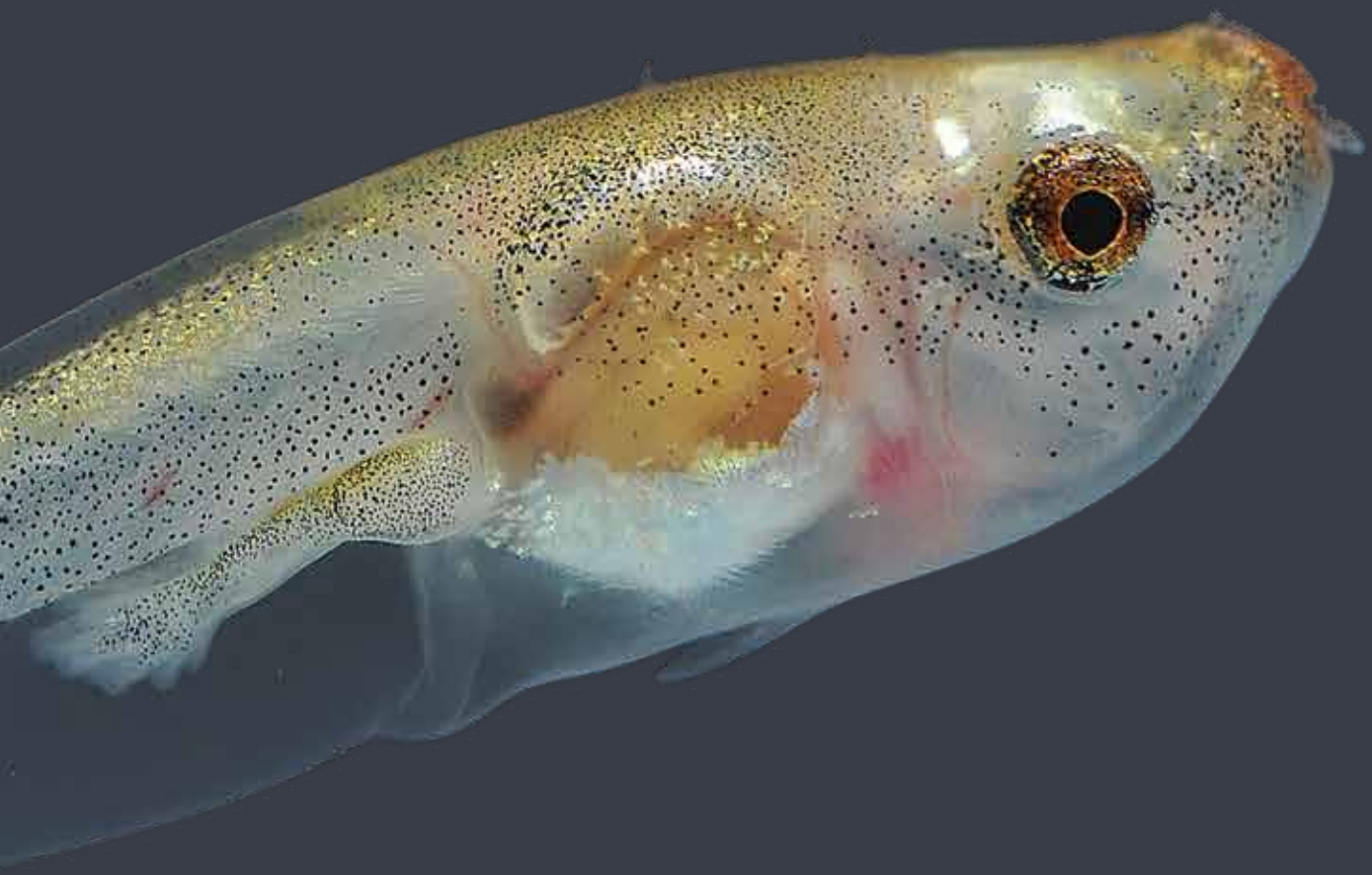
A Guide to the Tadpoles of Borneo

Alexander Haas, Indraneil Das, Stefan T. Hertwig,
Pia Bublies, Reinhard Schulz-Schaeffer



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Danum Valley canopy.

tredition

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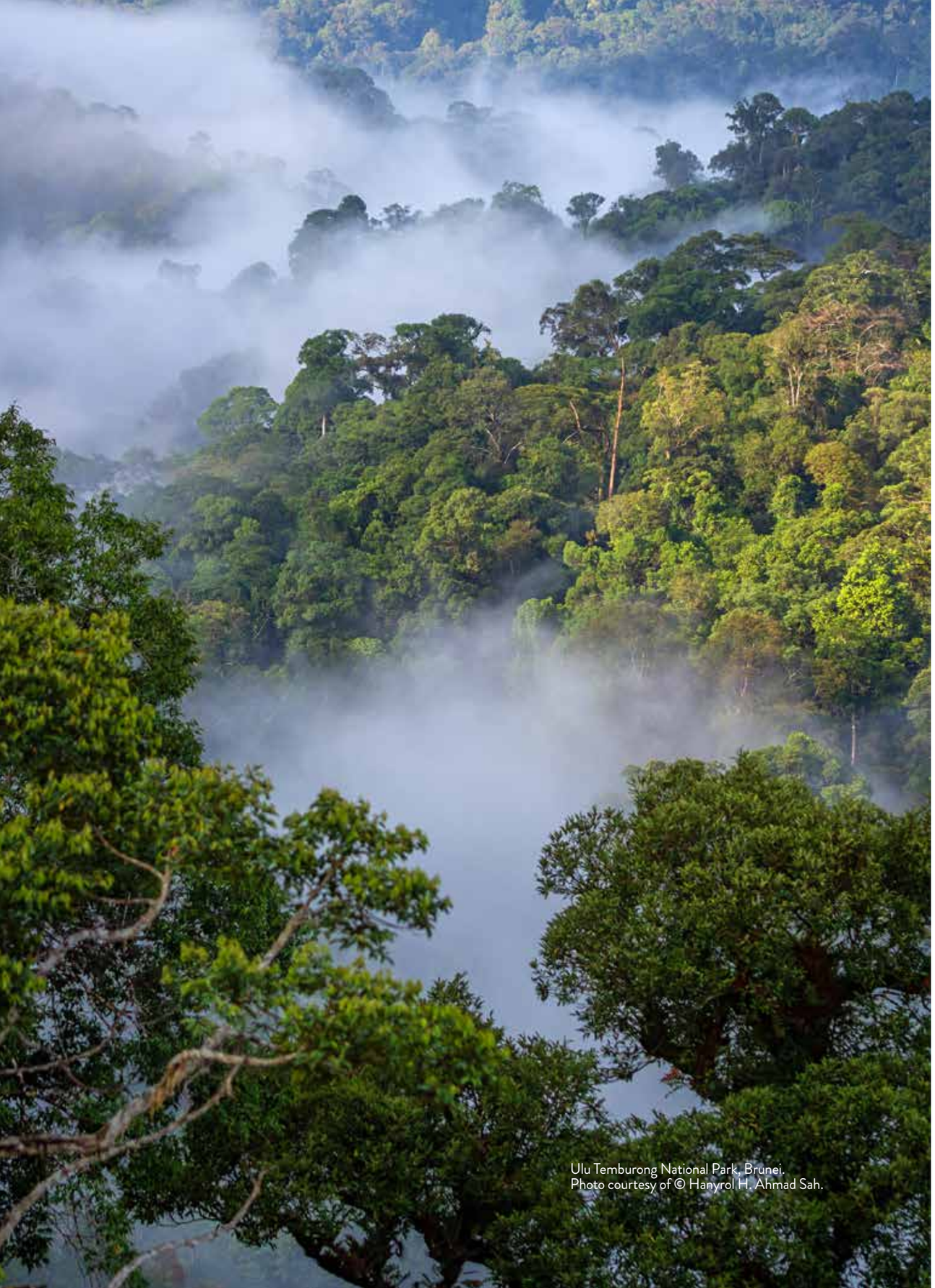
Phrynoidis juxtasper



Ulu Temburong National Park, Brunei.
Photo courtesy of © Hanyrol H. Ahmad Sah.

WE WILL NEVER FORGET …

our first trip together in 2001 to the interior of Sarawak and the kind Kelabit people of the Bario Highlands. It was a joyful productive exploration of the beautiful forests of Bario. The morale was high, discussions on shared scientific interests were productive and soon showed that we should try doing a project together. Soon after, we applied to Volkswagen Foundation for a four-year project on an inventory of East Malaysian tadpoles. In the consecutive years, we conducted many field trips together and amassed data far beyond tadpoles. The idea of writing a book on tadpoles always lingered in our heads, fascinating and intimidating us at the same time. It was only after Stefan T. Hertwig, Pia Bublies, and Reinhard Schulz-Schaeffer had later strengthened our team that we started the book writing journey. The time was ripe for a summary of what had been achieved.

When thinking about writing a book on the tadpoles of Borneo, we found us confronted with some tricky questions. How can a book be written about a fauna that is incompletely known at the time of writing? How can we dare writing about the tadpoles of Borneo when many tadpoles have either not been discovered or not been described scientifically? Why would we try to assemble a book if current knowledge is so patchy? And why risk the publication of a book that might be outdated by new discoveries and progress in taxonomy and systematics at the time of its release? These are only the biological and scientific questions raised by such a project. Many more questions concern the format: printed book, e-book, app for tablet PC? What would be the most useful and appealing format of such a publication in times of major changes in the markets. Who would use the book and how would it be used? What value in usability could we deliver?

The excellent previous work of colleagues certainly humbled us, for example Wen-hao Chou and Jun-yi Lin's *Tadpoles of Taiwan* and Marion Anstis' *Tadpoles and Frogs of Australia,* and Tsi Ming Leong's publications on Peninsular Malaysia tadpoles. At the same time, books such as *Frogs of Borneo* by Robert F. Inger, Robert B. Stuebing, T. Ulmar Grafe, and T. Maximilian Dehling inspired us with their book on frogs. The work and high standards of all theses authors encouraged us to fill a gap and experiment with our own ways to approach a publication on a localized tadpole fauna.

Many years of field work in the beautiful rainforests of Sarawak and Sabah have enriched us with insights that we want to share. Many students, with their keen enthusiasm have convinced us that producing a publications that facilitates access to the exceptional and fascinating amphibian fauna of Borneo is an effort well spent. The faith of our major financial sponsor for this research project, the Volkswagen Foundation, certainly encouraged us to take this challenge. Last but not least, the numbers of visitors to our website on the frogs of Borneo (🌐www.frogsofborneo.org) surprised us; we had not expected that attention. On this site, a few clicks lead the user to most of the Bornean species. Although incomplete in coverage and information for each species rather minimalistic, it has proven useful for many users. University students and general naturalists downloaded our imagery to build their personal pocket field guides. It convinced us that there is a need for simplicity among users.

Knowledge on amphibians and the tools of the trade are in constant change. That should not keep us from communicating the current status in the field in an accessible form. Our team of authors has proposed some new avenues in this book. For us it has been a joyful learning experience.

— Alexander Haas & Indraneil Das —

→ Author information p. 276

→ 🌐 www.frogsofborneo.org

ACKNOWLEDGMENTS

Over the years, numerous colleagues, friends, students, technicians, and field companions assisted in one way or another in our project to document the tadpoles of Borneo either by making the book a reality, working with us in the field, processing specimens in the laboratory, or just discussing Bornean amphibians with us. Needless to say that our endeavor was substantially motivated by previous groundbreaking scientific work on tadpoles by Robert F. Inger, Wen-hao Chou, Marion Anstis, and Tzi Ming Leong. Their wonderful work provided many inspirations for the present book.

First and foremost, we would like to thank the Volkswagen Foundation for enabling us with a grant to initiate our research on Bornean tadpoles, organize a symposium at Universiti Malaysia Sarawak in 2009, and produce this book. Furthermore, we would like to express our sincere gratitude to our scientific institutions for providing us with the possibility to conduct this research, namely the Institute for Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak; the Center for Natural History, Universität Hamburg, Leibniz-Institute for the Analysis of Biodiversity Change, and the Natural History Museum Bern. The Burgergemeinde Bern and German Academic Exchange Program (DAAD) generously provided funds for field assistants and travel expenses. We also gratefully acknowledge the generous support of our collaborating partners at the Universiti Sabah Malaysia, Charles Vairapppan and Kueh Boon-Hee.

Our research in protected areas of Sarawak and Sabah was only possible with the support and endorsement of the responsible authorities. We are indebted to the Economic Planning Unit, the Prime Minister's Department, Malaysia, and especially Munirah Abd. Manan. Sarawak Forest Department and Sarawak Forestry Corporation, especially (Datuk) Cheong Ek Choon, Engkamat Lading, Oswald Braken Tisen, Haji Azahari bin Omar, Zolkipli bin Mohamad Aton, Arabi Abang Aimran, (Datu) Haji Ali bin Yusop, Bolhan Budeng, Azahari bin Omar, Mohd. Shabudin Sabki, Nur Afiza Binti Umar, Dayang Nuriza binti Abang Abdillah, Mohamad bin Kohdi. We gratefully acknowledge the support of Sabah Biodiversity Center and Council, Abdul Fatah Amir, C.Y. Chung. Sabah Parks with our contact persons Jamili Nais, Maklarin Lakim, Paul Yambun, Nelly Majuakim. Yayasan Foundation and Maliau Management Committee, particularly Waidi Sinun, Rondy Milin, and Grace Pounsin supported our work at Maliau Conservation Area. Finally, we thank all local park managements and staff that we had the privilege to work with.

Many people contributed to our project. We needed support and assistance in the field, specimens had to be processed, tadpoles had to be barcoded, phylogenetically analyzed, and described. Some students produced Bachelor's or Master's Theses on tadpoles and frogs of Sarawak and Sabah as part of our project and moved on to make their own careers. First of all, our gratitude goes to Pui Yong Min who was our reliable, knowledgeable and kind partner and friend in many field trips. We thank him for his sustained support, his inter-cultural assistance, tremendous field work and endless enthusiasm.

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Ledlenser kindly provided some samples of their LED torches for field testing. Yeo Siew Teck (Cat City Holidays) provided valuable logistics support over the years. Nele Johannsen skillfully developed and contributed a sketched rainforest scenery (p. 46f) that shows where tadpoles live .

The authors hold copyrights for all photos in this book, except for several photos that were kindly provided by other photographers and are marked alongside with the photo. Especially Chien Lee, Hanyrol H. Ahmad, Lars Fehlandt, Pui Yong Min, Nikolay A. Poyarkov, Arne Schulze, and Wencke Krings. Marion Beeck gave some time-saving InDesign tips. We very much appreciate all their contributions!

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Two species of *Abavorana* have been described, *A. luctuosa* and, recently, *A. decorata*. At present, the limited genetic data available does not allow a definitive identification of this remarkable specimen from Lambir Hills National Park.

GENERAL SCOPE

Biodiversity research aims to uncover and understand the full biological richness of a given area. Southeast Asia includes several hotspots of biodiversity that are paralleled in species richness only by the Amazon river basin and adjacent regions in South America. One of the Asian hotspots is Sundaland, a shallow continental shelf on which Borneo, Sumatra, and Peninsula Malaysia are located (p. 26). Today's islands of Sundaland have been interconnected repeatedly during periods of low sea levels at former times.

The biodiversity of Southeast Asia has been vastly underestimated in the past and researchers are only beginning to comprehend the true richness of this region. Borneo is the largest island of Sundaland and plays a crucial role in the recording and understanding of the evolution of biodiversity in this region. In the past 20 years many species of frogs have been discovered on the island of Borneo. Some of these new species have been split from known taxa, acknowledging that known species had been complexes of several, closely related and morphologically similar, but genetically and ecologically distinct species. Progress is fast. A text like this can become outdated shortly after publication.

In this book we focus on species that we encountered in our own work in Sarawak and Sabah. For many known species, however, tadpoles have not been documented. The current list of Bornean frog species follows below (p. 18). Many more are likely to be described in the decades to come. It is unavoidable that the scientific information available for species and species' tadpoles (imagery, ecology) differs significantly. Some species are well known, widespread, and commonly found, others are restricted to certain areas, sometimes known only from their respective type localities and rarely seen. Our species accounts necessarily reflect that and are snapshots in an evolving field.

Feihyla kajau

While adults frogs live in numerous terrestrial habitats and niches, tadpoles are the larval aquatic stage in the biphasic life-cycle of frogs. The body shape, anatomy, and ecological requirements are completely different from the terrestrial frog. The tadpole eventually undergoes a metamorphosis to transform into a froglet. Metamorphosis is the process of physical transition from the aquatic larva to the terrestrial adult. The biology of tadpoles is just as fascinating as the biology of frogs and has been central in our own research. We believe that rather few publications have given tadpoles the attention they deserve. Clearly, understanding the ecology of tadpoles is essential for any conservation efforts. If an area does not provide proper habitats for tadpoles, there will be no frogs either! For the naturalist, ecologist or surveyor, tadpoles are an important indicator of the presence of a reproductively active population of that species.

After metamorphosis, the froglets leave the water and move to their different species-specific terrestrial habitats. Frogs occupy a large number of ecological niches, ranging from burrows in the forest floor to the canopy of the rainforests. This variety of living conditions is reflected by the adaptations of their body. Species that perch on shrubs or trees have slender bodies and long legs, while ground-dwellers often show a stocky body and short but strong legs.

All amphibian species from Borneo (and indeed from all over the world) have been described largely, if not entirely, on the basis of adult specimens, because frogs are found more often in the field than their larval stages. Tradition in herpetological research is another reason for the focus on adults and the neglect in tadpole research. Knowledge of tadpole descriptions has thus seriously lagged behind. Although many larval descriptions of species occurring on the island of Borneo have been published, we still lack information on the larval forms of many species. Larval descriptions currently available are sometimes derived from non-Bornean populations that may eventually prove to be non-conspecifics. Several familiar species have been shown in recent years to include morphologically similar albeit biologically distinct species.

Tawau Hills National Park, Sungai Gelas Waterfall.

Data quality is another problem, as a significant proportion of traditional larval descriptions lack voucher specimen information. Voucher specimens are specimens deposited in accessible museum collections for future reference. Many previously published larval descriptions have neglected DNA barcoding techniques for unambiguous matching of tadpoles and frogs. Assigning an unknown tadpole to a frog is no easy task; it may require rearing the tadpole through metamorphosis. Even then, in studies that have done so, wrong assignments have occurred. The froglet may look very unlike the adult frog—the famous Wallace's Flying Frog *Rhacophorus nigropalmatus* is one example. With the advent of DNA barcoding techniques it is now possible to match any tadpole with a frog from the same region, stream, or pond with a high reliability. This technique is far superior, less time consuming and less error-prone than rearing experiments. The only drawback is the access to a lab and the need to collect, handle and preserve tissue properly. Once the match and correct assignment has been established by DNA barcoding, morphological features can be re-examined to extract features that might allow to identify a tadpole without DNA barcoding.

In this book, we present pertinent morphological information for common species (if their tadpole is known to science) as a tool for field identification of tadpoles. With the help of this book, tadpoles should be identifiable to the species or at least to the generic level. The continuing discovery of new species and their tadpoles makes the development of reliable, classical dichotomous identification keys very difficult. New discoveries can overthrow existing keys easily. Keys, that where valid at the time of their publication, are included in some of the literature mentioned in this book, most notably in Inger (1985).

LITERATURE

Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

BORNEAN FROG SPECIES

Taxonomy is in constant flux. The list below gives the 200 recognized species of Borneo by the end of 2021**.** Please refer to *Amphibian Species of the World* (ASW) database for taxonomic details and updates. Currently, dozens of genetically distinct lineages have been recognized in the genera *Limnonectes*, *Occidozyga* and *Nyctixalus*. They represent potential candidate species. Therefore, the following list is a conservative estimate of Borneo's true frog diversity. More discoveries are expected in the future, especially from the still little know areas of Kalimantan.

taxonomic reference: http://research.amnh.org/vz/herpetology/amphibia/index.php

BOMBINATORIDAE: 1
Barbourula kalimantanensis Iskandar, 1978

BUFONIDAE: 35
Ansonia albomaculata Inger, 1960
Ansonia echinata Inger and Stuebing, 2009
Ansonia fuliginea (Mocquard, 1890)
Ansonia guibei Inger, 1966
Ansonia hanitschi Inger, 1960
Ansonia kanak Matsui, Nishikawa, Eto, and Hossman, 2020
Ansonia kelabitensis Matsui, Nishikawa, Eto, and Hossman, 2020
Ansonia latidisca Inger, 1966
Ansonia leptopus (Günther, 1872)
Ansonia longidigita Inger, 1960
Ansonia minuta Inger, 1960
Ansonia platysoma Inger, 1960
Ansonia spinulifer (Mocquard, 1890)
Ansonia teneritas Waser, Schweizer, Haas, Das, Jankowski, Min, and Hertwig, 2017
Ansonia torrentis Dring, 1983
Ansonia vidua Hertwig, Min, Haas, and Das, 2014
Duttaphrynus melanostictus (Schneider, 1799)
Ingerophrynus divergens (Peters, 1871)
Ingerophrynus quadriporcatus (Boulenger, 1887)
Leptophryne borbonica (Tschudi, 1838)
Pelophryne api Dring, 1983
Pelophryne guentheri (Boulenger, 1882)
Pelophryne linanitensis Das, 2008
Pelophryne misera (Mocquard, 1890)
Pelophryne murudensis Das, 2008
Pelophryne penrissenensis Matsui, Nishikawa, Eto, and Hossman, 2017
Pelophryne rhopophilia Inger and Stuebing, 1996
Pelophryne saravacensis Inger and Stuebing, 2009
Pelophryne signata (Boulenger, 1895)
Phrynoidis asper (Gravenhorst, 1829)
Phrynoidis juxtasper (Inger, 1964)
Pseudobufo subasper Tschudi, 1838
Rentapia everetti (Boulenger, 1896)
Rentapia hosii (Boulenger, 1892)
Sabahphrynus maculatus (Mocquard, 1890)

CERATOBATRACHIDAE: 3
Alcalus baluensis (Boulenger, 1896)
Alcalus rajae (Iskandar, Bickford, and Arifin, 2011)
Alcalus sariba (Shelford, 1905)

DICROGLOSSIDAE: 23
Fejervarya cancrivora (Gravenhorst, 1829)
Fejervarya limnocharis (Gravenhorst, 1829)
Hoplobatrachus rugulosus (Wiegmann, 1834)
Limnonectes asperatus (Inger, Boeadi, and Taufik, 1996)
Limnonectes cintalubang Matsui, Nishikawa, and Eto, 2014
Limnonectes conspicillatus (Günther, 1872)
Limnonectes finchi (Inger, 1966)
Limnonectes hikidai Matsui and Nishikawa, 2014
Limnonectes ibanorum (Inger, 1964)
Limnonectes ingeri (Kiew, 1978)
Limnonectes kenepaiensis (Inger, 1966)
Limnonectes kong Dehling and Dehling, 2017
Limnonectes leporinus (Andersson, 1923)
Limnonectes malesianus (Kiew, 1984)
Limnonectes moquardi (Mocquard, 1890)
Limnonectes palavanensis (Boulenger, 1894)
Limnonectes paramacrodon (Inger, 1966)
Limnonectes rhacodus (Inger, Boeadi, and Taufik, 1996)
Limnonectes sinuatodorsalis Matsui, 2015
Occidozyga baluensis (Boulenger, 1896)
Occidozyga laevis (Günther, 1858)
Occidozyga berbeza Matsui, Nishikawa, Eto, Hamidi, Hossman, and Fukuyama, 2021
Occidozyga sumatrana (Peters, 1877)

MEGOPHRYIDAE: 32
Leptobrachella arayai (Matsui, 1997)
Leptobrachella baluensis Smith, 1931
Leptobrachella bondangensis Eto, Matsui, Hamidy, Munir, and Iskandar, 2018
Leptobrachella brevicrus Dring, 1983
Leptobrachella dringi (Dubois, 1987)
Leptobrachella fritinniens (Dehling and Matsui, 2013)
Leptobrachella fusca Eto, Matsui, Hamidy, Munir, and Iskandar, 2018
Leptobrachella gracilis (Günther, 1872)
Leptobrachella hamidi (Matsui, 1997)
Leptobrachella itiokat Eto, Matsui, and Nishikawa, 2016
Leptobrachella juliandringi Eto, Matsui, and Nishikawa, 2015
Leptobrachella marmoratus (Matsui, Zainudin, and Nishikawa, 2014)
Leptobrachella maurus (Inger, Lakim, Biun, and Yambun, 1997)
Leptobrachella mjobergi Smith, 1925
Leptobrachella palmata Inger and Stuebing, 1992
Leptobrachella parva Dring, 1983
Leptobrachella pictus (Malkmus, 1992)
Leptobrachella sabahmontanus (Matsui, Nishikawa, and Yambun, 2014)
Leptobrachella serasanae Dring, 1983
Leptobrachium abbotti (Cochran, 1926)
Leptobrachium gunungense Malkmus, 1996
Leptobrachium hendricksoni Taylor, 1962
Leptobrachium ingeri Hamidy, Matsui, Nishikawa, and Belabut, 2012
Leptobrachium kanowitense Hamidy, Matsui, Nishikawa, and Belabut, 2012
Leptobrachium kantonishikawai Hamidy and Matsui, 2014
Leptobrachium montanum Fischer, 1885
Megophrys dringi Inger, Stuebing, and Tan, 1995
Pelobatrachus baluensis (Boulenger, 1899)
*Pelobatrachus edwardinae (*Inger, 1989)
Pelobatrachus kalimantanensis (Munir, Hamidy, Matsui, Iskandar, Sidik, and Shimada, 2019)
Pelobatrachus kobayashii (Malkmus and Matsui, 1997)
Pelobatrachus nasutus (Schlegel, 1858)

MICROHYLIDAE: 28
Chaperina fusca Mocquard, 1892
Gastrophrynoides borneensis (Boulenger, 1897)
Glyphoglossus brooksii (Boulenger, 1904)
Glyphoglossus capsus (Das, Pui, Hsu, Hertwig, and Haas, 2014)
Glyphoglossus flava (Kiew, 1984)
Glyphoglossus smithi (Barbour and Noble, 1916)
Kalophrynus baluensis Kiew, 1984
Kalophrynus barioensis Matsui and Nishikawa, 2011
Kalophrynus calciphilus Dehling, 2011
Kalophrynus dringi Fukuyama, Matsui, Eto, Hossman, and Nishikawa, 2021
Kalophrynus eok Das and Haas, 2003
Kalophrynus heterochirus Boulenger, 1900
Kalophrynus intermedius Inger, 1966
Kalophrynus meizon Zug, 2015
Kalophrynus nubicola Dring, 1983
Kalophrynus punctatus Peters, 1871
Kalophrynus puncak Fukuyama, Matsui, Eto, Hossman, and Nishikawa, 2021
Kalophrynus subterrestris Inger, 1966
Kaloula baleata (Müller, 1836)
Kaloula pulchra Gray, 1831
Metaphrynella sundana (Peters, 1867)
Microhyla berdmorei (Blyth, 1856)
Microhyla borneensis Parker, 1928
Microhyla maculifera Inger, 1989
Microhyla malang Matsui, 2011
Microhyla nepenthicola Das and Haas, 2010
Nanohyla perparva (Inger and Frogner, 1979)
Nanohyla petrigena (Inger and Frogner, 1979)

RANIDAE: 30
Abavorana luctuosa (Peters, 1871)
Abavorana decorata (Moquard, 1821)
Chalcorana megalonesa (Inger, Stuart, and Iskandar, 2009)
Chalcorana raniceps (Peters, 1871)
Huia cavitympanum (Boulenger, 1893)
Hylarana erythraea (Schlegel, 1837)
Indosylvirana nicobariensis (Stoliczka, 1870)
Meristogenys amoropalamus (Matsui, 1986)
Meristogenys dyscritus Shimada, Matsui, Yambun, and Sudin, 2011
Meristogenys jerboa (Günther, 1872)
Meristogenys kinabaluensis (Inger, 1966)
Meristogenys macrophthalmus (Matsui, 1986)
Meristogenys maryatiae Matsui, Shimada, and Sudin, 2010
Meristogenys orphnocnemis (Matsui, 1986)
Meristogenys penrissenensis Matsui, Nishikawa, Eto, and Hossman, 2017
Meristogenys phaeomerus (Inger and Gritis, 1983)
Meristogenys poecilus (Inger and Gritis, 1983)
Meristogenys stenocephalus Shimada, Matsui, Yambun, and Sudin, 2011
Meristogenys stigmachilus Shimada, Matsui, Yambun, and Sudin, 2011
Meristogenys whiteheadi (Boulenger, 1887)
Odorrana hosii (Boulenger, 1891)
Pulchrana baramica (Boettger, 1900)
Pulchrana glandulosa (Boulenger, 1882)
Pulchrana laterimaculata (Barbour and Noble, 1916)
Pulchrana picturata (Boulenger, 1920)
Pulchrana signata (Günther, 1872)
Staurois guttatus (Günther, 1858)
Staurois latopalmatus (Boulenger, 1887)
Staurois parvus Inger and Haile, 1959
Staurois tuberilinguis Boulenger, 1918

RHACOPHORIDAE: 48
Feihyla inexpectata (Matsui, Shimada, and Sudin, 2014)
Feihyla kajau (Dring, 1983)
Kurixalus absconditus Mediyansyah, Hamidy, Munir, and Matsui, 2019
Kurixalus chaseni (Smith, 1924)
Leptomantis angulirostris (Ahl, 1927)
Leptomantis belalongensis (Dehling and Grafe, 2008)
Leptomantis cyanopunctatus (Manthey and Steiof, 1998)
Leptomantis fasciatus (Boulenger, 1895)
Leptomantis gadingensis (Das and Haas, 2005)
Leptomantis gauni (Inger, 1966)
Leptomantis harrissoni (Inger and Haile, 1959)
Leptomantis malkmusi (Dehling, 2015)
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Philautus amoenus Smith, 1931
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TAXONOMY

taxonomic reference:
http://research.amnh.org/vz/herpetology/amphibia/index.php

Taxonomy is the science of describing and naming species and classifying them within the comprehensive scientific system of all living creatures on earth. Because of the ongoing discovery of new organisms, especially in the tropical realm, and the availability of new methods to study them, taxonomy is a highly dynamic field of research. From our point of view, a well justified hypothesis on phylogeny is the only acceptable way to order, describe, and name organisms. New insights on the evolution and phylogenetic relationships (relatedness by common descent) lead to new arrangement in the classification systems.

As science progresses, many scientific names of Bornean frogs have changed in recent times. What used to be *Rana malesiana* is now *Limnonectes malesianus*, for example. Such changes are necessary and document new research insights. For the naturalist or student in the field, however, changes in names can be very confusing, especially when using various books and articles to learn about the fauna; some sources may use old names, some more recent names. This is particularly true when researching Bornean taxa. Furthermore, if species have been split up into two or more, it is often difficult to assign previous tadpole descriptions to one of the new species, especially if DNA barcodes are not available. In order to avoid misunderstandings with names, it is a common procedure to cite the authors and year of first description of a species after its name. We provide this information in the individual species accounts. Comprehensive treatment on the taxonomic history of a species, including previous names (=synonyms) can be retrieved from the web site *Amphibian Species of the World*. We adopt the taxonomy of ASW herein (p. 18).

A crucial question in taxonomy is the understanding of the term 'species'. There is no universally accepted definition of a species, rather, there is a number of species concepts. Moreover, the criteria used for recognition and delimiting of species of a certain group of organisms are still hotly debated. Many understand species as independently evolving lineages or potentially reproducing meta-populations. Genetic, behavioral, ecological or morphological characters can be indicators of evolutionary independence or reproductive isolation from other such groups. Cryptic species can confound true diversity even more. In this book, we will deal with species pragmatically and consider all species that have been published according to the international rules of taxonomy.

WHO SHOULD USE THIS BOOK?

Be fascinated by the tadpoles and frogs of Borneo!

Our target audience include people with a genuine interest in going to the field and experience frogs in their natural environment. Therefore, a comprehensive expert textbook is not our goal. This may disappoint the expectations of some professionals and specialists. This book is meant to be an introductory guide to Bornean tadpoles for a broad audience: researchers, naturalists, biology students, amateur herpetologists, protected area staff, forestry staff, and travelers. Structure, appeal, look, style and usability are just as important to us as the scientific facts. Form must follow function. Visual representations (image knowledge) in some cases can transmit information better than text and may even render text superfluous; old traditions of scientific field guide books and textbooks need to be questioned, sometimes broken. The behavior of the readership also changes in times of social media and tablet PCs. Brevity and precision of information as well as fast and non-linear navigation through information seems key and defines usability. Reduction of jargon and text as well as exploiting the power of illustrations as information transmitters, however, is a challenge. We tried to apply image knowledge whenever feasible.

HOW TO USE THIS BOOK?

Each species of frog has a specific reproductive biology and chooses specific sites for egg deposition and larval development (see Tadpole Microhabitats p. 46). We grouped species in three sections that correspond to three major microhabitat classes of water bodies at which tadpoles or developmental stages (in direct-developing species) can be found: stagnant water bodies, flowing water, and terrestrial sites. We consider these categories most relevant for the field naturalist, who will most likely find herself or himself at a site that falls in one of these classes and wants to know, which kinds of tadpoles to expect. Sorting species according to microhabitat classes will facilitate getting familiar with specific faunas.

Terrestrial sites are used by species with direct development (lack of a free-swimming larvae; some *Philautus*). There are some species, however, which deposit eggs on land but still have free-swimming larvae later on; Guardian Frogs (*Limnonectes palavanensis* and *L. finchi*) are an example. In our scheme, the latter belong to the water body categories (stagnant or flowing) and not to the terrestrial category.

Phytotelma breeders lay their eggs into water bodies that are usually provided by plant cavities such as *Nepenthes* pitchers, bamboo internodes, tree holes or water in fallen log cavities. These situations are technically stagnant water bodies and phytotelma breeders shall be categorized as such in that section of the book.

For most species, these classes defined by the body of water are non-overlapping and clearly separate. Stagnant versus flowing water categories work reliably in tadpoles for the vast majority of species. A few exceptions exist in which case tadpoles of a particular species can be found in more than one of the four microhabitat classes. In adult frogs, things may be a bit more fuzzy, because some frogs can be encountered at a stream, yet lay their eggs into a water body that qualifies as stagnant (for example, an isolated side-pool of that stream). This must be considered in field situations, when using the book. Surprisingly few species can actually develop as tadpoles in either (slightly) flowing or (fully) stagnant water bodies, among them are mostly riparian species. If a species' tadpole can be found in more than one of the three microhabitat categories, appropriate comments will be made on the respective species' pages. Within the major categories, we present the species alphabetically, first by family name, then by scientific genus and species names.

The tadpoles of a given species are presented on a double page. Essential information (size, shape, color) is given immediately by photographs and graphic drawings, so that this information is available even before reading more details. We developed a reduced style of abstraction for mouthparts and body contours. In the field, size and body shape have proven very helpful as first clues for identification; both are essential to quickly recognize a tadpole, often to the genus level. More details in the text and from color photographs will allow, in many cases, for determination to the species level. The text repeats and deepens the information content of the photographs and drawings. Text is broken up into small blocks that cover specific topics. It makes non-linear reading and finding details more easy. Pictograms help to find the pertinent text block. Photographs vary in quality because they where taken over a long time period, when digital photography (and our skills) improved substantially.

In a common situation a naturalist will be in the field and will try to determine a tadpole right at the site where the tadpole is encountered. It is the priority to supply information that serves immediate identification to the best level; often genus level, sometimes species level. Similar species that could likely be confused with the given species under study will be mentioned and distinguishing features will be given if current knowledge allows that.

A complete literature survey is not the goal of this book. We suggest readings in appropriate places to guide the reader to pertinent or potentially interesting literature. Following the literature cited in those works will allow deeper research of the topic.

LITERATURE

This icon introduces publications for further reading that could be relevant to the respective section of the book or species in question..

A BRIEF HISTORY OF STUDIES

Map of Borneo and adjacent regions by Jodocus Hondius in Gerard Mercator's atlas (1613).

Portrait of botanist-explorer-turned administrator, Hugh Low (1824–1905).

Italian botanist, Odoardo Beccari (1843–1920).

A view of Gunung Kinabalu from John Whitehead's (1893) 'The Exploration of Mount Kina Balu'.

Borneo was not well known to western navigators before the 19th Century, being far from the trading routes of European naval powers. Perhaps the earliest accurately executed map of the island was prepared by Jodocus Hondius (Latinized version, Joost de Hondt) (1563–1612), a Flemish/Dutch engraver and cartographer. His maps in Gerard Mercator's (1613) atlas helped establish Amsterdam as the center of cartography in Europe in the 17th century. To the left: Hondius' hand colored 'Insulae Indiae Orientalis Praecipuae, In quibus Moluccae celeberrime sunt'.

At the time of publication of the 10th edition of Systema Naturae 1758, by Carolus Linneaus (1707–1778), the celebrated Swedish botanist, no frogs were described from Borneo. The earliest amphibian checklist for Borneo was published by the botanist-explorer-turned administrator, Hugh Low (1824–1905). Low was sent out to the East by his father to acquire horticultural specimens for the family business in London, and is perhaps best known for being the namesake for the highest peak on the island (Gunung Kinabalu's Low's Peak, at 4,095 m a.s.l.). His 1848 book, entitled: 'Sarawak. Its inhabitants and productions.' These notes taken during a residence in that country with His Excellency Mr. Brooke included a checklist that show two frog species, presumably made around the region of modern-day Kuching. The island was therefore terra incognita for herpetological studies during the visit by Odoardo Beccari (1843–1920) from Italy. Beccari's collection of amphibians was, of course, incidental to botanical collections, and made in collaboration and financial support by Marquis Giacomo Doria of Genoa (1840–1913), a patron of the Civic Museum of Natural History at Genoa, between 1865–1868. Collections were made from Sarawak, Kalimantan and Brunei, including the vicinity of Kuching, Gunung Pueh, Gunung Matang, Batang Lupar, Kapuas, Labuan, and several frog species (such as *Kalophrynus punctatus*) were described by the Curator of the Berlin Museum, Wilhelm Peters and by Peters and Giacomo Doria.

The next update of the fauna was provided by Edward Bartlett (ca. 1836–1908), Curator of the Sarawak Museum between 1895–1897. He wrote a three page account of the amphibians of Borneo that were represented in the Sarawak Museum or reported in the literature available to him. It lists 44 species (39 using contemporary taxonomy), and included localities, and if available, sizes, elevational distribution, color variations, vernacular names, abundance and habits.

By the middle of the 19th century, Enlightenment was sweeping Europe, with scientific discourse unshackled by superstition and especially, the rise of Darwinism and the need for empirical evidence, especially of human origins. At this time, Alfred Hart Everett (1849–1898), arrived in Borneo (in 1869), at the recommendation of the famous British scientist, Sir Charles Lyell, in order to examine cave deposits. For the first few years, he made natural history collecting for museums and collectors back home in England his primary occupation. Everett collected from Gunung Pueh and Gunung Penrissen, his material was worked on by Albert Günther and his successor, George Boulenger at the British Museum (Natural History), London. Outstanding amongst these (using contemporary day names) are *Alcalus baluensis* and *Rentapia everetti*. Another resident of Sarawak at the time was colonial administrator, Charles Hose (1863–1929), an amateur naturalist, geographer and anthropologist. Employed as Resident of Baram District by the Sarawak Civil Service, Hose authored a number of popular books that were based on his experiences in Borneo, and sole or donated collections of biological specimens to museums in Europe, North America and Asia. New frog species collected by Everett and Hose were described by Boulenger, and those that bear his name include *Odorrana hosii*, *Rentapia hosii* and *Philautus hosii*. Hose was also the collector of the holotype of arguably the most famous Bornean frog, the Wallace's Flying Frog, *Rhacophorus nigropalmatus*, from the 'Akar River'. Wallace's own specimen was apparently not preserved.

The English explorer, John Whitehead (1860–1899), visited the Gunung Kinabalu area in 1887–1888 to make zoological collections, reaching the summit in February 1888. His herpetological material from Kinabalu was reported by Boulenger (1887) at the British Museum London, and Mocquard (1890) at the Muséum National d'Histoire Naturelle, Paris. Whitehead's lasting contribution is the magnificent work, 'The Exploration of Mount Kina Balu' (1893), whose plates are often reprinted. The frog, *Meristogenys whiteheadi*, from the upper reaches of Kinabalu, honors Whitehead.

Robert Walter Campbell Shelford (1872–1912) was Curator of the Sarawak Museum between 1898–1905. His amphibian collections were also described by Boulenger. The frog species name, *Rhacophorus shelfordi* is named for him. Shelford was succeeded by the Swedish naturalist, Eric Georg Mjöberg (1882–1938), between 1922–1924. Mjöberg's herpetological collections, particularly from Gunung Murud, Gunung Gading, Gunung Penrissen and Gunung Pueh, were written up by the English physician-herpetologist, Malcolm Smith. The collections made from Murud were particularly remarkable. The mountain had been rarely visited. The trip resulted in the discovery of a large number of new species of amphibians and reptiles, and Mjöberg wrote a chapter on his observations on Wallace's Flying Frog. Mjöberg is the namesake for both *Leptobrachella mjobergi* and *Philautus mjobergi*.

The American field naturalist and philanthropist, William Louis Abbott (1860–1936), described as "...one of the greatest field naturalists that America has produced...", studied medicine in London, but decided to engage in scientific explorations. Abbott organized a number of expeditions, including to America, Africa, Seychelles, Madagascar, central Asia, the Himalayas, and the Dutch coastal portion of Borneo, from where he collected a frog that bears his name, *Leptobrachium abbotti*.

In the past half century, several teams contributed to amphibian collections from Borneo. Most notably Robert F. Inger (Field Museum of Natural History) and his collaborators. His and his team's work led to several book publications on the frogs of Borneo and a key publication on Bornean tadpoles. Major collecting efforts were initiated by Sabah Parks (Maklarin Lakim, Tan Fui Lian and Paul Yambun), the Universities of Kyoto (Masafumi Matsui and colleagues), Bandung Institute of Technology (Djoko Iskandar and colleagues), and finally, members of the Society for the Study of Southeast Asian Herpetology, Germany (particularly, Rudolph Malkmus and Ulrich Manthey).

Plate showing *Polypedates otilophus* collected by Alfred Everett and Charles Hose in Boulenger (reproduced from Proc. Zool. Soc. London 1893).

Robert Walter Campbell Shelford (1872–1912).

Wallace's Flying Frog, *Rhacophorus nigropalmatus*, an iconic frog species of Borneo.

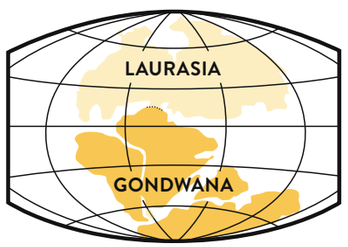
3 AMPHIBIAN STUDIES ON BORNEO

BIOGEOGRAPHY

With 200 recorded species (p. 18), Borneo boasts an astonishingly high number of frogs. Over 100 species have been recorded in the Gunung Mulu National Park (544 km^2) alone. This extraordinarily high species richness makes Borneo one of the global hot spots for amphibian diversity. The island is part of the biogeographical region of Sundaland, a recognized center of biodiversity for numerous groups of animals and plants. Sundaland also includes the Malay Peninsula, Sumatra, Java, Bali, and several smaller islands. Together they constitutes the emerged land masses of the Sunda shelf, which is a tectonically relatively stable extension of the Asian continent. The Sunda shelf consists of an assembly of old Gondwana blocks and subsequently amalgamated parts of the Asian continent. The contemporary shorelines of the Sunda islands, that are separated today by shallow seas less than 200 m deep, are geologically young: Borneo has been separated from the continent for just under five million years. Thus, the evolution of the amphibian diversity of Borneo can only be explained taking into account the biogeography and palaeogeography of the surrounding islands and archipelagos.

Plate tectonics and biogeography

Sundaland's current extraordinary biodiversity is largely a result of southeast Asia's complex geological and climatic history, that has influenced the distribution and composition of the fauna and flora. Sundaland is situated in the center of convergence between the Eurasian, Australian, Philippine Sea and Pacific tectonic plates. The movements and collisions of these surrounding tectonic plates caused subduction, volcanic activity, and mountain uplift. Subsequent erosion and deposition of sediments by river drainages on land, in deltas, coastal plains, and offshore have shaped—and continue to shape—the landscape of Sundaland. The collision between the Indian plate and the Asian continent, between 50 to 35 Mya, facilitated the exchange of fauna and flora between India and Asia. About 23 Mya, Australia began to collide with Sundaland and, as a result, the deep ocean that had hitherto separated Australia and Asia began to close. Subsequently, the Wallacea islands and the volcanic Banda arc emerged, while, on Borneo, mountains began to form. Northeast of Borneo, the oceanic archipelago of the Philippines emerged. Later, the rift and subduction of a micro-continental fragment from the South China margin north of Borneo had several repercussions: it caused the uplift of the extensive highlands in Borneo's interior, caused volcanism, changed the course of the large drainage systems, and brought the island of Palawan to its present position, close to Borneo's northern coastline.



Pangaea breakup approximately 200 million years ago

As a result of equatorial southeast Asia's turbulent geological history, Sundaland is today surrounded by the similarly diverse biogeographical regions of Indochina, the Philippines, and Wallacea, each boasting their own distinct fauna and flora. The western and southern boundaries of Sundaland are defined by deep open-water trenches. In contrast, the northern boundary (adjacent to the biogeographic region of Indochina), runs on the Malay peninsula along the Isthmus of Kra, the narrowest part of the Malay peninsula, or further south at the Kangar-Pattani Line, depending on the taxa that are considered. Indochina includes Thailand, Laos, Cambodia, Myanmar, and Vietnam up to southern China and the Himalayas. Many Bornean frog genera have ranges that include both Indochina and Sundaland, e.g. *Ansonia*, *Feihyla*, *Kurixalus*, *Leptobrachella*, *Limnonectes*, *Pelobatrachus*, *Microhyla*, *Polypedates* and *Rhacophorus*. The close relationship between the fauna of Borneo, the Malay peninsula, and Indochina is interpreted to be a result of the land connection until 5 Mya before present.

The island of Palawan, north of Borneo, is biogeographically considered to be part of Sundaland. However, geologically, Palawan is a relic of th micro-continental plate from the coast of southeast China which came into close proximity with Borneo about 10 Mya. It was eventually connected to Borneo during glacially-driven periods of low sea level. Biogeographically, Palawan serves as a bridge and transition zone between Sundaland and the Philippines, a theory borne out by the fact that the closest relatives of numerous species on Palawan are found either on Sundaland or the Philippines. Numerous closely-related frog species of *Hylarana*, *Limnonectes*, and *Occidozyga*, for example, are distributed throughout Palawan, Borneo and the Philippines. Sister species that occur on both Borneo and Palawan, are *Philautus everetti* (Palawan) and *P. macroscelis* (Borneo), and *Barbourula busuangensis* (Palawan) and *B. kalimantanensis* (Borneo). The evolutionary history of *Barbourula*, however, deviates from the usual pattern found in numerous groups of animals, in that Palawan and the other surrounding islands and biogeographic regions were colonized from northern Sundaland, which includes Borneo and the Malay Peninsula. The closest relatives of this genus are the fire belly toads *Bombina*, an ancient lineage of frogs widely distributed in Europe, east Asia and southern Vietnam. An ancestor of *Barbourula* probably rafted on emergent portions of Palawan, all the way from the Asian mainland to its present-day position. A subsequent dispersal from Palawan to Borneo resulted in the present disjunct distribution of *B. kalimantanensis* in a small area of central Borneo.

The north-eastern boundary of Sundaland corresponds to Huxley's modification of the Wallace Line. The Wallace Line is named after the English naturalist, Alfred Russel Wallace, who first noted the striking differences in mammal and bird fauna between the islands east and west of the Makassar and Lombok Straits. This faunal boundary line separates the islands of Wallacea in the east and the

Philippine archipelago in the northeast from the Asian ecozone. The Philippine archipelago, not counting the island of Palawan, consists of oceanic islands and is considered as a separate biogeographic region with a highly diverse fauna and flora. The chain of islands of the Sulu archipelago formed effective stepping stones, connecting the Philippines with the north-eastern tip of Borneo. These chains of volcanic islands along with Palawan probably provided a pathway for faunal exchanges between Sundaland and the Philippines. Examples of known genera from both Borneo and the Philippines are *Ansonia*, *Hylarana*, *Kurixalus*, *Limnonectes*, *Nyctixalus*, *Philautus* and *Staurois*.

The eastern boundary of Sundaland corresponds to the Wallace Line, that runs between Borneo and Sulawesi in the Makassar Strait and between Bali and Lombok in the Lombok Strait. The biogeographical region east of the Wallace Line is called Wallacea. It comprises Sulawesi and the Lesser Sunda Islands. Many species of mammals, birds, reptiles, and insects in Wallacea have Australian relatives, in contrast to the close affinities between the Sundaland fauna and the Asian continent. The anuran genera *Fejervarya*, *Hylarana*, *Limnonectes*, *Occidozyga*, *Polypedates* and *Rhacophorus*, however, are distributed on both sides of the Wallace Line. Again, these distribution patterns can only be explained by oversea dispersal out of Sundaland, since the Wallace Line was never bridged by terrestrial connections.

dispersal = spread of a population or species from one region to another.

vicariance = separation of populations by formation of geological barriers (e.g., mountains, rivers).

The role of dispersal

In general, the present distribution of organisms can be explained by dispersal (spread from one region to another), vicariance (separation by the formation of barriers), speciation, and extinction. Modern time-calibrated phylogenetic analyses of genetic data based on molecular clocks provide a way of identifying and dating dispersal events. Matching the resulting spatio-temporal patterns in an organism's evolution with palaeogeographical reconstructions, provided by geologists, in turn allows a deeper understanding of past biogeographical processes. The molecular clock is a technique that uses the substitution rate of nucleotide sequences of DNA to estimate the divergence time of different species. The calibration of molecular clocks is either based on fossils of known age, or uses estimates of gene evolution rates. Erroneous calibrations of molecular clock algorithms, however, will result in misleading reconstructions of divergence times.

The islands of Wallacea and the Philippine archipelagos, excluding for Palawan, were always separated from the Sunda shelf by deep oceanic trenches, which were never connected by continuous land bridges. Recent studies show that the occurrence of closely related anuran species on both sides of the Wallace Line has to be interpreted as the result of repeated oversea dispersal events. As frogs are normally saline intolerant, the probability of a successful dispersal increases as the distance between two islands decreases. Smaller islands can serve as stepping stones. Rafts consisting of plant material, that is washed into the sea after heavy tropical storms, can function as vehicles. The distribution patterns of several genera, such as *Ansonia*, *Hylarana*, *Kurixalus*, *Limnonectes*, *Occidozyga* and *Philautus*, representatives of which occur on both sides of the Wallace Line, may be explained by means of long-distance dispersal across shallow sea channels or deep oceanic trenches.

Climate, vegetation, and topography

Other factors influencing amphibian diversity and biogeography on Sundaland are climate, vegetation, and topography. Dramatic changes in climate, such as the ice ages in higher latitudes, have never interrupted evolutionary processes in tropical habitats close to the equator. However, changes in the global climate which affected sea levels have had a significant influence on the coastlines of Sundaland: there was a repeated emergence of land and subsidence below sea level of lower parts of the Sunda shelf. The fluctuating sea levels and the resulting consecutive episodes of isolation and connection of the different parts of Sundaland boosted the diversification of frogs. Periods of high sea levels isolated populations from each other and enabled the evolution of new species on the separated islands by allopatric speciation (evolution of species by geographic isolation). As the sea levels dropped again, the shallow Sunda shelf emerged or temporary land bridges provided pathways for faunal exchanges between the different parts of Sundaland. The new species were now genetically distinct, possibly reproductively isolated, and sympatric (after a range expansion when they came into secondary contact with related species). The Lampung High, for example, provided a connection between the southern part of Sumatra and the remaining landmasses of Sundaland at about 10 to 5 Mya and enabled the exchange of the anuran fauna. This scenario explains the close relationships between species of, for example, *Nyctixalus*, *Occidozyga*, and *Philautus* from Borneo, Java and Sumatra.

Frog species that also occur in other parts of Sundaland, the Asian continent or on the Philippines, such as *Duttaphrynus melanostictus*, *Kurixalus chaseni*, *Nyctixalus pictus*, *Polypedates leucomystax*, *P. macrotis* and *Leptomantis cyanopunctatus*, have reached Borneo only relatively recently during periods of low sea levels (a result of the most recent glaciations) and may have been isolated as the sea rose to its present level. Whether closely related but geographically separated populations represent biologically meaningful entities, i.e. valid species, or if isolated island populations of otherwise widespread species have to be regarded as one species remains a matter of debate and depends on the species concepts applied. Future phylogenetic studies could show that the isolated populations in different locations of the range of these frogs actually represent separate species. The famous Reinwardt's Flying Frog, for instance, was split up into *Rhacophorus reinwardtii* from Java and *R. borneensis* from Borneo.

Most of Sundaland has been covered by different types of tropical rainforests since the last glacial period and until anthropogenic deforestation began in the last century. Tropical rainforests grow in areas with annual precipitation in excess of 2,000 mm, with no more than four consecutive months of less than 100 mm, and with small variations in annual temperature. Nearly all recent amphibian species from Borneo, occur in the different types of evergreen tropical rainforests (lowland, *kerangas*, mangrove, montane forests, peat swamps). However, during southeast Asia's turbulent geological and climatological history, global fluctuations in climate—intensified by changes in ocean circulation—also altered precipitation amount, average temperatures, and the distribution of the predominant vegetation. In colder and dryer periods, parts of the emerged Sunda shelf were covered with dry, seasonal vegetation, like woodland savannas, resulting in a temporal fragmentation of wet forests. In subsequent warmer periods, with higher precipitation, wet rainforest covered Sundaland. These dynamics in the composition and distribution of the predominant vegetation types were additional drivers of the diversification of frogs in both lowland and montane forests.

The extensive mountain ranges of northern and central Borneo with their specific vegetation, high amount of precipitation and cooler temperatures play an important role in the amphibian diversity of the island, as they harbor a high proportion of endemic frog species (i.e. those restricted to a certain geographic region and found nowhere else). In fact, the amphibian diversity on Borneo follows a clear pattern, with the highest number of species being found in the highest mountains of the northern part of the island. Mountains provide ecological opportunities for species that are able to adapt to the cool, wet environments in higher elevations, but serve as barriers for lowland species.

endemics = species unique to a specified geographic region

Dense montane mixed oak-chestnut (Fagacea) forest, home of many frog species (Gunung Kinabalu).

Kerangas forest, Gunung Mulu National Park. This type of forest grows on nutrient-poor soil. Giant trees are absent and the majority of the trees has a small trunk cirumference.

Recent studies have demonstrated that the numerous endemic species adapted to cool and wet environments in Borneo's montane forests derived from local ancestors at lower altitudes, and are not related to species from similar vegetation zones beyond the island. Over time, the montane vegetation communities of Sundaland have also been affected by periodic changes in global climate, illustrated by the fact that Gunung Kinabalu has been capped by ice several times during the last 2 Mya. During cooler periods montane forests spread to lower elevations in the valleys and connected previously isolated habitats. As a result, the montane frog species could cross the valleys and colonize new mountains. Even in such drier periods, the climate of the tropical mountains remained relatively humid, as they act as a barrier to clouds and create their own weather. Later, during warmer and wetter periods, the montane forests retreated and lowland forests flourished in the valleys. In higher elevations, the montane frog populations have been separated from each other and have evolved in isolation into genetically distinct populations, or even new species. Examples of species recorded at higher elevations of several isolated mountains are *Philautus macroscelis, P. ingeri, Leptobrachella arayai*, *Leptomantis angulirostris*, *Leptobrachium montanum* and *Meristogenys kinabaluensis*. On the other hand, montane frog species can be endemic on a very small scale: Some Bornean frog species have a very restricted distribution area. Studying such micro-endemics requires extensive field work, with a dense sampling strategy to detect the species in their tiny ranges. *Kalophrynus nubicola, K. puncak*, and *K. dringi*, small microhylid frogs, exclusively inhabit the montane oak-laurel forests at higher elevations of Gunung Mulu. *Pelophryne linanitensis* has so far only been found in the mossy rhododendron forests on Batu Linanit, a small summit of the Gunung Murud Range. Today's warmer temperatures have effectively trapped these montane micro-endemic species on their isolated mountains, preventing their spread to lower elevations, different vegetation, and more competing frog species. Although most of the micro-endemics are from higher elevations, some lowland species also seem to be confined to certain localities or to special habitat types. For example, *Pelophryne api* is restricted to the Melinau limestone formation in the lowlands of Gunung Mulu National Park.

Another common phenomenon amongst tropical fauna and flora is 'cryptic' diversity. Cryptic species are closely-related, morphologically very similar species, that cannot be distinguished by external characteristics but only by using genetic analyses. Examples of groups of similar species with uncertain species boundaries are the rhacophorid frogs with rheophilous tadpoles (*Leptomantis angulirostris*, *L. belalongensis*, *L. gadingensis*, *L. gauni,* and *L. penanorum*), or the numerous bush frog species of the genus *Philautus*. Recently discovered, large complexes of cryptic, and mainly still undescribed species, are known from the dicroglossid genera *Limnonectes* and *Occidozyga*. The common ancestors of these clades diversified into separate evolutionary lineages as a result of non-adaptive radiations by allopatric speciation on Borneo. Later, some of these lineages spread and came into secondary contact with their congeners. Such complex spatio-temporal processes resulted in the distribution pattern evident in the (approximately) 20 cryptic species of Creek Frogs (formerly subsumed under *Limnonectes kuhlii* and *L. laticeps*), with up to three species in the same area. It is likely that there are a vast number of as yet undiscovered cryptic species, and therefore, the species diversity in amphibians on Sundaland has been considerably underestimated. However, future integrative taxonomic studies using significantly more genetic markers, as well as bio-acoustic and ecological data, need to test whether these observed genetically distinct evolutionary lineages, that we currently suspect to represent cryptic diversity, are actually valid species or not.

The distribution of amphibians depends not only on the vegetation but also on the availability of water bodies as habitat or for reproduction. In the montane forests, despite daily precipitation, permanent streams are quite rare, mainly because the mountain ridges of Borneo are often very steep and so water drains off very quickly. Therefore, species with direct development (phytotelma breeders or those without a free-swimming tadpole stage) are particularly common at higher elevations. The numerous species of bush frogs of the genus *Philautus* are the best examples of these reproductive strategies. In most species of frog, however, the most important stages for dispersal are probably the aquatic tadpole or the juvenile frogs (immediately after metamorphosis). River drainages influence the distribution of amphibians in different ways: they either act as barriers to or as pathways for the spread of species. During those periods when large parts of the Sunda shelf were exposed due to lower sea levels, the so-called paleo-drainage systems connected different areas of Sundaland. The north Sunda drainage system connected parts of west Borneo with Sumatra, while the east Sunda drainage system connected south Borneo with southeast Sumatra and Java.

Summary

Millions of years of interacting and dynamic evolutionary processes have shaped the unique diversity of the fauna and flora of Sundaland and adjacent biogeographic regions. As a result, the contemporary amphibian fauna of Borneo is a composite, consisting of a few species that have a wider distribution in southeast Asia but with most species recognized as being only from Borneo, or from small parts of the island itself. A permanently but relatively slow changing environment without serious interruption by mass extinctions provided new ecological opportunities and caused periodic fragmentations of populations, on the other hand. Subsequently allopatric speciation in geographic isolation, later range expansions, and secondary contact of the newly evolved species probably triggered relatively high speciation rates and resulted in the diversification in many groups of frogs. However, we still do not fully understand the extent to which many aspects of southeast Asia's complex geological and climatological history have influenced the evolution and distribution of the present amphibian fauna of Borneo. The reconstruction of these processes that shaped biogeographical patterns depends on a sound knowledge of real diversity, distribution, and phylogeny of the organisms studied. Reliable time scales of the evolutionary history, well-founded phylogenetic hypotheses are not yet available for many genera of frogs. The era of genomic studies, in which extensive genetic information from whole genomes is analyzed, will certainly result again in a re-examination of current taxonomy. These extensive data set will allow a more profound estimation of gene flow or genetic isolation between evolutionary lineages and thus a better assessment of the real species diversity. The overview presented here is, therefore, only a snapshot of the currently available knowledge.

Conservation

Today, habitats all over the world are at the mercy of human-induced alteration. One such change is the introduction of alien species. A few species of frogs were relatively recently introduced to Borneo by humans, either as a source of food, such as *Hoplobatrachus rugulosus* and *Lithobates catesbeianus*, or presumably accidentally, such as in *Kaloula pulchra* or *Duttaphrynus melanostictus*. These species have a limited distribution on Borneo and are restricted to disturbed habitats, such as human settlements or cultivated land. Nevertheless, such introduced species, are potentially dangerous for native

cryptic species = closely related valid species that are very similar in morphology or even indistinguishable in physical features

species, as they can displace native fauna or spread disease. In frogs, the chytrid fungus *Batrachochytrium dendrobatidis*, which is a serious global threat for amphibians, can be spread by these introduced species. This fungus was recently found in some regions on Borneo, but fortunately has not had any significant impact on anuran populations yet.

By contrast, deforestation and the resulting habitat loss represents a major threat for the biodiversity of Sundaland. Deforestation began in the middle of the last century and the resulting habitat destruction reached quickly such a high level, that now there are few untouched forests left on Borneo. The deforestation and subsequent conversion of the land for (human) habitation, agriculture and plantations result in permanent loss and fragmentation of natural habitats. The remaining amphibian populations, in their small and isolated residual ranges, face a high risk of extinction. In an effort to counteract this, the Malaysian federal state Sarawak, for example, has established new protected areas. But there is more yet to be done. One issue is that our current knowledge about many groups of Bornean frogs is still patchy and, every year, new species are being described.

Integrative phylogenetic studies suggested a surprisingly high amount of cryptic diversity in many groups of Bornean frogs. Consequentially, formerly widespread species of low concern have in numerous cases turned out to be complexes of several species with small distribution areas – this has real implications on the census of the actual biodiversity and, unfortunately, complicates its protection. It is clear, however, that efforts in research, politics—and biogeography—need to be significantly amplified if we are to ensure the long-term survival of the amphibian diversity on Borneo and elsewhere.

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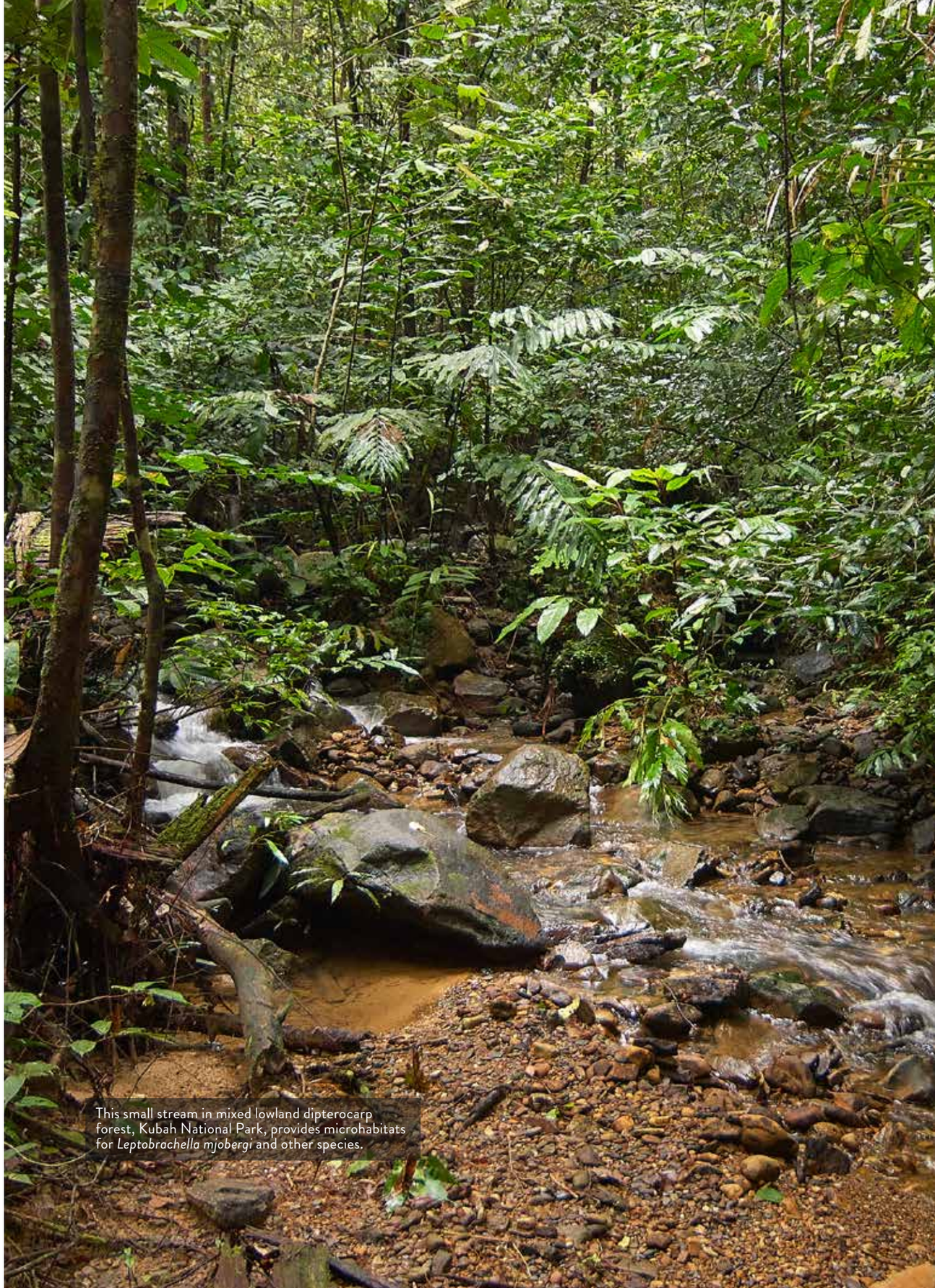


This small stream in mixed lowland dipterocarp forest, Kubah National Park, provides microhabitats for *Leptobrachella mjobergi* and other species.

NATURAL HISTORY

Researchers have mostly concentrated on exploring the diversity of Bornean amphibians, preparing inventories and describing new taxa. Relatively little, however, is known about the ecology of Bornean frogs and tadpoles. The knowledge on the ecology of the amphibian fauna clearly lags behind and more studies are needed on aspects of their natural history.

Dragonfly nymph feeding on *Pulchrana picturata* tadpole.

The complex life-cycles of frogs (p. 35) typically comprise eggs, larvae, metamorphic stages, froglets and adults (= the reproducing frogs). It has been argued that complex life-cycles with larval forms are only advantageous if the larva is a means to access otherwise inaccessible food resources for growth. Tadpoles are as much specialized to their specific aquatic niches, as are their adult kin to the terrestrial environment. Consequently, presence of both suitable terrestrial and aquatic habitats are prerequisites for a given species to survive in a region. Absence of suitable water bodies, in which reproduction can take place, and tadpoles can grow may exclude species from an area, despite the presence of adequate amount or type of forest habitat required by adult frogs.

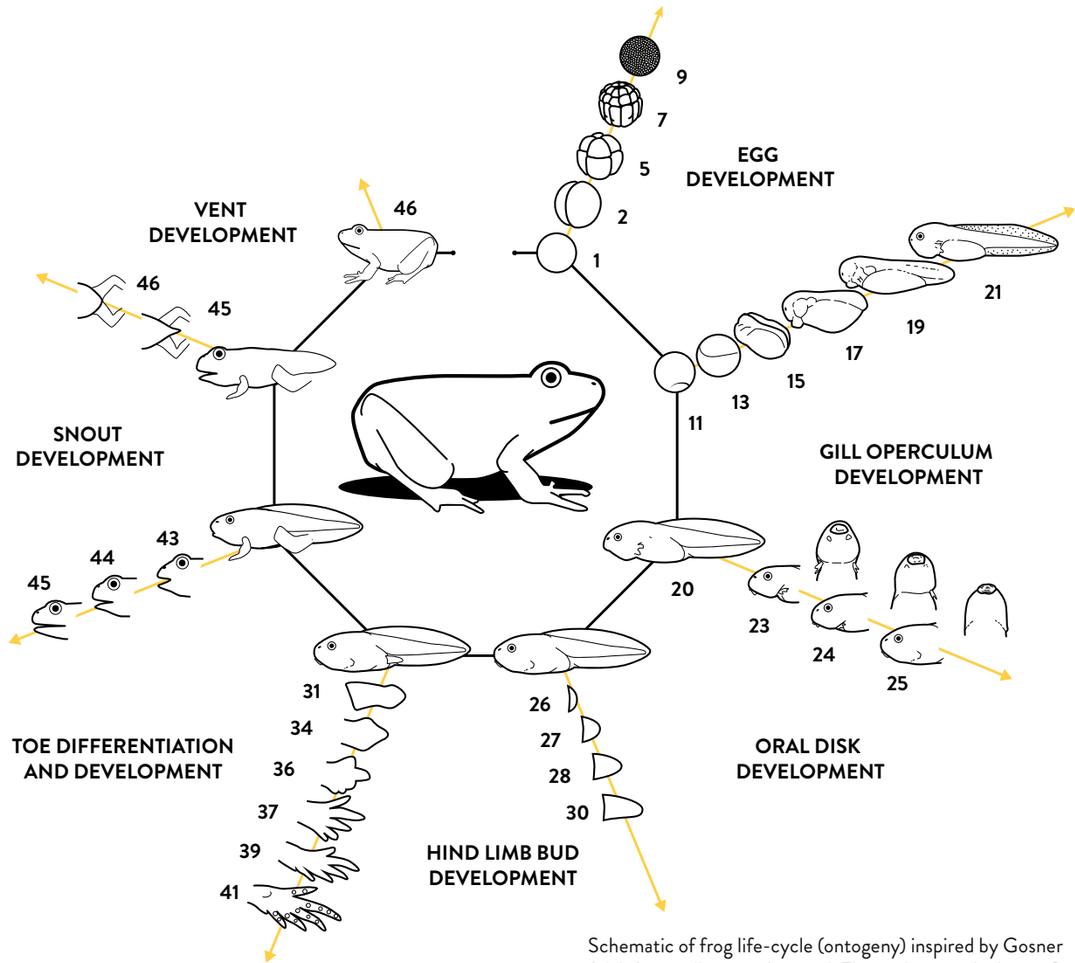
The exact environmental and spatial factors of tropical rainforests that shape various amphibian communities and their distributions are poorly understood. For what we know, canopy, leaf litter, mountain or stream communities may follow different assemblage rules. Structural features such as relief and elevation determine volume of precipitation, water retention, and water flow patterns. Elevation is connected to temperature. Mountain habitats are cooler than the lowlands. Some species are found exclusively in the sub-montane zone above 1000 m a.s.l., which indicates that these species are adapted to cooler temperature regimes. Also breeding habitat characteristics and availability is different in the highlands than in the lowlands. Their elevational range may have changed in historic times with rising or falling of global temperatures. The bed-rock, that may be limestone, sandstone or granite, influences soil and water acidity, floral composition and growth, and ultimately may have an effect on tadpole food resources. All such factors may explain that frog communities change spatially in tropical rainforests, that otherwise appear homogeneous to the untrained eye at first glance. Interactions with other organisms also have an affect on the abundance and composition of frog communities.

The role of competition of tadpoles in the same habitat is not well understood. Interaction with predators will influence a population of frogs or tadpoles. There are many snakes, birds, mammals, and lizards, even spiders or scorpions, that will prey on frogs. Tadpoles are eaten by many fish species, semi-aquatic spiders, snakes, beetle larvae, dragon- and damselfly larvae. Tadpoles are an important food source for many predators. Losses to predation can be high and many species compensate the losses by very high numbers of eggs per clutch, reaching several thousands in some species.

The utilization of breeding habitats that lack major predator groups (fish, dragonflies), such as phytotelmata, is a common evolutionary strategy. Another is to protect the eggs with foam nests (many rhacophorids) or guard the eggs (*Limnonectes palavanensis, L. finchi*).

The duration of the larval period from egg to metamorphosis is unknown in many of the Bornean species. It can be as short as three weeks, as in the tiny non-feeding tadpoles of *Microhyla nepenthicola* or much longer, four to eight weeks, in many other species.

Research on the diversity, composition, and dynamics of tadpole communities has just begun. Recent work by Ahmad Sah and Grafe (2020) has identified stream velocity, microhabitat width, and number of odonate larvae to significantly influence composition of the larval assemblage.

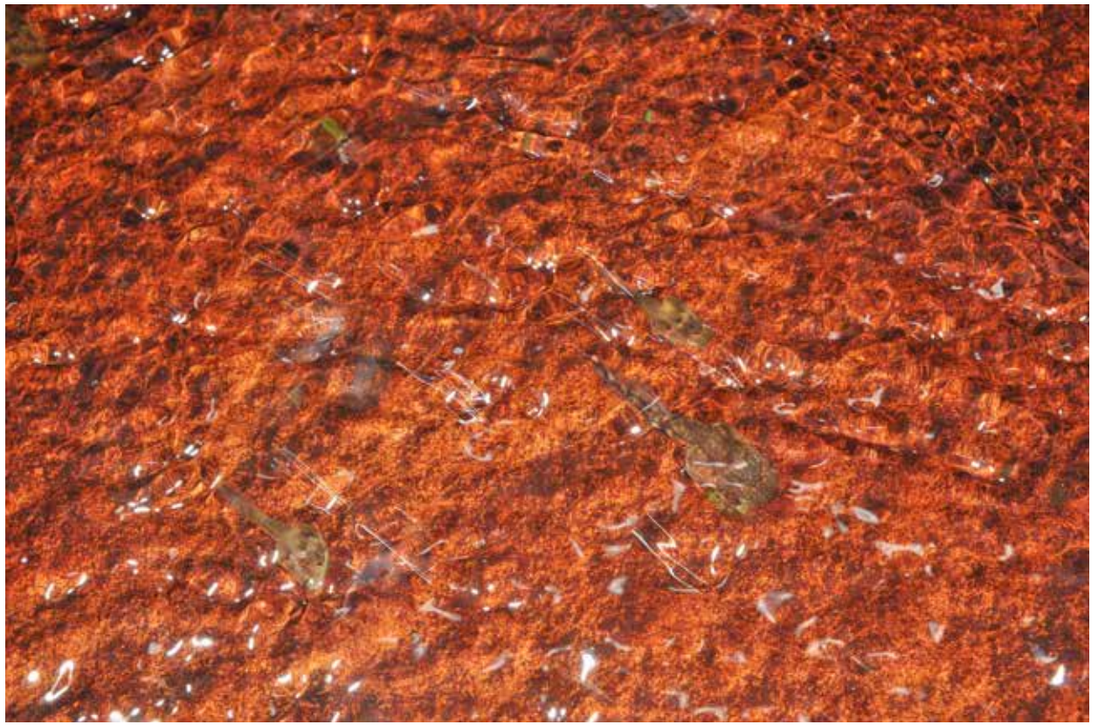


Schematic of frog life-cycle (ontogeny) inspired by Gosner (1960), not all stages depicted. The cycle goes clockwise. Specific character sets that change during development and that can be used to stage the embryo or larva according to Gosner are depicted radially.

Bottom-dwelling tadpoles may be well-camouflaged in their natural habitat. The photo shows an unidentified Creek Frog (*Limnonectes* sp.) tadpole from Mount Kinabalu in a shallow water puddle perfectly blending in with the bottom substrate.

Group of *Leptomantis harrissoni* tadpoles in a tree trunk phytotelma.

Tadpoles are an important food resource to a broad range of predators in Bornean ecosystems. Here a freshwater crab devours a *Huia cavitympanum* tadpole.



Gastromyzophorous tadpoles of *Meristogenys jerboa* while foraging at night on a rock surface that is overflown by water.

TADPOLE DIETS

Studying the diets of tadpoles is a difficult task. In most studies on the topic, the gut contents of freshly killed tadpoles are analyzed to draw conclusions about a tadpole's food items. However, there are major limitations to this approach: First, only the anterior parts of the gut will contain undigested food items and, thus, their analysis covers only a short time of feeding; the capture of the tadpole may have been outside its major feeding time. Second, some of the items present in the gut may actually not be digested and assimilated, but just pass through, and may represent incidental ingestions.

endotrophic larvae = larvae that do not have to take up food externally but grow and develop from yolk resources. **Exotrophic** larvae feed on external food sources.

For example, sand is a common component of the gut contents in ground-dwelling tadpoles. Obviously tadpoles do not digest sand grains. Rather, it is the microorganisms that live on the surface of and between the sand grains (e.g., microscopic algae, protozoans, small metazoans) that are the true food resources. Third, food items retrieved from a tadpole gut are difficult to identify under a microscope because the food is usually broken into pieces or in the process of digestion.

Nutrients come only from a portion of the materials ingested. Recently studies have started to investigate the isotope and fatty acid contents of tadpoles. The presence of nitrogen and carbon isotopes in the tadpole tissues depends on what the tadpole has been eating. Carnivorous species differ in their isotope and fatty acid signatures from mostly herbivorous tadpoles. These signatures can help establish a tadpole's position in the natural food web. Such approaches require high-tech equipment. The same applies to next generation sequencing, which allows recovering DNA traces from ingested food items for identification by DNA matching with databases. High-tech approaches are important but precise field observations can still contribute significantly to our understanding of tadpole feeding, especially in regions with scarce data. Sometimes tadpoles have been described as herbivores, eating mostly on algae or other plant materials. Recent observations from all parts of the world have shown that many tadpoles take up more animal matter than expected. In fact, the tadpoles of *Occidozyga* have been shown to swallow insect larvae in toto and attack other tadpoles. Oophagy, the eating of eggs, can be considered another form of carnivory. The larvae of *Rhacophorus harrissoni* can be oophagous (pp. 39 and 43). These tadpoles develop in tree holes and buttress. It is unclear if oophagy is mandatory in this species.

Other astonishing modes of feeding have been reported. Among microhylid species, tadpoles often are specialized high-efficiency suspension feeders. Microscopic floating particles (protozoans, debris, algae, pollen, dust, bacteria) are filtered and trapped in their highly elaborated gill or branchial apparatus by continuous pumping of water through that apparatus. Water intake is via the mouth and it is pumped over the internal epithelial gill filters and exits the gills via a gill chamber, in which the gills perform gas exchange. Microhylid tadpoles perform their suspension feeding in the water column at various depths;

Occidozyga baluensis feeding on the tail of a small *Rhacophorus pardalis* larva.

most microhylid tadpoles stay away from the bottom. In the evolution of this obligate filter-feeding mode, microhylid tadpoles have reduced keratinized mouthparts, jaw sheaths and keratodonts. When feeding and hovering in the water column, many microhylids keep the body at a certain inclination, head up, and hold their hovering position by incessantly beating the flagellate tip of their tail. Particularly tadpoles of *Glyphoglossus* maintain a steep angle and have a long flagellum. Rhacophorid tadpoles of the genus *Polypedates*, some *Rhacophorus* and *Leptomantis* also are highly efficient suspension feeders and can often be seen positioned stationary in the water column. They are less specialized than microhylids, in the sense that they maintain keratinized mouthparts that enable them to perform feeding with biting jaw motion as well.

Leptomantis harrissoni tadpole in ventral view. This species has tadpoles that are capable of oophagy (eating of eggs, p. 43). Note the egg-filled yellowish gut.

Megophryids have evolved different tadpole types. Tadpoles of *Pelobatrachus* and megorphrys species possess an oral disc of rhombic shape that is directed upwards. The tadpoles swim to the surface and the lips unfold and spread out under the surface film. The pumping mechanism of their internal branchial pump sucks in the water from the surface film over the oral disc. The water carries a load of microscopic food particles such as dust, pollen or bacteria. The megophryid tadpoles of *Leptobrachella* follow a different strategy. They are fossorial (p. 40), living in the superficial interstices of gravel beds in streams; they are rarely seen exposed. It is not fully understood what they feed on. Their jaws are quite strong and they probably feed on dead leaves or plant debris and organic overgrowth on it. The third tadpole type in megophryids, *Leptobrachium*, is a generalized bottom-dweller in quiet areas of rocky, clear streams. They can grow quite large. *Leptobrachium* tadpoles are likely opportunistic in their food resources.

Another ecomorph of tadpoles has specialized in grazing off the organic overgrowth on light exposed rock faces with overflowing water in mid-sized and large streams. They have developed mouth structures in the form of oral suckers to cling to rocks and prevent them from being flushed away. Such tadpoles that live in the flowing water are called rheophilous (literally "current-loving"). Some species of *Leptomantis*, most *Ansonia* and all *Huia* and *Meristogenys* belong to this category. *Huia* and *Meristogenys* tadpoles are unique in that they possess a large abdominal sucker in addition to an oral sucker (gastromyzophorous tadpole ecotype).

Tadpoles that eat external food sources for growth and development are called exotrophic. Yet, a few species have evolved endotrophic larvae that do not feed; rather, they live from endogenous food resources. Endotrophic larvae have a more or less typical body shape and still undergo metamorphosis Their internal food storage is yolk that is located

Pelobatrachus baluensis tadpole in dorsal view showing the funnel-shaped mouth used for surface feeding.

in their intestinal tissue; the yolk originally stems from the female frog that laid the eggs. Such yolk rich eggs are typically larger than other frog eggs, often 3-4 mm in yolk diameter, and the tadpoles that develop from it are small. Such non-feeding tadpoles have been confirmed for *Microhyla nepenthicola*, *Kalophrynus*, *Metaphrynella*, and some *Philautus* . These non-feeding tadpoles hatch from their egg, whereas direct-developing species go one step further: They complete their development in the egg. A finished froglet hatches from the egg. Nutrients are provided completely by the egg yolk. Although direct development is found in many frog species around the world, it has been confirmed only for few species on Borneo. All confirmed cases of direct development from Borneo belong to the genus *Philautus*.

Tadpoles of *Leptobrachella mjobergi* are capable of wiggling through the superficial interstices of the stream bed.

Tadpoles of the *Microhyla malang* are filter feeders. They float with slightly upward directed mouth in the water column, often close to the surface, while pumping water through their gill filters.

Larval specimen of *Philautus macroscelis*, an endotrophic larva.

Unidentified tadpoles of *Glyphoglossus*. These tadpoles assume an upward directed position in the water column when filter feeding.

Meristogenys sp. grazing on rock overgrowth and forming a dense congregation.

REPRODUCTIVE MODES & LARVAL HABITAT

Foam nest of a rhacophorid frog glued to a leaf 1.5 m above a pond.

phytotelma = pocket of water provided by plants, such as leaf axil, tree hole, buttress hole, bamboo internode, *Nepenthes* pitchers etc.

The place where a clutch is laid, the type of clutch, and how the larvae develop vary among frog species and dozens of different reproductive modes have been reported in frogs. Not all Bornean frogs have actually been observed laying their eggs and, thus, we do not know the reproductive modes for some with certainty.

Clutch of *Feihyla kajau*. Clutches are glued to the underside of leafs above water. Photo © A. Jankowski.

Some members of the rhacophorid tree-frogs are well-known for their foam nests. During mating the female secretes a albumin-like liquid from its ovarian ducts that the couple beats to foam with their hind limbs. The foam is made above a body of water and sticks to twigs, trunks or leaves. It is filled with fertilized eggs by the mating pair and left behind unattended after mating. The outer foam hardens and protects the clutch against intruders and desiccation. Once the tadpoles hatch from the eggs inside the foam nest, they secret substances that liquefy the foam. An opening forms at the bottom of the foam nest and the tadpoles will drop out of it into the water below. *Polypedates leucomystax* produces foam nests on the water surface, attached to aquatic vegetation. Most but not all Bornean Rhacophorids make foam nests. An exception are species of *Feihyla*, which lay eggs embedded in a jelly mass under leaves, without foam.

Some frogs have specialized in using small accumulations of water, such as root buttresses, tree holes, nut shells, hollow trunk or pitcher plants for larvae. The water volume may range from 100 ml to a few liters. Such small bodies of water that usually have plant origin are called phytotelmata. Phytotelma breeders include species of *Kalophrynus*, some *Microhyla*, *Metaphrynella, Chaperina*, *Nyctixalus*, some *Philautus*, *Theloderma* and some *Leptomantis*. Phytotelma breeders will occasionally accept water in human trash as reproduction sites such as cans, tires, or bottles.

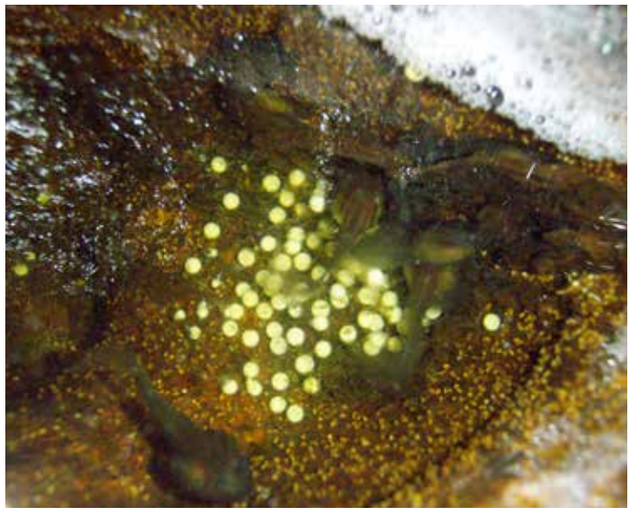
Terrestrial egg deposition helps avoid aquatic egg-eating predators. Species with terrestrial eggs include the direct-developing *Philautus*, but also *Limnonectes palavanensis* and *L. finchi*; the latter two have free-swimming tadpoles. In these *Limnonectes*, tadpoles hatch from the terrestrial clutch and climb the back of the male, which has been guarding the clutch. The male then transports the tadpoles to a near, suitable stream.

Many pond-breeding species lay their eggs in submerged clumps, attach them to vegetation or twigs in the water. Toads (Bufonidae) produce their eggs in strings. Other frogs have evolved clutches that float as thin layer of jelly eggs on the water surface. Some microhylids, such as *Microhyla malang* and *Kaloula pulchra* belong to this type, as well as *Fejervarya limnocharis*. In flowing water, drifting of eggs can be prevented by gluing eggs to rocks (e.g., *Meristogenys*). Ponds are water filled depressions. They can form for geological reasons, but can also be the result of uprooting of a tree or over time by the activity of pigs and rhinos that use wallows. Such small ponds are readily accepted as reproduction site by some species such as flying frogs (*Rhacophorus pardalis*, *R. borneensis*, *R. nigropalmatus*). Furthermore, stream sections may transform into stagnant pools during dry season and may be used for reproduction by *Ingerophrynus divergens* or *Abavorana luctuosa*, for example.

The territorial males of *Limnonectes leporinus* excavate shallow depressions in a small shallow streams. A female is attracted to the depression and mating occurs within this artificial structure. Eggs are single and sink to the bottom. After mating the male covers the eggs with sand and gravel, forming a small mound that protects the eggs from predators.

The site where the eggs are deposited is not necessarily the place where the tadpoles can be encountered later on. Tadpoles will choose their microhabitat within a stream or pond according to the accessibility of food, predation risk, temperature, light, and oxygen levels. The preferred microhabitats are diverse. Most *Limnonectes*, *Hylarana*, *Occidozyga*, and *Leptobrachium* species are bottom dwellers, that hide between pebble or rocks, under leaves or in the mud when disturbed. Other tadpoles make use of the mid-water column to filter small particles (for example some *Polypedates*, *Glyphoglossus*, *Microhyla*, *Chaperina*).

The tadpoles of some species seem to prefer the shelter of leaf litter accumulations (*Pelobatrachus*, *Staurois*, *Hylarana picturata*, *Odorrana*). Three genera have tadpoles with extraordinary rock clinging and rock climbing capabilities in flowing water, i.e., *Huia*, *Meristogenys* and *Ansonia*. All have large sucker structures to hold on to the rocks. During the day, they prefer resting places under the rocks but during the night these sucker-mouthed tadpoles crawl up to the upper side of overflown rocks to grace on algae that have grown there during the day. Tadpoles of *Meristogenys* and *Ansonia* can often be seen in mixed groups together. Sometimes they even crawl outside the water at the edge of a waterfall or cascade, as long as there is spray that keeps their gills and body wet.



Oophagy. Larvae of *Leptomantis harrissoni* feeding on eggs.

Developing stage of *Philautus acutus*.

The field of ecomorphology relates physical variables of size and shape to ecological adaptation of an organism. Once a relation has been established, predictions on the ecology of a tadpole can often be inferred from its morphology. For example, a tadpole with sloping head profile, extensive broad snout, muscular tail, oral sucker and reduced tail fin will certainly inhabit flowing water. For tadpoles a multi-category system has been proposed to sort tadpoles into ecomorphological guilds. We refer to life habits in the sections on the respective species.

Unidentified frog clutch glued to a wet rock cavity. Note that the eggs are wet but not submerged.

Mating pair of *Limnonectes leporinus* in a shallow section of a stream. In this species, the male (above) is larger than the female (below). Note the small white eggs already laid.

Several species of frogs reproduce in pig wallows, such as *Rhacophorus nigropalmatus*.

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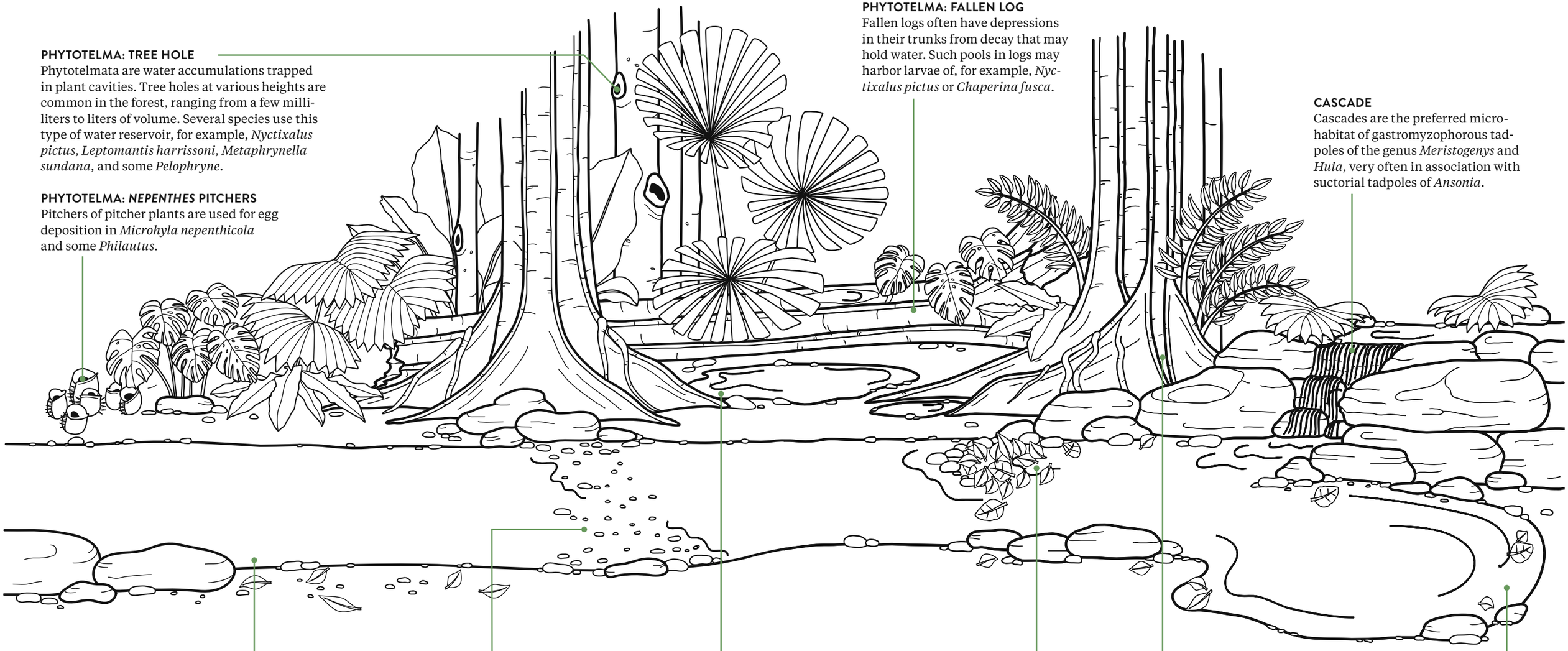
Eggs of *Staurois guttatus* laid in captivity. Photo © N. Potensky.

TADPOLE MICROHABITATS



PHYTOTELMA: TREE HOLE
Phytotelmata are water accumulations trapped in plant cavities. Tree holes at various heights are common in the forest, ranging from a few milliliters to liters of volume. Several species use this type of water reservoir, for example, *Nyctixalus pictus*, *Leptomantis harrissoni*, *Metaphrynella sundana,* and some *Pelophryne*.

PHYTOTELMA: *NEPENTHES* PITCHERS
Pitchers of pitcher plants are used for egg deposition in *Microhyla nepenthicola* and some *Philautus*.

PHYTOTELMA: FALLEN LOG
Fallen logs often have depressions in their trunks from decay that may hold water. Such pools in logs may harbor larvae of, for example, *Nyctixalus pictus* or *Chaperina fusca*.

CASCADE
Cascades are the preferred microhabitat of gastromyzophorous tadpoles of the genus *Meristogenys* and *Huia*, very often in association with suctorial tadpoles of *Ansonia*.

STREAM EDGE
Edges of streams have reduced flow velocity and are utilized by tadpoles of a number of stream-associated species, such as *Leptobrachium* species, *Limnonectes leporinus*, *Limnonectes ibanorum*, *Pelobatrachus nasutus*, *Ansonia leptopus, A. albomaculata*, *Ingerophrynus divergens*. The size of the stream and velocity play a role in a species' preference.

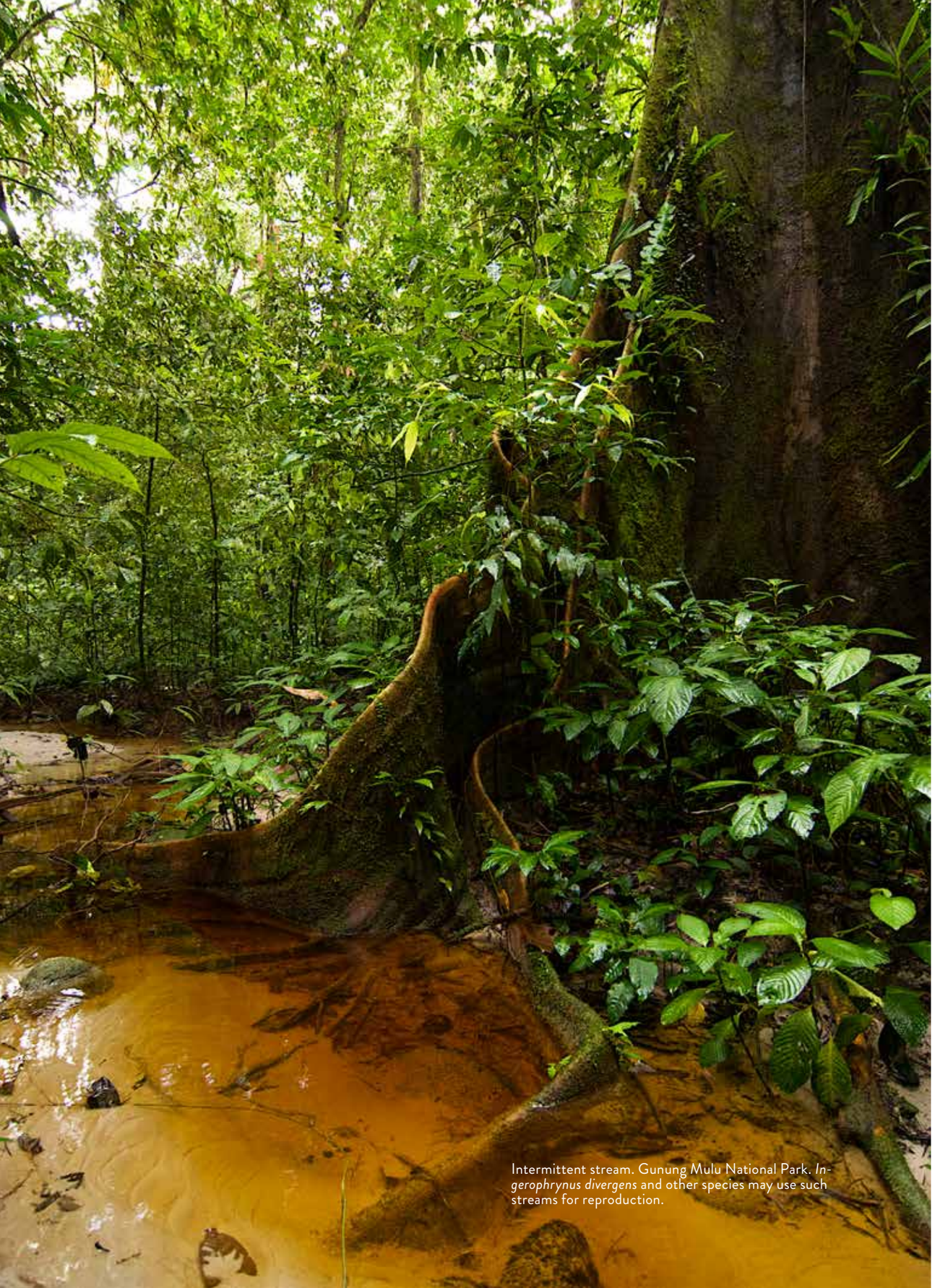
RIFFLE
Riffles are shallow parts in the river where the water overflows a sloping bed of gravel. Some specialized types of tadpoles can be encountered among the pebbles (rheophilous tadpoles of *Leptomantis gauni*, *Meristogenys*, *Ansonia*) or in the superficial interstices of the bed (species of *Leptobrachella*).

PONDS, POOLS & PUDDLES
These are stagnant bodies of water. Ponds are larger and hold water for longer periods whereas puddles are smaller and ephemeral. Small pools can be built by pig activity (wallows). A plethora of species populate such stagnant waters with their tadpoles, among them species of *Duttaphrynus*, *Fejervarya*, *Pulchrana, Chalcorana, Abavorana, Kaloula,* some *Microhyla*.

LEAVE ACCUMULATION
Leave litter is abundant in the forest. Leaves carried by the stream tend to accumulate in quiet sections or when barriers (rocks or logs) obstruct their way. *Pelobatrachus* and *Leptobrachium* tadpoles are frequently seen in such microhabitats.

PHYTOTELMA: BUTTRESS
Anastomoses at tree buttresses may form water-holding cavities, which are used by some species for reproduction, particularly *Chaperina fusca* and some *Kalophrynus*

SIDE POOL
Side pools are formed in outpocketings of the stream. The water in it may be stagnant or almost so. Side pools, for their lack of strong current, accumulate leave litter. Thick layers of leave litter are preferred habitats of, for example, *Pulchrana picturata*, *Leptobrachium nigrops*, *Odorrana hosii*, some *Limnonectes*, and *Staurois guttatus*.



Intermittent stream. Gunung Mulu National Park. *Ingerophrynus divergens* and other species may use such streams for reproduction.

ETHNOBIOLOGY

Frogs and humans show a strong association worldwide. On Borneo, the links are both cultural and culinary.

Frogs in plastic bag waiting to be sold on a local market.

Many beliefs and sayings center around frogs. Perhaps the most widespread is the wry observation of similarity between frogs and politicians (both allegedly with the capacity of hopping, the latter category, from a losing political party to a winning one). The Horned Frog (*Pelobatrachus nasutus*) is alleged to acquire magical powers during thunderstorms, and frogs of the genus have been considered to be so poisonous that they make plants wilt and perish. They are also considered dangerous to approach and touch, and a bite brings death. The Cinnamon Tree Frog (*Nyctixalus pictus*) is considered an agent of evil spirits; its low metallic call likened to the sound produced by a blacksmith sealing a coffin. Mass breeding in some species, interpreted as war between frogs, is thought in rural societies to precede conflict between ethnic groups, perhaps an example of imitative magic.

Two species of exotic frogs are farmed for food: the American Bullfrog (*Lithobates catesbeianus*) and the Taiwanese Bullfrog (*Hoplobatrachus rugulosus*). Frogs are sold in wet markets of many towns and cities across Borneo, and are offered cooked in Chinese restaurants, especially those specializing in Cantonese cuisine. Subsistence hunters wade through forested creeks in the interiors of Borneo, looking for the 'Pama' frog, the Giant River Frog (*Limnonectes leporinus*) for consumption—half a dozen would suffice as dinner for a small family. Other species thus hunted include its relatives (including *L. ibanorum*, *L. ingeri,* and *L. malesianus*). Smaller frogs (such as Creek Frogs and *L. paramacrodon*) are occasionally captured by children for providing a snack, and by hungry hunters, sometimes to accompany alcoholic drinks.

Several species (such as the River Toad, *Phrynoidis asper*, the Giant Toad, *P. juxtasper* and the Poisonous Rock Frog, *Odorrana hosii*) that bear powerful skin toxins may also be harvested by experienced hunters for food. The glandular skins that contains most of the poison are carefully removed before the flesh is cooked. Tadpoles of the Six-lined Treefrog (*Polypedates leucomystax*) are made into porridge for consumption by lactating mothers in the highlands of Bario in northern Sarawak. Frogs and tadpoles of the Mangrove Frog (*Fejervarya cancrivora*) and sometimes, its more common relative, the Cricket Frog (*F. limnocharis*), are captured for the local pet trade, specifically, for feeding the Dragonfish (*Scleropages* spp.). All parts of a frog are eaten, except the intestines of the large-growing species, and are typically made into soups.

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FINDING & OBSERVING TADPOLES

frog calls indicate reproductively active populations
https://soundcloud.com/frogvoicesofborneo

Please be aware that the following paragraphs contain scientific methods that require permits by the authorities to be conducted in the field. You are advised to consult with your local authorities prior to any field work and apply for appropriate permits. Furthermore, any wildlife should be treated humanely and respectfully and unnecessary stress is to be avoided according to animal welfare guidelines. Thirdly, hygiene and disinfecting equipment needs to be considered in times of aggressive fungi that can be transmitted from habitat to habitat.

Most Bornean tadpoles are unlikely to be seen by the casual observer. Looking for certain tadpoles can be frustrating and will require patience and effort. The incomplete coverage of species' tadpoles in this book and in the literature is telling in this respect.

In most species, tadpoles are less active during the day than during the night. Puddles that seem completely devoid of any tadpoles at daytime, may present an astonishing population of tadpoles at night. Many tadpoles hide in the mud or under submerged leaf litter, rocks or plants. At night, tadpoles are more likely to leave their shelter to forage and the search for tadpoles will often be more successful at night. Headlamps are essential, both hands are needed to catch tadpoles.

Background knowledge about the ecology of a tadpole is key to any endeavor to find the tadpoles of a given species. Streams have tadpole communities that are completely different from pond tadpole communities. Within each of these two major aquatic habitat categories, there are several different microhabitats inhabited by different tadpoles. Each of them has its own ecological niche. Each niche is composed of certain biotic and abiotic conditions such as flow velocity, sun exposure, plant growth, kind of substrate, depth, oxygen concentration, temperature, accessible food resources, predators, competitors, etc. The experienced naturalist will soon learn, which species to expect in which microhabitat (p.Tadpole Microhabitats 46).

In pond habitats, dip nets are most important. Over the years, we have experimented with various sizes and makes of nets and each naturalist may have slightly different preferences. We prefer nets with round or oval opening approximately 25 cm in diameter, a very stiff and durable frame, and net depth of 30-35 cm. A long handle can be helpful in some situations, but short handles of 50–70 cm have proven most versatile. Dark net screen is preferable over a light one, because a white net is more likely to scare away tadpoles whereas some tadpoles will swim more willingly into a dark net. The net needs to be extremely durable and easy to replace. When sweeping through the water or over bottom rocks and leaf litter, it is very common to hit sharp edged rocks and logs or get entangled with twig, that can easily rupture a delicate net. Black synthetic mesh that is commonly used for textile lining or backpack compartments works well as net. The meshes should not be too large (small tadpoles will pass through them) or too small (produces too much drag for fast strokes). If the net is wrapped around the rim of the frame at the opening, it is a good idea to protect this part by covering it with silicon tubing. Cable straps are an easy way to secure the tube along the net frame. In some situations, such as shallow puddles and phytotelmata, some additional commercial aquarium nets of various dimensions do a good job but often do not last long.

Tadpoles captured in a net need to be transferred quickly from the net to a plastic box or plastic bag containing water from the stream or pond. This can be done gently by hand or by inverting the net and dipping the tadpole into the water-filled container. Clear plastic bags will allow for a first assessment of the tadpole's features, such as coloration. Use a torch for examination. If more detailed observations are needed, the tadpole can be put to a portable field aquarium for photography. After examination the tadpole should be put back to the habitat where it has been caught.

Typically, finding frogs is easier than finding tadpoles. Almost all Bornean frogs are nocturnal and it is a waste of time to search for frogs during the day. Go out at night, properly equipped with good LED headlamps and torches and look around along the walking trails, particularly in the vicinity of streams and ponds. Many species perch on saplings and low vegetation, e.g., the common *Staurois* and *Chalcorana*. Species of *Limnonectes* and *Pelobatrachus,* however, will most likely be found on the forest floor or banks along bodies of water, whereas adult tree frogs need to be searched meters above the ground, often on tree branches that overhang water. The light of the headlamp will let the eyes of the frogs reflect a yellowish light. This method of searching frogs is called visual encounter survey.

Acoustic encounter is another method that works well, for example, for quantitative population surveys. Male frogs call to attract females. Learning and recognizing the calls of male frogs helps identify species in the field quickly and assess population size. Some frogs can be localized carefully in the field and examined without touching them. Others need to be caught by hand to have a closer look at some features such as toe webbing. Whenever you touch a frog remember that the skin can contain toxic substances; hands need to be washed thoroughly after handling frogs.

DESCRIBING & ILLUSTRATING TADPOLES

The lack of regional determination keys and field guides for tadpole identification is a hindrance for ecological and community studies. It is important to make rapid progress in describing hitherto unknown tadpoles. Although very similar tadpoles of cryptic species may exclude unequivocal identification by morphological methods in some cases, the paramount goal should be to optimize morphological determination for fast and reliable diagnostics as much as possible. In this respect, illustrations are essential to communicate information about body features.

In the past, many tadpole descriptions were in fact published without any illustrative figure of the tadpole concerned. Among those published tadpole descriptions that were equipped with figures, line drawings have been a frequently chosen option for more than a hundred years up to the present. The traditional predominance of line drawings in illustrating tadpoles has mainly been due to the ease of production in print and, in the beginning, lack of alternative technologies. Line drawings had clear advantages: easy to make, low cost, clarity (if done well), simple to reproduce and scale, and ease of grouping drawings on plates for interspecific comparisons. These advantages of line drawings are perhaps outweighed by several disadvantages: loss of color information and loss of pigmentation information; researchers may decide to hand the drawing process to an artist who is not familiar with the taxonomically relevant character states (a potential source of additional errors of detail). Tadpole drawn by two different artists can look quite different. Moreover, drawings were usually made from preserved specimens that may have altered body shapes (bending of axial skeleton, shrinkage caused by preservation). However, drawings have their merits to show certain features such as general body proportions and shape. Herein, we developed rather minimalistic computer vector drawings to show body shape, nostril and eye position of tadpoles in dorsal view.

The predominance of line drawings in the literature on tadpoles limits the immediate use of published information. An ecologist planning a community-level study on tadpoles in the tropics will hardly be able to compile enough information from the literature to be able to reliably identify living specimens in the field. Other approaches can replace drawings in many instances. High-resolution digital photographic techniques opened up new options for tadpole documentation and are, in our opinion, a necessary part in successful tadpole identification.

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Haas, A., Das, I. (2011) Describing East Malaysian tadpole diversity: Status and recommendations for standards and procedures associated with larval amphibian description and documentation. Bonner Zoologische Monographien 57: 29–46.

TADPOLE PHOTOGRAPHY

During the past decades, the advent and rapid progress of digital photography has profoundly changed our approach to image acquisition, processing, and archiving. For the first time, catalogues of vast numbers of high-quality images can be collected for biodiversity research projects at relatively low costs. Various software packages allow the handling and meta-data annotation of image catalogues containing thousands of images, allowing for rapid comparisons of tadpoles among regions or study sites.

The resolution and quality of images has steadily increased and any camera with 16 megapixel (MP) resolution or more likely will satisfy a biologist's needs for image quality in most cases. Flash control systems have evolved substantially. Wireless-controlled flash systems or radio trigger systems are readily available on the market for all systems, making multiple flash setups easy to handle in field situations. In synchronized, wireless through-the-lens (TTL) systems of the major camera manufacturers, lighting measurements and data exchanges between flash and camera are automatic. Images can be evaluated immediately after exposure on the camera screen and lighting can be adjusted (exposure compensation) if necessary. In modern flash systems, little intervention by the photographer is necessary and the technique is generally simple and reliable.

For tadpole photography a custom-made mini-aquarium is useful, 20x10x4 cm (width x height x depth) in dimension, glass thickness 4 mm. A bottom with sand, pebble stones or small rocks can serves as photo stage. The placement of the tadpole should be close to the front glass. A thin straw may help to gently direct the tadpole to the preferred spot in the tank. Great care should be taken to keep the water in the aquarium as clean as possible to avoid floating particles which become annoyingly apparent in flash photography on dark backgrounds. A leaf or plastic card inserted in front of the back glass will prevent reflections.

Dorsal views can best be obtained in a black or white plastic dish, preferably with shallow rim. For small individuals, even the rear cap of a lens has proven suitable.

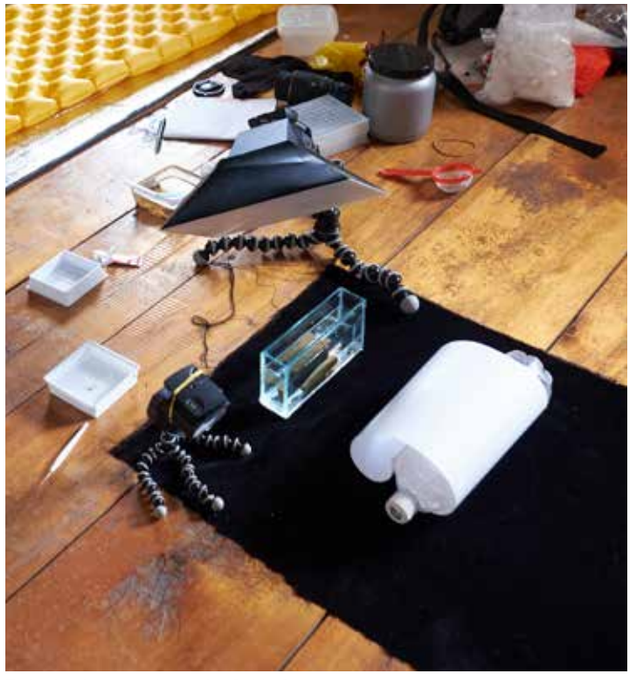
Tadpole photography will require a macro lens. 50–100 mm focal length macro lenses work well for tadpoles with APSC sensor SLR cameras; for full-format sensor cameras 100–200 mm focal length lenses will work great. Longer focal length macro lenses give sufficient distance between the front end of the lens and the aquarium to position flashes or reflectors. Additional extension tubes can increase magnification well beyond 1:1 and allow the documentation of finer patterns in pigmentation or details of mouthparts. Furthermore, the angles of view of 100 mm to 200 mm lenses reduce parallax effects. This is advantageous with respect to the refraction effects (distortion) in the aquarium, particularly towards the periphery of the image. Most of our tadpole photography in this book was done without a scale in the image, however, if measurements are intended to be taken from photographs, some appropriate scale should be placed near the tadpole, either outside the tank or inside. There will be some parallax error that needs to be determined; thus, long focal length lenses will tend to perform better if measurements from photographs are desired.

Good lighting can be achieved by placing the main flash unit (wireless-controlled) on top of the aquarium and a second flash with somewhat reduced power output to the left of the camera to fill in shadows from an angle. Alternatively, two flashes, one on either side of the camera and pointing to the subject can be used with good results. Flashes can be mounted on small table tripods. Some experimenting may be necessary to find your preferred setup, also depending on the color of the tadpole and of the substratum, the strength of flash output, and the camera and lens used. Diffusers (light modifiers) mounted on the flash will provide a diffuse, less harsh light.

A 80x80 cm piece of black velvet cloth under and behind the photo aquarium can make a good background and helps control light and reflections.

Tadpoles are always photographed facing to the left in order to show the position of the spiraculum on the left side of the body in most species. By choosing different background colors, it can be ensured that the outline of the tadpole tail fin is visible on the images. When using dark background, the reflection of the tadpole may be visible on the background glass of the aquarium. This can be avoided if a non-reflective object (color plastic card, rock, leaf) is put inside the tank behind the tadpole.

Properly lit, standardized lateral, dorsal and ventral digital photographs of tadpoles will capture the body shape, proportions, and pigmentation details in high quality. Digital high resolution imagery are an indispensable tool for tadpole identification. Large 16–36 megapixel images allow zooming in and evaluating valuable details in living specimens that vanish in museum specimens, such as silver and golden skin iridocytes.



Tadpole photography in the field often requires improvisation. A custom-made mini aquarium, a piece of black velvet, spoons and straws, some plastic dishes, two flashes, light modifiers and a table top tripod are useful items for a small and portable tadpole photography setup.

Different backgrounds can accentuate certain features, such as tail fin contour. Same specimen of *Limnonectes finchi* photographed with gray and black background, respectively. The photograph was taken using a small, portable table-top aquarium as depicted above.

MEASUREMENTS

A variety of external characters are accessible to measurement in tadpoles. Although various authors may use slightly different measurements, a certain standard has evolved. It has been shown that some external and internal features remain stable during larval life, whereas others (such as tail fin height) may vary with growth and as a response to external factors. Generally, formal tadpole descriptions should be based on developmental stages 32–40 (Gosner 1960 Table, p. 35). At stages 32–40 many taxonomically relevant character states are stable, e.g. relative tail length. In case of tadpole identification in the field, it is often the case that tadpoles are mostly in one age class (i.e., from one clutch); stages 32–40 may not be available.

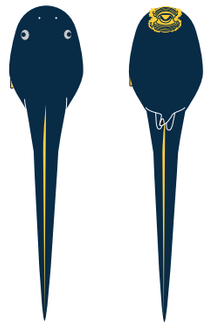
Measurements can be taken with vernier calipers in the field situation from anesthetized tadpole, but the results will lack precision. Taking measurements is much more efficient and precise in the laboratory performed under a stereo-microscope or with digital microscopy. If exact measurements are needed, tadpoles need to be brought to a lab and be measured with these modern measurement tools.

Most users of this book will not have access to laboratories equipment and will have to rely on qualitative features to identify tadpoles. The illustrations explain some terms that will be used in the tadpole descriptions. Tadpole measurements, apart from overall length and, for example, relative tail length, will be neglected in this book. In fact, in scientific papers, metrics of anuran tadpoles have not been used as the core of larval diagnosis, except for the number of keratodont rows. Metrics such as maximal body width and body height will obviously vary with the feeding condition of the tadpole. Tail fin height has been shown to vary with the presence of predators in some anuran tadpoles. Some distances and points for measurements are difficult to determine by nature, such as the point of maximum height of the tail, or need explanation, such as the body-tail junction which is defined specifically to be the point where the horizontal myoseptum meets the end of the body.

Combinations of qualitative characters can diagnose a tadpole in many cases, at least to the genus level. Furthermore, habitat type and locality (distributional information) help to narrow the range of possible species. In particularly difficult cases, however, the researcher must resort to molecular barcoding to identify a tadpole with certainty. We will point out other qualitative diagnostics whenever possible.

MEDIAL
at or towards the middle part or middle plane/axis of the body

LATERAL
at or towards the side; lateral view = viewed from the side



DORSAL
at or towards the upper part of the body. Dorsal view = viewed from above

VENTRAL
at or towards the lower part of the body. Ventral view = viewed from below

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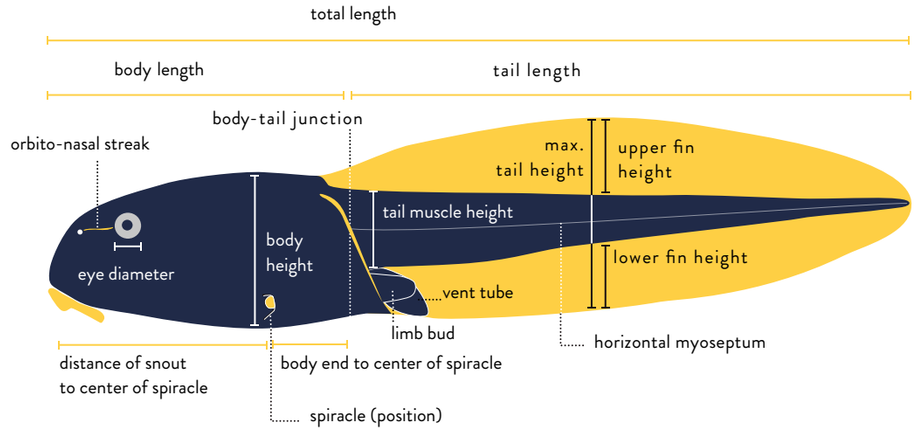

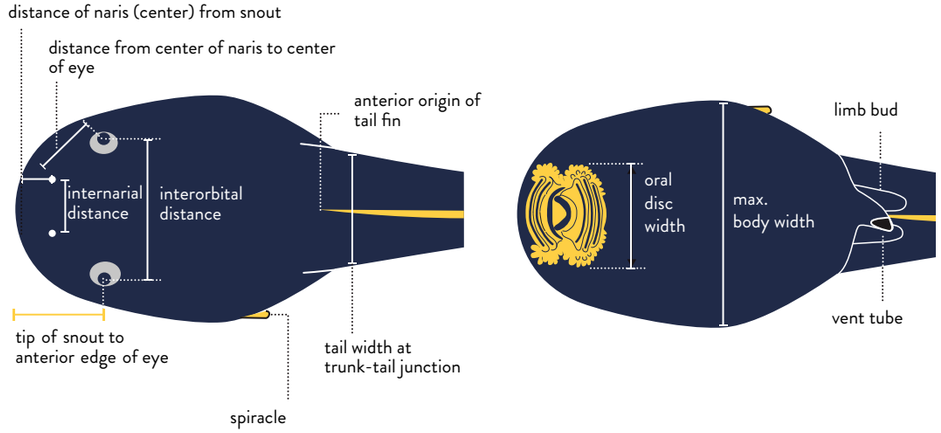

ANTERIOR
at or towards the front end of the body

VENTRAL

POSTERIOR
at or towards the hind end of the body

DNA BARCODING

DNA barcoding uses mitochondrial gene sequences that are extracted, amplified and sequenced, and compares it to known other such sequences for identification. Databases such as Genbank or International Barcoding of Life allow comparison with related taxa. DNA barcodes can facilitate species identification and description, reveal cryptic species, or link highly dimorphic males and females. Furthermore, in biphasic organisms with complex life-cycles, such as in certain arthropods and amphibians, barcoding techniques are an excellent tool to link eggs or tadpoles to their adults. Barcoding techniques have proven indispensable in tadpole research. Adult DNA samples can be obtained by mouth swapping for comparisons. DNA analyses are easy to perform and relatively cheap. They can be done by a contractor. DNA barcoding is highly reliable and unequivocal if tadpoles and frogs are sampled for DNA at the same site. In Amphibians, the mitochondrial 16S gene is most often used for DNA barcoding.

Genbank is a repository for genetic sequences
https://https.ncbi.nlm.nih.gov/genbank/

Before DNA techniques became readily available and affordable, researchers tried to identify tadpoles by raising them through metamorphosis and comparison with nearby found adults. This approach has been successful for a number of species that we can identify reliably by morphological features, without comparing their DNA sequences. The rearing of tadpoles is particularly successful with species that develop unique color patterns on their thighs or dorsum at pre- or mid-metamorphic stages, such as *Polypedates otilophus* or *Abavorana luctuosa* among Bornean species. In less conspicuous species, metamorphs may be indistinct from unrelated species that occur in syntopy or even highly divergent in their color pattern from adults (for example, *Rhacophorus nigropalmatus*) making assignments based on metamorphs ambiguous or erroneous in some species. Barcoding techniques could clarify previously ambiguous or wrong tadpole assignments.

Most of the tadpoles described in this book have been validated by DNA matching to adults from the same habitat or region. Selected genetic sequences from our work have been published in several papers and deposited at Genbank.

The morphologically highly divergent tadpole of *Philautus nepenthophilus* was successfully identified by DNA barcoding in Etter et al. (2020).

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VOUCHERS AND TISSUE PRESERVATION

In parts of the world in which new discoveries are a constant, it is necessary to document biodiversity scientifically by taking voucher specimens and tissue samples. Scientific sampling for the purpose of vouchering usually does not need large numbers. Scientific sampling is unlikely to damage local populations; many more individuals succumb to predators or habitat destruction. Proper permits, issued by the responsible authorities, are, of course, a prerequisite to scientific sampling of wildlife.

Tadpoles that need to be preserved for scientific purposes should be euthanized in accordance with animal welfare standards without causing unnecessary stress or pain. The qualified researcher applies certain chemicals in aqueous solution that will anesthetize the animals softly and will, in overdose, eventually kill them. In case of tadpoles, once deceased, one or a few tadpoles can be selected for tissue sampling. Small tadpoles can be transferred to absolute (100 %) alcohol completely. In larger tadpoles, cut out pieces of tail musculature, the tail tip, or the right hind limb (if present) are removed and transferred to vials with alcohol or other suitable fixatives. The volume of the alcohol in the vial should be at least 20 times the volume of the tissue. The alcohol must be free of additives that could potentially interfere with DNA analysis. Other solutions have been developed to preserve tissue samples for DNA analysis; RNAlater,® for example, works well. It has the advantage over ethanol that it is non-inflammable, has less evaporation problems, and can be carried on board of airplanes. In frogs, commonly tissue is excised from the underside of the thigh musculature or from the liver of the freshly killed specimen. Sharp forceps and laboratory dissection scissors are required for preparation. Whenever processing several specimens, utmost care must be taken to clean the dissection kit and workplace (wipe with ethanol; clear forceps and scissors in a flame) between samples to avoid DNA contamination.

Those tadpoles that will not be subject to DNA analyses, should be preserved and stored in 4 % formaldehyde solution (a 1:9 parts dilution of formaldehyde concentrate, which is traded at approx. 36 %). The formalin solution will partly transform into formic acid over time. The acid will decalcify the delicate bones of late tadpole stages and may destroy other tissue. Therefore, it is mandatory to buffer the formalin solution neutrally for long term storage. The following additives will work for 1 Liter or solution: 4 g of NaH2PO4 ; 6.5 g of Na2HPO4. Magnesium carbonate (MgCO3) can be used if the phosphates are not readily available, but specimens should be transferred to the phosphate buffered later on. Some laboratory suppliers provide ready-to-use buffered and stabilized formalin solutions for histology, that are good for long term storage. Alternatively, tadpoles that were fixed in formalin for a few days can be transferred to 70 % ethanol after rinsing thoroughly in water first and then transfer through steps of 30 % , 50 % , and 70 % alcohol, respectively.

Each vial with tadpoles needs to contain at least a field number, collector's name, date, and locality information. Field tags need to be good-quality (e.g., cloth-based) paper and all data need to be written either with pencil or water-proof ink. The ink needs to be dry before inserting the tag into fluid. There is no standard for field numbers, but putting your initials, the year, plus an index is a possible system; a time stamp (date+time) is a unique identifier that can be used. Field numbers need to correspond to a carefully written field logs. It must contain all pertinent field information for each of the specimens, such as date of collection, collector's name, locality, place, state, country, GPS coordinates, a short habitat description, short notes on circumstantial observations, notes that link the specimen to photos that were taken etc. This type of information is a prerequisite for depositing specimens in scientific collections.

Voucher tadpole collections used for this book are housed at the Zoological Museum Hamburg (ZMH), the Museum of the Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak (IBEC UNIMAS). and the Naturhistorisches Museum Bern (NMBE).

LITERATURE

Heyer, W.R., Donelly, M.A., McDiarmid, R.W., Hayek, L.A., Foster, M.S. (1994) Measuring and Monitoring biological Diversity. Standard Methods for Amphibians. Smithsonian Institution Press, Washington, London. 364 pp.

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TADPOLE MORPHOLOGY

Anuran tadpoles have a simple body plan: in most species, head and trunk (herein: body) are compact and the head is not or only indistinctly set off from the trunk. The head-trunk (body) is rounded and varies in relative length, height, width and shape among species. The transition from the trunk to the tail is abrupt in most species. At that the trunk-tail junction, the hind limb buds are located ventrally. They grow and differentiate over the larval period. The tail is long and bears dorsal and ventral semitransparent fins.

When tadpoles are observed in a pond or a stream, it is often impossible to see relevant body features immediately. Many species look similar for the untrained student. Catching the tadpole and having a close-up look will be necessary. Helpful tools for fieldwork are a hand-held torch and a good 10x magnifying glass. These will allow for having a closer look at tadpoles that where caught in a net. Digital photography (p. 52) is an excellent option for exploring morphological details. Properly lit high-resolution images of tadpoles reveal a wealth of features described in this book that will allow identification.

BODY SHAPES, EYES, AND NOSTRILS (HYPOTHETICAL COMBINATIONS)

nostrils closer to eyes than to snout, lateral eyes, rhomboid body

nostrils closer to snout than to eye, dorsolateral eyes, ovoid body

nostrils much closer to eyes than to snout, dorsal eyes, inverse tear drop shaped body

In the field, naturalists will likely seek features for tadpole identification that do not require precise measurements, except for body length and total lengths. Relative tail ratio (in % total length) can also be a helpful descriptor. Tadpoles offer a variety of qualitative features. Many of them refer to shape. It is in the nature of such qualitative verbal descriptions of shape that they have some ambiguity and are sometimes difficult to apply; an illustration can clarify the ambiguities. Some features may have to be checked in combination with other features to become diagnostic. Tadpoles in the second half of larval live, before metamorphosis (Gosner Stages 33–38), are most suitable for an assessment of morphological and coloration features.

The shape of the body (head-trunk unit) is an important feature, yet difficult to describe verbally and more easily expressed by drawings or photographs. It is necessary to document both the dorsal (or ventral) view and lateral view of a tadpole to describe body shape. The body of bottom dwelling species is dorsoventrally depressed (wider than high). Rheophilous tadpoles, i.e., tadpoles that live in the current of streams, are hydro-dynamically optimized. Usually they have expanded sloping snouts, giving them special body shapes, some of which can easily be recognized to the genus level. The highly specialized tadpoles of *Leptobrachella* are burrowers and have slender, long and cylindrical bodies with indistinct transition to the tail, giving them a peculiar eel-like appearance.

The head is a more or less rounded structure in tadpoles for the obvious hydrodynamic reason of swimming in the water. Yet, snout shapes, both in dorsal and lateral views, vary among species and need to be studied. Depending on the length of the snout, the nostrils may be located more to the snout than to the eye or more to the eye. Also, the nostrils can be narrowly or widely spaced, can have different rim structures, sizes, and orientations. The eye position is studied in dorsal view. The eye cornea can protrude beyond the body contour (lateral eye position) or reaches the contour (near lateral). In many species the eyes are further medial from the head contour (dorsolateral). Eye iris color and color pattern can present additional features that may help identify and distinguish tadpoles; they are best studied by high-resolution photographs of living specimens.

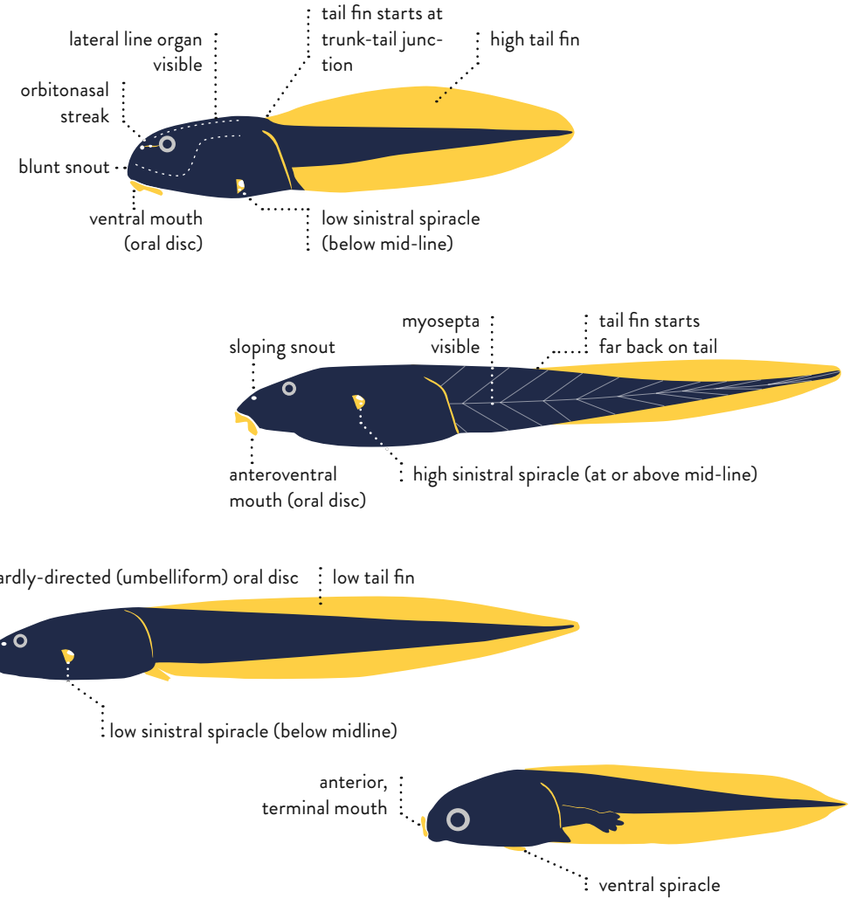
The mouth region with its extended lips has proven to be an important structure in species identification. It is relatively rich in structural features. The expanded lip structures are called oral disc in tadpoles. In relation to the head profile, the oral disc and mouth can have orientations that range from upward directed in *Pelobatrachus* to downward directed (ventral) in, for example, *Ansonia*. The mouth of filter-feeding microhylids and the predatory *Hoplobatrachus* are directed anteriorly and positioned terminally. The oral disc can be cup- or dome-shaped in stream-dwelling tadpoles. This type of oral disc is called oral sucker and helps to attach and anchor the tadpole to a rock surface in the current. These examples show that the orientation of the oral disc is related to the mode of feeding and microhabitat of the respective species. Apart from the orientation the relative size and shape of the oral disc need to be noted; some tadpoles have very large oral discs, in others they are rather small, reduced, or absent such as in species of *Microhyla* and *Nanohyla*.

The oral disc has two structural sub-elements, namely papillae and keratodonts. Both vary in arrangement, form and number among species. Papillae are epithelial, more or less conical or rounded structures mostly arranged along the rim of the oral disc (=marginal papillae) or at some distance to the rim (=submarginal papillae).

Keratodonts are keratinized spoon-shaped structures, commonly with serrated margin. Keratodont means 'horny tooth', although they have nothing in common with true teeth; tadpoles lack true teeth. Keratodonts are tiny and the investigation of their details requires a stereo-microscope or scanning electron microscope. Their specific arrangement in rows, however, is visible with magnification glasses or on high magnification photographs. It is the number and arrangement of rows (medial gap present or absent) that need to be recorded for identification. This information is summarized in a Labial Tooth Row Formula (LTRF).

BODY SHAPES AND QUALITATIVE FEATURES

Snout shape, oral disc position, spiracular position, tail fin height, lateral line organ, myosepta. Lateral views.



ORAL DISC AND SPIRACLE

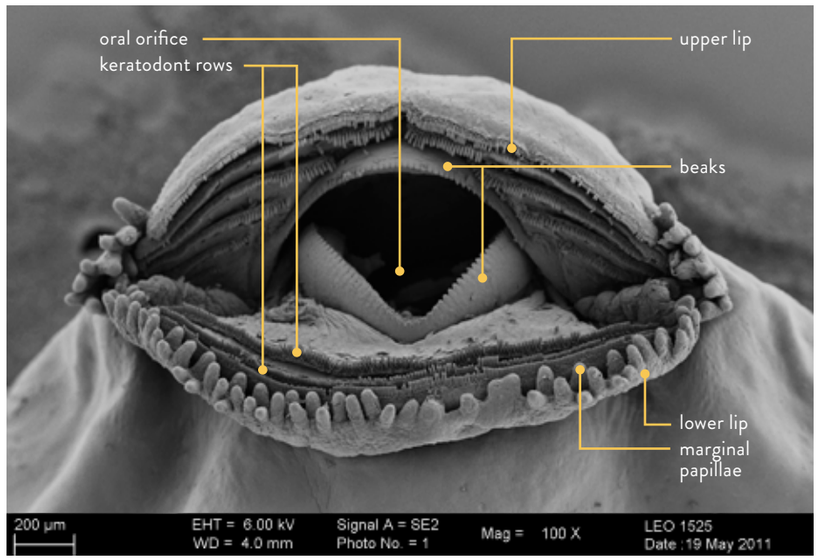
Examples of oral disc configurations and spiraculum position and shape; ventral views.

no expanded lips, no oral disc, median spiracle, (microhylids)

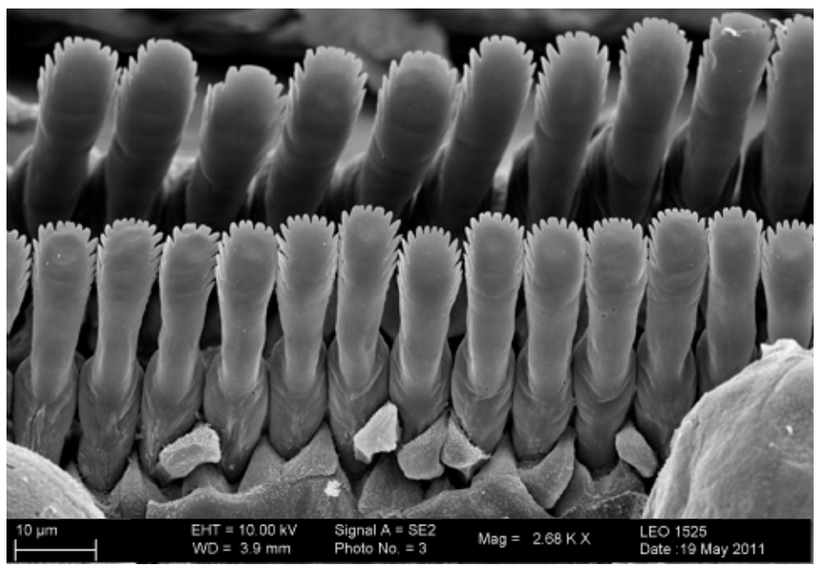
normal oral disc, often less than half body width, spiracle sinistral (= on left side of body), (many species)

oral disc forms wide sucker, spiracle sinistral, (*Ansonia*, and some rhacophorids)

oral sucker expanded, gastric sucker posterior to oral sucker , spiracle sinistral, (*Meristogenys*, *Huia*)

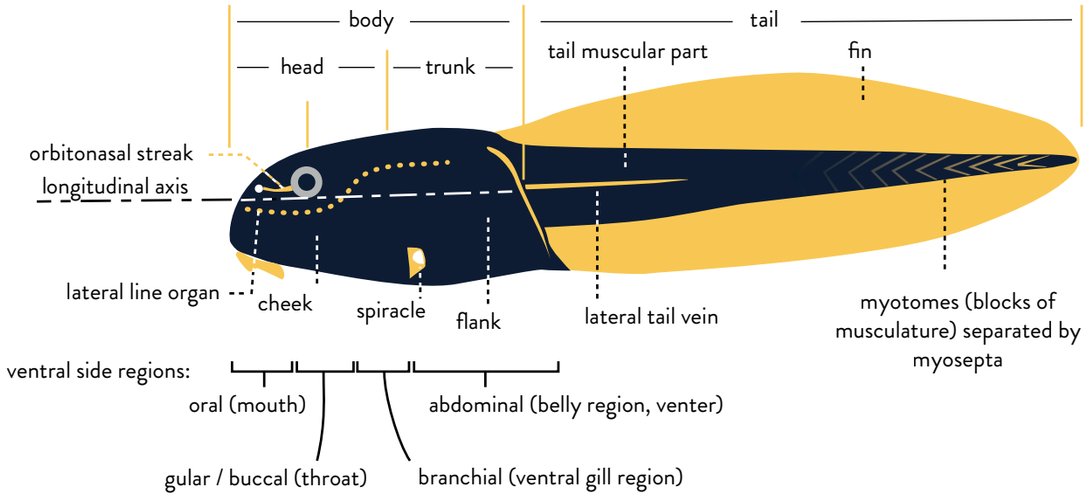


Scanning electron microscopy image of a *Zhangixalus dulitensis* tadpole. Ventral view. (SEM photo courtesy of Wencke Krings).



Same specimen as above. Keratodonts of the lower lip magnified. (SEM photo courtesy of Wencke Krings).

FEATURES AND REGIONS OF THE TADPOLE BODY



The LTRF records how many rows of keratodonts there are on the upper (anterior) and lower (posterior) lip of the oral disc, but also if they are continuous from side to side or with a gap; divided rows are given in parentheses.

The jaws are located at the center and deep in the oral disc. As mentioned, true teeth are absent in tadpoles, however, the jaws are reinforced with horny beaks, dark brown or black in color. Species may differ from each other by strength (height) of the beak, shape (angled or smoothly arched), and structure (finely or coarsely serrated margins). Obligate filter-feeding species of the Microhylidae lack keratinized beaks.

Oral disc and jaws work together in feeding. Biting and rasping movements of these structures remove food particles from the substrate. Particles are then sucked in with a water current generated by the musculature of the hyobranchial apparatus occupying the posteroventral part of the head. Below this musculo-skeletal complex, gill arches bear gill filaments that are passed by the water flow in the paired gill chambers. In many species, the gills can be seen shimmering through the skin in red color because they receive plenty of blood supply. The water exits the gill chambers through an unpaired spiracle. In addition to gill respiration, many tadpoles possess lungs and come to the surface to breath air from time to time. In fact, most tadpoles will die, if deprived from access to air. Bufonid

EXAMPLES OF ORAL CONFIGURATIONS

LTRF 0/0

(Microhylidae)

- keratodonts absent
- oral disc reduced
- no keratinized beaks

LTRF 2(2)/3(1–2)

- upper lip with two keratodont rows (second row divided)
- upper beak and lower beak keratinized
- three keratodont rows on the lower lip the two inner rows divided, outer row undivided

LTRF 2/3

- two undivided rows on upper lip
- upper and lower beak keratinized
- three undivided rows on lower lip

Note: Oral discs in this book are depicted in a schematic fashion. Although derived from actual specimens, herein oral discs are abstractions of taxonomically relevant features. They are not naturalistic drawings.

TAIL TIP SHAPES

tadpoles and tadpoles living in swift waters (rheophilous tadpoles) are different, however, and develop lungs only during metamorphosis.

Like fish, tadpoles possess sense organs in their skin to perceive water current and near-field pressure changes, the lateral line neuromasts. These are small groups of cells in the skin arranged as lines of dots over the head and trunk. In some species, the lateral line organs on the skin are hardly visible, in others they are more easily detectable. Recording the path of the system of lateral lines in a species may not be feasible during field observations; however, we will mention the general visibility of the system in species where noteworthy.

The trunk offers less structural features than the head, but can bear important coloration features for identification (see below). Structurally, the position of the spiracle and the vent are of importance. The spiracle, through which the water from the gills is expelled, is located on the left side of the body (sinistral) in most Bornean species, except for Microhylidae. In microhylids, the spiracle is in the mid-line of the belly (medio-ventral). Usually the spiracle can be seen on high magnification photographs. Its orifice can be attached to the body wall or detached and forming a free, albeit short tube (siphon).

COLORATION COMPARISONS

The images show the same specimen (*Indosylvirana nicobariensis*) before (above) and after (below) preservation. Taking images of living specimens is important in order to document color features. In preservation the color changes significantly and valuable information is lost. Silver, white or golden iridocytes disappear in preservation (from Haas and Das 2011).

The spiracle position along the anterior-posterior axis and its height along the dorso-ventral axis vary depending on the species, as well as the orientation. The vent opening is connected to the lower fin. Whether the vent is left, right, or in line embedded in the fin can be difficult to see on photographs and a microscope an forceps may be required if this is an issue that needs clarification.

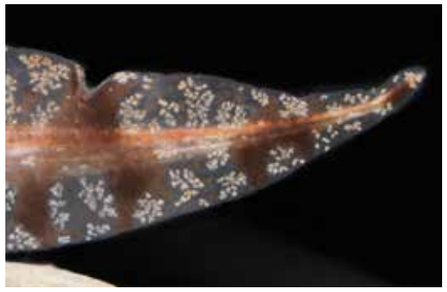
The tadpole tail fins have been shown in some species to vary in height in the presence of predators (higher when predators are present, such as dragonfly larvae). Despite this variation in dimension the overall shape of the tail fins offers reliable shape features. Such shape features are much better transmitted visually by good quality photographs than by verbal descriptions, which would leave more room for ambiguity. In that sense, text can only emphasize what can be seen on images.

Relative tail length (relative to overall length) contributes much to the general appearance of the tadpole. Significant differences in the dorsal tail fin are present in tadpoles. In some species, the dorsal fin begins on the trunk. In most species, the anterior onset of the dorsal fin is approximately at the body-tail junction. The onset of the dorsal fin is located further posteriorly in many stream-adapted tadpoles (esp. *Huia*, *Meristogenys*, some *Ansonia*). The position of the dorsal fin onset does not seem to vary much within a given species. The contour of upper and lower fins can be so minimally convex that they appear almost parallel for most of their lengths. In other species, the dorsal fin can be arched up significantly. In some species, the fin contour can form a soft concave line in the posterior part that result in an acuminate, cuspidate or flagellated tail tip. The tip itself can range from broadly rounded (obtuse) to narrowly rounded (acute).

The height of the muscular part of the tail relative to body height in lateral view varies among tadpoles. Species that live in fast-flowing waters usually have flat bodies and robust tails, making body height and tail muscle height at body-tail junction almost even. Pond-dwelling tadpoles, in contrast, may have high bodies and relatively shallow muscular parts of the tail.

The coloration is a severely underestimated source of pertinent information for identification. Only recently, scientists have begun paying more attention to color information in tadpoles. Before the mid 20th century analog color photography was not available and after the mid 20th century it was still difficult

Abavorana luctuosa. Advanced tadpole with well developed hind limbs. Note that at advanced stages, the hind limbs already bear the typical color pattern of this species.



Limnonectes paramacrodon tail tip. Note the arrangement of light iridocytes in groups reminiscent of rosettes. Such iridocyte arrangements are common in species of *Limnonectes*.

to handle and expensive. Researchers worked primarily with preserved tadpoles in which much of the color information was lost (colors bleach over time or dissolve in the preservative; blood looses its red color in preservation). With the evolution of digital photography, this changed. Digital photographs of living tadpoles taken under appropriate illumination reveal plenty of color pattern details without the need of a microscope.

Color and pattern in tadpoles stem from three types of color cells (chromatophores): the brown to black melanophores, the yellowish to reddish xanthophores, and the iridophores that reflect and diffract light and produce various colors such metallic shine, white, blue, and iridescence. Combinations, overlay and congregations of such cells produce the color pattern we perceive. Although the color cells (chromatophores) are small, they can be assessed from high magnification digital photographs. A number of verbal descriptors have been suggested to classify chromatophore shape: filiform, spindle-shaped, foliose, punctate, stellate. Unfortunately, the value and reliability of these chromatophore shapes in taxonomy and field work have yet to be investigated in depth.

The patterns that emerge from concentrations and combinations of the three chromatophore types are manifold and, again, it is difficult to find the most reliable verbal descriptors for all the varieties. Some terms have commonly been used: Stripe refers to a more or less lon-

gitudinal pattern, either as light stripes on dark background or vice versa, whereas bars on the tail are dark vertical structures with sharp boundaries; a bi-colored tail (most often a dark posterior part of the tail) can be considered a special case of barring. A dark or light band goes from side to side over the mid-line in dorsal view and has less sharp margins. If only one band is present, a band may also be described as patch. Finely and densely arranged small melanophores give tadpoles a stippled appearance. Many slightly larger, rounded aggregations of melanophores will render a spotted pattern. Such spots can be angular in their contour, rather than round, and the pattern that emerges may be called speckled. Spaced small iridophores on dark background can produce a dusted pattern. A dark background color with light openings of varying sizes and shapes, resulting in an irregular network of anastomosing areas, has been referred to as marbled pattern. Mottled patterns can be understood as random-sized markings of different darker and paler shades. If melanophores or iridophores are arranged tightly along the tail blood vessels, a venation pattern emerges.

Staurois guttatus tadpoles. The red color stems from the animal's blood and disappears in preserved museum specimens.

Conspicuous lateral tail vein in *Indosylvirana nicobariensis*.

Areas of transparencies offer further features. Especially in ventral and lateral views, transparent or semi-transparent sections may reveal details of the inner organization in some species that are completely covered by opaque skin in others. Therefore, visibility of the gills, the heart (located between the gills in the mid-line in ventral view, the gut coils or the lungs can be important details. The lungs, if present, are visible as faint bubbly structures in the upper half of the trunk in lateral view.

Vascularization influences the appearance of the color in tadpoles. This is probably the reason for the slight change in color that is noticeable when a tadpole has recently died. Color information is lost when tadpoles are preserved, largely because red blood cells and iridophores loose their color in preservation. In species with increased blood flow and vascularization of the skin (e.g., *Staurois*), the color of the blood causes a pink or reddish overall appearance. In general, some other blood vessel related features can be observed at the tail, where the major ventral vein or some lateral veins can be seen.

The color pattern of the tadpole can change dramatically at the event of metamorphosis, around the time when the forelimbs become exposed. At that time tadpoles develop the color pattern of the froglet, particularly on the back (dorsum) and the hind limbs. *Abavorana luctuosa* is an example (p. 63). At metamorphosis of this species, the banded pattern on the thighs and the red-brown dorsal coloration emerge. Green is rarely seen in tadpoles, whereas it is common in frogs. Green colors come out only at metamorphosis in species with greenish adults. For this reason and whenever specimens were available, we refer to pre-metamorphic stages (Gosner Stages 33–38; p. 35) when describing coloration.

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McDiarmid, R.W., Altig, R. (1999) Tadpoles: the biology of anuran larvae. University Chicago Press, Chicago, London. 444 pp.

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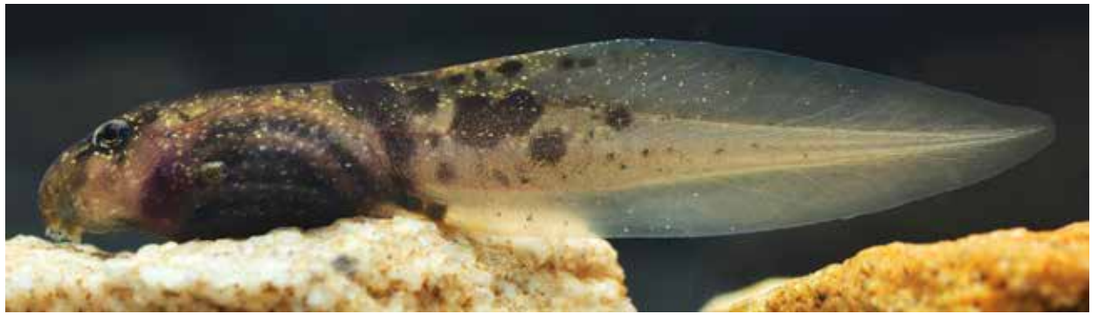
VARIABILITY IN TADPOLES

We are only beginning to understand the biology of Bornean tadpoles in their ecosystems and their interactions with other animals. Morphology and coloration may vary in tadpoles. Some of the variation can be profound. Variation falls into two categories: individual variation based on genetic background (no two individuals are identical) and induced variation (plasticity), i.e., induced by some external factor to which the tadpole is exposed and responds. Several such factors have been identified:

Crowding effects (high densities) can suppress growth and size at metamorphosis. Presence of predators, such as dragonflies, have been shown to lead to higher tail fins and may change the coloration pattern in some species; spots or black posterior parts of the tail can be more pronounced when predators are present. Substrate and food can also have an influence on growth and coloration. Patterns and sizes may vary geographically. Some tadpoles, just like their adults, seem to undergo daily changes of coloration. For example, larvae of *Abavorana luctuosa* are pale with strong black marking of the posterior half of the tail at night when these tadpoles leave their shelters and feed; they are more marbled with less indistinct tail markings during the day when they hide. Furthermore, coloration may change considerably with growth. Young stages of tadpoles commonly are paler than fully grown ones; tadpoles of *Leptobrachium* are a good example. They become progressively darker as they increase in size.

The known cases of variation in tadpoles should not confuse the student in the field. Many features discussed in this book have been proven reliable and less prone to variation, such as features of the oral disc, position of eyes, nostrils, mouth and spiracle, and shape descriptors of body and tail. The more experienced naturalist will soon recognize tadpoles on the basis of these features reliably to the genus level. Difficult cases, however, may require DNA matching techniques to assign them to known species. Much is to be learned about variation of Bornean tadpoles. Much more regional documentation of tadpoles and experimental laboratory work is necessary to assess the functional and evolutionary meaning of variation in tadpoles.

Ontogenetic change in pigmentation in *Leptobrachium abbotti*. Above: mid-larval stage with blotched pattern at posterior trunk and anterior tail. Below: A tadpole near metamorphosis with marbled pattern (specimens not to scale).



TADPOLE DESCRIPTIONS

This book covers tadpoles that we have documented within the Malaysia States of Sarawak and Sabah, for which, with few exceptions, photographic documentation was available. Thus, the account is necessarily incomplete as some remain unknown or have not been identified with certainty. Presenting the species that follow, most of which were confirmed by DNA barcoding, hopefully is an incentive to field biologists to fill the gaps in our knowledge in the future.

Habitat categories: Flowing (lotic) versus stagnant (lentic) water bodies

The tadpole descriptions are presented according to their type of aquatic habitat occupied, such as flowing water (lotic) versus stagnant water (lentic), and then alphabetically in the order of frog family, genus, and species. The distinction between lotic and lentic tadpole habitats or microhabitats draws a relatively clear separation line between species.

It is important to note that lentic habitats can exist in the immediate vicinity of rivers; for example, as isolated potholes or puddles on the riverbank. The key feature to classify them as stagnant is isolation and the absences of connection to the flowing water of the nearby stream. Furthermore, transitional habitats are common in which a pool is relatively quiet, mostly stagnant, yet is connected to the river. Species that utilize such habitats may be difficult to assign to either lentic or lotic categories and the reader will have to consult both major categories in such cases. Fortunately, there are not too many of cases.

Description components

For quicker access to information, components of the description are distributed in the form of defined blocks:

Color photographs are included for almost all species. Photographs have been edited slightly for contrast, saturation, sharpness and extraneous elements. Color photographs, often from different populations, were the basis for verbal descriptions of color patterns, however, in the future color patterns from new populations might expand the range of the coloration known within a species.

Oral disc features are presented in most species in a schematic form along with the description. Although these representations are derived from museum specimens (in a few cases, from publications), physical realism is neither a goal nor do we consider it particular-

ly helpful. In fact most of the oral disc schematics were produced by mirroring half side sketches to emphasize their schematic nature. We argue that abstractions are more suitable for identification through depiction of the main features of a tadpole oral disc, such as keratodont rows (labial tooth rows), conformation and thickness of beaks, arrangements of papillae. A schematic diagram can express these features in the most unobstructed manner. The Labial Tooth Row Formula (LTRF) in that text block summarizes the arrangement of keratodont rows.

Over the years in the field, we experienced that the tadpole's silhouette is invaluable for rapid field identification. Silhouettes were derived from real specimens. Variations exist depending on age (stage) of the larva and feeding status (gut empty or full). For the silhouette drawings, we usually avoided early larval stages or those in metamorphic climax. Information blocks are arranged around the body silhouette.

The **Size** that tadpoles of a given species can attain is presented in a silhouette drawing scaled to the original known maximum size.

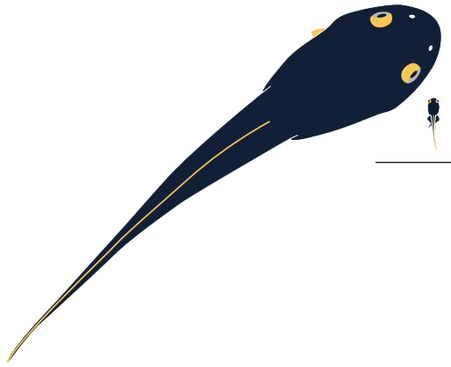
Maximum sizes were derived from either the literature or measurements of museum materials. However, scientific samples for some species remain small. For example, only one specimen of a *Philautus macroscelis* tadpole has ever been collected by us. In such cases, the numbers provided herein can only represent the largest specimen for which positive evidence exists. This does not exclude the possibility that larger specimens will be found in the future.

Similar species. This section mentions species that in the field could be confused with the species in question. Advice is provided as to which features to look for in order to discriminate them. In most cases, focus is put on similar species that inhabit similar habitat categories (such as phytotelma breeders, pond tadpoles, etc.), or are expected to occur syntopically in the same pond or stream. Clearly, because of current gaps in our knowledge, there are limitations and some tadpoles may only allow identification to the level of genus, unless the DNA barcoding technique is applied.

Body in the description refers to the head plus trunk. Most genera have characteristic body silhouettes, especially if the position of the nasal openings and the position and orientation of the eyes define important landmarks. For this reason, we do not consider body color pattern in our drawings of silhouette in dorsal view, preferring to emphasize these geometric relationships. The position and characteristics of the spiracle are features that are best studied in high quality photos.

Snout shape contributes to the overall silhouette and, thus, gives important information for field identification. The snout text block highlights the principal features to look for in dorsal and lateral views. Photographs taken of the specimens in the field in suitable dorsal and lateral views facilitate subsequent comparison with verbal descriptions.

Nostrils and eyes provide important landmarks for assessing the overall shape of the body. Additionally, they offer a series of features, such as nostril size and shape and iris coloration, that can help in identification.



Size range of Bornean tadpoles: *Leptobrachium abbotti* (90 mm) and *Metaphrynella sundana* (9 mm).

Good macro photography can help tremendously in assessing the character states of nostrils and eyes.

Tail muscularization, relative length, fin features, and shape of tail tip provide valuable information for field determination. The tail text block gives a verbal summary of major features to look for. The silhouette drawing provides supplementary information about the onset of the dorsal fin and thickness of the tail musculature. The lateral photograph (available for most species accounts) provides visual information about the tail tip shape, fin contour line, relative tail fin height and pigmentation. Although many studies on tadpoles describe the vent tube opening and its relation (dextral, sinistral, medial) to the lower fin, we ignore the feature in this book, because, first, vent position was of no relevance in our own field work and, second, the determination of its character state is not easily done in the field and almost always requires a stereo-microscope and transfer of the specimen to the lab.

Ecomorph assigns the species to general categories that are commonly used to delimit tadpole guilds.

Selection of silhouettes of Bornean tadpoles scaled to the same drawing size to highlight the diversity and disparity of shapes. From left: *Limnonectes ingeri*, *Kaloula baleata*, *Polypedates otilophus*, *Occidozyga baluensis*, *Phrynoidis juxtasper*, *Leptobrachella mjobergi*, *Meristogenys jerboa*, *Ansonia kanak*.

FLOWING WATER BODIES

Flowing waters are abundant on the island of Borneo. High precipitation, elevation, and inclination of the terrain, and the composition of the bedrock create a variety of flowing water habitats – suitable for diverse frog communities.

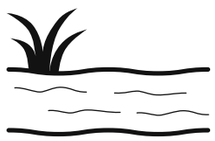
This book follows the major dichotomy between bodies of stagnant and flowing water. In both categories, several sub-categories can be defined that are common to the habitats of Borneo.

CASCADE / WATERFALL

Rapid overflow of water over boulders causes cascades or waterfalls to form. They are typical in upstream sections and headwaters of rivers. Certain tadpoles and frogs depend on cascades and waterfalls.

RIFFLE

A riffle is a moderately inclined section of a stream with gravel bed, overflown by shallow water. The water is so shallow that the gravel may break the surface of the water but does not make it foam.



STREAM

A stream can be many things. Usually some more qualities such as size, flowing velocity, bed composition, canopy cover, and forest type are needed to fully describe a stream and the tadpole microhabitats in it.

SIDE POOL

Quiet outpocketings of streams have been termed side pools. Although their water may seem stagnant, they are connected to the stream. Very often, leaves accumulate in side pools.

Cascading stream, Kubah National Park. Microhabitat for *Ansonia minuta*, *Meristogenys jerboa*, and *Meristogenys penrissenensis* tadpoles.

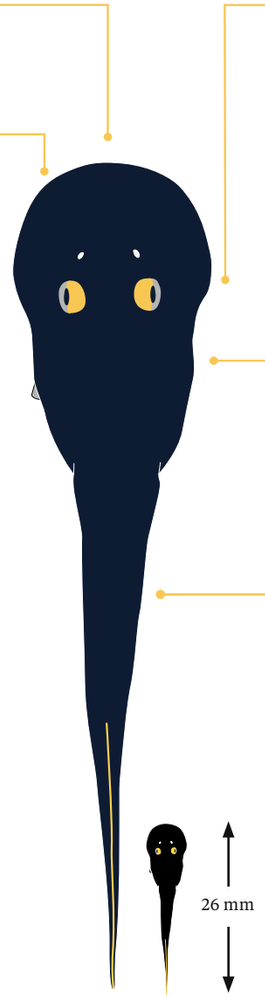
Ansonia echinata Inger and Stuebing, 2009

Thorny Slender Toad

SNOUT
Broadly expanded. Long and gradually sloping in profile, streamlined. In dorsal view, snout very broad.

ORAL DISC
Forms a large ventral sucker, almost as wide as maximum body width. Lips not emarginated. Lower lip with a row of low marginal papillae, upper lip with smooth bulge.

Two to three rows of submarginal, flat papillae on lower lip. Two undivided labial keratodont rows on upper, three undivided rows on lower lip (LTRF 2/3). Upper keratodont rows very long, reaching well beyond ends of lower keratodont rows, and curved inward at their lateral ends. Upper beak widely divided (no medial keratinization). Lower beak undivided, with wide angle, flat.



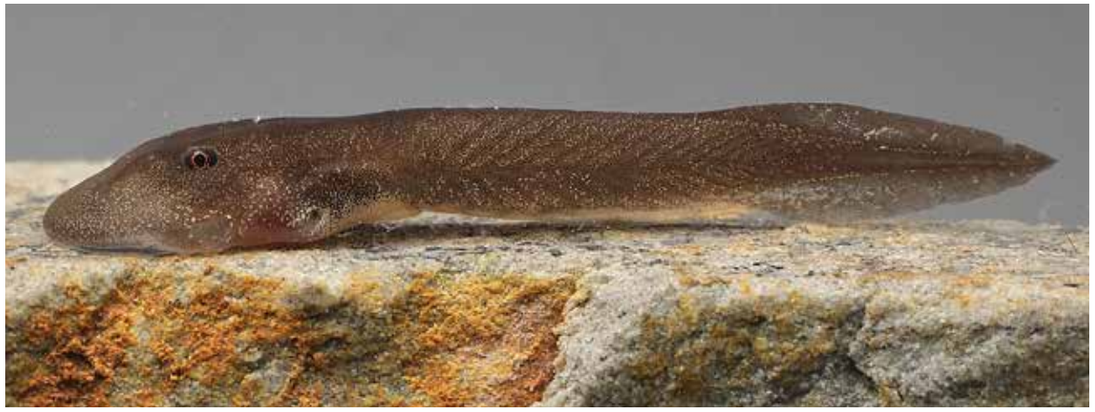
NOSTRILS & EYES
Eyes dorsolateral, far from body contour in dorsal view. Nostrils small, elliptical, located dorsally, directed anterolaterally, very much closer to eyes than to tip of snout. Nostril with marginal rim and tiny triangular fleshy projection on medial margin. Iris black with copper ring bordering the pupil.

BODY
Contour inverted pear-shaped in dorsal view. Body contour substantially narrowing behind level of eye. Body dorsoventrally depressed in lateral view. Abdomen flat, not bulging. Spiracle sinistral, tubular, attached to the body wall, far below mid-level in position in lateral view. Intestines coiled. Lateral line organs indistinct.

TAIL
Strong and muscular, as high as body in lateral view. Fins relatively low. Dorsal fin restricted to posterior 50% of tail. Lower fin as a soft keel for most of tail length, rising only in posterior 50% of tail. Both fins slightly arched. Lower fin slightly higher than dorsal fin. Fins taper gradually and terminate in a pointed tip. Myosepta slightly accentuated by pigmentation.

ECOMORPH
Lotic, suctorial, rheophilous, exotrophic.

SIMILAR SPECIES
Tadpoles of most *Ansonia* species are unique in terms of body shape (inverse pear-shaped in dorsal view). Within *Ansonia*, species can be differentially diagnosed by a combination of oral disc features, body shape, body size, coloration, elevational range and tail characters, especially extent of fins. *A. echinata* shares with *A. hanitschi* the very long and curving upper lip keratodont rows. The tadpole of *A. hanitschi* are adapted to high elevations and grow larger (although *A. echinata* might grow larger than has been reported so far). In general appearance, *A. echinata* tadpoles superficially resemble *A. minuta* tadpoles. Inger and Stuebing (2009) presented two 'cruciform' tadpoles associated with *A. echinata* adults at Bukit Kana. They did not match tadpoles by DNA (as in our sample) and based on own samples from the locality, we think that both 'cruciform' tadpoles belong to other *Ansonia* species. The syntopic larva of *A. kanak*, however, are different in color pattern and oral disc features.



Ansonia echinata *has only been reported from primary rainforest at Bukit Kana, Bintulu Division, in hilly terrain. The general body shape is streamlined and inverted pear-shaped as in other* Ansonia *species. Black and white markings are absent.*

HABITAT & ECOLOGY
Little is known about the ecology of this species. Individuals were found at Bukit Kana (250 m a.s.l.) and Batang Ai National Park, at large (13–15 m), clear, rocky streams with waterfalls, torrents, and riffles in lowland secondary forest. Tadpoles live in strong torrents on smooth rocks. Syntopic tadpoles are, for example, *A. kanak*, *Meristogenys* sp., *Huia cavitympanum*.

REPRODUCTION
Inger and Stuebing (2009) mentioned males perching on low vegetation, within 3.5 m from the water's edge. We observed adults resting and calling on low vegetation (small shrubs) near waterfalls.

COLORATION
Uniformly dusted dark brown or gray above, darker in the central parts of the dorsum. Pigmentation gradually extending from body onto muscular part of tail and fins. Tail fins pigmented more densely toward margins. Spots of golden iridocytes densely scattered over body and tail. Ventrally unpigmented in the pre-metamorphic stages examined, internal organs visible. As in other species, progressing pigmentation on the belly can be expected in advanced stages. Oral disc unpigmented.

LITERATURE

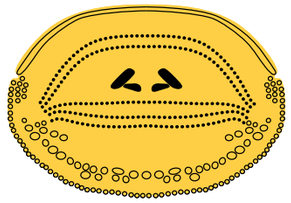
Inger, R.F. Stuebing, R.B. (2009) New species and new records of Bornean frogs (Amphibia: Anura). The Raffles Bulletin of Zoology 57: 527–535.

Ansonia guibei Inger, 1966

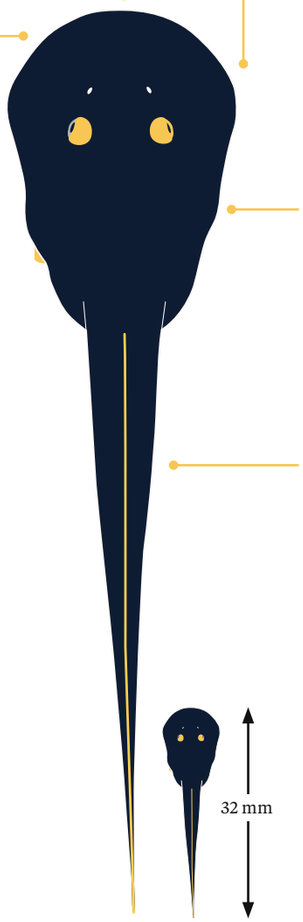
Guibé's Slender Toad

SNOUT
Broadly expanded. Long and sloping in profile. In dorsal view, snout very broad, appearing slightly truncated or less convex in the middle part. Slightly angular in dorsal view at the widest part of snout, giving the head silhouette a slightly rectangular appearance.

ORAL DISC
Forms a large, ventral sucker, as wide as maximum body width. Lower lip and lateral parts of upper lip with fine uniserial papillae along margin; ~80% of upper lip without papillae, bearing a bulged rim instead.



One to two rows of irregular submarginal papillae on lower lip. Two undivided labial tooth rows on upper, three on lower lip (LTRF 2/3); upper rows not reaching around lateral ends of lower rows. Upper and lower beaks divided.



NOSTRILS & EYES
Eyes dorsolateral, far from body contour in dorsal view. Iris with silvery-golden, thin ring edging the pupil. Nostrils small, oval, much closer to eye than to tip of snout.

BODY
Very broad relative to length, dorsoventrally depressed, inverted pear-shaped with angular side corners at level of oral disc; moderate but noticeable reduction of body width behind eyes. Spiracular opening attached to body wall, well below mid-body in lateral view.

TAIL
Fins start at trunk-tail junction, rising slowly in first third of tail. Fins remain relatively low, tapering gradually in the posterior half of the tail and ending in a narrowly rounded tip, without terminal filament.

ECOMORPH
Lotic, suctorial, rheophilous, exotrophic.

SIMILAR SPECIES
In general, *Ansonia* species can be differentially diagnosed by a combination of oral disc features, body shape, body size, coloration, and tail characters. *A. guibei* is a highland species, thus, many other species can be excluded by altitude. The tadpole of *A. hanitschi* and *A. platysoma* are less square and more pronounced pear-like in body shape in dorsal view. *A. guibei* tadpoles have an undivided lower jaw unlike other *Ansonia* species. The tadpoles of the other highland *Ansonia* at Kinabalu, *A. fuliginea* are unknown.

Ansonia guibei *is a highland species, ranging from about 1300 to 2000 m a.s.l. Tadpoles are common in Sungai Mesilau at Mesilau Nature Resort, Gunung Kinabalu, at approx. 1900 m a.s.l.*

HABITAT & ECOLOGY
Tadpoles can be found day and night at and on rocks in cold mountain streams of Gunung Kinabalu at 1300 to 2000 m elevation. The tadpoles cling to rocks with their sucker mouths and graze on algal overgrowth. *Ansonia guibei* tadpoles prefer moderate, non-foaming current.

REPRODUCTION
Details unknown.

COLORATION
Uniformly dark brown above, black in daylight. In tadpoles approaching metamorphosis (past Stage 40), the brown dorsal pattern of the toadlet emerges. Dark pigmentation of the body extends on muscular part of tail as dark band. Tail fins are pigmented at marginal parts, lightening up at junction with muscular part of tail. In ventral view, skin pale but inner organs wrapped in black deep layer of pigment cells, gut coils usually not visible. Gills bright red. Oral disc pale ventrally, slightly pigmented in those skin parts that face dorsal or lateral.

LITERATURE

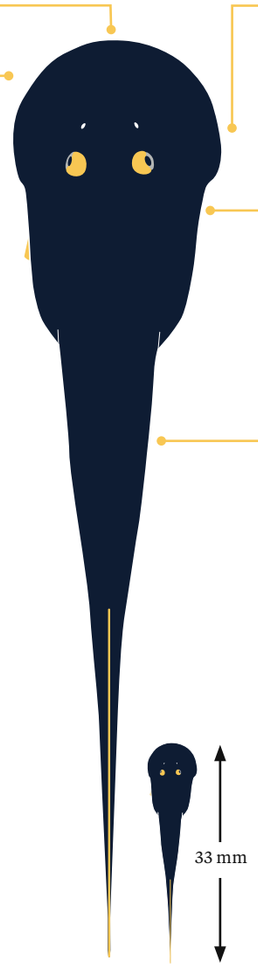
Malkmus R., Kosuch, J. (2000) Beschreibung einer neuen *Ansonia*-Larve (*Ansonia guibei*) von Borneo. Salamandra 36: 121–124.

Ansonia hanitschi Inger, 1960

Kinabalu Slender Toad

SNOUT
Flat, very broadly expanded. Long and sloping in profile, very much streamlined.

ORAL DISC
A large ventral sucker, as wide as maximum body width. Lower lip with row of small marginal papillae, upper lip with smooth bulge. Two rows of submarginal, flat papillae on lower lip. Two undivided labial tooth rows on upper, three undivided rows on lower lip (LTRF 2/3). Upper keratodont rows very long, reaching beyond ends of lower keratodont rows, and curved inward at their lateral ends. Upper beak widely divided, lower beak undivided, medially thin.



NOSTRILS & EYES
Eyes dorsolateral, far from body contour in dorsal view. Nostrils small, very much closer to eyes than to tip of snout. Iris black with silvery, sometimes coppery, ring edging the pupil.

BODY
In dorsal view, body contour inverted pear-shaped. Body contour abruptly narrowing at transition from head to trunk. Body dorsoventrally depressed. Spiracle sinistral and attached to body wall, far below mid-level in lateral view.

TAIL
Strong and muscular, almost as high as body in lateral view. Fins low, dorsal fin restricted to posterior half of tail, rising at approximately 40% of tail length. Lower fin starting at vent but low for most of its length. Fins taper gradually and terminate in a pointed tip, often forming a sharp, short terminal filament.

ECOMORPH
Lotic, suctorial, rheophilous, exotrophic.

SIMILAR SPECIES
A. hanitschi is the largest of the known Bornean *Ansonia* tadpoles. A combination of size (up to 33 mm), oral disc features (long coiled upper keratodont rows), reduced tail fins, present tail filament, and restriction to mountain ranges distinguish it from tadpoles of other *Ansonia* species, except for *A. kelabitensis*, to which distinguishing characters have not been established (Matsui et al. 2020). Furthermore, the tadpoles of some of the closely related species have not been found and described. *A. hanitschi* may live in association with tadpoles of *Meristogenys* and *Huia*, both of which posses a gastric sucker, which is absent in *Ansonia*.

Ansonia hanitschi *is a common toad of Gunung Kinabalu and Crocker Range, at elevations above 1.000 and below 1900 m a.s.l. The tadpoles are the largest known larvae in the genus* Ansonia *on Borneo, although the adults are not the largest toads in the genus. This toad and its tadpoles are very common along Sungai Silau-Silau and Sungai Liwagu at Gunung Kinabalu.*

HABITAT & ECOLOGY
A highland species. Tadpoles are found at and on rocks in mountain streams. The tadpoles cling tightly to rocks with their sucker mouth. They prefer strong currents, often with foaming water, such as small waterfalls and cascades. The tadpoles are most often seen at vertical smooth rock faces. When disturbed they are able to quickly detach and hide under rocks. Tadpoles have been seen venturing out of the water and grazing on algal overgrowth on rocks in the spray zone of small waterfalls. During the day the tadpoles hide at the base of rocks in the stream and crawl up to algae-rich areas of rocks at nighttime, when they can be observed grazing in groups.

REPRODUCTION
Malkmus et al. (2002) reported that males call from river banks and rocks during the day. Females in captivity produced 45–73 eggs in a jelly string that was attached to submerged rocks (Herrmann and Ulber 1992).

COLORATION
Uniformly and densely stippled dark gray above and partially on muscular part of tail. Tail fins pigmented at marginal parts with slightly less pigmented stripe at junction with muscular part of tail. Advanced stages with grown hind limbs develop the distinct dorsal color pattern of the metamorphosing toadlet. Ventrally unpigmented, internal organs visible but gradually covered by melanophores and iridophores from the sides on the belly in late stages.

LITERATURE

Haas A, Das I (2008) Larval identities of *Ansonia hanitschi* Inger, 1960 (Amphibia: Bufonidae) and *Polypedates colletti* (Boulenger, 1890) (Amphibia: Rhacophoridae) from East Malaysia (Borneo). Salamandra 44: 85–100.

Herrmann, H.J., Ulber, T. (1992) Über Haltung sowie Verhalten von *Ansonia hanitschi* Inger, 1960 (Anura: Bufonidae) in Biotop und Terrarium. Sauria 14: 15–18 [in German]

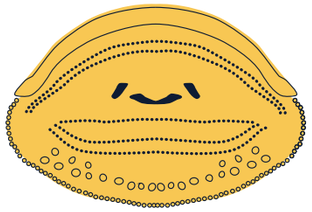
Malkmus, R., Manthey, U., Vogel, G., Hoffmann, P., Kosuch, J. (2002) Amphibians & Reptiles of Mount Kinabalu (North Borneo). Koeltz Scientific Books, Königstein. 424 pp.

Matsui, M., Nishikawa, K., Eto, K., Hossman, M.Y. (2020) Two new *Ansonia* from mountains of Borneo (Anura, Bufonidae). Zoological Science 37: 1–12.

Ansonia kanak Matsui, Nishikawa, Eto, and Hossman, 2020

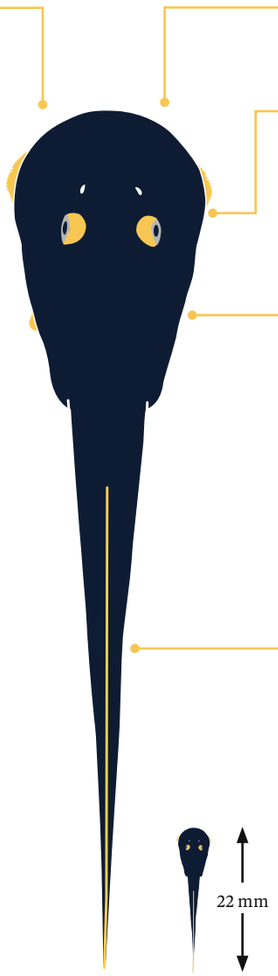
Kelabit Slender Toad

ORAL DISC
Ventral sucker, as wide as maximum body width or slightly beyond. Lower lip of the oral disc bears an uniserial row of marginal papillae; margin of the upper lip devoid of free papillae and bears a rim bulge instead. Flat, rounded submarginal papillae present on the lower lip. Uninterrupted posterior (distal) row of submarginal papillae (15–16 papillae).



A second, anterior submarginal row consists of 1–3 papilla per side at the far lateral part of the lower lip present or absent. Two keratodont rows on the upper, three rows on the lower lip (LTRF 2/3). Upper lip keratodont rows reach the level of the lower lip keratodont rows laterally but do not curl inward beyond them. Upper beak split in two short, widely spaced serrated edges; gap 2.0–2.6x length of one beak edge. Lower beak is very shallowly V-shaped, medially thin.

ECOMORPH
Lotic, suctorial, rheophilous, exotrophic.



SNOUT
Broadly rounded and greatly expanded. Long and sloping in profile.

NOSTRILS & EYES
Nostrils small and much closer to the eyes than to the snout. Eyes located dorsally, clearly away from the body contour in dorsal view. Iris is black with a golden ring around the pupil.

BODY
In dorsal view, body contour pear-shaped. The body is widest anterior to the eyes, approximately at the level of the nostrils. Only a mild constriction of the body contour behind the level of the eyes. Body dorsoventrally depressed. Spiracle sinistral and spiracular orifice is attached to the body wall medially. Spiracle low on the flank in lateral view.

TAIL
Relative tail length 64–69%. Tail fins start posterior to the trunk-tail junction, in the first third of tail. Fins increase in height only slightly in the proximal 50% of the tail. Dorsal and ventral tail fins low, lower fin slightly higher than the dorsal. Fins taper with mild convexity into an acuminate tip. In lateral view, tail musculature strong and almost as high as the trunk at the trunk-tail junction.

SIMILAR SPECIES
The tadpole of *A. kanak* has been reported under the name of *A. platysoma* (Haas et al. 2009), until its species status was reassessed by Matsui et al. (2020). Because of oral sucker presence (but lack of gastric sucker; see *Meristogenys* and *Huia*) and droplet-shaped body silhouette, it can only be confused with other sucker-mouthed *Ansonia* species. In terms of general body shape and coloration, the tadpoles of *A. kanak* are similar to *A. hanitschi*; however, the latter is larger and has conspicuously long and laterally curled keratodont rows on the upper lip. It is unclear whether the light area at the head-trunk transition is a characteristic color pattern of this species. Probably there is more diversity in *Ansonia* species and the taxonomy of *A. platysoma* might change as new evidence emerges.

Ansonia kanak *is a lowland species with suctorial tadpoles that are adapted to a life in the currents of clear, rocky mountain streams.*

HABITAT & ECOLOGY
These tadpoles live on rock faces in strong current within cascades in hillside streams (250–820 m a.s.l.). Many other frog species occur syntopically (see Matsui et al. 2020). Only if disturbed, they escape temporarily to areas with moderate currents such as pools between the cascades.

REPRODUCTION
Details unknown.

COLORATION
The background color of the back is brown with some darkened areas: the roof of the braincase between the eyes and the area dorsal to the vertebral column are densely pigmented. A light crossbar is located at the head-trunk transition. Also a diffuse, dark, broad band stretches from flank to flank forming a saddle. Loosely scattered, small golden pigment cells are found below the eye, on the dorsum, and laterally at the flank-venter transition. The dense pigmentation of the dorsum extends onto the muscular part of the tail. Dark margins form at the fins' edges.

LITERATURE

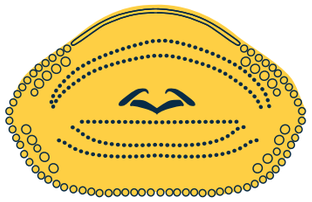
Haas, A., Wolter, J., Hertwig, S.T., Das, I. (2009) Larval morphologies of three species of stream toads, genus *Ansonia* (Amphibia: Bufonidae) from East Malaysia (Borneo), with a key to known Bornean *Ansonia* tadpoles. Zootaxa 2302: 1–18.

Matsui, M., Nishikawa, K., Eto, K., Hossman, M.Y. (2020) Two new *Ansonia* from mountains of Borneo (Anura, Bufonidae). Zoological Science 37: 1–12.

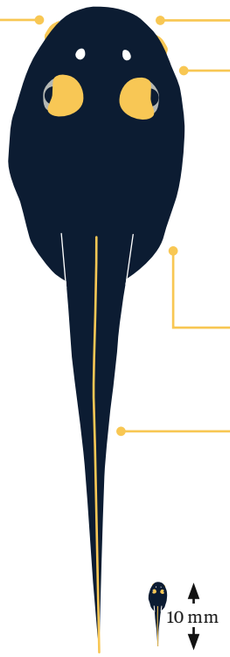
Ansonia leptopus (Günther, 1872)

Brown Slender Toad

ORAL DISC
Ventral. Two undivided labial tooth rows on upper, three on lower lip (LTRF 2/3). Upper rows do not wrap around lower rows laterally. Upper beak divided, lower beak undivided. Oral disc position ventral. Oral disc narrower than maximum body width.



Lower lip not flat and sucker-like. Lower lip margin and lateral parts of upper lip margin papillated. Upper lip papillation with broad gap; in medial third with soft bulge instead of papillae. Submarginal papillae on upper and lower lip.



SNOUT
In dorsal view, snout broadly rounded. Oral disc may slightly protrude from under snout laterally in dorsal view. Profile steeply sloping, almost obtuse.

NOSTRILS & EYES
Eyes dorsolateral. Iris and sclera black. Nostrils in dorsal view closer to eye than to tip of snout.

BODY
Oval, wider than high. Spiracle attached to body wall, low in position.

TAIL
Two thirds or less of total length. Muscular part moderately strong. Upper fin sloping gradually in first (proximal) third of tail and then rising more at beginning of second third of tail, ending in a rounded tip.

ECOMORPH
Lotic, clasping, exotrophic.

SIMILAR SPECIES
The color pattern of *A. leptopus* tadpoles is unique. *A. longidigita* also has black sharply delimited markings on light background but the markings are distinctly different from *A. leptopus*. In various publications, Inger called them 'cruciform', referring to the shape of crossing black bars. Currently, the two species are the only known *Ansonia* with contrast-rich "black & white" tadpoles. Also note the exceptionally small size of *A. leptopus* tadpoles.

The very small, yet distinctive tadpole of Ansonia leptopus *can be encountered in slow-moving, lowland streams. It is less well adapted to a life in water current than any of the other* Ansonia *tadpoles on Borneo. Despite its unique coloration, it may be easily overlooked due to its small size.*

HABITAT & ECOLOGY
A small tadpole in lowland to mid-elevation streams. It is found on or among leave drift, plant material or rocks clasping to the substrate or swimming around. These tadpoles avoid fast flowing waters and aggregate in quiet sections of streams. They can be encountered at day- and nighttime. Locally and at certain times of the year, the tadpoles can be abundant.

REPRODUCTION
Males call from the ground, on sandy stream banks or rocks. Often groups of dozens of males congregate at a stretch of a slowly moving stream. The call is a soft high-pitched trill.

COLORATION
Pale cream with distinct black markings on body and tail. Abdominal flanks black. A median stripe from runs from snout to tail dorsally. A dark stripe from snout curves below the eye to the posterior part of the head. Muscular part of the tail with a dorsal and lateral stripe. Ventral side unpigmented, inner organs visible.

LITERATURE

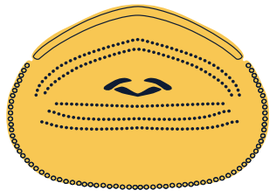
Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

Inger, R.F. (1992) Variation of apomorphic characters in stream-dwelling tadpoles of the bufonid genus *Ansonia* (Amphibia: Anura). Zoological Journal of the Linnean Society 105: 225–237.

Ansonia longidigita Inger, 1960

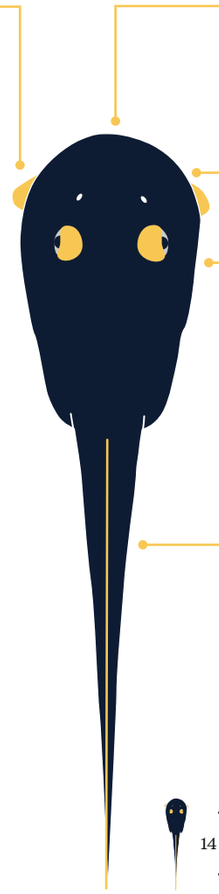
Long-fingered Slender Toad

ORAL DISC
Large ventral sucker, as wide as maximum body width or slightly wider, reaching beyond body contour in dorsal view. Lower lip margin and lateral parts of upper lip uni-serially papillated.



Upper lip mostly with soft bulge instead of papillae. Submarginal papillae absent. Two undivided labial tooth rows on upper, three on lower lip (LTRF 2/3). Upper labial tooth rows do not wrap around lower rows laterally. Upper beak divided, lower beak undivided.

ECOMORPH
Lotic, suctorial, rheophilous, exotrophic.



SNOUT
Expanded, sloping profile in lateral view, streamlined.

NOSTRILS & EYES
Nostrils small, much closer to eyes than to tip of snout, embedded in black blotch. Eyes dorsolateral in position. Iris and sclera black.

BODY
Depressed and streamlined in lateral view; in dorsal view, inverted droplet- shaped. The body is broadest at the level of the oral sucker and tapers gradually (no pronounced constriction) towards the base of the tail. The spiracle is low on the flank, well below mid body axis in lateral view.

TAIL
Less than two thirds of total length. Muscular part moderately strong, more than 50% if body height in lateral view. Fin low; upper fin rises shortly posterior to trunk-tail junction and rises moderately from there. Tail fins more or less parallel in the mid and end third of the tail. Rounded tip.

SIMILAR SPECIES
The conspicuous color pattern in combination with transverse gut orientation of *A. longidigita* tadpoles are unique features. Superficially *A. leptopus* tadpoles look somewhat similar but have different shape and pattern of their black markings, a much smaller oral disc, and more pond type tadpole body shape. Currently, the two species are the only known *Ansonia* with contrast-rich "black & white" tadpoles.

Ansonia longidigita *is a small suctorial tadpole with distinct black and white pattern. The mouthparts form a ventral sucker with which the tadpole clings to rock surfaces in the stream.*

HABITAT & ECOLOGY
A small tadpole of lowland to high elevation streams, in stream sections with moderately fast currents. It adheres to rocks where it feeds on algal overgrowth. It prefers faster current than *A. leptopus* and, in contrast to that species, continuously maintains position in the current with its oral sucker attached to the substrate. The tadpoles rarely occur in abundance and due to its small size, finding them may require careful search in appropriate habitats.

REPRODUCTION
Males call from rocks and boulders at the shores of or in clear streams. Males can call solitary or in small aggregations. The call is a forceful high-pitched trill.

COLORATION
Pale cream with characteristic black „cruciform" markings on body and tail: medial black stripe on head and trunk with extensions towards and beyond the eyes, and further posteriorly on the flanks. Another blotch embeds the nostrils area and extends rostrally and laterally. A thick black stripe covers the muscular tail laterally. Tail fins are clear. Venter mostly unpigmented. The gut is visible from below; it winds in a unique transverse fashion.

LITERATURE
Haas, A., Wolter, J., Hertwig, S.T., Das, I. (2009) Larval morphologies of three species of stream toads, genus *Ansonia* (Amphibia: Bufonidae) from East Malaysia (Borneo), with a key to known Bornean *Ansonia* tadpoles. Zootaxa 2302: 1–18.

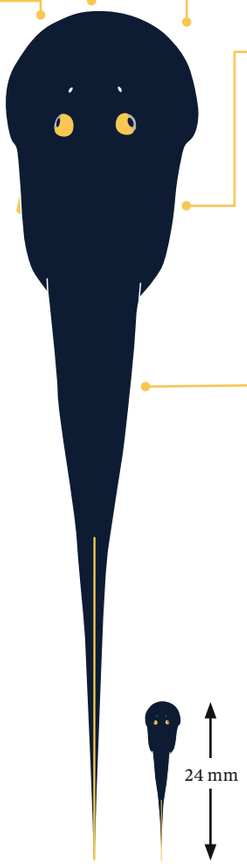
Ansonia minuta Inger, 1960

Dwarf Slender Toad

SNOUT
Broadly expanded and almost half circular in dorsal view. Long and sloping in profile, streamlined.

ORAL DISC
Large ventral sucker, as wide as maximum body width. Uniserial row of marginal papillation is present on the lower lip of the oral disc. The upper lip lacks papillae and has a circumferential bulge instead. The oral disc possesses an inconspicuous lateral indentations at the end of the papillae row.

Flat, rounded submarginal papillae are present on the lower lip: one complete posterior row (18–21 papillae) and an incomplete anterior one (3–6 papillae on each side; gap medially). Labial ridges bear two keratodont rows on the upper and three on the lower lip (LTRF 2/3). Upper lip keratodont rows reach or go beyond the level of the lower lip keratodont rows posteriorly. Upper beak comprises two short, widely spaced beak edges. Lower beak is undivided and shallow V-shaped, medially thin.



NOSTRILS & EYES
Nostrils small, much closer to eyes than to tip of snout. Eyes dorsolateral, at clear distance from body contour in dorsal view. Iris black with a golden ring around the pupil

BODY
In dorsal view the body contour is inverted pear-shaped with a slight constriction behind the level of the eye. Body is widest anterior to the eyes and dorsoventrally depressed. Spiracle is sinistral and spiracular orifice is attached to the body wall medially, free laterally. Spiracle low on the flank (well below mid body axis) in lateral view when the tadpole is attached to a rock.

TAIL
Musculature strong and almost as high as trunk (in lateral view) at trunk-tail junction. Dorsal tail fin starts only at ca. 50% of tail length. Dorsal and ventral tail fins of approximately equal heights. Tail reaches its maximum height at mid-tail position. Edges of fins are only slightly convex in lateral view. Fin shape spear-shaped and tapers towards a narrowly rounded tip, sharp flagellum absent.

ECOMORPH
Lotic, suctorial, rheophilous, exotrophic.

SIMILAR SPECIES
Presence of oral sucker,lack of gastric sucker (see *Meristogenys* and *Huia*), and droplet-shaped body silhouette, let *Ansonia minuta* only be confused with other sucker-mouthed *Ansonia* species. The shape of the tail fins and the coloration markers allow for the identification of this tadpole. Tadpoles of the closely related *A. hanitschi* and *A. platysoma* may appear most similar at first glance but differ from *A. minuta* in elevation of habitat, size, and oral disc features. *A. spinulifer* differs most notably in tail shape and microhabitat (slower current).

Ansonia minuta *inhabits lowland streams in hilly primary and secondary forests of western Sarawak and Kalimantan. In suitable habitats, the toad and its tadpoles can be common. Adults specialize on ants for prey.*

HABITAT & ECOLOGY
Tadpoles of this species live at rock faces in strong, foaming current. They are active at daytime and more so at night. We observed them on a spectrum of rock inclinations, from flat to vertical, but always in quite strong current. Tadpoles were found in hilly areas below 700 m a.s.l.

REPRODUCTION
Little is known about the reproductive habits of this species. Males call along suitable, clear and rocky hillside streams. Locally males occur in numbers. Males perch on low vegetation on the river bank or on boulders in the river. Females produce clutches of 40–223 eggs, with mean egg diameter 1.54 mm.

COLORATION
Background color of the back is dark brown, almost black in daylight. A distinct pattern is absent, yet the pigmentation is darkest between the eyes and the mid-dorsum of head-trunk region. In the populations investigated so far, tadpoles possessed conspicuous clusters of golden epidermal pigment cells located on the lower cheek and a larger and denser one on the lower flank and lateral parts of the venter, respectively. Less well defined groups of golden cells may be present far rostrally on the snout, above the eye, on the dorsum in the trunk region, and scattered on the tail (mostly dorsal). The venter and oral disc are mostly unpigmented and translucent, except for the lateral parts at the transition to the flanks. The gills and the heart are visible through the ventral skin. The gut coil is arranged spirally and clearly visible in ventral view.

LITERATURE

Haas, A., Wolter, J., Hertwig, S.T., Das, I. (2009) Larval morphologies of three species of stream toads, genus *Ansonia* (Amphibia: Bufonidae) from East Malaysia (Borneo), with a key to known Bornean *Ansonia* tadpoles. Zootaxa 2302: 1–18.

Direp, Y., Das, I., Haas, A. (2009) Reproductive and trophic ecology of *Ansonia minuta* (Amphibia: Bufonidae). Malayan Nature Journal 61: 307–314.

Ansonia spinulifer (Mocquard, 1890)

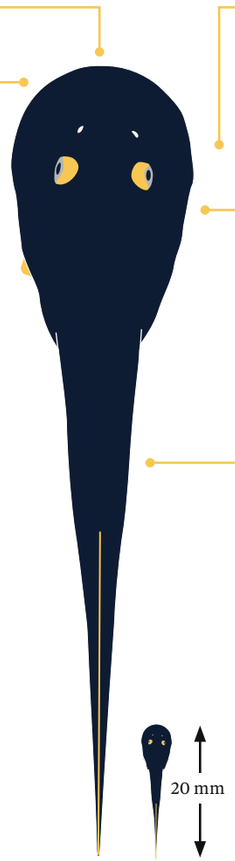
Spiny Slender Toad

SNOUT
Broadly expanded, smooth arch in dorsal view. Profile long and sloping, sstreamlined.

ORAL DISC
As wide as maximum body width. Marginal papillae on lower lip, upper lip with circumferential rim bulge. Two clear rows of flat submarginal papillae on lower lip. Keratodont rows undivided, two on upper three on lower lip (LTRF 2/3).

Upper keratodont rows do not curl around the lower ones laterally. Upper beak divided and widely spaced, lower beak undivided, medially thin.

ECOMORPH
Lotic, suctorial, rheophilous, exotrophic.



NOSTRILS & EYES
Nostrils much closer to the eyes than to snout. Nostrils oval and small. Eyes dorsolateral in position. Iris mostly black with scattered bronze pigment. Iris edge with bronze tinge around pupil.

BODY
Droplet-shaped contour in dorsal view, widest just anterior to eye level, moderate constriction at head-trunk transition. Body dorsoventrally depressed, streamlined. Spiraculum sinistral, attached to the body wall, very low in vertical position.

TAIL
Approximately two thirds of total length, strong and muscular. Muscular part almost equals body height in lateral view. Tail fins low. Upper fin rising only in second third (>40 % tail length) of tail. Edges of upper and lower fin slowly converging posteriorly. Tip of tail narrowly rounded, pointed.

SIMILAR SPECIES
The species can only be confused with other sucker-mouthed *Ansonia* species (gastric sucker absent, compare *Meristogeny*s and *Huia*). *A. spinulifer* is a small tadpole, much smaller than, for example, *A. hanitschi*. It differs, among other things, in the described oral disc features from *A. hanitschi*, *A. guibei*, and *A. platysoma*; and in coloration profoundly from *A. leptopus* and *A. longidigita*. It is most similar to *A. minuta,* yet the tadpole of *A. minuta* seems to grow larger, has a more spear-shaped tail fin, even more posterior origin of fins, and possesses more extensive areas of golden iridocytes; clearly these distinguishing features are preliminary.

Ansonia spinulifer *is a fairly common lowland toad, however, rarely seen in large numbers. Its small, black tadpoles can be encountered in rocky, clear lowland streams, usually in small numbers.*

HABITAT & ECOLOGY
The tadpole inhabits clear lowland rocky streams. It can be found in moderate current or in riffles and on coarse gravel and rocky bottom. The tadpole feeds on algal overgrowth that is rasped off with the jaws while the oral sucker keeps the tadpole adhered to the rock. It can be observed at daytime, although it might be more active at night.

REPRODUCTION
Males call from low vegetation or logs near streams, at or away from the stream bank. Males do not aggregate in calling groups but maintain single posts.

COLORATION
Dark brown to black above with snout and parts below eye dusted with golden pigment cells (only visible in high magnification). Another area of scattered golden pigment (iridocytes) is on the lower flank, extending slightly onto the belly. Ventrally, the tadpole is unpigmented, internal organs are visible. The lateral pigmentation ends abruptly on the ventral side forming a sharp edge of pigmentation laterally in ventral view, with concentrations of golden pigment posterolaterally of oral sucker and laterally of gut coils. Dark coloration of body extends onto muscular part of tail. Tail fins with scattered dark pigment cells along margins, base of fins mostly clear.

LITERATURE

Inger, R.F. (1992) Variation of apomorphic characters in stream-dwelling tadpoles of the bufonid genus *Ansonia* (Amphibia: Anura). Zoological Journal of the Linnean Society 105: 225–237.

Malkmus, R., Manthey, U., Vogel, G., Hoffmann, P., Kosuch, J. (2002) Amphibians & Reptiles of Mount Kinabalu (North Borneo). Koeltz Scientific Books, Königstein. 424 pp.

Ingerophrynus divergens (Peters, 1871)

Forest Toad

SNOUT
Slightly tapering but broadly rounded at tip in dorsal view. Profile smoothly rounded, moderately long.

ORAL DISC
Ventral in orientation. Papillation on both lips only laterally, wide medial areas of lips without papillae. Clear lateral indentation between upper and lower lip.

Submarginal papillae in both lips, more on lower lip. Two undivided labial tooth rows on upper, three on lower lip; the second upper row with tiny medial gap (LTRF 2(2)/3). Upper and lower beaks undivided. Beaks narrow, moderately strong.

NOSTRILS & EYES
Nasal opening moderately large to large, rimmed. Dorsal rim with triangular process. Nostrils closer to eyes than to tip of snout. Eyes dorsolateral. Iris black with scattered iridophores.

BODY
Small, depressed ovoid in lateral view. Weakly rhomboid in dorsal view with slight constriction at head-trunk transition. Wider than high, i.e., slightly depressed dorsoventrally. Widest point of body silhouette is behind the eyes. Spiracle sinistral and attached to the body wall, below mid-body axis in lateral view.

TAIL
Moderately long, less than two thirds of total length. Tail muscle weak; thickness of muscular part of tail thin compared to width of body in dorsal view. Fins start at trunk-tail junction. Fins become moderately high, relatively flat in contour, ending in a blunt, rounded tip. Overall fin shape slightly lanceolate.

ECOMORPH
Lentic, benthic, exotrophic.

SIMILAR SPECIES
The tadpole is similar to that of *Ingerophrynus quadriporcatus*. The latter lacks the dark blotch in the upper flank behind the gill region. *Duttaphrynus melanostictus* is similar in body silhouette but deeply black (even ventrally). Ecology separates the species as well: larvae of *I. quadriporcatus* are found in peat swamps whereas *I. divergen*s is a lowland dipterocarp and alluvial forest inhabitant, and *D. melanostictus* occurs exclusively in open areas near or in human settlements. *Rentapia hosii* is exclusive to mid-size clear lowland streams. Except for *R. hosii*, these species are distinct in having broad unpapillated middle parts on their upper and lower lips. Tadpoles of *Kurixalus chaseni* (Rhacophoridae) are similar at first glance in their small size and general body shape and live in forest ponds and puddles; however, they are distinguished from *Ingerophrynus* by their fully papillated lower lip and different keratodont arrangement, as well as in general coloration (p. 236).

Ingerophrynus divergens *is common in forested regions of Borneo below 700 m a.s.l. The tadpole is small.*

HABITAT & ECOLOGY
Tadpoles of this species have been seen in forest floor puddles, pools of intermittent forest streams and nearly stagnant sections of small forest streams. We found the tadpoles mostly in quiet sections of small streams. The tadpoles are bottom dwellers that feed on the small particles at the bottom of sandy or silty side-pools, such as microbes, algae, protozoans, or decaying plant matter.

REPRODUCTION
Males call close to the breeding body of water, often in groups that form choruses. The call is a rasping trill. Calling congregations are loud and can be heard from the distance. Males clasp females around the armpits (axillary amplexus). Hundreds of eggs are laid in mucous strings.

COLORATION
Dark brown above. Braincase (between and behind eyes) pigmented dark. Blurry paired dark spots dorsally on upper flanks. Brown pigmentation extends onto tail but fades towards tail tip. Unpigmented below, inner organs visible.

LITERATURE
Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

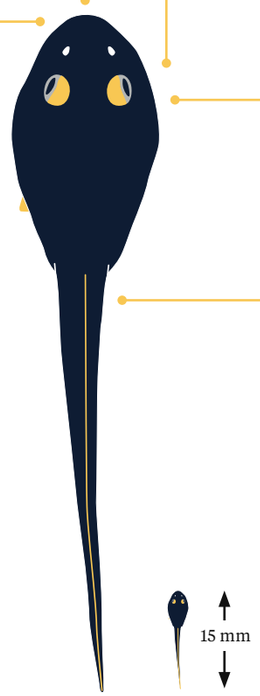
Leptophryne borbonica (Tschudi, 1838)

Hour-glass Toad

SNOUT
Not expanded, rounded in lateral view and moderately tapering from the level of eyes forward in dorsal view.

ORAL DISC
Oral disc ventral, much narrower than max. width of body. Single row of marginal papillae of upper lip restricted to lateral quadrant, wide middle section of upper lip without papillae. Lower lip completely papillated uniserially along margin.

Two keratodont rows on the upper lip (row 1 or rows 1+2 divided), three undivided rows on the lower lip (LTRF 2(2)/3 or 2(1-2)/3). Beaks undivided, narrow, rather weak.

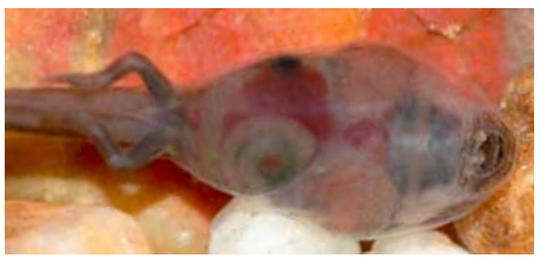


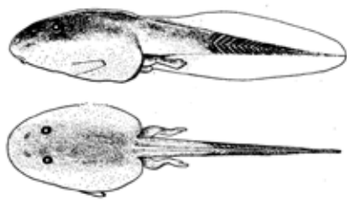
NOSTRILS & EYES
Nostrils elevated in snout profile, relatively large. Eyes dorsolateral. Iris black with few silvery iridophores.

BODY
Ovoid in lateral view, slightly depressed dorsoventrally; oval to moderately rhomboid in dorsal view; widest point of body posterior to level of eyes. Spiracle tubular, free orifice, visible from above.

TAIL
Moderately long. Dorsal tail fin starts at trunk-tail junction but rises only slowly for a short distance before it rises up more pronouncedly into an only moderately high fin. Tail tip rounded.

ECOMORPH
Lotic, benthic, exotrophic.





Leptophryne borbonica, from Berry (1972)

SIMILAR SPECIES
The body shape and small size are similar to other bufonids (see remarks for *Rentapia hosii*), however, *L. borbonica* differs from other *Ingerophrynus*, *Rentapia* and *Duttaphrynus* by possessing divided second keratodont row on upper lip and an uninterrupted row of marginal papillae on the lower lip. Species of *Ansonia* possess a sucker-like oral disc. Other species that potentially could occur in the same stream, such as *Limnonectes, Leptobrachella* or *Feihyla,* can be eliminated by body shape and keratodont configuration.

Although not very common in general, Leptophryne borbonica *can be abundant locally. It lives from the lowlands up to the lower montane elevations. Previously, drawings of the tadpoles have been published (Berry 1972).*

HABITAT & ECOLOGY
Toads gathers around small streams with gravel and sand bottom or at seepage areas for reproduction. The species is distributed widely in the lowland rainforests of Borneo up to elevations of 1100 m a.s.l. Despite the wide distribution, we encountered populations only in certain areas. The ecological demands of this species are not well understood.

REPRODUCTION
Eggs are deposited in clusters of 200–300 eggs between gravel of the stream in quiet sections, also in seepage areas (Berry 1972). Eggs are 1.29 mm in diameter. We found clutches with embryos attached to the gravel and covered by leaf litter (see photo). Embryos were found over a larger area, possibly indicating that several females had spawned simultaneously.

COLORATION
Head-body blackish brown above without clear pattern, tail muscle the same. In our sample, an area from the eye and nostril down to the oral disc was without pigmentation. Also the dark dorsal pigmentation fades down the flanks. Ventral side unpigmented, translucent, and the inner organs are visible. Tail fins are clear.

LITERATURE

Berry, P.Y. (1972) Undescribed and little known tadpoles from West Malaysia. Herpetologica, 28: 338–346.

Inger RF (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89

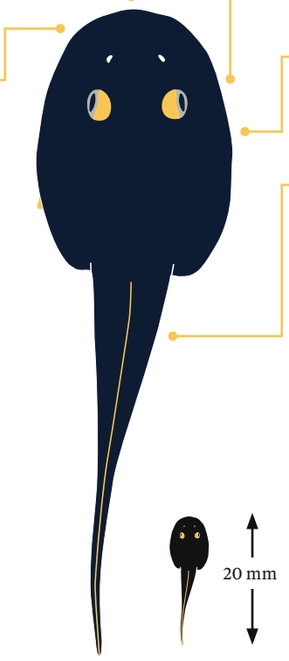
Phrynoidis juxtasper (Inger, 1960)

Giant River Toad

SNOUT
Bluntly rounded in dorsal view, moderately extended and steeply sloping in profile.

ORAL DISC
Ventral, almost as wide as width of body. Two keratodont rows on upper, three keratodont rows on lower lip; rows undivided (LTRF 2/3) or anterior two on lower lip divided (LTRF 2/3(1-2)). Lower lip with

uniserial row of papillae.
Upper lip with papillae in lateral parts and a fleshy rim in medial papillae-free part. Beaks moderately developed, undivided.



NOSTRILS & EYES
Nostrils much closer to eyes than to tip of snout. Eyes dorsolateral.

BODY
Oval, slightly depressed dorsoventrally. Spiracle sinistral, below mid-body axis in lateral view.

TAIL
Relatively short, less than two thirds of total length. Muscular part moderately strong, slightly more than half of body height in lateral view. Dorsal tail fin originating shortly posterior of trunk-tail junction; rising in a relatively straight line in the first third, then forming a smooth peak at approximately mid-tail, and shallowly curving toward the broadly rounded tip. Overall fin shape bluntly lanceolate to spatulate. Myosepta indistinct.

ECOMORPH
Lotic, benthic, suctorial, exotrophic.

Tadpole of *Phrynoidis asper*, from Berry (1972)

SIMILAR SPECIES

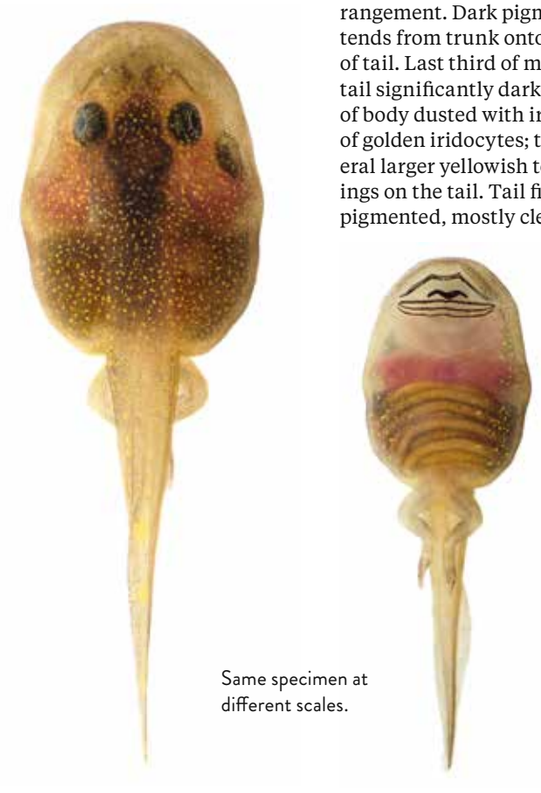
Phrynoidis juxtasper possesses a large oral sucker and is dark in color, these features can led one to confuse them with some *Ansonia* larvae. *P. juxtasper* is most easily distinguished from *Ansonia* larvae by a oval head-body (vs. droplet-shaped), undivided beaks (vs. upper beak divided), and distinct ventral abdominal pattern. Despite the abundance of adult *P. asper* in some habitats, tadpoles have been rarely found. Inger (1985) described the tadpole of *P. asper* as being similar to the larva of *Ingerophrynus divergens* and further speculated that the high similarity with larvae of *I. divergens* might be a source of confusion and might explain that the tadpoles of *P. asper* had not been collected more often. However, Berry (1972) described the larva of *P. asper* from West Malaysia. The tadpole he described was a stream adapted larva, very much similar in size, oral disc, and body and tail fin shape to *P. juxtasper* tadpoles as described here (verified by DNA barcoding). These discrepancies in published records indicate that the breeding biology and tadpoles of *P. asper* need further research.

Tadpoles of this relatively common lowland toad have rarely been documented on Borneo. Descriptions for Phrynoidis juxtasper *tadpoles from Sumatran tadpoles have been published by Manthey and Grossmann (1997) and also mentioned in Malkmus et al. (2002).*

HABITAT & ECOLOGY
Tadpoles live in quiet, sun exposed, warm shore side-pools of rocky lowland streams. Tadpoles are active day and night and feed on organic rock overgrowth. Short busts of breeding activity and the development in the warm stream side pools might result in very fast growth and development and might explain why the tadpoles of this common species are not seen regularly. These speculations, however, need confirmation by more research.

REPRODUCTION
P. juxtasper reproduce along mid-size to large lowland streams with coarse gravel and rock bed. The calls of the males can be heard from far.

COLORATION
Dark brown above and on flanks; gold dusted below, oral disc without pigmentation. Gut, gills, and heart visible through ventral skin. Gut with conspicuously transverse arrangement. Dark pigmentation extends from trunk onto muscular part of tail. Last third of muscular part of tail significantly darker. Vast parts of body dusted with irregular groups of golden iridocytes; they form several larger yellowish to golden markings on the tail. Tail fin moderately pigmented, mostly clear.



Same specimen at different scales.

LITERATURE

Berry, P.Y. (1972) Undescribed and little known tadpoles from West Malaysia. Herpetologica, 28: 338–346.

Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

Malkmus, R., Manthey, U., Vogel, G., Hoffmann, P., Kosuch, J. (2002) Amphibians & Reptiles of Mount Kinabalu (North Borneo). Koeltz Scientific Books, Königstein. 424 pp.

Manthey, U., Grossmann, W. (1997) Amphibien & Reptilien Südostasiens. Natur und Tier Verlag, Münster. 511 pp.

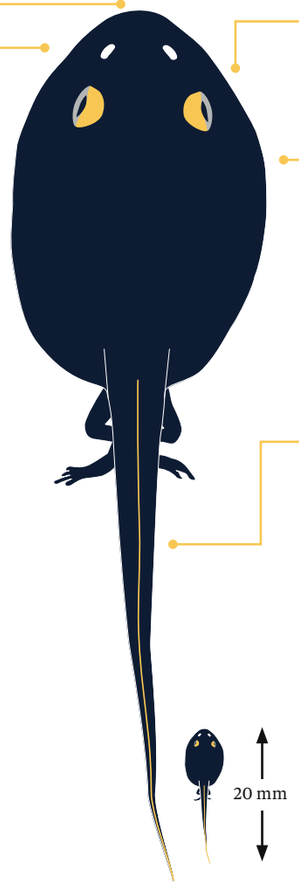
Rentapia hosii (Boulenger, 1892)

Brown Tree Toad

SNOUT
Short and obtuse in lateral view with a soft bulge between nostrils. In dorsal view, moderately tapering with smooth rounded tip.

ORAL DISC
Ventral, much narrower than maximum width of body. Papillae on upper and lower lip restricted to lateral forth of lips. Submarginal papillae often arranged in rows. Lateral emargination between upper and lower lip pronounced.

Two keratodont rows on upper, three keratodont rows on lower lip; second row on upper lip divided; first row on lower lip angled but not divided (LTRF 2(2)/3). Beaks undivided. Jaw sheaths weak and narrow, very finely serrated.



NOSTRILS & EYES
Nostrils relatively large, located between eye and snout tip. Nostrils with elevated rim. Eyes dorsolateral. Iris black.

BODY
Oval to ovoid in dorsal view, flat oval in lateral view. Wider than high, i.e., slightly depressed dorsoventrally. Widest point of body silhouette behind the eyes. Spiracle sinistral and attached to the body wall, orifice directed laterally; spiracle below midbody axis in lateral view, not visible from above.

TAIL
Moderately long; less than two thirds of total length. Muscular part relatively weak, much narrower than body width in dorsal view, moderately high in lateral view. Fins start at trunk-tail junction. Fin height moderate. Upper and lower fin contours mostly parallel, ending in a broadly rounded tip. Myosepta faintly visible in distal tail.

ECOMORPH
Lentic, benthic, exotrophic.

SIMILAR SPECIES
The size, body, and tail proportions are a common bufonid tadpole features that are shared by *Ingerophrynus* and *Duttaphrynus*. The most likely candidates for confusion on Borneo are the tadpoles of *Duttaphrynus melanostictus* (fully black even ventrally, dusted with light spots, pond breeder), *Ingerophrynus divergens* (dark diffuse areas on trunk, small streams and intermittent streams) and *I. quadriporcatus* (lighter color, more extended snout, higher arched fin, peat swamp pools). These bufonid species and *R. hosii* are distinct in having an oral disc with wide medial areas devoid of papillae on both their upper and lower lips.

Choruses of male Rentapia hosii *can be heard from bushes and trees along mid-sized lowland streams. Although the species is quite abundant locally, we have not encountered tadpoles in the wild. The image above is a tadpole from a captive breeding group.*

HABITAT & ECOLOGY
According to Inger and Stuebing (2017), the tadpoles live at the bottom of quiet side pools of medium sized lowland streams, among plant debris. Bufonid tadpoles do not develop lungs until metamorphosis, so they do not come to the surface for additional breathing as other species do. This and the small body size of the tadpoles may make it difficult to spot them in the field.

REPRODUCTION
Male calling is synchronized to unknown cues that make males gather along stream banks for one or two nights in sometimes large numbers. Just as unexpected as the choruses form, the calling activity may cease. Most males call from bushes and trees but also from branches and logs near the bank (see photo). Females are much larger than males and strikingly different in color pattern.

COLORATION
Dark brown to black on dorsal side of head and body. Ventrally the skin lacks dense pigmentation and is mostly translucent. Dark pigmentation of the dorsum extends onto the muscular part of the tail and the base of the upper fin, fading distally towards the distal third of the tail and fin. Other parts of fin, and lower tail fin in particular, clear.

LITERATURE

Inger, R.F. (1966) The systematics and zoogeography of the Amphibia of Borneo. Fieldiana Zoology 52: 1–402.

Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

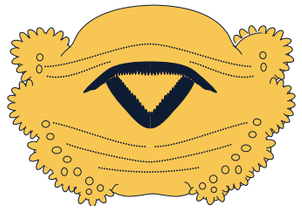
Inger, R.F., Stuebing, R.B., Grafe, T.U., Dehling, J.M. (2017) A field guide to the frogs of Borneo. 3rd ed. Natural History Books, Kota Kinabalu. 228 pp.

Limnonectes conspicillatus (Günther, 1872)

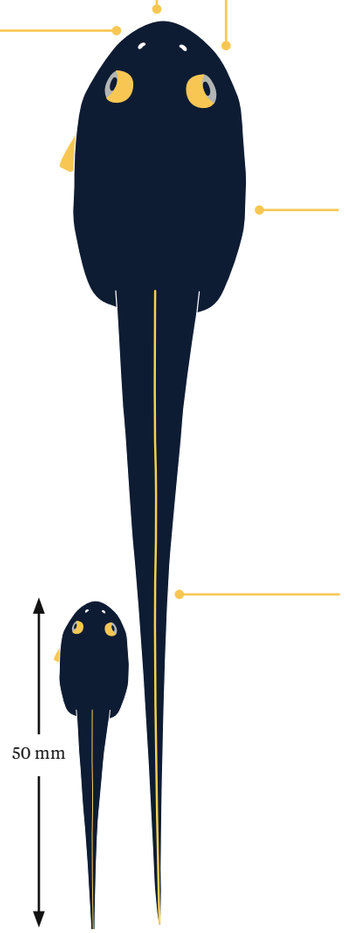
Broad-headed Creek Frog

SNOUT
Smooth and triangular in dorsal view; in lateral view, moderately long, blunt, and smoothly arched. Oral disc does not project beyond the snout in dorsal view.

ORAL DISC
Ventral, moderately large (a third of head width), not projecting beyond the snout contour.



A clear emargination separates upper and lower lips; lower lip further segmented by one major and two minor indentations. Oral disc with blunt papillae along their margins, except for a broad gap in papillation medially in the upper lip and a smaller, yet still substantial, medial gap in the lower lip. Submarginal papillae present on both the upper and lower lips, more numerous on lower. LTRF 2(2)/3(1). Beaks moderately strong, well keratinized but not thick; beak edges bear fine serrations. Upper beak a broad, shallow arch; lower beak V-shaped.



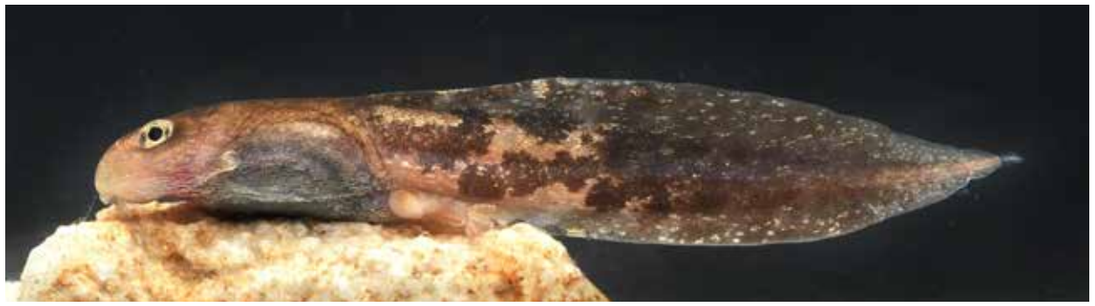
NOSTRILS & EYES
Eyes dorsolaterally. Nostril relatively large, without projection. Nostril closer to the snout than to the eye, and oriented anterolaterally. The iris bears dense brass to gold iridocytes. The iridocytes form a complete ring around the pupil and are less dense in the anterior and posterior sectors, both of which may appear darker.

BODY
Medium-sized to large, oval in dorsal view. Body dorsoventrally depressed. Head as wide as the trunk. The widest point of the body is at the gill region of the head or at the trunk, depending on stage and feeding condition. Head weakly triangular in dorsal view. Spiracle sinistral, opening posteriorly. Medial rim of spiracular orifice free, a short tube is formed; orifice below the mid-body in lateral view. Lateral line organs visible, particularly at head and along upper trunk.

TAIL
Long, 68% of total length. Muscular part strong, distinctly higher than half of body height in lateral view, more than half of the maximum trunk width in dorsal view. The upper fin starts at the trunk-tail junction reaching the posterior trunk. Upper and lower fin contours relatively similar and arching moderately. Upper fin is higher than lower fin. In the posterior quarter, the fins converge with straight edges into a narrowly rounded tip. Maximum tail height approximately at mid-tail. Lateral tail vein indistinct; tail myosepta indistinct.

ECOMORPH
Lotic, benthic, exotrophic.

SIMILAR SPECIES
The Creek Frogs used to be known with two species, *L. kuhlii* and *L. laticeps* on Borneo. Recent studies synomymized the old names and uncovered multiple genetically distinct lineages. Numerous Creek Frog species might be described in the future. Morphological diagnosis of all the candidate species have not been worked out. Tadpoles of all species of Creek Frogs are expected to be relatively similar in general shape, proportions, and snout shape. We found markedly different color patterns in tadpoles from different populations (barred vs. blotched tail pattern, silver-white abdomen vs. clear abdomen etc.). In order to sort out the diversity and understand interspecific variation, Creek Frogs and their larvae need further research. With some experience, Creek Frog tadpoles can be distinguished easily from other *Limnonectes* species (such as River Frogs or Guardian Frogs) by a combination of features of body shape, fin shape, snout shape, and their oral disc.



Creek Frogs, on Borneo formerly subsumed under the names Limnonectes kuhlii *and* L. laticeps*, turned out to be phylogenetically much more diverse with dozens of distinct lineages. The description herein is based on a tadpole sample from the Matang Range that was genetically matched with adults (photo) from the area (Lineage 6 in Matsui et al. 2016).*

HABITAT & ECOLOGY
Limnonectes conspicillatus tadpoles have so far only been known from quiet pools in small, sometimes intermittent streams. During the day they mostly hide under leave litter and seem to forage mainly at night.

REPRODUCTION
No data available.

COLORATION
Generally brown to chocolate brown above. On head and trunk, there is no well defined pattern, rather, it shows diffuse lighter and darker areas. In lateral view, the lower face of the head and the lower flank turn more translucent, from brown to gray with dense horizontally oriented dashes of silver iridocytes. Skin of venter translucent, but finely hatched with vermiculate melanocytes; red gills visible through skin. Abdomen is covered with silver-gold sheet, median line absent; gut coil is indistinct but visible in ventral and lateral views. The body background color continues onto the tail, however, there are sharply defined dark blotches on the proximal muscular part of the tail and dorsal tail fin (less so on proximal lower fin). In the distal half of the tail, dark markings may further fuse to form large dark area. Other populations with much less dark markings might indicate high variability. Tail and tail fins bear scattered patches of iridocytes.

LITERATURE

Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89. [*Limnonectes kuhlii* and *L. laticeps*]

McLeod, D.S. (2010) Of Least Concern? Systematics of a cryptic species complex: *Limnonectes kuhlii* (Amphibia: Anura: Dicroglossidae). Molecular Phylogenetics and Evolution 56: 991–1000.

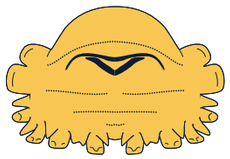
Matsui, M., Kuraishi, N., Eto, K., Hamidy, A., Nishikawa, K., Shimada, T., Yambun, P., Vairappan, C.S., Hossman, M.Y.B. (2016) Unusually high genetic diversity in the Bornean *Limnonectes kuhlii*-like fanged frogs (Anura: Dicroglossidae). Molecular Phylogenetics and Evolution 102: 305–319.

Limnonectes leporinus (Anderson, 1923)

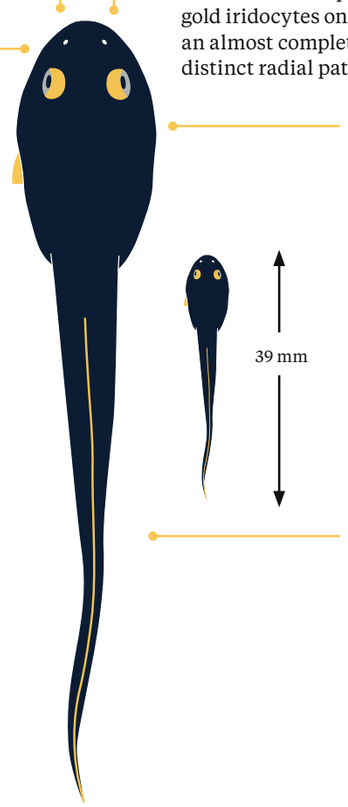
Giant River Frog

SNOUT
Smoothly arched in dorsal view. In lateral view, moderately long and bluntly rounded.

ORAL DISC
Approximately 30% of maximum head width, anteroventral in orientation, and not projecting beyond the snout contour in dorsal view. An emargination sets upper and lower lips apart.



Oral disc bears papillae along its margin, with two gaps: a wide gap in the upper and a narrow gap in the lower lip. Marginal papillae thick and low in number. Upper lip bears flat, broad papillae (as if 2-3 papillae were fused), whereas on the lower lip flat, broad and moderately curled-in papillae as well as more conical ones. On lower lip, papillae arranged in a single staggered row generating the impression of a double-row. Submarginal papillae absent. LTRF 1/3(1), the outer keratodont row of the lower lip particularly short. Beaks thin, well keratinized; edges bear fine serrations. Upper beak smoothly convex medially and arched concavely laterally. Lower jaw sheath has the shape of a flat V.



NOSTRILS & EYES
Eyes dorsolateral. Nostrils anterolaterally oriented, small and closer to the snout than to the eye; nostril rim without distinct projection. Iris is dotted with brass to gold iridocytes on a black background. Iridocytes form an almost complete ring around the pupil. Iris with a distinct radial pattern of four dark radii.

BODY
Medium sized. In dorsal view, body contour oval. Head slightly wider than the trunk; widest point of the body at the gill region. Head contour smoothly rounded in dorsal view. Body dorsoventrally depressed. Spiracle sinistral and opening posteriorly; spiracular orifice free from the body wall medially for a short distance, a short free tube is present. Lateral face of the spiracular tube more extended than the medial part. Spiracle at the mid-body level in lateral view. Lateral line organs indistinct.

TAIL
Up to 70% of total length. Muscular part of tail moderately strong. In dorsal view, tail muscle equal to or slightly wider than half of the maximum trunk width; in lateral view, it is clearly higher than half trunk height. Dorsal fin originates posterior to the trunk-tail junction, approximately at 5–7% of tail length. Upper fin higher than the lower fin. The upper fin contour forms a shallowly convex curve. In the posterior fourth of the tail, fins converge into an acute tip (often damaged). Some individuals possess a shallow concavity in the contour of the upper fin close to the tip. In others, the tail is elegantly lancet shaped. Maximum tail height in the mid third of the tail. Lateral tail vein masked by pigmentation; tail myosepta indistinct.

ECOMORPH
Lotic, benthic, exotrophic.

SIMILAR SPECIES
Our genetically confirmed samples showed lateral horizontal black streak at tail base, and differed in this feature from other River Frog species. Otherwise, River Frog tadpoles (and other *Limnonectes*) are superficially similar and may be difficult to identify in the field, especially since *L. leporinus* tadpoles can occur sympatrically with *L. malesianus* and *L. ingeri* in the same habitat, and sometimes, even the same water body. *L. ingeri*, *L. leporinus*, *L. malesianus*, and *L. paramacrodon* possess a single upper keratodont row that distinguishes them from many other tadpoles. Further research is needed to show whether the subtle differences between River Frog tadpoles are beyond the range of intraspecific variation. DNA barcoding is recommended for identification.

The tadpoles of Limnonectes leporinus *live in riparian settings, mostly in quiet side pools or edges where they inhabit the bottom among leaf litter.*

HABITAT & ECOLOGY
Streams from small to large with sand and gravel bottom. Tadpoles hide amongst leaf litter and plant debris. The weakly developed mouthparts suggest that they consume fine organic particles (such as algae, protists, bacteria, and decaying matter) opportunistically. Inger (2009) suggested that this species and related river frogs mostly consume the suspension of organic matter that they stir up by their activities at the bottom of their aquatic habitats.

REPRODUCTION
Limnonectes leporinus reproduces in streams with moderate current. In larger streams, they spawn at the quiet bank areas. They lay their eggs in circular depressions in shallow water that the male excavate in the gravel bed (p. 44). When laid, the eggs do not stick together but trickle into gravel interstices. After completion of spawning, the male covers the circular depression with gravel, often creating a small mound.

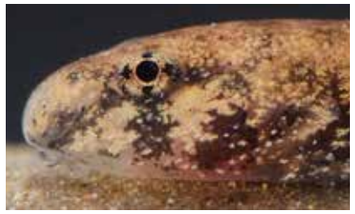
COLORATION
Generally sandy brown to mid-brown above, with irregular blurred dark or olive marbling and few scattered black dots. The body is densely dusted with iridocytes above. Dark blotch or saddle marking is positioned at the trunk-tail junction dorsally. Flank darker than dorsum, marbled. Three fuzzy dark areas present on the lateral face: a dark streak from the eye to the oral disc, a dark patch below the eye, and one posterior to eye; sometimes another patch laterally at gill area. In the lower head and lower flank, the dorsal dense iridocyte cover breaks up into irregular, light patches. Skin of venter is mostly unpigmented, transparent. Few scattered iridocytes and melanocytes in the gular, buccal, branchial, and anterior abdominal ventral skin areas. Brown body background color continues onto dorsal tail, becomes lighter there and fades distally. Blotches of lateral tail base are typically merged to form a horizontal streak for one fifth of the tail length. Numerous distinct rosette-like clusters of iridocytes cover the tail and tail fins. Black blotches accentuate the distal part of the tail.

LITERATURE

Inger, R.F. (1966) The systematics and zoogeography of the Amphibia of Borneo. Fieldiana Zoology 52: 1–402.

Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

Inger, R.F. (2009) Contributions to the natural history of seven species of Bornean frogs. Fieldiana (Zool.) 116: 1–25.

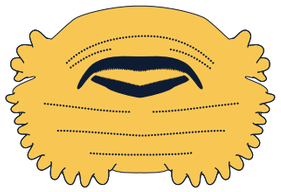


Limnonectes ibanorum (Inger, 1964)

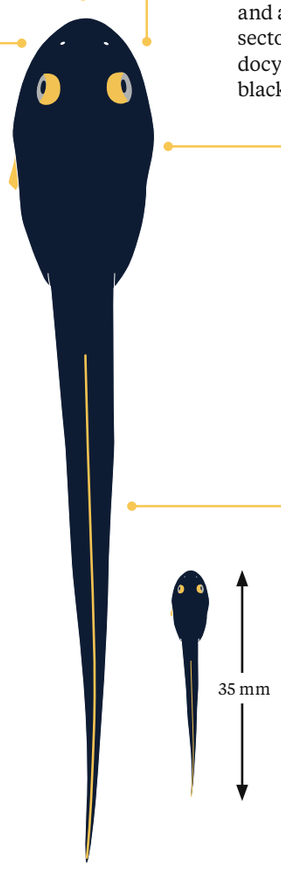
Rough-backed River Frog

SNOUT
In dorsal view, smoothly arched. In lateral view, moderately long; the contour is bluntly rounded, not distinctly tapering.

ORAL DISC
Moderately large, approximately 40% of head width. Anteroventral to ventral in position and does not project beyond snout contour in dorsal view. An emargination separates upper and lower lips.



Oral disc bears blunt papillae along its margin, except for a wide gap in the upper lip and a narrower gap in the lower lip. The marginal papillae are thick and low in number, arranged in a staggered line on the lower lip, so that they may appear to stand in a double-row. Submarginal papillae are absent. LTRF 2(2)/3(1). Beaks moderately well keratinized, not strong; their edges bear fine serrations. Upper beak weakly convex medially and arched laterally; lower beak a very flat V.



NOSTRILS & EYES
Eyes dorsolateral. Nostril anterolaterally oriented closer to the snout than to the eye; nostril rim smooth. Iris dotted with gold iridocytes. Iridocytes form a complete ring around the pupil and are less dense in the anterior and posterior sectors. There are narrow areas devoid of iridocytes in the upper and lower sector forming black spots or vertical streaks.

BODY
Medium-sized. In dorsal view, general body contour oval. Head slightly wider than the trunk. Widest point of the body at the gill region of the head. Shape of the head smoothly rounded in dorsal view. Body dorsoventrally depressed. Spiracle sinistral, opening posteriorly. Medial rim of the spiracular orifice attached to the body wall. Spiracle below the mid-body level in lateral view. Lateral line organs indistinct.

TAIL
68% of the total length. Muscular part of the tail strong, slightly less high than trunk in lateral view; it is approximately half of the maximum trunk width in dorsal view. Dorsal fin originates posterior to the trunk-tail junction, at approximately 10% of tail length. Upper fin slightly higher than the lower fin. In the posterior third of the tail, fins converge into an acute tip. Overall, the tail is elegantly lancet-shaped. Maximum tail height approximately at mid-tail level. Lateral tail vein visible. Tail myosepta faintly visible distally.

ECOMORPH
Lentic/lotic, benthic, exotrophic.

SIMILAR SPECIES
There is some similarity among *Limnonectes* tadpoles in body shape, relatively small oral disc, low count of keratodont rows, benthic habits that separates them from other genera. It is important to note in what habitat setting the respective tadpole was encountered. *Limnonectes ibanorum* tadpoles are restricted to the microhabitats described above. Although ecologically different, *L. leporinus*, can occasionally occur in the same pools with *L. ibanorum*; *L. leporinus* tadpoles show greater contrast in color pattern, commonly with a black horizontal line at the base of the tail, and a different tail shape. Creek frog tadpoles have an even more bluntly rounded snout in lateral view than *L. ibanorum*. In *Limnonectes finchi* and *L. palavanensis* tadpoles, the origin of the upper tail fin is clearly more posterior than in *L. ibanorum* and they are well separated in habitat choice.

The tadpoles of Limnonectes ibanorum *can be encountered in quiet, sun exposed side pools of mid-sized lowland or hillside streams.*

HABITAT & ECOLOGY
Quiet sections of mid-sized streams, especially in pools that are fully or partially cut off from the main water by gravel bars. They have also been reported from potholes on river banks. The tadpoles are benthic, staying close to the bottom of their pools, and can be observed foraging by day. Their color pattern provides excellent camouflage on the gravel-sand bottom. When disturbed, they will quickly swim to seek shelter under the nearest rock.

REPRODUCTION
Details of egg laying, nesting site and early development remain unknown.

COLORATION
Generally sandy brown to light olive brown above, with irregular blurred marbling, densely dusted with iridocytes above. At higher magnification, vermiculate melanocytes can be seen dorsally. Two distinct blotches located dorsally at the trunk-tail junction. Flank darker than dorsum. Sometimes there is a dark streak from the eye to the oral disc. Scattered, horizontally oriented dashes of silver iridocytes at the lower head and lower flank. Mid-flank bears clusters of iridocytes, reminiscent of rosettes. Skin of venter mostly unpigmented; only the anterior two thirds of the abdomen tend to have a silver sheath of iridocytes; some scattered iridocytes in the gular region; gills and gut coil visible. Body background color continues onto the dorsal tail and fades distally. Diffuse clusters of melanocytes may form a blurred marbling along the tail, including the fins. Rosette-like clusters of iridocytes at the flanks continue from trunk to tail and tail fins.

LITERATURE

Inger, R.F. (1966) The systematics and zoogeography of the Amphibia of Borneo. Fieldiana Zoology 52:1–402.

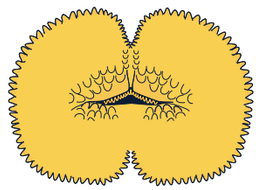
Inger, R.F. (2009) Contributions to the natural history of seven species of Bornean frogs. Fieldiana Zoology 116: 1–25.

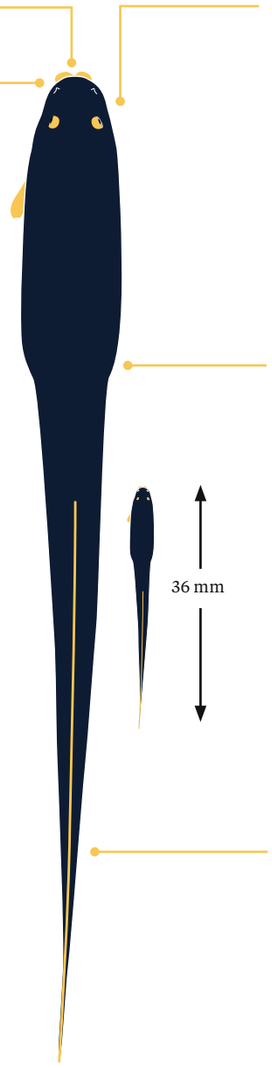
Leptobrachella baluensis Smith, 1931

Kinabalu Dwarf Litter Frog

SNOUT
Contour broadly rounded in dorsal view, blunt, and moderately long (relative to head). In lateral view, head bluntly conical in shape and nostril positioned elevated.

ORAL DISC
Anteroventral, approximately half of body width or more. Oral disc a peculiar funnel that protrudes perpendicular from body. Medial emarginations present in both upper and lower lip and the lips folded-in at these emarginations. Both lips bear short, numerous, marginal papillae in a continuous row.
Deep in the oral disc, mouth surrounded by irregular rows of submarginal papillae on upper and lower lips. Keratodonts absent (LTRF 0/0). Beaks strong, well keratinized, black, with sharp serrations. Beaks sit deep at the base of oral disc. They are partly covered by additional transverse ridges, barely visible without dissection.





NOSTRILS & EYES
Eyes positioned dorsolaterally, non-protruding in pre-metamorphic stages. Eyes small in early stage tadpoles increasing in size with development. Eyes surrounded by a unpigmented, white orbits. Iris (in late larval stages) black with a thin silvery circle around the pupil. Nostril closer to the snout than to eye. Nostril orifice oriented anterolaterally; its rim bears a triangular projection dorsally.

BODY
Very elongate, narrow. In lateral view, head slightly depressed, trunk subcylindrical. In dorsal view, body very slender, only slightly wider than base of the tail. Body-tail transition smooth, inconspicuous. Trunk section of body long and head much shorter than trunk. Body widest at the trunk. Spiracle sinistral and opens posterodorsally. Its orifice is positioned above the longitudinal body axis in lateral view. The spiracular orifice is free from the body wall and forms a free tube. Lateral line organs visible as series of dots on the head, along the flanks, and along the side of the tail.

TAIL
Long, up to 70% of total length. Muscular part of the tail strong, as high as body in lateral view. Upper fin starts well posterior to trunk-tail junction. It rises in an almost straight flat line and forms a shallow arch posteriorly to slope down to the narrowly rounded tip. Lower fin starts at body-tail junction, low and almost straight in contour. Maximum height of the tail is approximately in the middle section (no pronounced peak in tail fins). Upper fin slightly higher than the lower fin. Skin glands absent.

ECOMORPH
Lotic, exotrophic; gravel interstice specialist, fossorial.

SIMILAR SPECIES
Currently, the lack of sufficient data on intraspecific and ontogenetic variation and the paucity of features (reduced or lack of keratodonts) do not allow establishing reliable diagnostics for each of the *Leptobrachella* species. In case of *L. baluensis* tadpoles, there is potential for confusing them with tadpoles of other species of the genus that live in the same mountain ranges. DNA barcoding will be required to determine the tadpoles collected in such situations. See comments and literature for *Leptobrachella mjobergi*.

The tadpoles of Leptobrachella baluensis *live in interstices of small to mid-sized mountain streams. Their body shape is strikingly "eel-like", meaning that the head and trunk are long and slender, and the transition from trunk to tail is smooth.*

HABITAT & ECOLOGY
The species occurs in submontane and montane primary and secondary forests from above 900 m a.s.l. Often, the presence of calling males suggest the presence of tadpoles in a nearby body of water. Tadpoles are interstice specialists in the gravel bed of the streams. Tadpoles are unlikely to be seen in the open but will have to be dug up from the gravel. As inhabitants of interstices, they do not necessarily need surface water as long as there is water in the gravel layer.

REPRODUCTION
Males call from near stream banks on moist substrates. They will commonly perch on low vegetation or fallen leaves. Males can occur in numbers and form calling choruses. The call is a series of buzzing notes. The call sound pressure is considerable taking into account the small size of the males. Details of egg-laying are unknown.

COLORATION
Advanced larval stages are uniformly dark brown above and unpigmented, semi-translucent below (including oral disc). Early stages are more lightly pigmented and may appear pinkish-gray. In close-up, the skin has a hatched texture (reminiscent of fabric) and a bluish iridescence in life. Iridophores are mostly absent. Gut coil visible through the abdominal skin. Heart and gills visible through ventral skin as red areas, more clearly at early larval stages. The body coloration extents seamlessly onto the muscular part of the tail. Tail fins are dark pigmented, lightening towards their edges. Myosepta are faintly visible, somewhat accentuated by pigmentation. A thin lateral tail vein faintly visible in the proximal part of the tail.

LITERATURE

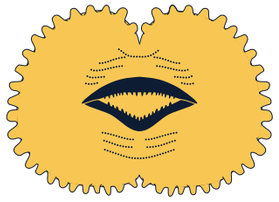
Malkmus, R., Manthey, U., Vogel, G., Hoffmann, P., Kosuch, J. (2002) Amphibians & Reptiles of Mount Kinabalu (North Borneo). Koeltz Scientific Books. 424 pp.

Leptobrachella dringi (Dubois, 1987)

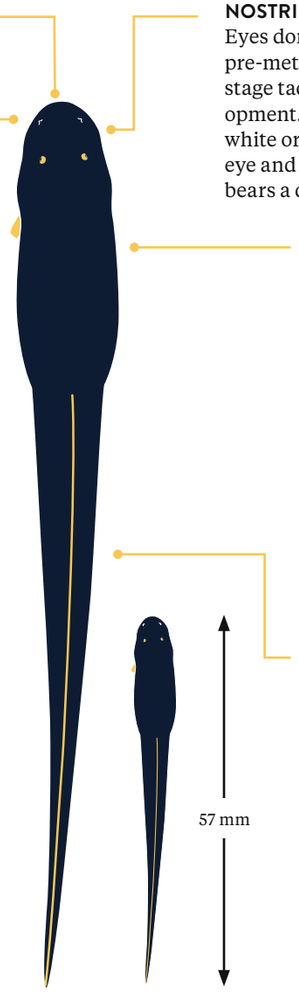
Dring's Slender Litter Frog

SNOUT
Contour broadly rounded blunt in dorsal view and moderately long. In lateral view, sloping and rounded. In profile, nostrils located on a small bulge.

ORAL DISC
Subterminal; width up to half of body width. Oral disc formed as funnel that protrudes from body. Emarginations are present in the medial plane of both upper and lower lips and the oral funnel is folded in at these emarginations. Both lips bear short, numerous, marginal papillae in a continuous row, except for a tiny anterior gap.



Deep in the oral disc funnel (not shown), the lower lip bears irregular rows of submarginal papillae. Keratodont rows short, with the peripheral ones on upper and lower lip, respectively, undivided; LTRF 5(2–5)/3(1–2). Beaks strong, well keratinized, black, with small and sharp serrations above, more blunt below. Upper jaw sheath high (difficult to see in full extent) and arched, lower sheath high and V-shaped.



NOSTRILS & EYES
Eyes dorsolateral, deep, not protruding in pre-metamorphic stages. Eyes tiny in early stage tadpoles, increase in size with development. Eyes surrounded by unpigmented, white orbita. Nostril closer to snout than to eye and oriented anterolaterally. Its dorsal rim bears a distinct projection. Iris black.

BODY
Mid-sized and elongate; tadpole eel-like. In lateral view, head and trunk are depressed. In dorsal view, the body is slender, only slightly wider than the base of the tail, body-tail transition smooth. Trunk part of the body long; the head shorter than the trunk and weakly set off from it. Body widest at the trunk. Spiracle is sinistral. Spiracular opening free from the body, i.e., a free tube opens posterolaterally. Spiracular opening positioned anterior to the mid head-trunk length. Skin glands absent.

TAIL
Long, up to 73% of total length. Muscular part strongly developed, virtually as high as body at base of tail. Fins begin at the trunk-tail transition but stay low in the anterior part of the tail. Upper fin with a straight edge, whereas lower fin slightly convex. Fins almost equal in heights. Posteriorly, fins end in a broadly rounded tip.

ECOMORPH
Lotic, exotrophic, gravel interstices specialist, fossorial.

SIMILAR SPECIES
Few samples of *Leptobrachella* tadpoles have been collected. Sample sizes make inferences about reliable identification of species and differential diagnosis between species difficult. Currently, reliable identification rests on DNA barcoding. *Leptobrachella* tadpoles can easily be distinguished from any other tadpole on Borneo by the combination of specific microhabitat, the slender eel-like body, small eyes, and the unique shape of the protruding oral disc. *L. dringi* (Oberhummer et al. 2014) is distinguishable from a tadpole identified by Malkmus et al. (2002) as *L. arayai*. The latter lacked iridophore dots on the body and head (present on tail only), had two short keratodont rows on upper lip, and more submarginal papillae on lower lip. Malkmus et al. (2002) provided no genetic information for that specimen, and recently, *L. sabahmontanus*, was described from the same locality. Thus, currently it is impossible to assign the tadpole described by Malkmus et al (2002) to one of the two sympatric species with certainty.

Some Leptobrachella *tadpoles have only been known from few specimens and any descriptions are preliminary.* Leptobrachella *tadpoles are uniquely "eel-like". The trunk-tail transition is smooth. Head and body are flexible and take part in undulating movements when the tadpoles wiggle through gravel interstitial space.*

HABITAT & ECOLOGY
Tadpoles have only been reported so far from Gunung Mulu, at high elevations (1700 m a.s.l), the type locality of the species. Tadpoles inhabit gravel beds in shallow sections of mountain streams. Food resources have not been determined yet, but decomposed leaf litter in the gravel interstitial spaces could be a possible dietary component.

REPRODUCTION
The call consists of a short series of 2–11 high frequency notes between 6100–6400 Hz, without frequency modulation.

COLORATION
Ash gray, milky semi-transparent skin with a bluish-white sheen on head and trunk. Upper head, upper trunk and tail with brown pigmentation in advanced stages. Brown pigmentation of the body fades towards venter. Buccal, gill, and abdominal skin milky semi-transparent, without brown pigment but with bluish sheen. Gills and heart visible as red areas. Gut coils visible in ventral and lateral views. Tail fins semi-transparent, dusted moderately with brown pigment cells (in advanced stages). Scattered blueish iridophores present on dorsal face of body and along the tail including fins; myosepta accentuated by pigmentation.

LITERATURE

Oberhummer, E., Barten, C., Schweizer, M., Das, I., Haas, A., Hertwig, S.T. (2014) Description of the tadpoles of three rare species of megophryid frogs (Amphibia: Anura: Megophryidae) from Gunung Mulu, Sarawak, Malaysia. Zootaxa 3835: 59–79.

Matsui, M., Dehling, J.M. (2012) Notes on an enigmatic Bornean megophryid, *Leptolalax dringi Dubois*, 1987 (Amphibia: Anura). Zootaxa 3317: 49–58.

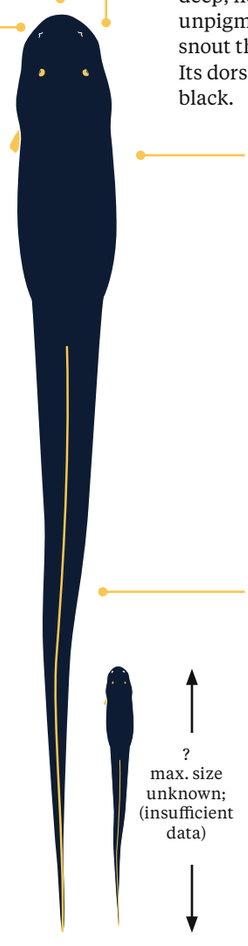
Leptobrachella fritinniens (Dehling and Matsui, 2013)

Twittering Slender Litter Frog

SNOUT
Broadly rounded, blunt, and moderately long in dorsal view; set off from the posterior part of the head by a shallow convexity. In lateral view, head smoothly sloping downward into the rounded snout giving the head a blunt conical shape. In profile, nostril positioned elevated on a bulge.

ORAL DISC
The details of the oral disc could not be studied with confidence because only two specimens of relatively early stage could be examined. However, oral disc features follow the general features in the genus *Leptobrachella*: disc funnel-shaped and conspicuously protruding from the body.

ECOMORPH
Lotic, exotrophic, gravel interstices specialist, fossorial.



NOSTRILS & EYES
Eyes very small, positioned dorsolaterally, deep, not protruding. Eyes surrounded by an unpigmented, white orbita. Nostril closer to snout than to eye and oriented anterolaterally. Its dorsal rim bears a distinct projection. Iris black.

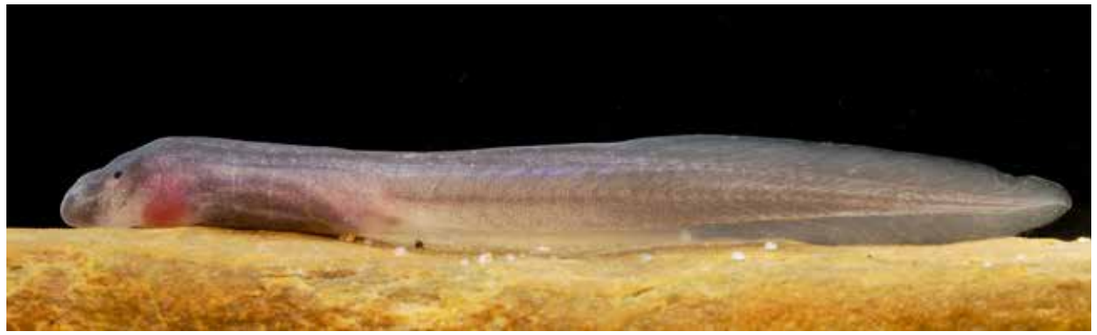
BODY
Mid-sized and elongate; tadpole eel-like. In lateral view, head and trunk slightly depressed. In dorsal view, body slender, only slightly wider than base of tail. Body-tail transition smooth. Trunk is elongate; the head is shorter than the trunk and weakly set off from the trunk. Body widest at the gill region or the trunk. Spiracle sinistral. The spiracular opening free from the body with free spiracular tube opening posterolaterally. The opening is positioned anterior to the mid head-trunk length. Skin glands absent.

TAIL
Long, approx. 67% of total length. Muscular part strongly developed, virtually as high as body at base of tail. Dorsal fin begins posterior to the trunk-tail transition and stays low in the anterior part of the tail. It has a straight edge in the first third of the tail, then, with a very smooth but noticeable change of curvature. Dorsal fin contour assumes a slightly convex course in the posterior two thirds of fin. Lower fin starts at the trunk-tail transition. Lower and upper fin similar in maximum height. The fins converge into a rounded tip.

SIMILAR SPECIES

Only a few samples of tadpoles of *Leptobrachella* species have been collected by scientists so far. Sample sizes have been small in most cases making inferences about reliable identification of species and differential diagnosis between species difficult. Currently, reliable identification rests on DNA barcoding. Differences in the descriptions of this and other species should be interpreted with common sense with respect to the available evidence.

Leptobrachella tadpoles can easily be distinguished from any other tadpole on Borneo by the combination of specific microhabitat, the slender body, small eyes, and the unique shape of the protruding oral disc. Inger (1985) gave a description of *L. gracilis* tadpoles that, according to the locality information provided and the taxonomic changes since then, would probably be considered the larvae of a different *Leptobrachella* species, possibly *L. fritinniens*.



We could secure only three specimens, one of which is used here for photo documentation and description. L. fritinniens *probably is a common* Leptobrachella *of lowland and mid-elevational levels (<700 m a.s.l.) in Sabah and northeast Sarawak. The dearth of knowledge on its larval form is due to the effort it takes to collect these elusive inhabitants of gravel interstitial spaces.*

HABITAT & ECOLOGY
The tadpoles we report here were collected at Poring, Kinabalu Park, and Crocker Range National park, from the lower altitudes of these mountain ranges. Tadpoles inhabit interstitial spaces in gravel beds in clear mountain streams.

REPRODUCTION
Males call from low vegetation along streams, usually less than 1 m above the ground. The vocal sack is bipartite. The twittering call has a dominant frequency between 7225–9190 Hz (frequency modulation).

COLORATION
Upper body and tail skin has a bluish iridescence in live specimens. Upper head, upper trunk and tail with brown pigmentation in advanced tadpoles. Brown pigmentation of the body fades towards the ventral side. Buccal, gill, and abdominal skin semi-transparent, without brown pigment. Gills and heart visible as reddish areas shining through skin. Gut coils visible in ventral and lateral views. Tail fins semi-transparent, dusted moderately with brown pigment cells (probably less pigmented at early larval stages). Few scattered silver-blueish iridophore dots present on the dorsal face of the head and body and along the upper parts of tail root. Myosepta accentuated by pigmentation, lateral tail vein visible.

LITERATURE

Dehling, J. M., Matsui, M. (2013) A new species of *Leptolalax* (Anura: Megophryidae) from Gunung Mulu National Park, Sarawak, East Malaysia (Borneo). Zootaxa 3670: 33-44.

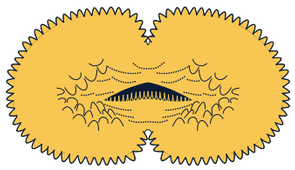
Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

Leptobrachella gracilis (Günther, 1872)

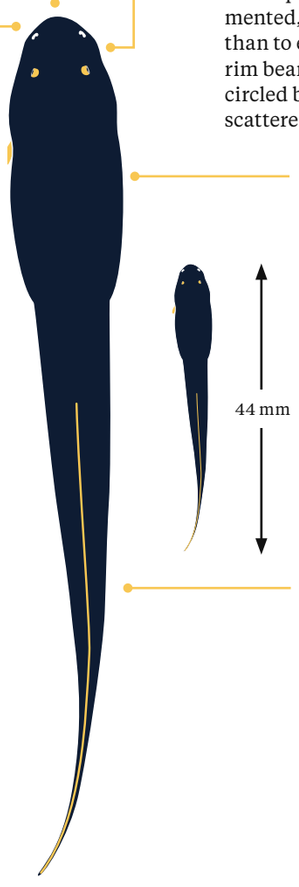
Sarawak Slender Litter Frog

SNOUT
Broadly rounded, blunt, and moderately long in dorsal view. In lateral view, head smoothly sloping into a rounded, blunt snout. Nostril positioned elevated on a small bulge.

ORAL DISC
Subterminal; width up to half of body width. Disc funnel-shaped, protruding from body. Emarginations present in the medial plane of both upper and lower lips.



Oral funnel folded in at the emarginations. Upper and lower lips bear short, numerous, marginal papillae in a single continuous row. Oral disc bears many submarginal papillae. Keratodont rows short, peripheral rows on upper and lower lip, respectively, undivided; LTRF 4(2–4)/3(1–2). The 3rd and 4th upper lip rows each consist of two keratodont-bearing ridges. Keratodonts loosely spaced. Beaks strong and well keratinized, black, beak edges bear serrations. Both beaks are high, however, the beaks due to their deep position. Upper jaw smoothly arched; the lower one slightly more angled, more V-shaped.



NOSTRILS & EYES
Eyes dorsolateral, siting deep, not protruding in pre-metamorphic stages. Eyes tiny in early stage tadpoles, they increase in size with development. Eyes surrounded by an unpigmented, white orbits. Nostril closer to snout than to eye, oriented anterolaterally. Its dorsal rim bears a distinct projection. Nostril rim encircled by a brown ring. Iris black with a ring of scattered silver iridophores around the pupil.

BODY
Medium to large in size and elongate. Head and trunk depressed in lateral view. In dorsal view, body slender, only slightly wider than the base of the tail. Body-tail transition smooth. Trunk part of the body long, slightly longer than head. Head only slightly set off from trunk. Body widest at trunk. Spiracle sinistral. Spiracle opening is free from the body; spiracular tube opens posterolaterally. The opening is positioned posterior to the mid head-trunk length. Skin glands are absent.

TAIL
Long, up to 70% of total length. Muscular part strongly developed, virtually as high as body at base of tail. Dorsal fin begins posterior to the trunk-tail transition at approximately 20% of tail length. It stays low in the anterior part of the tail. Both fins straight, without much convexity. Fins subequal in height. Posteriorly, the fins end in a narrowly rounded tip.

ECOMORPH
Lotic, exotrophic, gravel interstices specialist, fossorial.

SIMILAR SPECIES
Leptobrachella tadpoles are rarely collected and confirmed by DNA barcoding. The subtle differences we saw in various *Leptobrachella* samples are difficult to assess. For the time being, DNA barcoding is highly recommended for identification, especially in areas where species are sympatric. *Leptobrachella* tadpoles can easily and reliably be distinguished from any other Bornean tadpoles on the basis of their microhabitat choice, relatively slender body, small eyes, plus the unique shape of the protruding oral disc; a few short keratodont rows are present in some species, absent in others. In the light of current knowledge, recent taxonomic changes, and the locality information provided, the tadpoles described by Inger (1985) as *L. gracilis* (then still in *Leptolalax*) from various sites could represent larvae of several species.

As in other species of Leptobrachella, *to find the tadpoles of* Leptobrachella gracilis *requires the right search strategy (suitable microhabitats) and tools (reinforced nets). The casual observer is rather unlikely to encounter them in the field.*

HABITAT & ECOLOGY
Larvae of *L. gracilis* are inhabitants of crevices and interstices of gravel. We discovered the tadpoles depicted here in a roadside ditch in slow-flowing water, under piles of accumulated leaf litter and amongst gravel. Interestingly, tadpoles of *L. gracilis* where associated with larvae of a total of nine more anuran species in the same body of water, at the time of sampling!

REPRODUCTION
Males call from elevated perches, usually <1 m, on branches or low vegetation along streams, often several meters from the water. The call is a harsh trill composed of pulsed notes. The dominant frequency is approximately 2500 Hz.

COLORATION
Body background color gray, with a bluish-white sheen. Upper head, upper trunk, and tail with brown pigmentation in advanced stages. Brown pigmentation of the body fades towards the ventral side. Buccal region, gill region, and abdominal skin semi-transparent, without brown pigment but with bluish sheen. Gills and heart visible as reddish areas; gut coils visible in ventral and lateral views. Tail fins semi-transparent, dusted moderately with brown pigment cells (in advanced stages). Scattered iridophores present on the dorsal face of head and body and along the tail including the dorsal fin. Myosepta and lateral tail vein visible.

LITERATURE
Inger, R.F. (1983) Larvae of Southeast Asian species of *Leptobrachium* and *Leptobrachella* (Anura: Pelobatidae). In: Rhodin, A. G. J., Miyata K. (eds) Advances in Herpetology and Evolutionary Biology. Essays in Honor of Ernest E. Williams: 13–32. Cambridge, Massachusetts, Museum of Comparative Zoology, Harvard University.

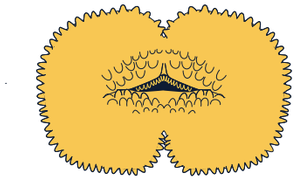
Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

Leptobrachella mjobergi Smith, 1925

Mjöberg's Dwarf Litter Frog

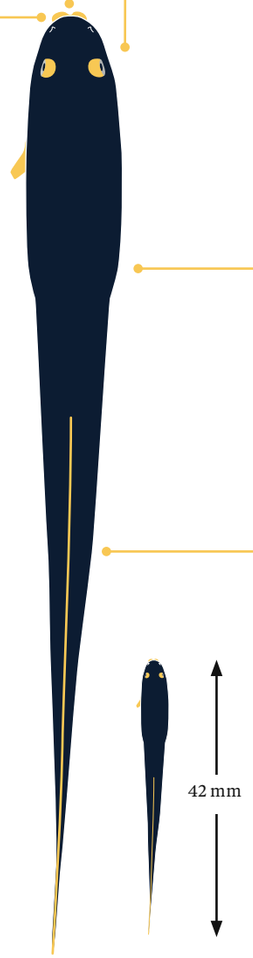
SNOUT
Snout broadly rounded, blunt, and moderately long in dorsal view. In lateral view, head conical in shape, snout profile blunt. Nostril located on a small bulge in lateral view.

ORAL DISC
Anteroventral, approximately half of body width or more, funnel-shaped. It protrudes from the body. Medial emarginations are present in upper and lower lips. Oral funnel folded-in at these emarginations. Both lips bear short, numerous, marginal papillae in a continuous row.



Deep in oral disc, the mouth is surrounded by irregular rows of submarginal papillae on upper and lower lips. Keratodonts absent (LTRF 0/0). Beaks thick, strongly keratinized, black, with sharp serrations. Beaks sit deep at the base of the oral funnel, behind additional transverse ridges, barely visible without removing tissue.

ECOMORPH
Lotic, exotrophic, gravel interstice specialist, fossorial.



NOSTRILS & EYES
Eyes dorsolaterally, non-protruding in pre-metamorphic stages, tiny in early stage tadpoles. They increase in size with development. Eyes surrounded by an unpigmented, white orbit. Iris (in late larval stages) black with a thin silvery circle around the pupil. Nostril closer to snout than to eye, oriented anterolaterally. Rim of the nostril with a triangular projection dorsally.

BODY
Mid-sized and elongate, eel-like. In lateral view, head slightly depressed. Trunk subcylindrical, almost circular in cross-section. In dorsal view, body slender, only slightly wider than the base of the tail. Body-tail transition smooth and the trunk section of the body is long. Head much shorter than trunk. Body widest at the trunk. Spiracle sinistral directed posterodorsally. Spiracular orifice above the longitudinal body axis in lateral view and not fused to the body wall (free tube). Lateral line organs visible as series of dots on the head, along the flanks, and along the side of the tail.

TAIL
Long, 66–68% of total length. Muscular part of the tail is strong, as high as body in lateral view. Upper fin starts well posterior to trunk-tail junction at almost one third of tail. It rises in a very shallow arch and slopes downward towards the tip. Lower fin starts at the body-tail junction, is low and almost straight in contour. Upper and lower fins taper in the end part in the tail to form a triangular, narrowly rounded tip (damages of the tips are common). Maximum height of the tail is approximately in middle section (no pronounced peak in tail fins). Upper fin slightly higher than the lower fin. Skin glands absent.

SIMILAR SPECIES
All known tadpoles of *Leptobrachella* live in the interstices of gravel. They are usually found in riffles of streams. Their slender, eel-like bodies and peculiar funnel-shaped, protruding oral disc distinguish them from all other Bornean tadpoles. Within *Leptobrachella*, descriptions of tadpoles have been based on small samples. Ontogenetic and intraspecific variations are mostly unknown. Lack of data and features do not allow establishing reliable diagnostic characters for the species in the genus. Researchers are advised to apply DNA barcoding to match adults with larvae.

The tadpoles of Leptobrachella mjobergi *are secretive and live in gravel interstices of lowland streams in western Sarawak.* Leptobrachella *tadpoles are uniquely "eel-like" in body shape, also expressed by their body undulations when moving. The trunk is hardly set off from the tail. The head is more movable than in other tadpoles and allows them to maneuver through gravel interstices.*

HABITAT & ECOLOGY
The species occurs in lowland and hillside primary and secondary forest and seems to tolerate even lightly-disturbed forests. Individuals are always found in close association with streams. These streams typically have sections with shallow riffles, where tadpoles seem to live preferentially. It is still not fully understood what food items *L. mjobergi* tadpoles ingest in its interstice microhabitat but Inger (1985) suggested a diet on dead leaves. This hypothesis is supported by gut contents and powerful jaw morphology. Several anatomical features have been linked to their adaptation to interstices (Haas et al. 2006).

REPRODUCTION
Males are found calling along stream banks. Males may call from the ground or rocks or perch slightly elevated, often 5–30 cm high on vegetation, usually facing the stream. The call is a series of very high-pitched chirps. Males can form choruses. Despite the small size of the frogs, the calls are loud and assemblages of synchronously calling males can produce an impressive sound pressure level.

COLORATION
Advanced larval stages are uniformly dark brown above and unpigmented, semi-translucent below (including oral disc). Early stages more lightly pigmented and appearing pinkish-gray. In close-up, the skin has a hatched texture, reminiscent of fabric, and a bluish iridescence in life. Iridophores absent. Gut coil visible through the abdominal skin. Heart and gills appear red through the ventral skin, at least in early larval stages. The body coloration extents seamlessly onto the muscular part of the tail. Tail fins dark pigmented, lightening towards their edges. Myosepta faintly visible.

LITERATURE
Inger, R. F., (1983) Larvae of Southeast Asian species of *Leptobrachium* and *Leptobrachella* (Anura: Pelobatidae), pp. 13-32. In Rhodin, A., and K. Miyata (eds.). Advances in Herpetology and Evolutionary Biology. Museum of Comparative Zoology, Cambridge, Mass.

Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

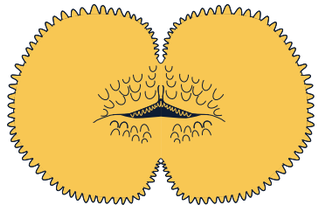
Haas, A., Hertwig, S., Das, I., (2006) Extreme tadpoles: The morphology of the fossorial megophryid larva, *Leptobrachella mjobergi*. Zoology 109: 26–42.

Leptobrachella itiokai Eto, Matsui, and Nishikawa, 2016

Itioka's Dwarf Litter Frog

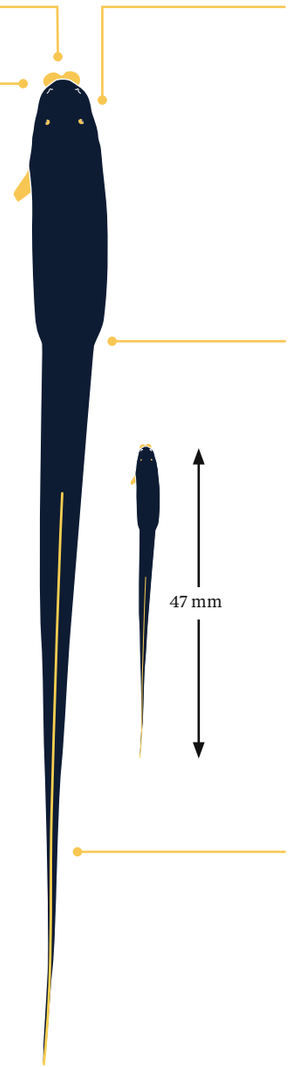
SNOUT
In dorsal view, the snout is broadly rounded, blunt, and moderately long relative to head. In lateral view, the head is bluntly conical. A small bulge supports the nostril in lateral view.

ORAL DISC
Anteroventral, approximately half of body width. Oral disc funnel-shaped, protruding from body. Emarginations and in-foldings present in mid-line of upper and lower lip, respectively.



Upper and lower lips bear short, numerous, marginal papillae in a continuous row. At the base of the oral funnel, the lips bear irregular rows of papillae. Keratodonts are absent (LTRF 0/0). Beaks are strong, well keratinized, black, with sharp serrations. Beaks are deeply recessed in the funnel-shaped oral disc, partly hidden by transverse ridges.

ECOMORPH
Lotic, exotrophic, gravel interstice specialist, fossorial.



NOSTRILS & EYES
Eyes dorsolateral, tiny and non-protruding in early stage tadpoles; they increase in size and become more bulging during metamorphosis. Eye socket (orbits) unpigmented, whitish. Iris black with (in late larval stages), with a faint silvery circle around the pupil. Nostril closer to snout than to eye and oriented anterolaterally. Nostril rim bears a triangular projection dorsally.

BODY
Mid-sized, "eel-like"; body very elongate. In lateral view, head and trunk slightly depressed, trunk is subcylindrical. In dorsal view, body slender, only slightly wider than the base of the tail. Body-tail transition smooth. Trunk section of the body long, head much shorter than trunk. Body widest at the trunk. Spiracle sinistral and opening posterodorsally. Spiracular orifice positioned above longitudinal body axis in lateral view. Spiracular orifice free from the body wall. Spiracular tube long. Lateral line organs clearly visible as a series of light dots on the head, along the flanks, and along the side of the tail.

TAIL
Long, approximately 70% of total length. Muscular part strong, almost as high as body in lateral view. Upper fin starts well posterior to trunk-tail junction. Upper fin low in the proximal half of tail, increases in height in the posterior half. Height of lower fin is constant and low in the proximal half of the tail and increases slightly in the posterior half. Tail end triangular, tip narrowly rounded, acuminate. Skin glands absent.

SIMILAR SPECIES
Leptobrachella itiokai tadpoles are morphologically similar to other species in the genus. Few known samples and lack of distinct features (lack of distinct color pattern, lack of keratodonts) require DNA analysis for reliable identification, especially in cases, as in *L. itiokai*, when different species occur in sympatry or even syntopy. See also comments for *Leptobrachella mjobergi*.

Prior to the discovery of Leptobrachella itiokai*, its tadpole had been assigned to* L. brevicrus *(Oberhummer et al. 2014). The description presented here is preliminary, as not many specimens have ever been found. The larvae are interstice specialists in clear montane streams.* Leptobrachella itiokai *tadpoles are morphologically similar to other species in the genus.*

HABITAT & ECOLOGY
This species occurs in clear streams of montane forests at the higher elevations of Gunung Mulu. Tadpoles live in interstices in the gravel and under rocks. The feeding ecology of tadpoles is unknown.

REPRODUCTION
Males typically call on leaves or branches 20–60 cm above the ground at steep montane streams. The call of males consists of series of chirps.

COLORATION
Early larval stages are lightly pigmented and appear yellowish in color; advanced larval stages are uniformly brown above. Silvery iridophores are absent. In close-up, skin reminiscent of fabric with a hatched texture; it has a bluish iridescence in life. Venter, including oral discs, unpigmented, cream-colored, semi-translucent. Gut and gills are faintly visible through the abdominal skin. Heart and gill region reddish. The brown body coloration continues onto muscular part of tail. Tail fins pigmented at their base and clear towards their edges. Myosepta visible distally.

LITERATURE

Oberhummer, E., Barten, C., Schweizer, M., Das, I., Haas, A., Hertwig, S.T., (2014) Description of the tadpoles of three rare species of megophryid frogs (Amphibia: Anura: Megophryidae) from Gunung Mulu, Sarawak, Malaysia. Zootaxa 3835: 59–79.

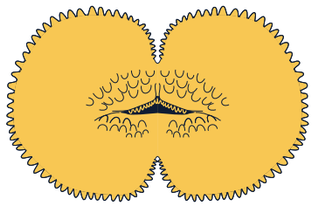
Eto, K., Matsui, M., Nishikawa, K. (2016) A new highland species of dwarf litter frog genus *Leptobrachella* (Amphibia: Anura: Megophryidae) from Sarawak. The Raffles Bulletin of Zoology 64: 194–203.

Leptobrachella juliandringi Eto, Matsui, and Nishikawa, 2015

Dring's Dwarf Litter Frog

SNOUT
Broadly rounded in dorsal view, blunt, and moderately long relative to head. In lateral view, the head is bluntly conical. A small bulge supports the nostril in lateral view.

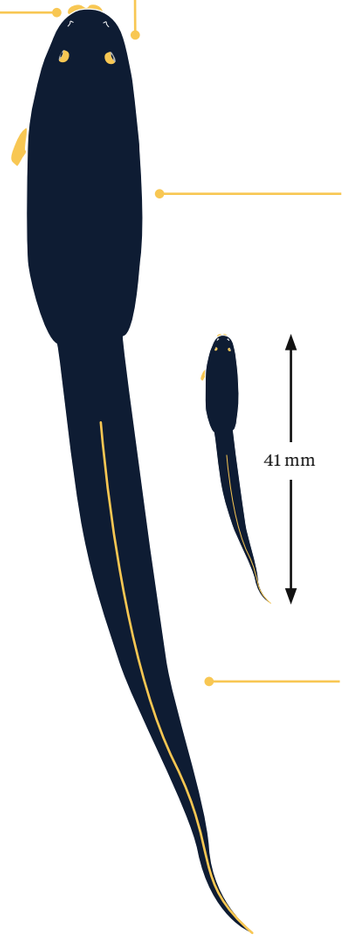
ORAL DISC
Anteroventral, approximately half of body width. Oral disc funnel-shaped, protruding from body. Emarginations and in-foldings are present in the mid-line of upper and lower lip, respectively.



Upper and lower lips bear short, numerous, marginal papillae in a continuous row. At the base of the oral funnel, the lips bear irregular rows of papillae. Keratodonts are absent (LTRF 0/0). Beaks are strong, well keratinized, black, with sharp serrations. Beaks deeply recessed in the funnel-shaped oral disc, behind transverse ridges; not easily visible.

ECOMORPH
Lotic, gravel interstice specialist, fossorial.

SIMILAR SPECIES
See comments for *Leptobrachella mjobergi*.



NOSTRILS & EYES
Eyes dorsolateral, tiny and non-protruding in early stage tadpoles; they increase in size and become more bulging during metamorphosis. Eye socket (orbits) unpigmented, cream-colored. Iris black, in late larval stages with a thin silvery circle around the pupil. Nostril closer to snout than to eye and oriented anterolaterally. Nostril rim bears a triangular projection dorsally.

BODY
Mid-sized, "eel-like" in shape, elongate. In lateral view, head and trunk slightly depressed, trunk subcylindrical. In dorsal view, body slender, only slightly wider than the base of the tail; trunk-tail transition smooth. Trunk section of body long, head much shorter than trunk. Body widest at trunk. Spiracle sinistral and opens posterodorsally. Spiracular orifice positioned above the longitudinal body axis in lateral view. Spiracular orifice free from the body wall, extended into a long, free tube. Lateral line organs present as series of light dots on the head, along the flanks, and along the side of the tail.

TAIL
Long, approximately 68% of total length. Muscular part of tail strong, almost as high as trunk in lateral view. Upper fin starts well posterior to trunk-tail junction; low in the proximal half of the tail. It becomes higher gradually, reaching its maximum height only at the posterior third of the tail. Upper fin only slightly higher than the lower fin. Lower fin starts at trunk-tail junction; it is low and almost straight in contour. In its posterior third, tail fins converge in relatively straight lines towards the narrowly rounded tip (tail tips often damaged). Skin glands absent.

Leptobrachella juliandringi *inhabits low and hilly forests in eastern and north-eastern Sarawak. The larvae are interstice specialists in stream riffles.* Leptobrachella *tadpoles are "eel-like" in body shape and are able to move in undulating, snake-like motion. These tadpoles will only rarely surface from the gravel.*

HABITAT & ECOLOGY
The species occurs in clear streams of lowland and hilly forests. Tadpoles live in interstices in the gravel and under rocks, particularly in low-depth riffles over shingle bed. The feeding ecology of tadpoles remains unknown.

REPRODUCTION
Males call along stream banks. They often perch on leaves 20–80 cm above the ground. Male calls can be described as a series of high-pitched chirps and can form choruses. Details of the reproduction, such as number of eggs and oviposition site are unknown.

COLORATION
Early larval stages lightly pigmented, appearing pinkish gray; advanced larval stages uniformly dark brown above. Silvery iridophores absent. In close-up, skin shows a hatched texture and a bluish iridescence in life. Venter, including oral discs, unpigmented, semi-translucent. Gut coil visible through the abdominal skin. Gill region and heart indicated in red. Dark body coloration continues seamlessly onto the muscular part of the tail. Tail fins dark pigmented, lightening towards their edges. Myosepta faintly visible.

LITERATURE

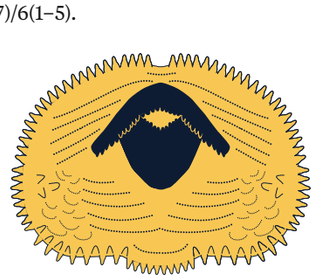
Eto, K., Matsui, M., Nishikawa, K. (2015) Description of a new species of the genus *Leptobrachella* (Amphibia, Anura, Megophryidae) from Borneo. Current Herpetology 34: 128–139.

Leptobrachium abbotti (Cochran, 1926)

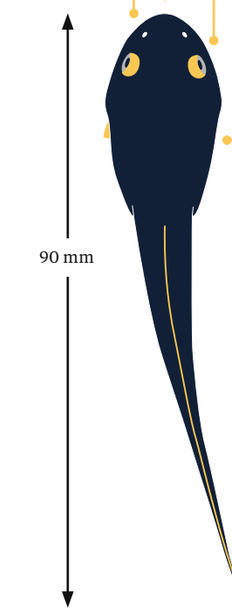
Lowland Litter Frog

SNOUT
Broadly rounded, blunt, and moderately long in dorsal view. In lateral view, head and snout smoothly curving downward, forming a rounded profile with the part bearing the nostrils slightly bulging.

ORAL DISC
Anteroventral to almost ventral, less than half of the body in width. Emarginations between upper and lower lip are absent. Both lips bear conical, marginal papillae in a single row that may have stretches with papillae in staggered arrangement. Marginal papillation nearly continuous, with a tiny medial gap in the upper lip papillation. Keratodont formula: LTRF 6(2–6)/6(1–5) to 7(2–7)/6(1–5).



First upper and last lower lip keratodont rows are short. Laterally on the oral disc, with some submarginal papillae and up to 16 additional short submarginal ridges with short keratodont rows. Beaks heavily built, strongly keratinized, deep black, bearing coarse serrations along their edges.



ECOMORPH
Lotic, exotrophic, benthic.

NOSTRILS & EYES
Eyes positioned dorsolaterally. Iris and scleral part of the eyeball black with densely scattered iridophores, silver on the scleral part, copper on iris. Nostril distinct, relatively large. Nostril slightly closer to snout than to eye, oriented anterolaterally. Nostril dorsal rim with a soft, bulging projection.

BODY
Large and robust, slightly dorsoventrally depressed. In dorsal view, body contour oblong oval. Trunk clearly wider than base of tail. Body widest at the anterior trunk or the gill region (depending on feeding status). Spiracle sinistral, opening posteriorly to posterolaterally. Spiracular orifice positioned slightly below mid-body level in lateral view; free from the body wall; a short tube is formed. Lateral line organs distinct. Broken lines of dash-like lateral line organs conspicuous on the head, along flanks, and along side of the tail.

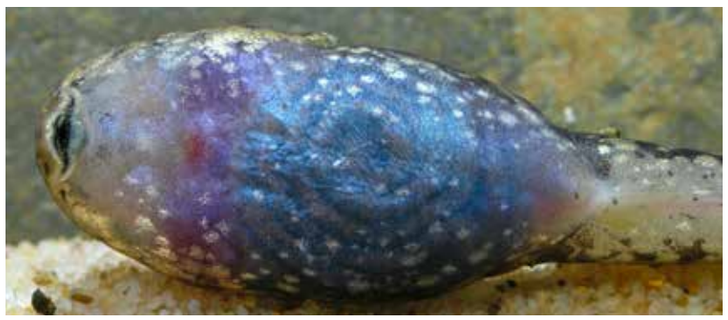
TAIL
Long, 66–68% of total length. Muscular part strong, almost as high as body in lateral view. Upper fin rises gradually from the trunk-tail junction. It rises relatively straight to mid-tail, weakly arches there and runs in a almost straight line to the narrowly rounded tip. Lower fin starts at the body-tail junction; it is shallowly arched in contour. Maximum height of tail fins approximately at mid-tail section. Upper fin higher than lower fin. Skin glands absent.

SIMILAR SPECIES
Leptobrachium tadpoles are easily diagnosed at the genus level by habitat (rocky or gravel bed streams), generally dark to black color, large size, and oral disc features. Further studies are needed to reliably establish interspecific diagnostics in *Leptobrachium*. However, *L. abbotti* appears to have 1) the most dense and pronounced 'hatched' pigmentation pattern that even covers the skin of the venter, and 2) higher numbers of additional lateral submarginal keratodont rows than *L. montanum* and *L. gunungense*. *Leptobrachium ingeri* has blackish tadpoles (tadpole of the closely related *L. kanowitense* unknown). Tadpoles of the Creek Frog complex may occur in syntopy and could be potentially confused superficially with *L. abbotti*, but they never reach their size and are mostly lighter in color and have different papillation patterns on the oral disc.

Leptobrachium abbotti *is widely distributed in lowland Borneo and probably represents more than one species. Its tadpoles are large. They live in clear streams with rock and gravel bed. When disturbed, they hide under and between rocks, under logs, or among leaf drift.*

HABITAT & ECOLOGY
The species can be encountered in lowland to hillside primary and secondary forests (< 1000 m a.s.l.). The tadpoles prefer sections of gravel- or rock-bottom streams with low to moderate current (side pools, bays, shores, shingle areas). They inhabit the bottom layers in the stream. At night, they can be observed in numbers grazing on bottom rocks and leaf debris or just resting on the substratum. Often, mixed stages are present in the same stream, indicative of extended breeding periods. At daytime, the tadpoles spend most of the time in hiding places. They are seen in more exposed situations at greater densities at night. Despite their size, they are difficult to catch because of their alertness and swimming speed.

REPRODUCTION
Males call from leaf litter at varying distance from the stream banks and neighboring forests. The loud call consists of 1-3 „quack" notes.



COLORATION
Variable, from mottled to blotched; generally dark brown above with a dark markings on somewhat lighter background. Early tadpole stages with overall less dark pigmentation. Individuals become darker and more mottled towards metamorphosis. Distinct dark blotches are positioned at the tail root, at least in early stages. Early stages show a pair of whitish structures posteriorly at the head. Golden iridophores arranged in patches, present dorsally and laterally, but can occur ventrally, too. In close-ups, conspicuous hatched pattern of pigment cells evident. Ventral side semi-translucent to opaque (depending on stage). Gut coil visible at early stages but hardly visible in tadpoles at the pre-metamorphic stage; same with heart and gills. In living specimens, abdominal skin with a bluish-silvery iridescence (absent in preserved specimens). Body coloration continues onto muscular part of tail. Along the tail, the pattern breaks up into blotches and spots distally in early stages. In more advanced stages, mottling of body continues seamlessly onto tail. Myosepta and lateral tail vein indistinct.

LITERATURE

Inger, R. F. (1983) Larvae of Southeast Asian species of *Leptobrachium* and *Leptobrachella* (Anura: Pelobatidae), pp. 13-32. In Rhodin, A., and K. Miyata (eds.). Advances in Herpetology and Evolutionary Biology. Museum of Comparative Zoology, Cambridge, Mass.

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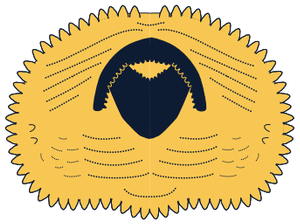
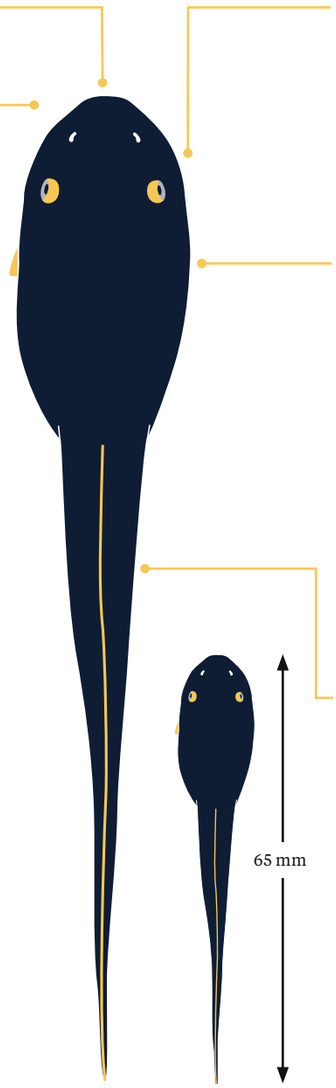
Leptobrachium gunungense Malkmus, 1996

Kinabalu Large-eyed Litter Frog





SNOUT
Broadly rounded in dorsal view, blunt to somewhat obtuse tip, moderately long. Part anterior of the level of nostrils weakly set off in dorsal view. In lateral view, Head smoothly sloping, snout rounded. In profile, nostril slightly elevated.

ORAL DISC
Anteroventral to almost ventral, less than half of body in width. No distinct emargination between upper and lower lip. Both lips bear relatively large, bluntly conical, marginal papillae in a single row.

Row of marginal papillae nearly continuous, with only a small medial gap in the upper lip papillation. Lower lip bears a few scattered submarginal papillae; some of them as short ridges that bear short keratodont rows. Keratodont formula: LTRF 6(2–6)/5(1–4). Additionally, there are 7–10 short keratodont rows in the submarginal area of the lower lip. First upper lip keratodont row particularly short. Beaks massive, well keratinized, black, bearing coarse serrations along their edges.

ECOMORPH
Lotic, exotrophic, benthic.

NOSTRILS & EYES
Eyes dorsolateral, relatively small. Iris and sclera black with densely scattered silvery or golden iridophores. Nostril distinct and relatively large, closer to snout than to eye. Nostril oriented anterolaterally. Its dorsal rim forms an inconspicuous projection bulging laterally.

BODY
Large. In lateral view, head and trunk slightly dorsoventrally depressed. In dorsal view, body elongated oval in shape, much wider than base of tail. Body widest at the anterior trunk or posterior gill chamber. Spiracle sinistral, opening posterolaterally. Spiracular orifice positioned at approximately mid-body in lateral view. Its rim free, forming a very short tube, or fused to the body wall. Lateral line organs distinct as series of light dashes. Myosepta indistinct. Lateral tail vein mostly visible.

TAIL
Long, 64–67% of total length. Muscular part of the tail strong, almost as high as body in lateral view. Upper fin rises slowly from the trunk-tail junction. It rises relatively straight to mid-tail, weakly curves convexly, and runs downwards in a shallow arch, straight posteriorly, to a narrowly rounded tip. Lower fin starts at body-tail junction, low and shallowly arched in contour. Maximum height of tail and tail fins is approximately in mid-section of tail. Upper fin higher than lower fin. Skin glands absent.

SIMILAR SPECIES
If the habitat is high enough to exclude *L. montanum*, tadpoles of *L. gunungense* are easily recognized by their size and color pattern. Papillation and keratodont pattern clearly separates them from all other tadpoles at the generic level; however, reliable diagnostic characters that separate *L. gunungense* from *L. montanum* have not yet been established. See comments under *L. montanum*.

The tadpoles of Leptobrachium gunungense *can grow large. They live in the cold, clear waters of rocky mountain streams at high elevation (> 1700 m a.s.l.). They are fast swimmers and will disappear quickly under rocks when disturbed. Tadpole morphology is similar to* L. montanum. *Adults of the two species can be distinguish by their call (Malkmus 1996).*

HABITAT & ECOLOGY
Highland primary forests, 1750–2200 m a.s.l reaching the mossy forest zone. The inhabited streams are rocky, clear, often steep and narrow. However, we have also seen them in high elevation blackwater streams. The tadpoles are not specifically adapted to live in strong current; rather, they are always found in quiet sections of a stream with low or only moderate current; bottom dwellers. Details of development have not been recorded, however, it is likely that development takes rather long in the cold waters of mountain streams. Mixed developmental stages are commonly found in the same stream.

REPRODUCTION
Males call from the ground at some distance from the streams from the slopes of the stream banks. The call has been described as a series (4–16) of relatively stifled, nasal notes, higher than in the similar and sometimes sympatric *L. montanum* (Malkmus et al. 2002). Males stimulate each other and choruses can form temporarily.

LITERATURE

Inger, R.F., Stuebing, R.B., Grafe, T.U., Dehling, J.M. (2017) A field guide to the frogs of Borneo. 3rd ed. Natural History Books, Kota Kinabalu. 228 pp.

Malkmus, R. (2002) Amphibians and Reptiles of Mount Kinabalu (North Borneo). Koeltz Scientific Books, Königstein. 424 pp.

Malkmus, R. (1996) *Leptobrachium gunungensis* sp. n. (Anura: Pelobatidae) vom Mount Kinabalu, Nord-Borneo. Mitteilungen aus dem Zoologischen Museum in Berlin 72: 297–301.

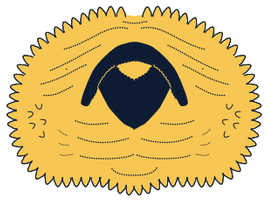
COLORATION
Variable with age, advanced tadpoles darker than early stages. Generally, above with some dark irregular markings on somewhat lighter gray or brown background. Distinct dark blotches are present dorsally at tail root; these are less distinct in advanced stages. Young individuals show a pair of whitish structures at the posterior head region. Scattered groups of iridophores can be found dorsally and some also ventrally. In close-up, a hatched pattern of the pigment cells is discernible. Venter translucent or opaque, depending on stage. Gut coil visible at early stages, less so in advanced stages. In life, abdominal skin with a bluish-silvery iridescence (absent in preserved specimens). Buccal and gular regions mostly translucent, with moderate pigmentation; gills and heart visibly, red. Body coloration extends onto muscular part of tail. There, the pattern transforms into a pattern of blotches and spots. Both, muscular and fin parts of tail bear blotches and spots. Myosepta, lateral line, and lateral tail vein visible.

Leptobrachium ingeri Matsui, Nishikawa, and Belabut, 2012

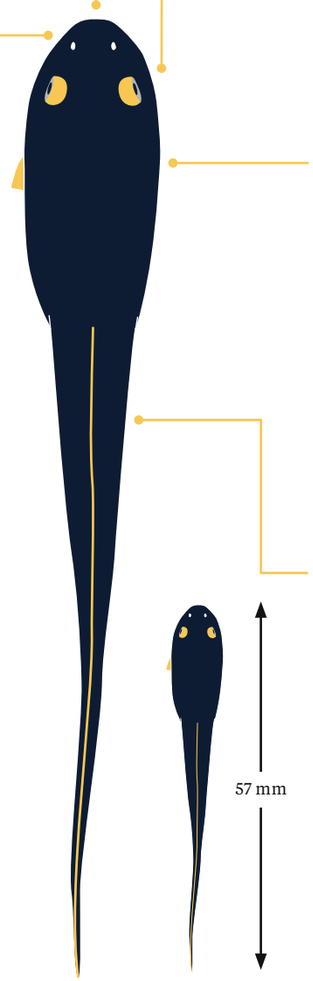
Inger's Large-eyed Litter Frog

SNOUT
Broadly rounded, blunt, and moderately long in dorsal view. In lateral view, head slopes smoothly. Snout blunt and rounded, giving the impression that it is slightly flexed ventrally.

ORAL DISC
Anteroventral to almost ventral in position, less than half of body in width. No distinct emargination between upper and lower lip.



Marginal papillae relatively large, slightly conical in shape form an almost complete row around the oral disc, with a small medial gap in the upper lip papillation. Lower lip bears few submarginal papillae laterally. Keratodont formula: LTRF 5(2–5)/4(1–3), additionally, there are 0–5 short keratodont rows in the submarginal area of the lower lip. First and most peripheral upper lip keratodont row particularly short. Beaks strong, well keratinized, black, and bear coarse moderately sharp serrations along their edges.



NOSTRILS & EYES
Eyes positioned dorsolaterally, low in profile, non-protruding. Iris and the scleral part of the eyeball black. Nostril distinct and relatively large, closer to snout than to eye. Nostril oriented laterally; mediodorsal nostril rim slightly projecting laterally.

BODY
Medium to large in size. In lateral view, head and trunk dorsoventrally depressed. In dorsal view, body is elongated, slightly wider than base of tail. Body widest at the level of the gill chambers. Spiracle sinistral, opening posterolaterally. Spiracular orifice positioned below mid-body in lateral view. Spiracle free from the body wall and forms a short tube. Lateral line organs visible as series of light dashes on the head, along the flanks, and along the side of the tail.

TAIL
Long, 65–67% of total length. Muscular part of tail strong, almost as high and wide as body. Upper fin rises in a soft convex arch from the trunk-tail junction. Lower fin similar to but lower than upper fin. In the posterior half, tail fins taper into a narrowly rounded tip. Maximum height of tail and tail fins approximately in the tail mid-section. Skin glands absent.

ECOMORPH
Lotic, exotrophic, benthic.

SIMILAR SPECIES
The tadpole of *Leptobrachium ingeri* can easily be distinguished from the known tadpoles of its congeners by its homogeneously black appearance, relatively slender body, and lower count of keratodont rows. In fact, this species can be confused superficially with tadpoles of *Pulchrana picturata* or *P. signata*, because of the similarities in body shape and black color. However, from the latter, *L. ingeri* can easily be distinguished by features of the oral disc and lack of skin glands (abundant in *P. picturata*). The tadpole of the closely related *L. kanowitense* has not been described yet; it seems likely, however, that *L. ingeri* and *L. kanowitense* tadpoles are similar.

The tadpoles of Leptobrachium ingeri *are relatively large. They are more slender and darker in color than larvae of the sympatric* L. abbotti. *The taxon has recently be separated from* L. nigrops.

HABITAT & ECOLOGY
Leptobrachium ingeri tadpoles are known from coastal Sarawak, where they live in clear rocky streams in hillside settings. Tadpoles are not adapted to strong current and prefer quiet or almost stagnant sections, shores, and bays associated with streams of low water velocity. In those sections of the stream, accumulations of leaves are common and the tadpoles seek shelter among the leaves. At night, they forage more active over the stream substrate than during the day.

REPRODUCTION
Males call at some distance from streams, slopes of banks, or the ground. Little else is known about the reproductive biology of this species.

COLORATION
Homogeneously black above. Abdominal skin with bluish-silvery iridescence (absent in preserved specimens). In close-ups, a finely hatched pattern of pigment cells is discernible particularly ventrally. Abdominal region semi-translucent to milky (gut coils visible) with a bluish hue. Gill region red and buccal region dark pigmented. Oral disc partly pigmented, particularly the papillae. Black color of the dorsal trunk continues onto the tail. Along the tail, the dark pigmentation fades somewhat towards the tip, the fin edges, and generally the lower parts of the tail. Myosepta and lateral tail veins inconspicuous. Inger (1985) and Inger et al. (2017) mentioned a golden stripe down the center of the back; a feature we could not confirm in our samples.

LITERATURE

Inger, R.F., (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

Inger, R.F., Stuebing, R.B., Grafe, T.U., Dehling, J.M. (2017) A field guide to the frogs of Borneo. 3rd ed. Natural History Books, Kota Kinabalu. 228 pp.

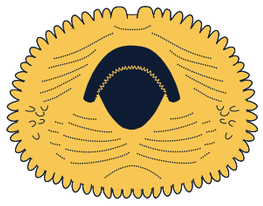
Leong, T.M., Chou, L.M. (1999) Larval diversity and development in the Singapore Anura (Amphibia). The Raffles Bulletin of Zoology 47: 81–137. [describing *Leptobrachium nigrops*]

Leptobrachium montanum Fischer, 1885

Mountain Large-eyed Litter Frog

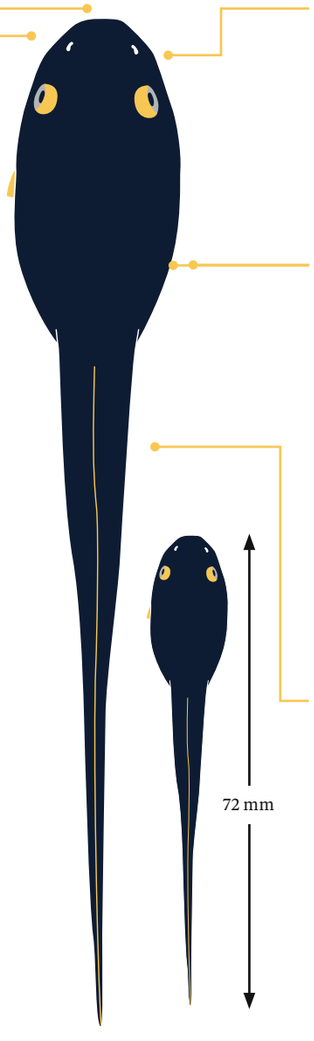
SNOUT
Broadly rounded, blunt, moderately long in dorsal view. The part anterior to the nostrils is slightly set off in dorsal view. In lateral view, head smoothly sloping into a rounded snout. Snout slightly bulging where the nostril is located.

ORAL DISC
Anteroventral to almost ventral, less than half of the body in width. Emarginations between upper and lower lip indistinct. Both lips bear relatively large, bluntly conical, marginal papillae in a single and nearly continuous row, with a small medial gap in the upper lip papillation. First anterior papilla next to that gap broadened.



Few scattered submarginal papillae present on the lateral lower lip. Keratodont formula: LTRF from 5(2–5)/5(1–4) to 7(2–7)/6(1–5), variably with additional short submarginal rows laterally. First upper lip row very short. Beaks are massive, well keratinized, black, and bear coarse serrations along their edges.

ECOMORPH
Lotic, exotrophic, benthic.



NOSTRILS & EYES
Eyes positioned dorsolaterally. Iris and scleral part of eyeball black with densely scattered silvery or golden iridophores. Nostril distinct, mostly unpigmented and closer to the snout than to the eye. Nostril oriented anterolaterally. Its dorsal rim bears a projection.

BODY
Large. In lateral view, head and trunk slightly dorsoventrally depressed. In dorsal view,body a long oval, clearly wider than the base of the tail. Body widest at the anterior trunk (following gill chambers). Spiracle sinistral, opening posterolaterally; its orifice is positioned at approximately mid-body in lateral view. Spiracular orifice with free rim in most specimens; a short tube is formed. Lateral line organs distinct. Broken lines of dash-like lateral line organs visible. Myosepta indistinct. Lateral tail vein visible.

TAIL
66–67% of total length. Muscular part strong, almost as high as the body in lateral view. Upper fin rises slowly from the trunk-tail junction. It is almost straight to mid-tail, changes directions and descends in a shallow arch to a narrowly rounded tip. Lower fin starts at the body-tail junction, continues low and shallowly arched in contour. Maximum height of the tail and tail fins approximately at middle section of tail. Upper skin higher than the lower fin. Skin glands absent.

SIMILAR SPECIES
Leptobrachium tadpoles (all species) are easily diagnosed to the genus by habitat (rocky stream), generally dark to black color, large size, and oral disc features; however, diagnostics for the tadpoles within the genus have not been established successfully. With respect to *L. abbotti*, Malkmus et al. (2002) mention the absence of network pigmentation pattern on the venter (body and tail) in *L. montanum*. We cannot confirm absence, but found the ventral hatched pigmentation pattern much less pronounced in *L. montanum* tadpoles. The number of submarginal papillae and additional lateral keratodont rows appears variable according to the samples for both species that we could examine. The anterior-most papilla was broader than the other papillae in some but not all *L. montanum*, and may also be variable or a feature restricted to some populations. *Leptobrachium nigrops* has all-black tadpoles. The larva of *L. kanowitense* remains undescribed.

Tadpoles of Leptobrachium montanum *grow large. They live in clear rocky mountain streams. They seek shelter under large rocks or in crevices. Despite their body mass, these tadpoles can swim fast, and will disappear quickly under rocks when disturbed.*

HABITAT & ECOLOGY
Highland primary and secondary forests at elevations between 900–1,685 m a.s.l. These tadpoles are not adapted to live in strong current and are always found in rocky bottoms or quiet sections of streams with low or moderate current. The tadpoles inhabit the bottom layers in the stream. Often, a mix of stages populates a stream, indicating that breeding activities extend over some time. The species probably takes a long time to metamorphose.

REPRODUCTION
Males sitting on the ground call at some distance from the slopes of stream banks. The call is a series of relatively deep „quack“ notes. The call frequency is deeper than in the morphologically similar *L. gunungense* (Malkmus et al. 2002). Males stimulate each other and their rising choruses in the colony may be followed by periods of complete silence.

COLORATION
Advanced larval stages are generally dark brown above, with dark markings on somewhat lighter background; young tadpole stages are less dark pigmented. Distinct dark blotches are positioned at the tail base. Young individuals bear a pair of whitish structures at the posterior end of the head region. Golden iridophores are arranged in patches and are present dorsally and laterally, some ventrally. In close-up, a hatched pattern of pigment cells becomes evident. Ventral side semi-translucent to opaque (depending on stage). Gut coil visible, at least faintly (more clearly at earlier stages). Abdominal skin has a bluish-silvery iridescence (absent in preserved specimens). Buccal and gular regions mostly translucent, with little pigmentation. Gills and heart indicated in red. Body coloration continues onto the muscular part of tail. Along the tail, the pattern breaks up into blotches and spots distally, on both, the muscular and fin parts of the tail. Myosepta, lateral line, and lateral tail vein visible.

LITERATURE

Inger, R. F., Stuebing, R. B., Grafe, U., Dehling, M. (2017) A Field Guide to the Frogs of Borneo. 3rd ed. Kota Kinabalu: Natural History Publications (Borneo). 228 pp.

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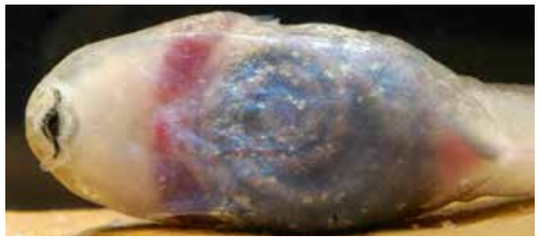
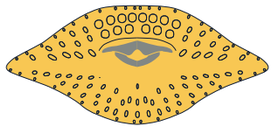


Megophrys dringi Inger, Stuebing, and Tan, 1995

Dring's Horned Frog

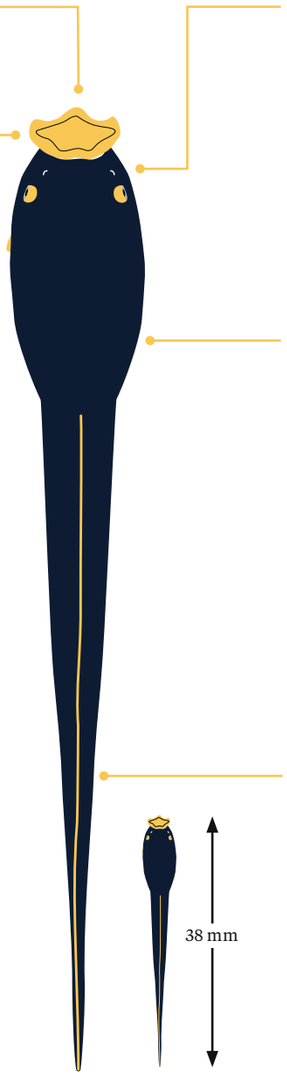
SNOUT
Smoothly narrowing toward the base of the oral funnel, both in lateral and dorsal views.

ORAL DISC
Terminal, umbelliform, and turned upward. Expanded disc as wide as body; rhomboid with lateral pointed corners. Ventral (anterior) lip sinuate and deeper than upper lip. In its resting position, the disc's edges are curled in and the two corners stand up like horns.



When feeding at the water surface, oral disc gets fully spread out. Marginal papillae absent. Numerous dark brown, round and elongate submarginal papillae (ridges) present, arranged in rows and oriented towards mouth. In the sector dorsal to the mouth, large papillae are present. Beaks thin, and not strongly keratinized (not black in color), difficult to see because deeply recessed in the oral funnel. Upper jaw bears a medial embayment.

ECOMORPH
Lotic, exotrophic, surface feeder.

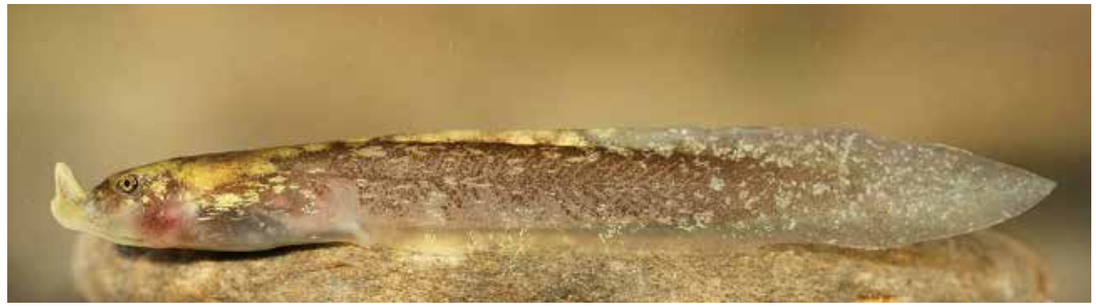


NOSTRILS & EYES
Eyes dorsolateral, widely spaced but without the cornea protruding beyond the body contour in dorsal view. Oval nostrils open laterally, closer to eye than to snout. Rim of nostril slightly raised from body wall and exhibits a small, short mid-dorsal projection. Sclera black with a gold-yellow stippling of iridocytes. Iris stippled dark gold-yellow to orange on black background.

BODY
Moderate in size, slender. In lateral view, head and trunk only slightly depressed dorsoventrally. In dorsal view, body long, twice as long as wide, and more parallel sided than oval, broader in head part than in trunk. Trunk wider than the base of the tail. Body widest at the gill region. Spiracle sinistral and extending into a short siphon with a free round spiracular orifice. Opening of spiracle situated below the horizontal mid-trunk line. Spiracular siphon directed posterodorsally. Lateral line organs indistinct.

TAIL
70% of total length (including funnel). Muscular part strong, virtually as high as body in lateral view. Dorsal fin inserts shortly posterior to trunk- tail junction. Lower fin connected to the trunk. Edges of fins almost straight. Posteriorly fins taper into a pointed tip. Fins are approximately equal in height. Skin glands absent.

SIMILAR SPECIES
Currently, *Megophrys dringi* and some *Pelobatrachus* tadpoles are known from small samples, representing limited ontogenetic stages. The intra-specific variation of these surface feeder larvae needs more research. In some areas, diagnosis at the species level may be difficult. Yet, some differences among the species have been noted (see comments on other species): *M. dringi* differs from known *Pelobatrachus* tadpoles by its golden pigmentation on head and dorsum and by possessing a V-shaped band anterior to the eyes. In addition, it differs from *P. nasutus* by showing reduced pigmentation ventrally and by absence of the radial iris pattern. *M. dringi* lacks distinct black spots at the ventral base of the oral disc (present in *P. baluensis*).



The tadpoles of Megophrys dringi *have only been reported from 1700 m a.s.l. at Gunung Mulu. Like its congeners, this tadpole bears the typical terminal mouth with an upward-directed oral disc.*

HABITAT & ECOLOGY
Tadpoles have been observed in small, shallow pools at the edges of a high elevation stream where the current was moderate and the bottom consisted of rocks or coarse gravel. These pools were connected by steep, narrow (50 to 150 cm width), fast–flowing cascades over bedrock. The tadpoles have been encountered near the banks of the stream, particularly among accumulations of leaf litter or among coarse gravel mixed with leaves and other organic debris.

REPRODUCTION
Details unknown.

LITERATURE

Oberhummer, E., Barten, C., Schweizer, M., Das, I., Haas, A., Hertwig, S.T. (2014) Description of the tadpoles of three rare species of megophryid frogs (Amphibia: Anura: Megophryidae) from Gunung Mulu, Sarawak, Malaysia. Zootaxa 3835: 59–79.

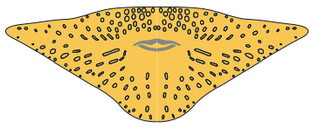
COLORATION
Generally brown above. Background color of the body and tail grayish (slightly lighter at the snout) with beige or brown pattern elements. Dorsal and lateral faces of the body and tail show a conspicuous pattern of intense dark brown and gold pigmentation. Dorsal face of the head and trunk covered by shiny gold pigmentation that reaches laterally to below the eye. Two diffuse bands of dark brown melanocytes present dorsolaterally. Between the anterior edges of eyes and the medial point of the upper lip a distinct, broadly V-shaped dark band is present. Lips are light beige. Lateral tips of the lips golden. Venter grayish semi-transparent with scattered melanocytes (possibly more densely pigmented towards end of larval life); in addition, scattered iridocytes particularly in the abdominal region. Tail dark pigmented with melanocytes. Myosepta somewhat accentuated by melanocyte density. Melanocyte pigmentation of the tail includes the tail fins, especially posteriorly (lower tail fin lightly pigmented anteriorly). Gold iridocyte blotches from the dorsum extend toward the upper tail fin, particularly along the anterior third of the upper fin that is marbled in golden beige and dark flecks. Lateral tail vein faintly visible.

Pelobatrachus baluensis (Boulenger, 1899)

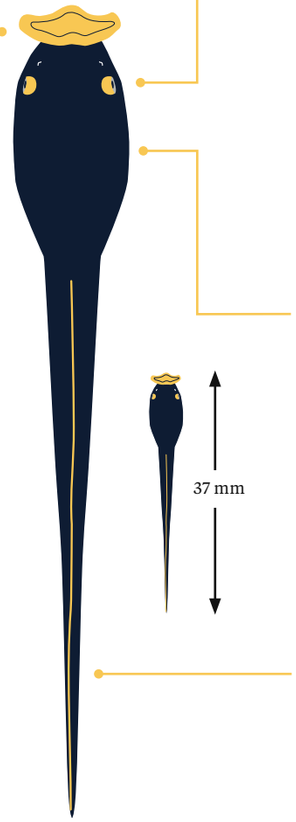
Kinabalu Horned Frog

SNOUT
Smoothly narrowing toward base of the oral funnel, both in lateral and dorsal view.

ORAL DISC
Terminal and turned upwards, umbelliform. Fully opened disc wider than body; pointed laterally. Lower (anterior) lip sinuate, deeper than upper lip. Oral disc forms a large rhomboid structure.



In its resting position, disc's edges are curled in and the two corners stand up like horns. When feeding at the water surface, oral disc spreads. Marginal papillae absent. Oral disc bears numerous round and elongate submarginal papillae (ridges); they are arranged in rows and oriented towards the mouth. Submarginal papillae particularly dense in the sector dorsal to the mouth. Beaks deeply positioned in oral disc, hidden. Beaks thin, weakly keratinized. Upper beak sinuate with medial embayment, lower is a simple arch.



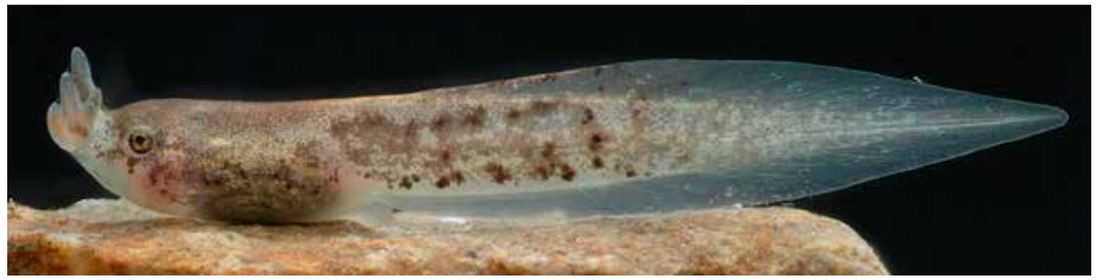
NOSTRILS & EYES
Eyes dorsolaterally, widely spaced but without the cornea protruding beyond the body contour in dorsal view. Iris densely scattered with gold to copper iridophores on black background. Pupil slightly rhomboid. Peripheral scleral part of eye bears scattered gold or silver iridophores on black background. Nostril small, positioned in a concavity of the snout; slightly closer to eye than to snout, oriented anterolaterally. Dorsal nostril rim bears a tiny triangular projection.

BODY
Moderately large, slender. In lateral view, head and trunk only slightly depressed dorsoventrally. In dorsal view, body long, twice as long as wide, and more parallel-sided than oval. Trunk clearly wider than base of the tail. Body widest at gill region. Spiracle sinistral; it opens posteriorly to posterolaterally, below the mid-body axis in lateral view. Spiracular orifice attached to body wall, no free tube. Lateral line organs indistinct.

TAIL
Long, 70% of total length (including funnel). Muscular part strong, almost as high as body in lateral view. Upper fin originates posterior to trunk-tail junction. It first rises in a flat convex arch and then gradually descends to the tail narrowly rounded tip. Lower fin also starts at the body-tail junction. It is only slightly convex in contour. Maximum height of the tail and tail fins approximately at 50% of tail length. Fins are approximately equal in height. Skin glands absent.

ECOMORPH
Lotic, exotrophic, surface feeder.

SIMILAR SPECIES
Tadpoles of *Pelobatrachus* (and *Megophrys dringi*) are easily recognized by the uniquely upward-directed oral disc. This feature is unique and renders misidentification with tadpoles from other Bornean genera unlikely. Within *Pelobatrachus*, however, reliable differential diagnoses of tadpoles have not been established. Auxiliary criteria such as geographic area and elevation may narrow the options. Features that have been described here and elsewhere need to be related to intra-specific variation before they can be used in inter-specific diagnoses. Color patterns in megophryids can change considerable with growth of the larvae, further complicating field identification. Malkmus et al. (2002) presented a description and drawing of the very similar, sympatric tadpoles of *P. kobayashii*; however, reliable diagnostics remain unclear and more research on how to distinguish the two sympatric tadpoles is necessary. See *M. dringi* and *P. nasutus* for further information.



Pelobatrachus baluensis *is a beautiful horned frog that inhabits undisturbed forests at higher altitudes. Its tadpoles live in small mountain brooks and streams. They possess elaborate upwardly-directed funnel mouths, a unique character in* Pelobatrachus *and* Megophrys *species.*

HABITAT & ECOLOGY
A montane species recorded from the pristine forests of Gunung Kinabalu and Crocker Range, at approximately 1200–2000 m a.s.l. Small streams in which tadpoles live have rather low flow velocity with nearly still sections. The tadpoles are shy and will quickly seek shelter when exposed. They are rather stationary and do not swim around much. They filter-feed among leaf litter, plant debris or close to rocks. When feeding, the tadpole assumes an upward-directed posture, with the oral disc spread at the water surface. The surface layer of water, which is loaded with small particles, is sucked into the mouth. Although they do not possess a specialized sucker, we observed tadpoles adhere to rocks with their gular region (ventral to the oral disc).

REPRODUCTION
Details of reproduction are mostly unknown. Malkmus et al. (2002) recorded that males particularly call between 5:30–6:00 and 18:00–19:00 hrs from the banks of small streams.

COLORATION
Dark brown above, consisting of diffuse mottling of darker areas on lighter brown background. Brass to golden iridophores are scattered over the dorsal surface and flanks of the head and trunk; dense groups of iridophores form a conspicuous accentuated light edge along the uprising dorsal fin. Dense groups of melanocytes are arranged as a row of diffuse flecks along the upper muscular part of the tail, at the base of the anterior part of the dorsal fin. Fins mottled as well and dark in appearance. Specimens become more pigmented (darker) with development. Venter is grayish semi-transparent (at least in early stages), sometimes with scattered iridophores in the abdominal region. Gut coil visible. Heart and gills are visible through the skin as red areas. Oral disc lightly pigmented, more so on the dorsal lip; sometimes it bears dark stripes dorsally and laterally. Submarginal papillae and ridges pigmented. Ventrally, a conspicuous black spot on each side at the transition from snout to oral disc is present. Oral disc often with orange tinge. Myosepta and lateral tail vein indistinct.

LITERATURE

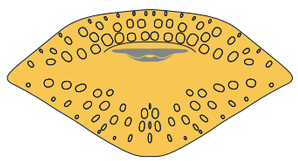
Malkmus, R. et. al. (2002) Amphibians & Reptiles of Mount Kinabalu (North Borneo). Koeltz Scientific Books, Königstein. 424 pp.

Pelobatrachus nasutus (Schlegel, 1858)

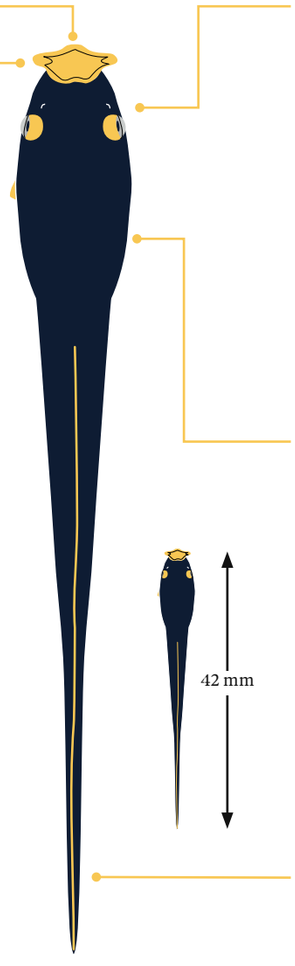
Borneo Horned Frog

SNOUT
Smoothly tapering toward the base of the oral funnel, both in lateral and dorsal views.

ORAL DISC
Terminal and directed upward, umbelliform. A large rhomboid structure, pointed laterally. Ventral (anterior) lip sinuate, deeper than upper lip. In resting tadpoles, disc edges are curled in and the two corners stand up like horns.



In order to feed at the water surface, the oral disc spreads out. Marginal papillae absent. Oral disc bears numerous round and elongate submarginal papillae (ridges). Submarginal papillae arranged in irregular centripetal rows towards the mouth. Larger round submarginal papillae present in the sector dorsal to the mouth. Beaks are thin, not strongly keratinized, not black in color. Upper jaw sheath with medial embayment, the lower jaw a simple U-arch.



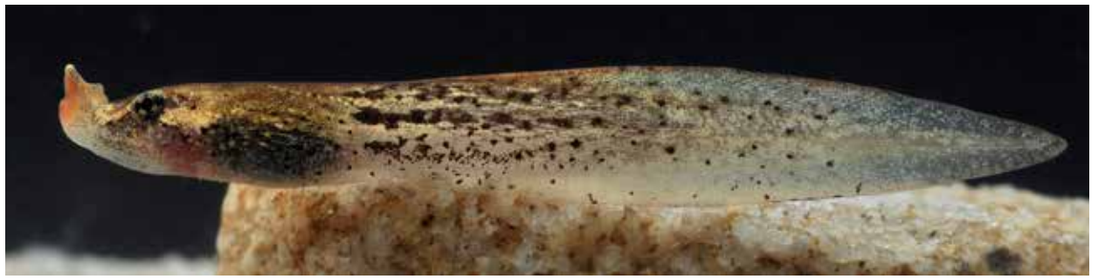
NOSTRILS & EYES
Eyes are positioned laterally, cornea slightly protruding beyond the body contour in dorsal view. Iris densely scattered with golden iridophores on black background in four sectors separated by black areas, forming a distinct four-radial pattern. Peripheral scleral part of the eye bears scattered gold or silver iridophores on black background. Nostril small, positioned in a concavity of the snout. Nostril slightly closer to eye than to snout, oriented anterolaterally. Dorsal nostril rim bears a tiny triangular projection.

BODY
Moderately large, but relatively slender tadpole. In lateral view, head and trunk moderately dorsoventrally depressed. Trunk approximately as high as wide. In dorsal view, body long, twice as long as wide, and more parallel sided than oval. Trunk wider than base of tail. Body is widest at gill region. Spiracle sinistral. Spiracular orifice opens posteriorly to posterolaterally, located below the midbody axis in lateral view. Spiracular orifice attached to the body wall; no free tube formed. Lateral line organs indistinct.

TAIL
Long, 70% of total length (including funnel). Muscular part of tail strong, as high as body in lateral view. Upper fin rises behind the trunk-tail junction; it gains height only slightly in the first third of tail and is only slightly convex in the middle part of the tail. Lower fin similar to the upper fin in shape, slightly lower. Both fins taper into a narrowly rounded tip. Skin glands absent.

ECOMORPH
Lotic, exotrophic, surface feeder.

SIMILAR SPECIES
The umbelliform oral disc is unique to *Pelobatrachus and Megophrys dringi*. Within the genus *Pelobatrachus*, reliable differential diagnoses of tadpoles have not been established, although preliminary differences can be noted (e.g., size and shape of the oral disc, submarginal papillae and ridges, iris pattern). Pending further corroboration, we observed only in *P. nasut*us 1) the conspicuous radial pattern on the iris, 2) the strongly pigmented ventral side, and 3) white flecks, and often striped pattern, not in *P. baluensis*; neither reported for *P. kobayashii* by Malkmus et al. (2002). *P. nasutus* specimens from the Malay Peninsula showed similar coloration (Wildenhues et al. 2012). Intra-specific variation appears to be high in *P. nasutus* and our assessment remains preliminary. See other species for more information. A short description of *P. kalimantanensis larvae* was given by Munir et al.; larval distinguishing features to *P. nasutus* still need to be worked out.



Tadpoles of Pelobatrachus nasutus *inhabit small to medium streams in the lowlands, hills, up to submontane limits of Borneo. The tadpoles can be difficult to find because they often live among leaf drift and seek shelter at the slightest disturbance. Their coloration provides perfect camouflage among leaves and sediment in the water.*

HABITAT & ECOLOGY
Recorded from 200–1300 m a.s.l. The larvae are specialized filter-feeders that exploit the organic matter on the water surface, such as plankton, pollen, plant debris, etc. Their upwardly directed, large oral disc is aligned with the water papillated surface during feeding and its structure helps channeling the water to the mouth. Due to their feeding mode, the tadpoles require quiet sections in a stream, areas with leaf drift, such as side channels, with little current.

REPRODUCTION
The reproductive biology is mainly known from captive breeding (Wildenhues et al. 2012). Male calls are a single “honk” or series of “honks” that can be heard from afar. Males call from near streams during dawn and dusk. Rainfall further stimulates calling activities. Amplexus of the small male with the much larger female is inguinal and eggs are attached to rocks, under logs or to plants in quiet areas of forest streams (Malkmus et al. 2002; Wildenhues et al. 2012).

COLORATION
Variable. Generally dark brown to black above with diffuse dark marbling and mottling on lighter brown background. There are areas of densely congregated iridophores forming white, cream or golden flecks or stripes, particularly at the body flanks, the edge of the (anterior) upper tail fin, and at lower part of tail base. Between these areas longitudinal concentrations of melanocytes are present, especially at the flank and/or base of the tail. These features of light and dark elements give many specimens a longitudinally striped appearance. The fins are mottled as well and dark in overall appearance. Specimens become more pigmented with growth and development. The ventral side is well-pigmented and mostly opaque (semi-transparent in early stages), sometimes with white or cream spots and stippling in the abdominal region. The gut coil is faintly visible or invisible; heart and gills are indistinct (more distinct in early stages). The oral disc is well-pigmented and ventrally without conspicuous black spots. Some individuals have an orange tinge to their oral disc. Myosepta and lateral tail vein are invisible.

LITERATURE

Malkmus, R. et. al. (2002) Amphibians & Reptiles of Mount Kinabalu (North Borneo). Koeltz Scientific Books, Königstein. 424 pp.

Wildenhues, M., Rauhaus, A., Karbe, D., van der Straeten, K., Hertwig, S.T., Ziegler, T. (2012) Husbandry, captive breeding, larval development and stages of the Malayan horned frog *Megophrys nasuta* (Schlegel, 1858) (Amphibia: Anura: Megophryidae). Amphibian and Reptile Conservation 5: 15–28.

Munir, M., Hamidy, A., Matsui, masafumi, Iskandar, D.T., Sidik, I. Shimada, T. (2019) A new species of *Megophrys* Kuhl & Van Hasselt (Amphibia: Megophryidae) from Borneo allied to *M. nasuta* (Schlegel, 1858). Zootaxa 4679: 1–24.

Huia cavitympanum (Boulenger, 1893)

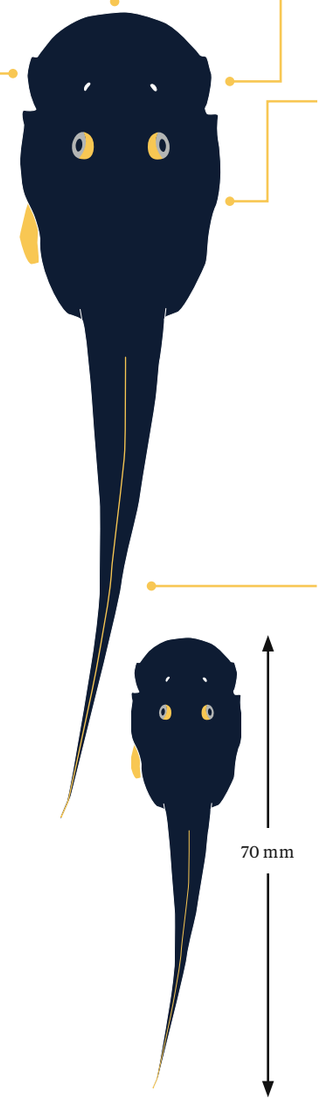
Hole-in-the-head Frog

SNOUT
In dorsal view, snout expanded, broadly rounded. In lateral view, snout elongated and sloping in a smooth slightly convex curve; streamlined

ORAL DISC
Ventral, wide, and expanded posteriorly by a large abdominal sucker. Abdominal sucker has a thick rim and covers most of the trunk ventrally. Oral disc and sucker cover approx. 85% of the body length.

Brown friction areas are discernible inside the abdominal sucker rim. Marginal papillation of oral disc reduced. Emarginations between upper and lower lip absent. LTRF: 12(4–9)/6(1) or 11(4–8)/6(1). Beaks well-keratinized, strong, undivided; edges bear blunt serrations. Upper beak broadly arched, inversely V-shaped, thin medially; lower jaw sheath V-shaped.

ECOMORPH
Lotic, rheophilous, suctorial, gastromyzophorous, exotrophic.



NOSTRILS & EYES
Eyes positioned dorsolaterally. Nostrils closer to eyes than to snout, oriented anterolaterally. Iris from densely stippled to solid golden on a black background. Pupil slightly rhomboidal.

BODY
Depressed and streamlined in lateral view, anteriorly with very long sloping snout profile. In dorsal view, the body contour is somewhat rectangular, long (length approximately 1.5 x width). Snout broadly rounded, set off from rest of body by a distinct notch in the body contour. Body widest at the level of the eyes in dorsal view. In lateral view, trunk as deep as the head; belly not bulging. Spiracle sinistral. Spiracular tube opens posteriorly and well below the longitudinal body axis in lateral view. Spiracular orifice free from the abdominal wall, at the end of a free spiracular tube.

TAIL
Approximately 62% of total length. Muscular part of tail strong and high, almost equal to body height. Dorsal fin starts posterior to the trunk-tail junction, gradually sloping up to an almost angular point in the dorsal fin, from where it descends with slightly concave contour towards the sharply pointed tip. Lower fin originates just before mid-tail and runs with slightly convex contour toward the tip. Maximum height of the tail is approximately at mid-point of tail. Skin glands absent.

SIMILAR SPECIES
Huia cavitympanum larvae can only be confused with tadpoles of *Meristogenys* species, but are easily distinguished from any *Meristogenys* by the combination of: spotted pattern, high number of upper lip keratodont rows, undivided upper jaw sheath. These characters, combined with the presence of an abdominal sucker, distinguish the species from any other Bornean tadpoles.

The tadpoles of Huia cavitympanum *are among to the most amazing tadpoles of Borneo, on account of their large size and strength. Their enormous oral and abdominal suckers can create an astonishing suction force.*

HABITAT & ECOLOGY
Tadpoles are well adapted for a life in cascades and rapids. We have seen them cling to rocks in a variety of water velocities, but most often in turbulent, very fast-moving current in clear mountain streams (250–1000 m a.s.l.). Among the Bornean species, tadpoles of *H. cavitympanum* appear to withstand the highest water velocities of all species.

REPRODUCTION
Males perch along steep river banks and produce high-frequency calls. A portion of the call is completely in the ultrasonic (inaudible) frequency range. The vocal repertoire is highly variable in frequency modulation and spectral composition. The audible part or the call is a high, sharp whistle.

COLORATION
Body and tail dark brown to gray, sometimes with an olive hue. Distinct cream to pale yellow spots are scattered over the snout, the cheek and the tail. The spotted pattern is a distinctive and unique character of this species. Dorsally and laterally, conspicuous iridocytes absent. The pigmentation of the trunk extends seamlessly onto the muscular part of the tail. Tail fins dark pigmented, except for a light zone at bases of dorsal and lower fins. Ventral body skin covered with silvery-golden iridocytes laterally, as is the rim of the abdominal sucker. Medial sucker lacks pigmentation except for scattered iridocytes in the anterior and medial part. Specialized epithelium (friction areas) along the inner side of the sucker rim visible as light brown areas. Gut coils, red heart, and red gills visible through the venter skin, but hidden behind opaque sucker tissue. Myosepta of the tail accentuated by melanocytes. Tail veins visible at proximal part of tail.

LITERATURE

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Arifin, U., Chan, K.O., Smart, U., Hertwig, S.T., Smith, E.N., Iskandar, D.T., Haas, A. (2021) Revisiting the phylogenetic predicament of the genus *Huia* (Amphibia: Ranidae) using molecular data and tadpole morphology. Zoological Journal of the Linnean Society 193: 673–699.

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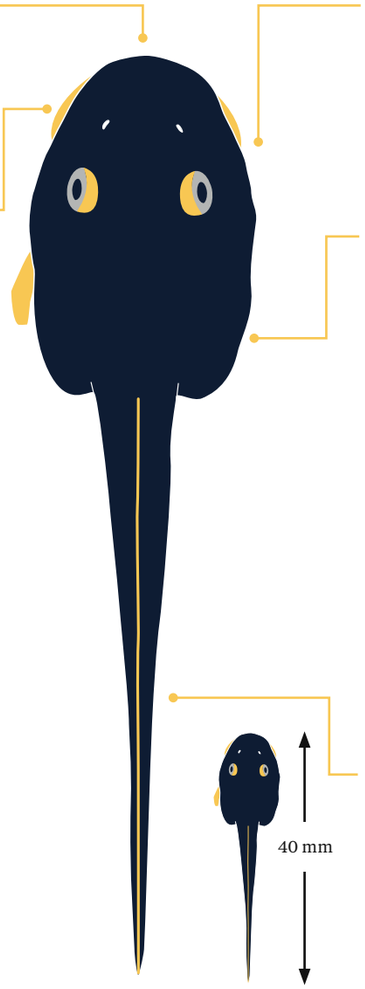
Meristogenys amoropalamus (Matsui, 1986)

Mountain Torrent Frog

SNOUT
Exapnded and broadly rounded in dorsal view. In lateral view, snout long, sloping in a smooth convex curve, with a slight bulge above the oral disc. Oral disc set off from the snout by a groove.

ORAL DISC
Ventral in position, wide, followed posteriorly by a large abdominal sucker. Abdominal sucker thick-rimmed and covering part of the trunk ventrally.

A horseshoe-shaped faintly brown friction area is discernible inside the abdominal sucker rim. Posterior rim at approx. 80% of body length in ventral view. Marginal papillation of oral disc present at the lateral upper lip and the lower lip. Marginal papillae short, rounded and indistinct. Several submarginal papillae at the lateral upper lip. LTRF 7(4–7)/6(1). Beaks strongly keratinized, deep black. Upper beak widely divided. Lower beak narrowly divided in early and undivided in late stages, V-shaped. Beaks bear coarse serrae (ribs).



ECOMORPH
Lotic, rheophilous, suctorial, gastromyzophorous, exotrophic.

NOSTRILS & EYES
Eyes dorsolateral. Nostrils closer to eyes than to snout, oriented anterolaterally. Iris black with a ring of silvery to golden iridocytes that forms around the pupil. Scattered iridocytes more peripherally. Sclera with silvery iridocyte stippling.

BODY
Depressed and streamlined in lateral view, anteriorly with a long sloping snout profile. In dorsal view, body contour between oval and rectangular, snout slightly set off. Trunk bulges posteriorly on both sides of tail root. Body widest at the level of the gill region. In lateral view, trunk just as deep as head, i.e., ventral side flat, belly not bulging. Spiracle sinistral; spiracular tube opening posterodorsally and well below the longitudinal body axis in lateral view. Spiracular orifice at the end of a free long spiracular tube. Small groups of skin glands located at the cheek, anterior to the spiracle, behind the eyes, and at posterior bulges of the trunk.

TAIL
64–65% of total length. Muscular part of the tail strong and high, slightly less than body height. Dorsal fin starts only slightly posterior to the trunk-tail junction, gradually slopes up straight to the highest point and changes abruptly to a downward slope, tip pointed. Lower fin originates at approximately one third of tail length. Lower fin lower than upper fin. Maximum height of tail approximately at the mid-point of tail length. Both upper and lower fins bear lines of skin glands.

SIMILAR SPECIES
Meristogenys amoropalamus tadpoles can be confused with other tadpoles of other *Meristogenys* species, especially *M. dyscritus*; see characters there. Keratodont formula, skin glands, jaws, and skin protuberances need to be examined carefully when identifying *Meristogenys* tadpoles. *Ansonia* tadpoles can occur in the same streams, in fact, sometimes populate the same rocks with *Meristogeny*s tadpoles, but do not possess an abdominal sucker. Tadpoles of *Huia cavitympanum* (abdominal sucker present) are easily distinguished by their undivided upper and lower jaws and spotted pattern.

The tadpoles of Meristogenys amoropalamus *live in clear, cool mountain streams and possess large abdominal suckers (gastromyzophorous) to withstand the current.*

HABITAT & ECOLOGY
Meristogenys amoropalamus tadpoles are inhabitants of clear high elevation cascading streams (>1300 m a.s.l.). Their abdominal sucker allows them to hold on to rocks in the current as they graze over the rock surface. Tadpoles forage on exposed rock surfaces at night, whereas during the day, they conceal themselves under rocks. Particularly attractive rock faces may attract many tadpoles and schools may form. Habitat and microhabitat are often shared with *Ansonia* tadpoles.

REPRODUCTION
Reproductive behavior is unknown. Eggs of 2.2 mm diameter and 400–600 ovarian eggs per female have been reported.

COLORATION
Body and tail generally grayish to dark brown, the trunk being darker dorsally and laterally than the head. Diffusely dark areas have been recorded at the nostrils and between the eyes. At the lower flanks and the lateral abdominal skin are fields of scattered iridocytes. More medially, the abdomen is black or semi-transparent; gut coils not or faintly visible. Oral disc and abdominal sucker are unpigmented; gills and heart are not visible. Specialized epithelium (friction areas) along the inner side of the sucker rim are present as light brown areas. Pigmentation of the trunk extends seamlessly onto muscular part of tail, although lighter in appearance. Tail fins stippled with melanocytes, with lighter zone at bases of dorsal and lower fins, respectively. In advanced stages, melanocytes along blood vessels accentuate the myosepta and can create a reticulate pattern on the tail fins.

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Shimada, T., Matsui, M. (2019) Re-examination of larval assignment of *Meristogenys poecilus* in Sarawak, Borneo, with a diagnostic table of *Meristogenys* larvae. Current Herpetology 38: 23–31.

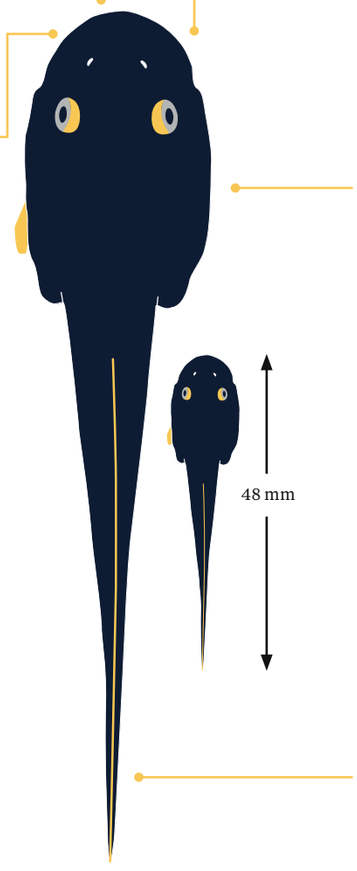
Meristogenys dyscritus Shimada, Matsui, Yambun, and Sudin, 2011

Liwagu Torrent Frog

SNOUT
Expanded, broadly rounded in dorsal view. In lateral view, snout long, sloping in a smooth convex curve, with a slight bulge above the oral disc. Oral disc set off from snout by a groove.

ORAL DISC
Ventral, wide, followed posteriorly by a large abdominal sucker. Abdominal sucker thick-rimmed and covers parts of trunk ventrally.

Faintly brown friction area discernible inside the rim, U-shaped. Posterior rim of abdominal sucker is at approximately 80% of body length in ventral view. Marginal papillation of oral disc present at the lower lip and the lateral upper lip, respectively. Marginal papillae short, rounded and indistinct. Several submarginal papillae are located at the lateral parts of the upper lip. LTRF 6(4–6)/6(1) to 6(4–6)/8(1). Beaks strongly keratinized, deep black. Upper beak widely divided. Lower beak divided. The beaks bear coarse serrae (ribs).



ECOMORPH
Lotic, rheophilous, suctorial, gastromyzophorous, exotrophic.

NOSTRILS & EYES
Eyes dorsolateral. Nostrils closer to eyes than to snout, and oriented anterolaterally. Iris with black background color, on which a thin ring of golden iridocytes forms around the pupil; peripherally of that ring the iris is dusted with golden iridocytes. Scleral iridocyte stippling is silvery.

BODY
Depressed and streamlined in lateral view, anteriorly with long sloping snout profile. In dorsal view, body contour long oval to rectangular, snout slightly set off, trunk bulges posteriorly on both sides of the tail root. Body widest at the level of the gill region. In lateral view, trunk just as deep as the head, i.e., ventral side flat, belly not bulging. Spiracle sinistral. Spiracular tube opens posteriorly and is well below the longitudinal body axis in lateral view. Spiracular orifice at the end of a free, relatively long spiracular tube. Small groups of skin glands at the cheek, anterior to the spiracle, behind the eyes, and at the posterior bulges of the trunk (see also tail). Lateral line organs indistinct. Dense pointed skin protuberances on snout (in at least advanced larvae).

TAIL
Muscular part strong and high, slightly less than body. Dorsal fin starts from posterior to trunk-tail junction (approx. at 10% tail length), gradually sloping up straight to highest point and changing immediately to a downward slope. Tip pointed. Lower fin originates at approximately one third of tail length; it is lower than upper fin. Maximum height approximately at the mid-point of tail. Skin glands on lower fin only.

SIMILAR SPECIES
Huia and *Meristogenys* are the only Bornean taxa with gastromyzophorous tadpoles. *Meristogenys dyscritus* tadpoles are distinguished from *M. amoropalamus* larvae by possessing six upper lip keratodont rows (seven in *M. amoropalamus*). Glands at the tail are absent in the upper fin in *M. dyscritus*. The dorsal tail fin is originating more posteriorly than in *M. amoropalamus*. Keratodont formula, skin glands, jaws, and skin protuberances need to be examined carefully when identifying any *Meristogenys* tadpole. Tadpoles of *Huia cavitympanum* are easily distinguished by their undivided jaws and spotted color pattern. *Ansonia* tadpoles do not possess an abdominal sucker.

The tadpoles of Meristogenys dyscritus *live in clear, cool mountain streams and possess a large abdominal sucker (gastromyzophorous) to cling to rocks in cascades.*

HABITAT & ECOLOGY
Meristogenys dyscritus tadpoles have been reported from Gunung Kinabalu Park and Crocker Range Park, where they inhabit clear cascading streams. Their abdominal sucker allows them to hold on to rocks in the current. As all other tadpoles of *Meristogenys*, these larvae are grazers that feed on organic overgrowth (algae, small animals, bacteria) on the rock surfaces. The habitat and microhabitat are often shared with *Ansonia* tadpoles.

REPRODUCTION
Males perch on low vegetation along the river bank. The male call is an unpulsed, sharp, whistle, with several minutes of pause between calls. The dominating frequencies are high, between 6.000–10.000 Hz. 700–1.500 eggs have been counted in gravid females.

COLORATION
Body and tail generally grayish to brown, the trunk being darker dorsally and laterally than the head. Diffusely dark areas have been recorded at the nostrils and between the eyes. Abdomen covered by a sheath of white-silvery iridocytes concealing the gut. Oral disc and abdominal sucker are unpigmented, yet gills and heart are not visible. Pigmentation of the trunk extends seamlessly onto the muscular part of the tail, although lighter in appearance. Tail fins stippled with melanocytes, except for a light zone at the bases of dorsal and lower fins, respectively. In advanced stages, melanocytes along the blood vessels accentuate the myosepta and can create a somewhat reticulate pattern on the tail fins.

LITERATURE

Shimada, T., Matsui, M., Yambun, P., Sudin, A. (2011). A survey of morphological variation in adult *Meristogenys amoropalamus* (Amphibia, Anura, Ranidae), with a description of a new species, Zootaxa, 2905: 33–56.

Shimada, T., Matsui, M. (2019) Re-examination of larval assignment of *Meristogenys poecilus* in Sarawak, Borneo, with a diagnostic table of *Meristogenys* larvae. Current Herpetology 38: 23–31.

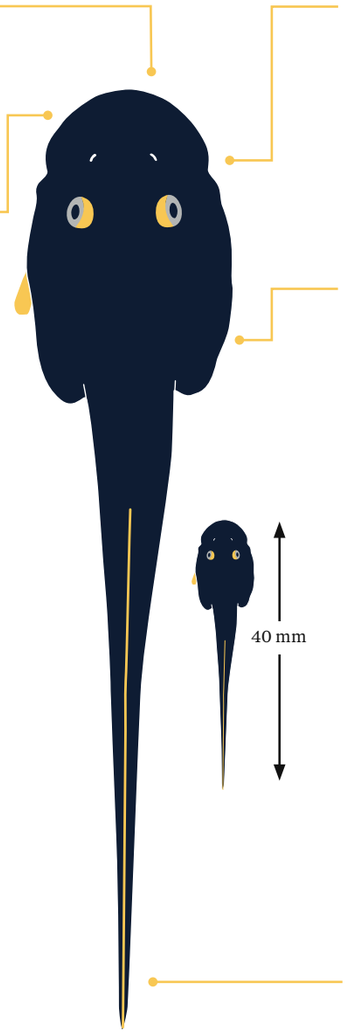
Meristogenys jerboa (Günther, 1972)

Western Torrent Frog

SNOUT
Expanded and broadly rounded in dorsal view. In lateral view, snout long, sloping in a smooth convex curve, with a bulge above the oral disc. Oral disc set off from the snout by a groove.

ORAL DISC
Ventral, wide, followed posteriorly by a large abdominal sucker. Abdominal sucker thick-rimmed. In ventral view, snout to posterior rim of the abdominal sucker covers approximately 70–75% of body length.

Faintly brown friction areas discernible inside the rim. Marginal papillation of oral disc present along the lower and lateral upper lips, respectively. Marginal papillae short, rounded and indistinct. A dense irregular row of submarginal papillae located at lateral upper lip. LTRF 6(4–6)/6(1) to 6(4–6)/7(1). Beaks strongly keratinized, deep black. Upper and lower beaks widely divided, both bearing several coarse serrae (ribs).



ECOMORPH
Lotic, rheophilous, suctorial, gastromyzophorous, exotrophic.

SIMILAR SPECIES
Meristogenys jerboa tadpoles can occur in sympatry with *M. penrissenensis*. *M. jerboa* tadpoles are distinguished from *M. penrissenensis* by possessing six (three divided) upper lip keratodont rows (seven, four divided, in *M. penrissenensis*). *Ansonia* tadpoles can live in the same habitat with *M. jerboa* tadpoles but are easily distinguishable from the latter by the lack of a abdominal sucker.

NOSTRILS & EYES
Eyes dorsolateral. Nostril oval, closer to eyes than to snout, and oriented anterolaterally. Iris with a black background color, on which a thin ring of golden iridocytes forms around the pupil; peripherally of that ring, iris dusted with golden iridocytes. Sclera stippled with silvery iridocyte.

BODY
Depressed and streamlined in lateral view, anteriorly with a long sloping snout profile. In dorsal view, body contour oval to rectangular, snout set off by a notch. Trunk bulges posteriorly on both sides of tail root. Body widest at the level of gill region. In lateral view, trunk just as deep as head, i.e., ventral side flat, belly not bulging. Spiracle sinistral, spiracular tube opening posteriorly; spiracle well below the longitudinal body axis in lateral view. Spiracular orifice at the end of a free, relatively long spiracular tube. Small groups of skin glands located at the cheek, anterior to the spiracle, behind the eyes, and at the posterior bulges of the trunk (also see tail); posterior, ventral abdominal glands are absent. Glands may be difficult to see. Lateral line organs are indistinct. In advanced larvae, dorsal head and trunk bear dense pointed protuberances.

TAIL
Long, 63–66% of total length. Muscular part strong and high, almost as high as body in lateral view. Dorsal fin starts only well posterior at 10–20% of tail length, gradually arching up to the highest point,softly changing direction and sloping down in a straight line to the pointed tip. Lower fin originates at approximately one third of tail length and much lower than upper fin. Maximum height of the tail slightly before the mid-point of tail length. Skin glands present on lower fin only.

The mid-sized tadpoles of Meristogenys jerboa *live in clear streams in lowland hills of Western Sarawak. As all other* Meristogenys, M. jerboa *has a conspicuous large abdominal sucker (gastromyzophorous), which is used as an adhesive organ to cling to rocks.*

HABITAT & ECOLOGY
Clear hillside streams of western Sarawak. Their abdominal sucker allows them to hold on to rocks in the current. *Meristogenys jerboa* tadpoles are grazers that feed on organic overgrowth (algae, small animals, bacteria) on rock surfaces. Although they prefer to feed right in the current of overflown rocks at night, *M. jerboa* seems to prefer moderate flow velocities and not very strong and turbulent sections. Sometimes, tadpoles form groups of up to 30 to feed on the same rock face. Often rock overgrowth also attracts *Ansonia minuta* tadpoles, that feed side by side with *M. jerboa* in western Sarawak habitats.

REPRODUCTION
Males perch on low vegetation, roots or rocks along the steep river bank, or on boulders. The male call is an unpulsed, sharp, high-pitched whistle, with several minutes of pause between calls.

COLORATION
General coloration of upper and lateral sides of the body and tail is a light brown or ocher background with dark dense dotting or marbling. Dotting becomes more blotchy and shows greater contrast on the tail. Additional iridocyte clusters on body and tail contribute to the pattern. Abdomen covered by a sheath of white-silvery iridocytes concealing the gut. Oral disc and abdominal sucker unpigmented. Gills and heart invisible. Tail fins may bear larger dots. In advanced stages, melanocytes along the blood vessels accentuate the myosepta and can create a reticulate pattern on the tail fins.

LITERATURE
Shimada, T., Matsui, M., Nishikawa, K., Eto, K. (2015). A new species of *Meristogenys* (Anura: Ranidae) from Sarawak, Borneo. Zoological Science, 32: 474–484.

Meristogenys kinabaluensis (Inger, 1966)

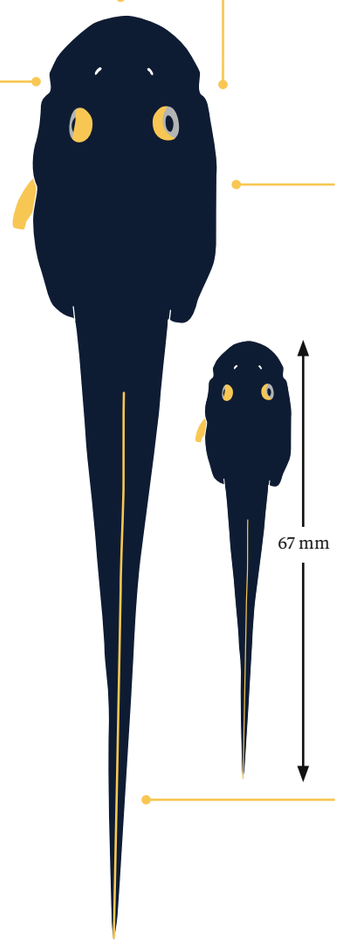
Kinabalu Torrent Frog

SNOUT
Expanded, broadly rounded in dorsal view. In lateral view,snout long and sloping downward in a smooth convex curve. Oral disc set off from the snout by a groove.

ORAL DISC
Ventral and wide; large abdominal sucker present posterior to the oral disc. Abdominal sucker thick-rimmed; posterior rim at approximately 75% of body length.

A horseshoe-shaped friction area discernible inside the sucker rim. Marginal papillation present at lower lip and lateral upper lip. Marginal papillae short, rounded, indistinct. Dense irregular row of submarginal papillae located at the lateral upper lip. LTRF 6(4–6)/6(1). Beaks strongly keratinized, deep black. Upper beak widely divided, lower beak undivided. Upper and lower beaks bear coarse serrae (ribs).

ECOMORPH
Lotic, rheophilous, suctorial, gastromyzophorous, exotrophic.



NOSTRILS & EYES
Eyes dorsolateral. Nostril closer to eye than to snout, and oriented anterolaterally. Iris with black background color, on which a thin ring of golden iridocytes forms around the pupil; peripherally of that ring iris dusted with golden iridocytes. Scleral part of eye stippled with silvery iridocytes.

BODY
Depressed and streamlined in lateral view, anteriorly with a long sloping snout profile. In dorsal view, body contour oval to rectangular. Snout set off by a notch. Posterior trunk end extended as bulges on both sides of tail root. Body widest at the level of gills. Venter flat. Spiracle sinistral. Spiracular tube opens posteriorly and is well below the longitudinal body axis in lateral view. Spiracular orifice at the end of a free, relatively long spiracular tube. Small groups of skin glands at cheek, anterior to spiracle, behind the eyes, and at the posterior bulges of trunk (close to limb buds) (see tail). Glands may be difficult to see and subject to variation. Lateral line organs indistinct. Head and trunk smooth, pointed skin protuberances absent.

TAIL
Long and strongly built, approximately 65–67% of total length. Muscular part strong and high, almost as high as body in lateral view. Dorsal fin starts slightly posterior to trunk-tail junction. It rises up relatively straight to the highest point and softly changing direction and sloping down in a straight or slightly concave line to the pointed tip. Lower fin originates posterior to the trunk-tail junction (10–15% of tail length); it remains low in the proximal third of the tail. Lower fin lower than the upper fin. Maximum height at the mid-point of tail length. Skin glands absent in fins.

SIMILAR SPECIES
Meristogenys kinabaluensis is the only *Meristogenys* known with six upper lip keratodont rows and undivided lower beak, furthermore, it is larger than most other *Meristogenys*. Presence of skin glands at the posterior end of the venter have been reported as diagnostic feature, but were absent in our samples from Gunung Kinabalu.

The tadpoles of Meristogenys kinabaluensis *grow large. They live in clear highland streams of north-eastern Sarawak and eastern Sabah. These tadpole possesses a large abdominal sucker (gastromyzophorous), which is used as an adhesive organ to cling to rocks.*

HABITAT & ECOLOGY
Tadpoles require pristine highland streams, with clear, cool water. By virtue of their abdominal sucker, they can withstand the current even in cascades or waterfalls. *Meristogenys kinabaluensis* tadpoles are grazers that feed on organic overgrowth (algae, small animals, bacteria) on rock surfaces. They are most likely seen at night grazing on rock faces in the current. Grazing congregation of tadpoles may form. Often, *Ansonia* tadpoles can be seen together with *Meristogenys* tadpoles.

REPRODUCTION
Adults perch on logs and boulders in streams, presumably these microhabitats are also where amplexus takes place.

COLORATION
General coloration of upper and lateral sides of body and tail ocher, even yellowish on the tail, with darker mottling. The mottling is more blotchy on tail. Dorsally, the flanks are darker than the head due to deep pigmentation of the abdomen. Abdomen ventrally covered by a sheath of white-silvery iridocytes concealing the gut. Oral disc and abdominal sucker are unpigmented. Gills and heart are not visible. Tail fins blotched. In advanced stages, melanocytes along the blood vessels accentuate the myosepta and can create a somewhat reticulate pattern on the tail fins.

LITERATURE
Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

Shimada, T., Matsui, M. (2019) Re-examination of larval assignment of *Meristogenys poecilus* in Sarawak, Borneo, with a diagnostic table of *Meristogenys* larvae. Current Herpetology 38: 23–31.

Meristogenys maryatiae Matsui, Shimada, and Sudin, 2010

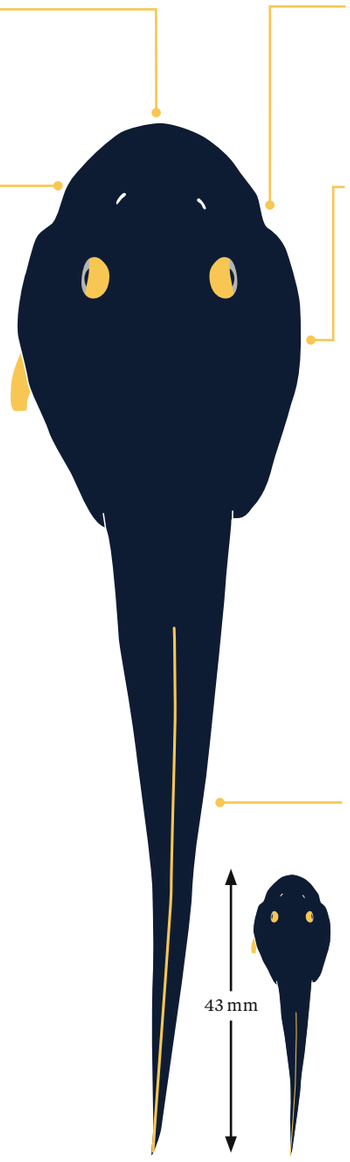
Maryati's Torrent Frog

SNOUT
Broadly rounded in dorsal view. In lateral view, snout long, sloping downward in a smooth convex curve. Oral disc set off from the snout by a groove.

ORAL DISC
Ventral and wide. Very large abdominal sucker present posterior to oral disc. Abdominal sucker wide and thick-rimmed. Its posterior rim at approximately 85-90% of body length in ventral view.

A horseshoe-shaped friction area lies inside the sucker rim, additional round friction areas laterally. Marginal papillation of the oral disc present at lower lip and lateral upper lip. Marginal papillae short, rounded and indistinct. A row of submarginal papillae located at the lateral upper lip. LTRF 7(4–7)/6(1). Beaks strongly keratinized, deep black. Upper beak widely divided; lower beak narrowly divided, V-shaped. Upper and lower beaks bear coarse serrae (ribs).

ECOMORPH
Lotic, rheophilous, suctorial, gastromyzophorous, exotrophic.



NOSTRILS & EYES
Eyes dorsolateral. Nostril closer to eyes than to snout, oriented anterolaterally. Black iris densely stippled with golden iridocytes that fuse to a thin, solid, golden ring around the pupil.

BODY
Depressed and streamlined in lateral view, anteriorly with a long sloping snout profile. In dorsal view, body contour broadly oval. Snout set off by a notch in the body contour. Posterior trunk end extended as moderate bulges on both sides of the tail root. Body widest at the level of gill region. Ventral side flat, belly not bulging. Spiracle is sinistral. Spiracular tube opens posterodorsally and well below longitudinal body axis in lateral view. Spiracular orifice at the end of a free, relatively long spiracular tube. Small groups of skin glands are located at cheek, anterior to spiracle, behind eyes, and at posterolateral bulge of trunk; no glands at posterior end of venter (also see description of tail). Lateral line organs are indistinct. Head, dorsum and flanks with small and short skin projections above.

TAIL
Approximately 64% of total length. Muscular part strong and high, almost as high as body in lateral view. Dorsal fin starts posterior to the trunk-tail junction. It arches up to the highest point, and gently slopes down in a straight or slightly convex line to the pointed tip. Lower fin originates at approximately half of tail length and remains lower than upper fin. Maximum height of tail at mid-point of tail length. If present, skin glands located in lower fin.

SIMILAR SPECIES
Abdominal suckers are exclusive to *Huia* and *Meristogenys* Tadpoles of *Meristogenys* differ from *Huia* in the divided upper beak. Within *Meristogenys,* close examination of all features is necessary (lower beak, skin glands, tail fins, LTRF). *M. maryatiae* has a narrowly divided lower beak and the most expansive abdominal sucker among *Meristogenys* tadpoles.

Tadpoles of Meristogenys maryatiae *are mid-sized larvae. They live in hilly terrain (155–1000 m a.s.l.) in clear rocky streams. They possess a large abdominal sucker, which is used to adhere to rocks in the current. In* M. maryatiae*, the abdominal sucker is impressively large.*

HABITAT & ECOLOGY
Meristogenys tadpoles require streams with clear water, because only in clear streams, rocks develop an organic overgrowth composed by small organisms, such as algae. *Meristogenys* tadpoles feed on this overgrowth. Although there are no published observations, it is likely that these larvae are mostly active (grazing) at night as has been observed for other *Meristogenys* tadpoles.

REPRODUCTION
Details unknown.

COLORATION
Background color of body and tail yellowish to brown; combined with darker brown mottling over body and tail muscles. Clusters of iridocytes along the dorsal line of the tail muscle and the margin of the dorsal fin add some color variation. Oral disc and abdominal sucker mostly unpigmented, except for their dorsal faces and rims. Gills and heart not visible. Tail fins blotched. In advanced stages, melanocytes along the blood vessels accentuate the proximal myosepta and produce a reticulate pattern on the tail fins. Lateral part of abdomen covered by dense white-silvery iridocytes; the medial part of the abdomen may be devoid of iridocytes, semi-translucent.

LITERATURE
Matsui, M., Shimada, T., Sudin, A. (2010) A new species of *Meristogenys* (Amphibia, Anura, Ranidae) from Sabah, Borneo. Zoological Science, 27: 61–66.

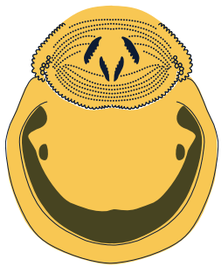
Shimada, T., Matsui, M. (2019) Re-examination of larval assignment of *Meristogenys poecilus* in Sarawak, Borneo, with a diagnostic table of *Meristogenys* larvae. Current Herpetology 38: 23–31.

Meristogenys orphnocnemis (Matsui, 1986)

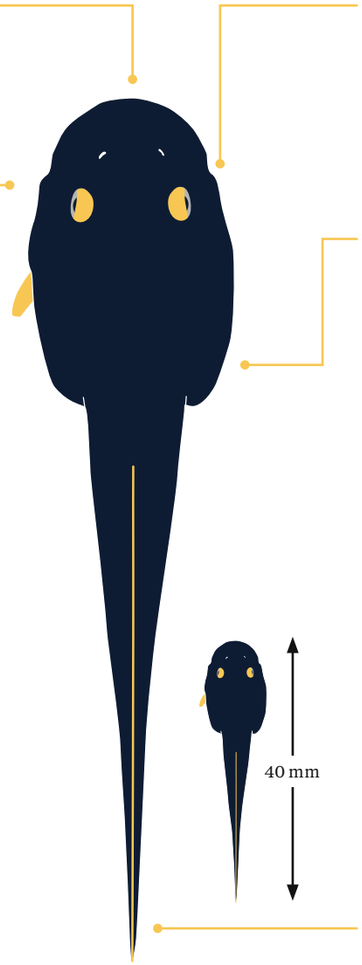
Northern Torrent Frog

SNOUT
Broadly rounded in dorsal view. In lateral view, snout long; contour curves downward in a smooth convex line. Oral disc set off from the snout by a groove.

ORAL DISC
Ventral and wide. Thick-rimmed large abdominal sucker posteriorly adjacent to oral disc. Posterior rim of sucker at approximately 85% of body length in ventral view.



Broad horseshoe-shaped friction area set inside the sucker rim; additional small round frictions areas laterally at the sucker. Marginal papillation of oral disc present at lower and lateral upper lip. Marginal papillae short, rounded, indistinct. Row of submarginal papillae located at the lateral upper lip. LTRF 6(4–6)/6(1). Beaks strongly keratinized, deep black. Upper beak widely divided; lower beak divided, V-shaped. Upper and lower beaks bear coarse serrae (ribs).



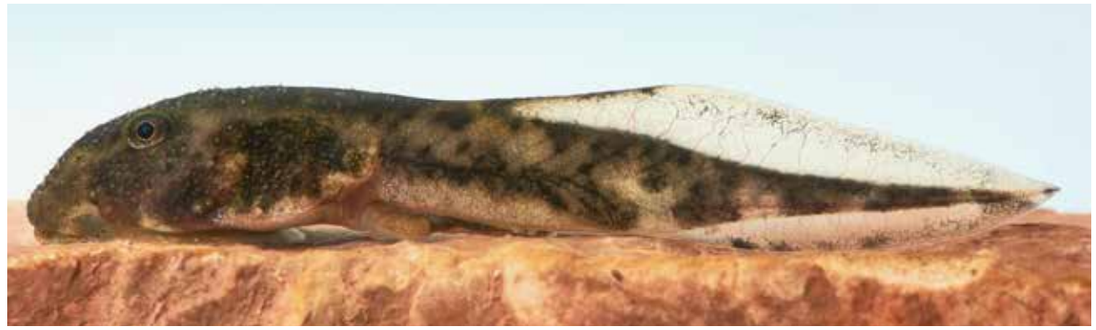
ECOMORPH
Lotic, rheophilous, suctorial, gastromyzophorous, exotrophic.

SIMILAR SPECIES
Only tadpoles of *Huia* and *Meristogenys* possess abdominal suckers and are easily recognized by this feature. *Meristogenys* differs from *Huia* in the divided upper beak. Within *Meristogenys*, several species with fused lower beaks can be excluded (divided in *M. orphnocnemis*). Examination of all features (size, skin glands, tail fins, LTRF, skin protuberances) will be necessary to distinguish species with divided lower beaks. The taxonomy of larval *Meristogenys* is poorly-known. Reliable identification may not be possible in all cases.

NOSTRILS & EYES
Eyes positioned dorsolaterally. Nostrils are closer to eyes than to snout, and oriented anterolaterally. Iris bears a thin ring of golden iridocytes around the pupil; more peripherally iris densely stippled with golden iridocytes on black background.

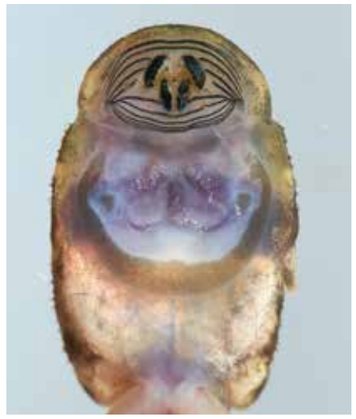
BODY
Depressed and streamlined in lateral view. In dorsal view, body contour is more rectangular than oval. Snout set off by a notch from rest of the head. Posterior trunk end bulges posteriorly on both sides of the tail root. Body widest at the level of eyes or gills. Body flat ventrally. Spiracle sinistral. Spiracular tube opens posteriorly and well below the longitudinal body axis in lateral view, close to the substrate. Spiracular orifice at the end of a free, relatively long spiracular tube. Small groups of skin glands located at the cheek, anterior to spiracle, behind the eyes, and at posterolateral bulge of the trunk; glands at posterior end of venter absent (see also tail). Skin glands may be difficult to see in living specimens, more easily noted in preserved larvae. Lateral line organs indistinct. Head, dorsum and flanks above with many conspicuous, pointed skin projections.

TAIL
Makes up 63–66% of total length. Muscular part strong and high, virtually as high as body in lateral view. Dorsal fin starts posterior to trunk-tail junction (20–25% tail length); rises up in a straight line to highest point, and slopes down in a straight line to tip. Tip triangular, pointed. Lower fin originates at approximately 45% of tail length; lower than the upper fin and slightly convex. Maximum height of the tail at the midpoint of tail. Few skin glands in the lower fin, or absent.



The tadpoles of Meristogenys orphnocnemis *are mid-sized. The species is common in lowland to hillside forests of Sabah. Like some other* Meristogenys*, this tadpoles possesses skin projection on the body.*

HABITAT & ECOLOGY
The species has been described from Bundu Tuhan, at the lower elevations of Gunung Kinabalu, Sabah, at 990 m a.s.l., but is also found in even lower localities. Tadpoles can be found in clear, medium to large, rocky hill streams. They feed on organic rock overgrowth (algae, protists). We observed these larvae mostly at night, grazing over rock surfaces.



REPRODUCTION
Males call from low vegetation, roots or rocks along the stream; females are mostly on the ground. Males call at irregular intervals, and sometimes calls are several minutes apart. Up to 800 eggs are attached onto a rock surface in the current. Hatching takes 24 days. Freshly hatched tadpoles tend to stay together in a group for about four days before they leave the natal site and disperse in the river.

COLORATION
The coloration is variable. Upper side of body in shades of brown, gray or olive. Diffuse spots and blotches create a diffusely mottled or marbled pattern. The blotches become more clear and contrasty along the tail muscles. Scattered iridocytes present but do not form distinct patches. Oral disc and abdominal sucker are mostly unpigmented, except for their dorsal faces and rims. Gills and heart are not visible. The tail fins are pigmented, more intensely in the periphery. In advanced stages, melanocytes along the blood vessels accentuate the proximal tail myosepta and produce a reticulate pattern on the tail fins. Lateral part of abdomen covered by dense white-silvery iridocytes; the semi-translucent medial belly skin may or may not possess scattered iridocytes.

LITERATURE
Malkmus, R. (2002) Amphibians & Reptiles of Mount Kinabalu (North Borneo). Koeltz Scientific Books, Königstein. 424 pp.

Matsui, M. (1986) Three new species of *Amolops* from Borneo (Amphibia, Anura, Ranidae). Copeia, 1986: 623–630.

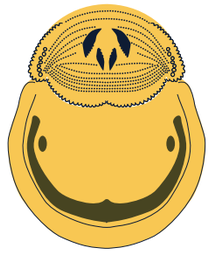
RANIDAE

Meristogenys penrissenensis Shimada, Matsui, Nishikawa, and Eto, 2015

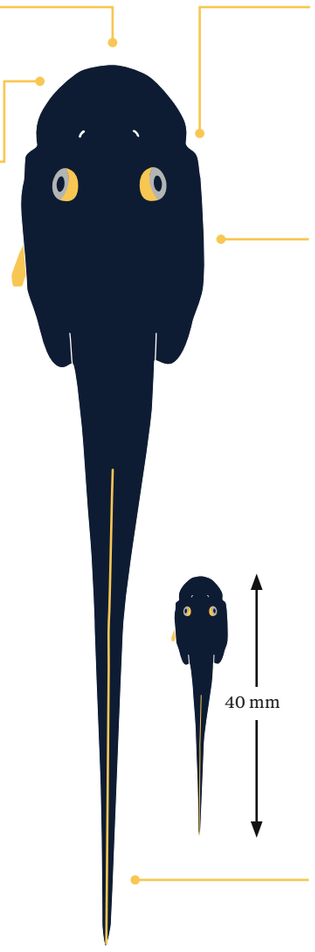
Penrissen Torrent Frog

SNOUT
Broadly rounded in dorsal view. In lateral view, long and sloping in a slightly convex curve. Oral disc set off from snout by a groove.

ORAL DISC
Ventral, wide, followed posteriorly by a large abdominal sucker. Abdominal sucker thick-rimmed, covering much area ventrally.



In ventral view, posterior rim of abdominal sucker reaches approximately 70–75% of the body length. Faintly brown friction areas are discernible inside the rim. Marginal papillation of oral disc present along the lower and lateral upper lips. Marginal papillae short, rounded and indistinct. A dense irregular row of submarginal papillae located at lateral upper lip. LTRF from 7(4–7)/7(1) to 7(4–7)/8(1). Beaks strongly keratinized, deep black. Upper and lower beaks are both widely divided, possessing coarse serrae (ribs).



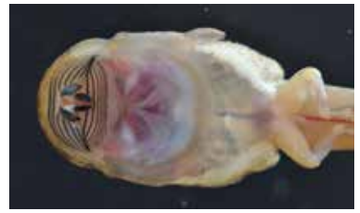
ECOMORPH
Lotic, rheophilous, suctorial, gastromyzophorous, exotrophic.

SIMILAR SPECIES
Meristogenys penrissenensis tadpoles are distinguished from sympatric *M. jerboa* larvae (and several other *Meristogenys* larvae) by possessing seven (four divided) upper lip keratodont rows (six, four divided, in *M. jerboa*). Close examination of lower beak, skin glands, tail fins, LTRF, and skin protuberances is necessary to exclude other *Meristogenys*. *Ansonia* tadpoles can occur in the same streams but can be easily excluded by their lack of an abdominal sucker.

NOSTRILS & EYES
Eyes dorsolateral. Nostrils closer to eyes than to snout, oriented anterolaterally. Iris black with a thin ring of golden iridocytes around pupil, peripherally dusted with golden iridocytes. Sclera stippled with silvery iridocyte.

BODY
Depressed and streamlined in lateral view. Body contour oval to rectangular, snout slightly set off by a notch. Trunk bulges posteriorly on both sides of tail root. Body is widest at the level of gill region. In lateral view, the trunk is just as deep as the head, i.e., venter flat. Spiracle as free long tube, sinistral, opening posteriorly well below mid-height of body, close to the substrate when the tadpole is attached to the substrate. Small groups of skin glands located at cheek, anterior to spiracle, behind eyes, and at the posterior bulge of trunk (also see description of tail). Ventral glands at the posterior end of abdomen absent. Glands may be difficult to see. Lateral line organs indistinct. Head and upper trunk bear dense, small, conical skin protuberances; also scattered along flanks.

TAIL
Approximately 64–68% of total length. Muscular part strong and high, almost as high as body in lateral view. The dorsal fin starts well posterior (~15% tail length) to the trunk-tail junction. The upper fin rises up in a straight line to the highest point, often changes direction fairly abruptly to slope down in a straight or slightly concave line to the tip.; tip pointed. Lower fin originates at approximately 40% of tail length. It is much lower than the upper fin. The maximum height of the tail is slightly before the mid-point of tail. Fins devoid of skin glands or a few present in the lower fin.



The tadpoles of Meristogenys penrissenensis *live in the current of clear, mid-sized rocky streams in the hillsides of western Sarawak. They are mid-size and have an abdominal sucker (gastromyzophorous), which is used as an adhesive organ to cling to rocks.*

HABITAT & ECOLOGY
Meristogenys penrissenensis tadpoles have been described from clear hillside streams of western Sarawak where they are sympatric and even syntopic with *M. jerboa*. Their abdominal sucker allows them to hold on to rocks in the current. *M. penrissenensis* tadpoles graze over organic rock overgrowth (algae, small animals, bacteria), most actively during the night. They prefer moderate flow velocities. Groups of tadpoles may feed together on the same rock face, often associated with larvae of *Ansonia*.

LITERATURE

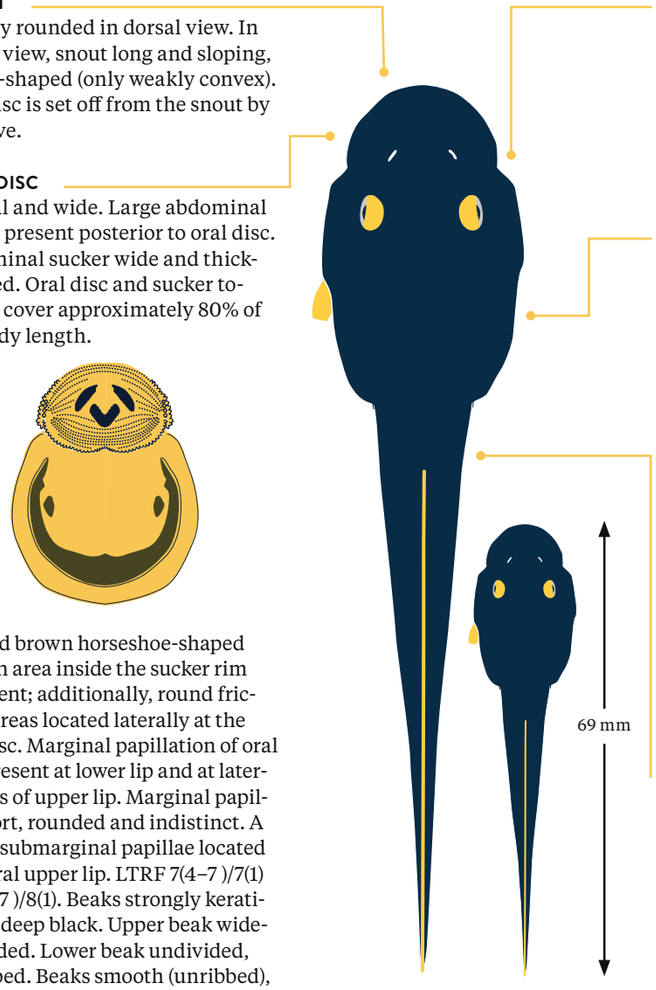
Shimada, T., Matsui, M., Nishikawa, K., Eto, K. (2015) A new species of *Meristogenys* (Anura: Ranidae) from Sarawak, Borneo. Zoological Science, 32: 474–484.

REPRODUCTION
Males commonly perch on low vegetation, clay embankments, roots or rocks along the steep river bank. The male call is an unpulsed, sharp, high-pitched, whistle. Calls are emitted at seemingly random intervals of several minutes at times.

COLORATION
Dark brown irregular spots on a beige background give the tadpole a mottled appearance. The mottling becomes more blotchy and with greater contrast on the tail. There is significant variation in the pattern and the pattern is most pronounced in late stage tadpoles. Iridophores are abundant over body and muscular tail and can form light patches on the fins. Lateral abdomen covered by a sheath of silver iridocytes; medial abdominal skin semi-transparent; gut covert by deeper layers of pigmentation and not clearly visible. Oral disc and abdominal sucker unpigmented; gills and heart invisible. Specialized epithelium (friction areas) along the inner side of the sucker rim are visible as light brown areas. Tail fins may bear some diffuse dark and light blotches of pigmentation (melanocytes and iridocytes) at their margins. In advanced stages, melanocytes along the blood vessels accentuate the myosepta. Melanocytes can create a reticulate pattern on tail fins.

Meristogenys stenocephalus Shimada, Matsui, Yambun, and Sudin, 2011

Narrow-headed Torrent Frog



SNOUT
Broadly rounded in dorsal view. In lateral view, snout long and sloping, wedge-shaped (only weakly convex). Oral disc is set off from the snout by a groove.

ORAL DISC
Ventral and wide. Large abdominal sucker present posterior to oral disc. Abdominal sucker wide and thick-rimmed. Oral disc and sucker together cover approximately 80% of the body length.

A broad brown horseshoe-shaped friction area inside the sucker rim is present; additionally, round frictions areas located laterally at the oral disc. Marginal papillation of oral disc present at lower lip and at lateral parts of upper lip. Marginal papillae short, rounded and indistinct. A row of submarginal papillae located at lateral upper lip. LTRF 7(4–7)/7(1) to 7(4–7)/8(1). Beaks strongly keratinized, deep black. Upper beak widely divided. Lower beak undivided, V-shaped. Beaks smooth (unribbed), their edges bear serrations.

NOSTRILS & EYES
Nostrils closer to eyes than to snout, oriented anterolaterally. Eyes dorsolateral. Iris with a thin ring of golden iridocytes around the pupil; otherwise iris densely stippled with golden iridocytes on black background. Sclera stippled golden above, silver below.

BODY
Depressed and streamlined. In dorsal view, body contour oval to rectangular. A notch sets off the snout from the rest of the head. Posterior trunk end bulges posteriorly on both sides of tail root. Body widest at the level of gills. Venter flat. Spiracle tube free and long, sinistral; spiracle opens posteriorly and well below mid-body, close to the substrate in attached larvae. Skin glands may be difficult to see. Small groups of skin glands located at cheek, anterior to spiracle, behind eyes, and at posterolateral bulge of the trunk; glands at posterior end of the venter absent. Lateral line organs indistinct. Skin projections on upper side of body, densest on snout and head, scattered over flanks.

TAIL
Approximately 64–69% of total length. Muscular part strong and high, as high as body in lateral view. Dorsal fin starts posterior (10–13% tail length) to trunk-tail junction. It rises up straight to the highest point, curves and slopes down in a convex line to the pointed tip. Lower fin originates at approximately 45% of tail length and is convex. Upper fin much higher than lower. Maximum height at the mid-point of tail length. Skin glands along base of lower fin only.

ECOMORPH
Lotic, rheophilous, suctorial, gastromyzophorous, exotrophic.

SIMILAR SPECIES
Only species of *Huia* and *Meristogenys* possess larval abdominal suckers and are easily recognized by this feature. *Meristogenys* differs from *Huia* in the divided upper beak. *Meristogenys stenocephalus* share seven upper lip keratodont rows (four divided), undivided lower beak, skin projections, lack of dorsal fin glands with *M. whiteheadi* and *M. stigmachilus*, yet *M. stenocephalus* larvae seem to grow larger than the other two species. Reliable distinguishing characters have not been established and DNA matching with adults is required.

The tadpoles of Meristogenys stenocephalus *are among the largest in the genus. The distinguishing characters between larval* M. stenocephalus, M. whiteheadi, *and* M. stigmachilus *have not been fully established and the account herein remains preliminary (samples from Gunung Mulu Nationals Park)*

HABITAT & ECOLOGY
The tadpoles live in clear, medium to large rocky lowland and hillside streams of western Sabah and northern Sarawak. They feed on organic rock overgrowth (algae, protists). We encountered these larvae at small cascades under openings in the canopy, in otherwise not very steep, rather broad streams.

LITERATURE

Shimada, T., Matsui, M., Nishikawa, K., Eto, K. (2015) A new species of *Meristogenys* (Anura: Ranidae) from Sarawak, Borneo. Zoological Science 32: 474–484. [with key to species]

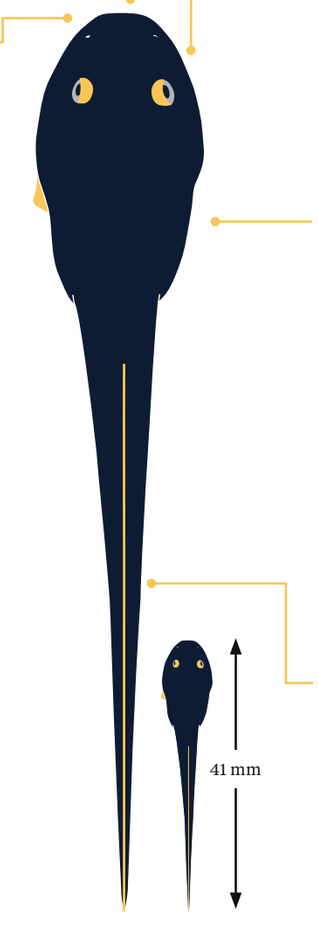
Shimada, T., Matsui, M., Yambun, P., Sudin, A. (2011) A taxonomic study of Whitehead's torrent frog, *Meristogenys whiteheadi*, with descriptions of two new species (Amphibia: Ranidae). Zoological Journal of the Linnean Society, 161: 157–183.

REPRODUCTION
No details have been reported for this species.

COLORATION
Mottled above with dark brown diffuse spots on lighter brown background. This patterns extends onto the tail, where it has a higher contrast and larger spots. Light spots of iridocytes are present along the dorsal edge of the tail muscle, dorsal and lower fins. At the tip, they may form a bright stripe (occasionally also seen in other *Meristogenys*) with sometimes bright orange hue in advanced tadpoles. Tail pigmentation is more intense in advanced than in early stages. In advanced stages, melanocytes along the blood vessels accentuate the proximal tail myosepta and produce a reticulate pattern on the tail fins. Oral disc and abdominal sucker are mostly unpigmented, except for their dorsal faces and rims. Gills and heart not visible. The lateral sections of the abdomen covered by dense white-silvery iridocytes. Medial abdominal skin unpigmented, semi-transparent; gut hidden by pigmentation of the abdominal lining.

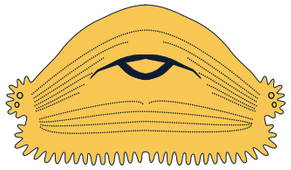
Odorrana hosii (Boulenger, 1891)

Poisonous Rock Frog



SNOUT
Broadly rounded, but obtuse medially, in dorsal view. In lateral view, relatively long, sloping to the tip in a moderately convex curve. Each nostril positioned on a small bulge.

ORAL DISC
Nearly ventral. Emarginations present at lateral margin between upper and lower lips. One row of marginal papillae present along ventral lip; papillae alternate in direction so that they appear as if standing in double-row.



Upper lip mostly devoid of papillae, except for far lateral part, where one row of marginal papillae and few submarginal papillae are developed. Marginal papillae moderately long. LTRF 6(3–6)/4(1) or 6(2–6)/4(1); division of first keratodont row on lower lip may be indistinct (very narrow gap). Beaks well keratinized, black, but thin; their edges bear fine serrations. Upper beak shallowly arched; lower beak V to U-shaped.

ECOMORPH
Lotic (quiet sections), exotrophic, leaf litter specialist.

NOSTRILS & EYES
Eyes relatively small, dorsolateral. Nostrils closer to snout than to eyes, and oriented anteriorly. Each nostril sitting on the anterior face of a bulge. Iris color pattern consists of a thin ring of orange iridocytes around pupil; peripherally of that ring iris densely stippled with golden iridocytes on generally black background, however, four sectors of the iris remain black instead, and give the eye a radial appearance.

BODY
Mid-sized tadpole. In lateral view, the body is depressed; snout relatively long and gently sloping with a moderately convex curve to a rounded tip. In dorsal view, body contour generally oval, but head wider than the trunk part. Body widest at the level of the gills, posterior to eyes. Ventral side flat, belly not bulging. Spiracle sinistral. Spiracular tube opens posterodorsally, well below the longitudinal body axis in lateral view. Spiracular orifice at the end of a short free tube. Lateral line organs visible on the snout in close-ups, but otherwise indistinct.

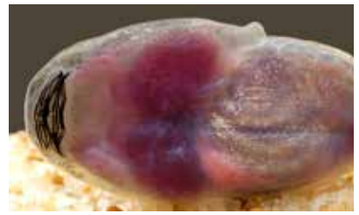
TAIL
Very long, up to 70% of total length. Muscular part of tail strong and high, nearly as high as body in lateral view. Dorsal fin originates clearly posterior to trunk-tail junction. It rises and runs smoothly, and a shallow arch leads to a narrowly rounded tip. Lower fin similar to the upper fin in height and contour shape, both fins are relatively low. Maximum height of tail approximately at midpoint of tail. Lateral tail vein clearly visible.

SIMILAR SPECIES
The most likely candidates to confuse *Odorrana hosii* tadpoles with are larvae of *Staurois* and *Pulchrana*, because of their dark color, long tails, low tail fins and usage of similar microhabitats (leaf litter). Apart from some differences in oral disc features (see descriptions of *Staurois* and *Pulchrana*), *O. hosii* lacks skin glands in tail fins (present in *Pulchrana*). The nasal bulges and anteriorly oriented nostrils are unique in *O. hosii*, but may require examination under high magnification.

Although the adult stage of Odorrana hosii *is abundant in many rocky hill stream areas, its tadpoles have rarely been reported from their natural habitat.*

HABITAT & ECOLOGY
Only few observations of the tadpoles have been available (Manthey and Grossmann 1997) and, thus, inferences on the tadpole's ecology and habitat preferences are limited. We found *Odorrana hosii* tadpoles in quiet side-pools or isolated troughs of rocky, mid-sized streams. These pools were more than 50 cm deep and partially filled with leaf litter. Tadpoles were dip-netted from the deeper portion of the pool, sometimes in association with larvae of *Staurois guttatus*. It is unclear, if these tadpoles normally prefer isolated rock pools (standing waters, lentic) or inhabit quiet, flowing sections in streams as well (lotic).

REPRODUCTION
No data available.



COLORATION
Uniformly dark brown to dark gray above on the body and the muscular part of the tail; distinct markings are absent. Irregular clusters of iridocytes present at the cheek and at the tail, more pronounced so towards metamorphosis. The lateral tail vein is clearly visible in the first third of the tail and its side branches (lined with melanocytes) accentuate tail muscle myosepta. The fins are mostly clear except for some pigmentation along their respective bases. Ventral skin of body in the buccal and branchial regions transparent, mostly devoid of pigment cells; the ventral skin shows slight iridescence (not in preserved specimens). Gills, heart and some of the head muscles are visible through the skin in red. The abdominal skin is semi-transparent, but dense scattering of iridocytes may prevent a clear view of the gut.

LITERATURE

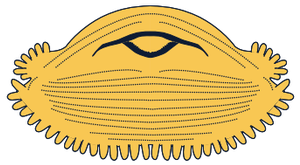
Manthey, U., Grossmann, W. (1997) Amphibien und Reptilien Südostasiens. Natur und Tier Verlag, Münster. 511 pp.

Staurois guttatus (Günther, 1858)

Black-Spotted Rock Skipper

SNOUT
Long, tapering in dorsal view, yet apex broadly rounded, obtuse. In lateral view, dorsal face continuation of the downward slope of the forehead; apex of snout positioned low.

ORAL DISC
Ventral; width slightly more than half of maximum body width. Emarginations present laterally between upper and lower lips.



Upper lip mostly devoid of papillae; with only a single row of several marginal papillae on small lateral flaps. Submarginal papillae absent. One uninterrupted row of marginal papillae along lower lip. Marginal papillae moderately long, blunt. LTRF 2(2)/8(1) to 2(2)/10(1); peripheral keratodont row number on lower lip increases with tadpole stage. A single short accessory keratodont row located laterally at the transition from lower to upper lip; it is somewhat longitudinal in orientation. Beaks keratinized, black, and thin; their edges bear very fine serrations. Upper beak a broad smooth and shallow arch; lower beak widely V- to U-shaped.

NOSTRILS & EYES
Eyes small and covered by skin for most of larval life; they grow and become functional towards metamorphosis. Eyes dorsolateral. Iris (in late larval stages) black with a silvery sector above and below. Nostrils small, much closer to snout than to eyes, at level dorsal to oral disc. Nostrils supported medially by a slight bulge of snout, directed anterolaterally.

BODY
Mid-sized tadpole. Body depressed, flat above and below; head slightly wedged, sloping down to snout, only slightly convex, long. In dorsal view, body slender, with a blunt somewhat triangular head; trunk less wide than head. Body widest at the level of the gills, posterior to eyes. Spiracle sinistral. Spiracular tube opens directed posteriorly and is positioned slightly below longitudinal body axis in lateral view. Spiracle forming a short, free tube. Lateral line organs inconspicuous.

TAIL
Long, approximately 72% of total length. Muscular part of the tail moderately strong, less than body height in lateral view. Dorsal fin starts shortly behind trunk-tail junction; it remains low for the first 10–15% of the tail, then slopes up gradually. It then arches shallowly at approximately mid-tail and slopes downward with only slight convexity towards the moderately rounded tail tip. Lower fin with a flat, almost straight contour. Both tail fins relatively low. Maximum height approximately at mid-point of tail length. Both fins similar in height or dorsal fin slightly higher at mid-tail point. Skin glands absent. Lateral tail vein clearly visible.

ECOMORPH
Lotic to lentic, exotrophic, leaf litter interstice specialist, fossorial.

SIMILAR SPECIES
The general features described for *Staurois guttatus* apply for all species of *Staurois*. *S. parvus* lacks the accessory keratodont rows and usually has 2~3 interrupted keratodont rows on lower lip. Grosjean and Preininger (2020) report the absence of accessory keratodont rows in *S. guttatus*. Our limited samples do not confirm that. The tadpole of *S. latopalmatus* is unknown. *Odorrana hosii* and *Pulchrana picturata* may occur in the same microhabitat with *Staurois* tadpoles. Both species lack the reddish appearance (in life) and the retarded ocular development of *Staurois*. *Staurois* lacks the skin glands found in *Pulchrana* tadpoles.

Although Staurois guttatus *is a common frog along Bornean streams, its tadpoles are difficult to find. Their morphology is unusual and they strongly resemble the tadpoles of neotropical Glass Frogs (family Centrolenidae) to which they are unrelated. Little is known about their biology.*

HABITAT & ECOLOGY
The species is known from lowland, mid-elevation, and montane streams. The tadpoles live in rock troughs and side-pools that are partially or completely disconnected from the main stream and filled with deep leaf litter and detritus. Tadpoles are elusive; they avoid light (photophobic) and hide deep under leaf litter at least at daytime. Most likely feeding happens at night.

LITERATURE
Arifin, U., Iskandar, D., Bickford, D., Meier, R., Kutty, S.N., Brown, R., (2011) Phylogenetic relationships within the genus *Staurois* (Anura, Ranidae) based on 16S rRNA sequences. Zootaxa 2744: 39–52.

Inger, R.F., Tan, F.L. (1990) Recently discovered and newly assigned frog larvae (Ranidae and Rhacophoridae) from Borneo. The Raffles Bulletin of Zoology 38: 3–9.

Inger, R.F., Wassersug, R.J., (1990) A centrolenid-like anuran larva from Southeast Asia. Zoological Science 7: 557–561.

REPRODUCTION
See comments on reproduction for *S. parvus*.

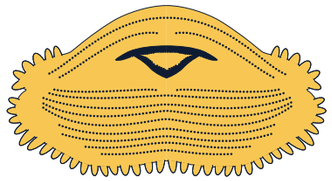
COLORATION
Uniformly dark gray above (at least in advanced tadpoles) in daylight; distinct markings absent, yet the general appearance of living specimens is reddish due to high blood volume, high vascularization of skin and semi-transparency of lateral and ventral body skin. Skin with bluish iridescence in living specimens. Fins mostly clear, dorsal fin darkly pigmented at anterior base. Skin of venter semi-transparent mostly unpigmented, with bluish iridescence (lost in preserved specimens). Scattered silvery iridophores may be present ventrally at the ventral gill region and anterior abdominal region, laterally at the gill region, and as irregular patches of iridocytes scattered along the proximal tail. The oral disc is unpigmented. Gills, heart, and gut visible through skin. Patches of iridophores arranged in irregular pattern along the muscular part or the tail, in some specimens on lateral gill region as well.

Staurois parvus Inger and Haile, 1959

Lesser Rock Skipper

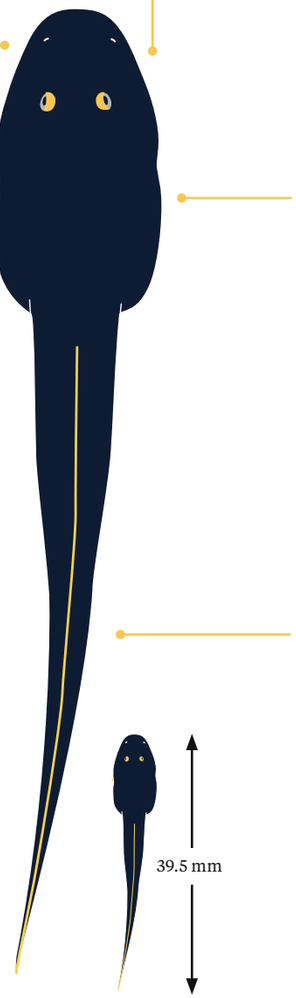
SNOUT
Tapering in dorsal view, apex broadly rounded, obtuse. In lateral view, its dorsal face is a continuation of the downward slope of the forehead. Apex positioned low.

ORAL DISC
Subterminal, width up to 59% width of body. Emarginations present at lateral margin between upper and lower lips.



Upper lip mostly devoid of papillae, it only bears a single row of several marginal papillae on small lateral flaps; sometimes with 1-2 submarginal papillae. One uninterrupted row of marginal papillae present along the margin of the lower lip. Marginal papillae moderately long. Submarginal papillae absent. LTRF 2(2)/10(1) to 2(2)/11(1-3). Lateral accessory keratodont row absent. Beaks keratinized and black, thin; their edges bear very fine serrations. Upper beak almost straight, slightly arched; the lower beak smoothly V- to U-shaped.

ECOMORPH
Lotic (quiet sections), exotrophic, leaf litter interstice specialist, fossorial



NOSTRILS & EYES
Eyes very small and covered by skin for most of larval life, but grow and differentiate towards metamorphosis; positioned dorsolaterally. Iris (in late larval stages) black with a silvery sector above and below. Nostrils small, much closer to snout than to eyes; above the region of oral disc. Nostril supported medially by slight bulge of snout and directed anterolaterally.

BODY
Mid-sized tadpoles. In lateral view, Body depressed, flat above and below; the snout is slightly wedged, sloping down to snout, only slightly convex and long. In dorsal view, Body slender, with a bluntly triangular head and a less wide trunk. Body widest at level of gills, posterior to eyes. Spiracle sinistral, spiracular tube opening posteriorly and positioned below the longitudinal body axis in lateral view. Spiracular orifice free from body wall, forming a short tube. Lateral line organs inconspicuous.

TAIL
Very long, approximately 72–73% of total length. Muscular part of tail moderately strong to strong, slightly less than body height in lateral view. Dorsal fin starts slightly posterior to trunk-tail junction, but remains low for the first 10–15% of the tail. It then rises gradually and arches shallowly at approximately mid-tail and slopes downward with only light convexity towards the moderately rounded tail tip. Lower fin with a flat, almost straight contour. Both tail fins relatively low. Maximum height of the tail approximately at mid-point of tail length. Both fins similar in height, dorsal fin slightly higher at mid-tail point.

SIMILAR SPECIES
Very few *Staurois* tadpoles have been collected in the field. Valuable information came from breeding in captivity (Preininger et al. 2012; Grosjean and Preininger 2020). Lack of accessory keratodont rows, 2–3 interrupted rows on lower lip and pattern of whitish glands (at least in preservation) distinguish it from *S. guttatus* and *S. tuberilinguis*. See *S. guttatus* for further comments.

Staurois parvus *is a small species of the genus* Staurois. *The tadpoles have not yet been observed in the field and published descriptions stem from captive breeding colonies (Grosjean and Preininger (2020)). The specimens from which the description was derived also stem from this breeding and were kindly provided by Doris Preininger.*

HABITAT & ECOLOGY
The species is known from mid-elevation rocky streams of eastern Sarawak. According to observations in captivity, tadpoles of *S. parvus* live in leaf litter containing rock troughs and quiet side-pools of cascading streams. Tadpoles are wary and photophobic.

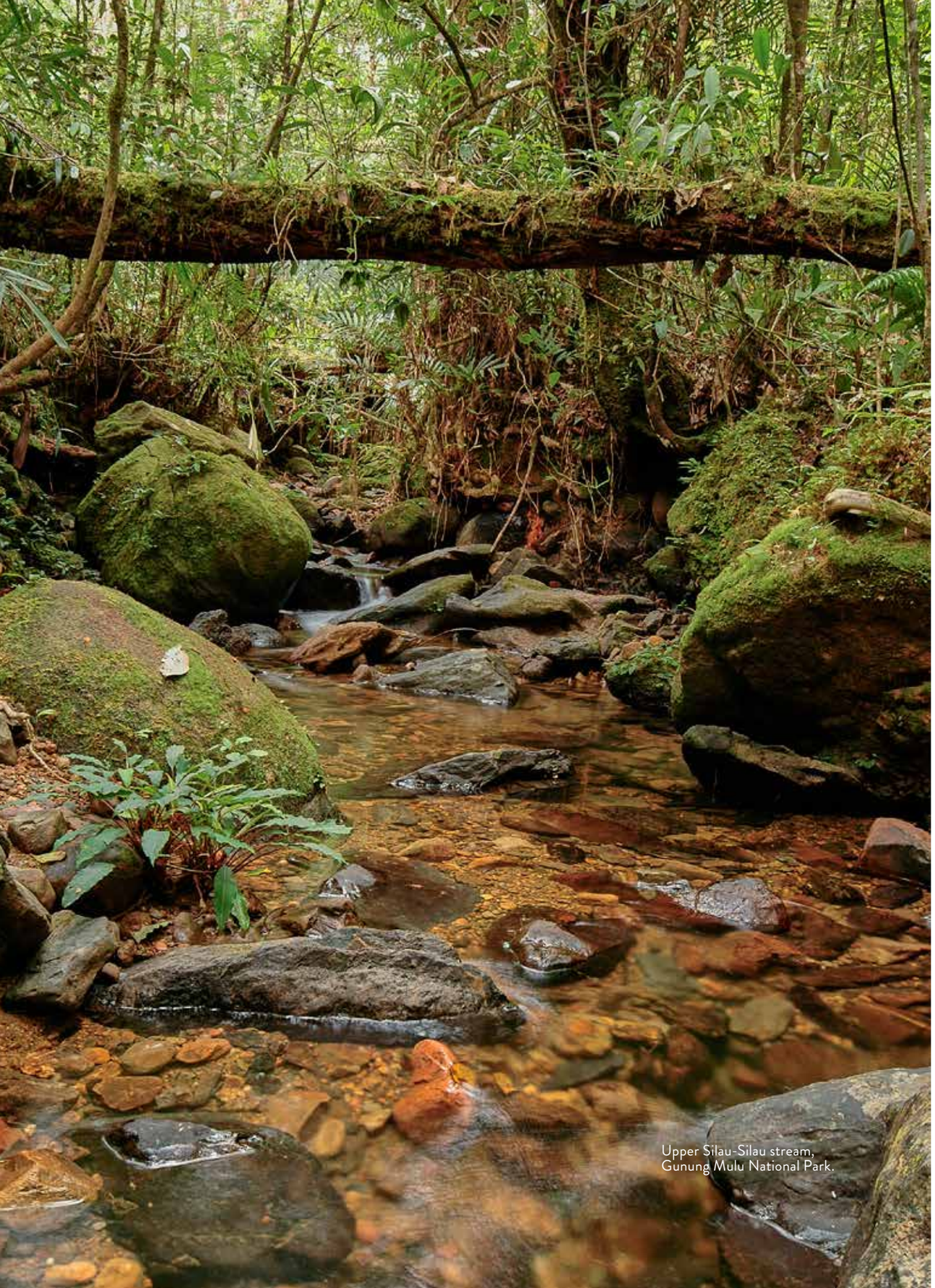
REPRODUCTION
Preininger et al. (2012) reported that in a terrarium, two clutches with 14 and 26 eggs, respectively, were discovered under submerged rocks in a quiet section of an artificial stream. Troughs under cascades may also be sites where the species deposits eggs. It is unclear whether or not an amplectant pair lays one or several clutches. Larval life may extend over three months; metamorphs measure 11.8 mm in snout-vent length.

COLORATION
A band of dark pigmentation above from head over trunk to dorsal muscular part of tail. Apart from that, skin mostly transparent or semi-transparent and tadpoles with a reddish appearance. The skin has gray-bluish iridescence in living specimens. Fins mostly clear. Ventral skin of body semi-transparent to transparent with bluish iridescence (in life). The oral disc is unpigmented. Gills, heart, and gut visible through skin. In preserved specimens, a pattern of whitish dots (glands/acini?) has been described and proposed as a diagnostic character of the tadpoles of this species.

LITERATURE

Preininger, D., Weissenbacher, A., Wampula, T., Hödl, W. (2012) The conservation breeding of two foot-flagging frog species from Borneo, *Staurois parvus* and *Staurois guttatus*. Amphibian and Reptile Conservation 5: 45–56.

Grosjean, S., Preininger, D. (2020) Description of two *Staurois* tadpoles from Borneo, Staurois parvus and Staurois tuberilinguis (Anura: Ranidae). Zootaxa 4896: 523–534.



Upper Silau-Silau stream, Gunung Mulu National Park.

Staurois tuberilinguis Boulenger, 1918

Green Spotted Rock Skipper

Descriptions of S. tuberilinguis *tadpoles were provided by Malkmus et al. (1999) and Grosjean and Preininger (2020). Both teams sampled tadpoles from Gunung Kinabalu and identified them by DNA matching to adults.*

TADPOLE DESCRIPTION

Body depressed, elliptical elongate in dorsal view, widest at level of internal gills, with constriction between head and body (see silhouette of *S. guttatus*). Body flat ventrally. Snout long, obtuse. Eyes dorsal, oriented dorsolaterally, not bulging. Nostril round, small, rimmed, and much closer to snout than to eye. Tail length 69–74% of total length; strong tail musculature. Tail fins low. Upper fin only starts proximally with second third of tail. Tail tip moderately rounded.
Sinistral spiracle with short free tube, opening directed posteriorly.

Total length up to 46.6 mm.
Oral disc subterminal. LTRF 2(2)/6(1) to 2(2)/11(1). Oral disc width approximately 60–63% of body width. Two rows of papillae on lateral lower lip, one row medially. A short accessory keratodont row located laterally on each lateral corner of oral disc. Beaks weak, finely serrated, weakly arched. Body and tail pigmented above but pigmentation rapidly decreases more ventrally; flank and venter skin semi-transparent, organs shine through; highly vascularized skin; general appearance pinkish.

HABITAT & ECOLOGY

This species has been recorded from mid to high elevations, 200–1800 m a.s.l., mostly above 500 m. It is closely associated with small rocky streams. Adults perch on low vegetation along streams or on rocks, and vegetation growing in the streams. The call of males is similar to the trill of crickets. Malkmus et al. (1999) found the tadpoles in 40 cm deep rock troughs of a rocky stream. The trough was fully filled with leaf litter. Tadpoles were reported to be strongly photophobic.

SIMILAR SPECIES

The general body shape is similar to *S. guttatus* and *S. parvus;* see descriptions there. Grosjean and Preininger (2020) proposed distinguishing characters between *S. guttatus* and *S. tuberilinguis*. Some of their diagnostic larval characters for *S. guttatus* (smaller size, absence of lateral accessory keratodont rows, presences of small gap in lower lip row of marginal papillae) were in conflict with our own samples. Malkmus et al. (1999) did not draw a lateral accessory keratodont row in their depiction of a *S. tuberilinguis* oral disc; yet Grosjean and Preininger (2020) found the row present in their samples of *S. tuberilinguis;* we noted it in our samples of *S. guttatus* in contrast to these authors. It is possible that there is more variation in *Staurois* larvae than currently known and more research is needed.

LITERATURE

Malkmus, R., Kosuch, J., Kreutz, J. (1999) Die Larve von *Staurois tuberilinguis* Boulenger, 1918. Eine neue centrolenidenähnliche Kaulquappe aus Borneo (Anura: Ranidae). Herpetozoa, 12: 17–22.

Grosjean, S., Preininger, D. (2020) Description of two *Staurois* tadpoles from Borneo, *Staurois parvus* and *Staurois tuberilinguis* (Anura: Ranidae). Zootaxa 4896: 523–534.

Feihyla kajau (Dring, 1983)

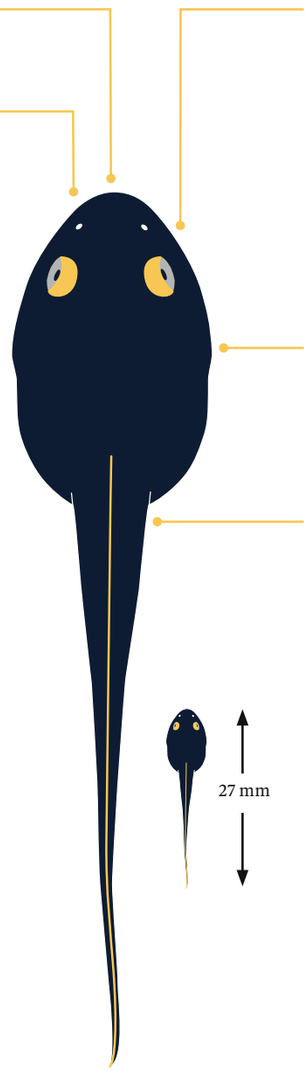
White-eared Tree Frog

SNOUT
Rounded, blunt, moderately tapering in dorsal and lateral views.

ORAL DISC
Oriented anteroventrally. Marginal papillation with wide gap on upper lip, gap absent on lower lip. Oral disc marginal papillae mostly arranged in a single row but submarginal papillae located in lateral areas of the upper and lower lips, thus, forming double-row papillation laterally.

Marginal papillae moderately long, blunt. Lateral oral disc indentations present. Labial ridges bear uniserial keratodont rows. LTRF 4(2–4)/3.

ECOMORPH
Lotic (here: very low current) to lentic, exotrophic, benthic.



NOSTRILS & EYES
Nostrils round and fairly large, widely spaced, closer to snout than to eyes. Eyes relatively large, positioned and facing dorsolaterally. Iris golden in upper and lower sectors around the pupil. Anterior and posterior sectors of iris show copper-red color. Scleral part of eye densely covered with silvery to golden (depending on light conditions) shiny pigments.

BODY
Oval to ovoid, wider than deep. Spiracle sinistral. Spiracular tube fused to body and directed posterolaterally, opening ventral to longitudinal body axis in lateral view.

TAIL
Long, up to 68% of total length. Muscular part of tail only moderately strong, much less in height than body. Dorsal tail fin rises at or slightly anterior to trunk-tail junction. Fins are arched and taper posteriorly into an acuminate tip (many specimens have damaged tail ends that become rounded). Dorsal and lower fins approximately of same height. Maximum height of in the middle third of tail length.

SIMILAR SPECIES
Because of its size and the general brown appearance, this tadpole can be confused with some *Limnonectes* tadpoles that inhabit the same streams and stream pools. The brown "saddle" and the reddish anterior and posterior sectors of the iris (close-up!) are usually sufficient characters to identify *Feihyla kajau* tadpoles in the field and separate it from similar species. The tadpole of *F. inexpectata* is markedly different from *F. kajau* by its high contrast black and white markings on the body and hitherto has been reported only from stagnant pools.

Feihyla kajau *is widely distributed on the island of Borneo. Under favorable weather conditions small to large aggregations of this species may form for reproduction. The tadpole has a plump body and is easily identified by a combination of characters but first and foremost the dark "saddle" across the trunk dorsally.*

HABITAT & ECOLOGY
The tadpole inhabits quiet sections in small intermittent streams below 1000 m a.s.l. In most cases, we found the tadpoles in virtually stagnant water pools (yet, often with some inflow and outflow) in small streams with rocky, gravel, or sandy bottom and some leave litter. Such tadpole habitats are mostly in the forest under canopy cover, however, they also reproduce in suitable small roadside streams in more open situations.

REPRODUCTION
Males call from low to moderately high vegetation (1–3 m) overhanging water. Males commonly aggregate in calling groups. Species of *Feihyla* do not build foam nests as in *Rhacophorus* and *Leptomantis*. Clutches are laid in jelly masses below leaves.

COLORATION
Brown dorsally. The trunk bears a darker brown dorsal cross band ("saddle"). Generally, the dorsum of the body has a brown background color, with groups of lighter bronze pigment cells on the trunk region and scattered lighter pigmentation on forehead region. At the flanks, dark pigmentation decreases towards the venter and larger, silvery shining iridocytes are present. Clusters of bronze pigmentation are positioned at the gill region; small groups along the flanks and cheeks. Ventral skin transparent; gills, heart and gut coils are clearly visible. Some iridophores may be present below gill region. At the base of the tail, spindle-shaped melanocytes give it an overall brown ground color. Groups of round, larger melanocytes form mottling, predominantly on the muscular part of the tail, but also extending onto the dorsal fin; lower fin clear. Blood vessels inconspicuous, myosepta moderately visible.

LITERATURE

Dring, J. (1983) Some new frogs from Sarawak. Amphibia-Reptilia 4: 103–115.

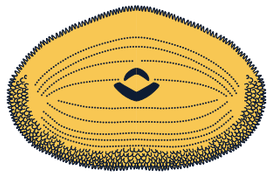
Das, I., Hedeir, H., Pui, Y.M., Hertwig, S.T., Haas, A. (2016) Larval external description and development in *Feihyla kajau* (Dring, 1983) (Amphibia: Anura: Rhacophoridae). Raffles Bulletin of Zoology 64: 319–328.

Leptomantis angulirostris (Ahl, 1927)

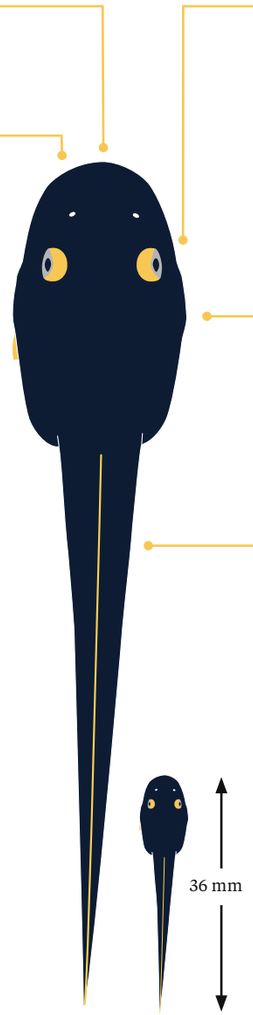
Masked Flying Frog

SNOUT
Expanded, broadly rounded. Snout profile sloping in a smooth convex curve.

ORAL DISC
Ventral and wide (ca. 80% of max. body width). Sucker without emargination between upper and lower lip.



Lower and side parts of lip bear multiple rows of papillae that are reduced on the upper lip. Marginal row consists of fine pointed papillae, whereas the papillae towards the mouth are blunt and gradually shorter. LTRF 4(3-4)/4 to 4(3-4)/5. Upper and lower lip keratodont rows long, spanning most of the oral disc. Relative to the disc, jaws small yet strongly built, black. Keratinized (black) part of upper jaw much less wide than the lower jaw. Jaw edges bear coarse, blunt serrations.



NOSTRILS & EYES
Nostril closer to eye than to snout. Eyes dorsolateral in position and do not reach the body contour. Iris and sclera outside iris densely stippled with pale golden iridocytes on a black background. Towards pupil, golden iridocytes merge into a solid golden ring.

BODY
Streamlined in lateral view. In dorsal view, body contour oval; dorsoventrally depressed. Head broader than trunk; widest at level posterior to eyes. Spiracle sinistral and low, below mid-body axis in lateral view. Spiracular orifice free, not fused to the body wall. Spiracle directed posteriorly.

TAIL
Strongly muscular, very long, approximately 68% of total length. Tail base almost as deep as trunk at their junction. Dorsal fin starts slightly behind the trunk-tail junction. Dorsal fin exceeds lower fin in height. Maximum tail height at about mid-tail position. Fin contours are shallowly convex. Tail fins taper gradually and end in a moderately narrow rounded tip.

ECOMORPH
Lotic, exotrophic, adherent-suctorial, rheophilous.

SIMILAR SPECIES
Among Bornean species, *Leptomantis penanorum* tadpoles are most similar to *L. angulirostris* tadpoles. See further comments for *L. penanorum*.

LITERATURE

Malkmus R, Manthey U, Vogel G, Hoffmann P, Kosuch J (2002) Amphibians & Reptiles of Mount Kinabalu (North Borneo). Koeltz Scientific Books, Königstein. 424 pp.

Inger, R.F., Tan, F.L. (1990) Recently discovered and newly assigned frog larvae (Ranidae and Rhacophoridae) from Borneo. The Raffles Bulletin of Zoology, 38: 3–9.

Tadpoles of Leptomantis angulirostris *occur at mid to high elevations. They live in clear, rocky mountain streams. Their streamlined body, sucker mouth, and strong tail are indicative of a life in lotic waters.*

HABITAT & ECOLOGY
The tadpoles of this species are known from approximately 500–1650 m a.s.l. in Sabahan primary forest. The tadpoles are adapted to clear mountain streams. Usually they are not found in abundance. They live in stony pools with moderate current. The tadpoles can cling to rocks and hold position in the current, but do not seem to be equipped to live in strong current or cascades.

REPRODUCTION
Malkmus et al. (2002) reported that males perch on vegetation in 1–4 m hight above water at streams of Gunung Kinabalu. Males call from approximately 6 pm to 5:30 am. The call is similar to arboreal crickets of the subfamily Pseudophyllinae. Males are brown above, whereas the larger females are green.

COLORATION
The general color of the tadpole ranges from light to dark brown, with grayish or olive hues above. Dark brown dusting is on the trunk and the muscular part of the tail. Scattered iridophores may be found on snout, cheek and flank. Red gills shine through the cheek skin. Gills and heart are visible through the translucent ventral skin, although partly covered by patches of iridophores at the heart and each of the gill areas, respectively. Abdomen opaque silver. A longitudinal streak runs at the mid-line of the abdomen (Vena abdominalis). Gut coils are not clearly visible. A few round black spots are present on the tail fins. Otherwise the fins are clear. Major tail vein and some myosepta are visible.

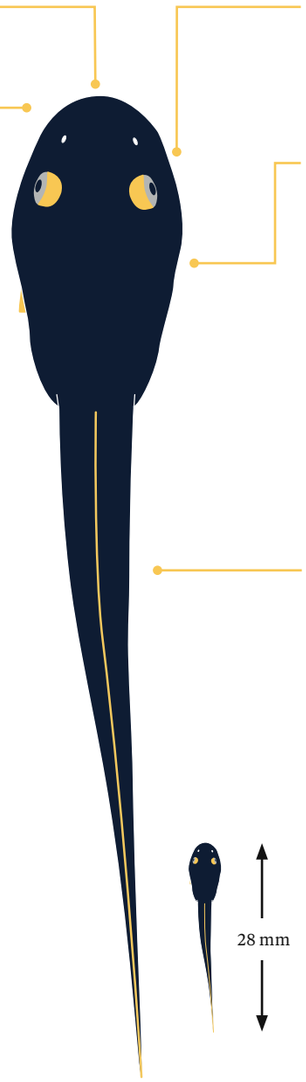
Leptomantis cyanopunctatus (Manthey and Steiof, 1998)

Blue-spotted Tree Frog

SNOUT
Rounded in dorsal view. In lateral view, snout long. Profile bluntly rounded.

ORAL DISC
Ventral and cup-shaped, 57–62% width of body. Marginal papillae of the upper lip occupy lateral thirds of lip. Size (length) of individual papillae increases from inner towards outer papillae. An additional infra-marginal row present at lateral quarters of upper lip. Marginal papillae of lower lip continuous, with 2–3 rows of evenly spaced/sized infra-marginal papillae. Nine rows of keratodonts on upper and three on lower lip (LTRF 9(5–9)/3(1)) in fully grown specimens; one row less on the upper row in earlier stages of development. Margin of upper jaw sheath curved downwards; lower jaw sheath broadly arched. Both jaw sheaths keratinized and serrated at their margins. Degree of keratinization on lower jaw sheath more extensive (wider) than that of upper jaw.

ECOMORPH
Lotic, exotrophic, adherent.



NOSTRILS & EYES
Eyes positioned dorsolaterally. Nostril oval. In dorsal view, nostril approximately equidistant between eyes and snout; opening laterally.

BODY
Medium in size. Slightly depressed in lateral view, flat above. In dorsal view, body contour is elliptical to smoothly rhomboid. Spiracle sinistral. Spiracular tube opens posteriorly. It is low, well-below longitudinal body axis in lateral view. Medial part of the spiracular orifice free from the abdominal wall, forming a free tube that is visible from above and below. Spiracle is positioned at 55–58% of body length. Lateral line pores are faintly discernible. Orbitonasal streak indistinct.

TAIL
Relatively long, approximately two times body length. Muscular part strong. Dorsal fin weakly convex at tail midpoint. Dorsal fin slightly deeper than lower fin. Fins taper gradually in the posterior third of tail to end in a narrowly rounded tip.

SIMILAR SPECIES
The black body may cause confusion with *Ansonia* tadpoles, which also breed in streams. *Leptomantis cyanopunctatus*, however, is easily distinguished from any species of *Ansonia* by its many keratodont rows on the upper lip (only two in *Ansonia*). Tadpoles of *L. gaun*i and *L. gadingensis* might occur in the same streams but are lighter in color than *L. cyanopunctatus*.

The description of the Leptomantis cyanopunctatus *tadpole follows Leong (2004).*

LITERATURE

Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89. [as *Rhacophorus bimaculatus*]

Leong, T.M. (2004) Larval descriptions of some poorly known tadpoles from Peninsular Malaysia (Amphibia: Anura). The Raffles Bulletin of Zoology 52: 609–20.

Habitat of *L. cyanopunctatus* at Maliau Basin Conservation Area.

HABITAT & ECOLOGY
Little is known about the tadpoles of this species. Larvae were reported from small forest streams, not more than 2 m wide, in moderate current situations with leaf drift.

REPRODUCTION
Similar to other rhacophorid tree frogs, *L. cyanopunctatus* will likely be encountered in the vicinity of a suitable breeding habitat, in this case a stream, where adults perch on bordering vegetation. The clutch deposition has, to our knowledge, not been described, but the formation of a foam nest is likely in this species as in other species of *Leptomantis*.

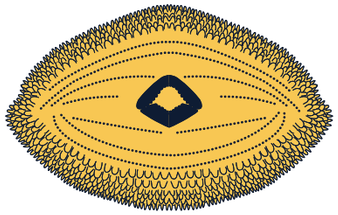
COLORATION
The general coloration of the larval body and tail is jet black. The body color extends onto the muscular part of the tail, but the tail fins are mostly clear, except for parts immediately adjacent to the dorsal and ventral margins of the tail musculature. The ventral side is light gray.

Leptomantis gadingensis Das and Haas, 2005

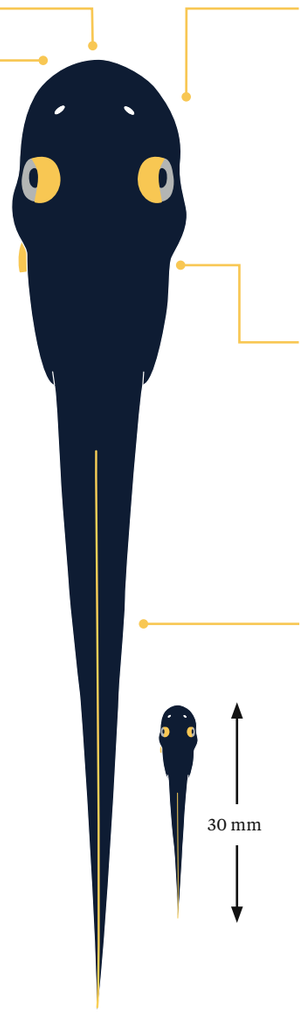
Gading Tree Frog

SNOUT
Expanded and broadly rounded viewed from above. Sucker-like oral disc ventral. Snout profile sloping in a convex curve, however, the elevation of the nostrils gives the snout a slightly angular profile in lateral view.

ORAL DISC
Ventral and wide (approximately 85% of maximum body width). Sucker without emargination between upper and lower lip. Lips bear multiple rows of papillae. Marginal row consists of fine papillae.



Papillae towards the mouth are blunt and gradually shorter. LTRF 4(3–4)/3(1). Outer upper and lower lip keratodont rows are long and spanning most of oral disc width. Relative to disc, jaws small yet strongly built, black. Jaws V-shaped and subequal in width. Jaw edges bear coarse and blunt serrations.



NOSTRILS & EYES
Nostril approximately midway between eye and snout. Eyes dorsolateral. Eyes not reaching or projecting beyond the body contour viewed from above. Iris with a black background with a narrow golden ring around the pupil and dense golden stippling beyond it. Black eyeball outside the iris is densely stippled with iridocytes; stippling denser below than above.

BODY
Streamlined. In dorsal view, body contour oval to rectangular; dorsoventrally depressed. Head broader than trunk; widest at level posterior to eyes. Spiracle sinistral and low, well below mid-body axis in lateral view. Spiracular orifice free, not fused to body wall. Spiracle points posteriorly.

TAIL
Strongly muscular. Tail base almost as deep as trunk at their junction. Dorsal fin starts behind the trunk-tail junction. Dorsal fin slightly exceeds the lower fin in height. Maximum tail height at about mid-tail position. Fin contours shallowly convex. Tail fins taper gradually and end in a broadly rounded tip.

ECOMORPH
Lotic, exotrophic, adherent–suctorial.

SIMILAR SPECIES
Little is known about the tadpoles of what could be dubbed the "*Leptomantis* -complex", which includes the closely related species *Leptomantis gauni*, *L. gadingensis*, *L. belalongensis*, and *L. malkmusi*. Actually, some of these species have been questioned in their species status. For those for which the tadpoles are known, clear distinguishing features have not been established. In body shape, these tadpoles are similar to *L. penanorum* and *L. angulirostris*, however, the latter two bear conspicuous black spots on the tail.

The tadpoles of Rhacophorus gadingensis *live in rocky streams in lowland and hilly terrains. Originally known from Gunung Gading National Park, the species probably has a wider distribution in western Borneo. As in this image, only relatively early tadpole stages have been documented and variability in characters towards older stages is still uncertain.*

HABITAT & ECOLOGY
The tadpoles of this species have so far been found at approximately 100–300 m elevation. The tadpoles are adapted to clear cascading streams. They live dispersed in the stream and may be difficult to find. We have seen them in pebble and rock pools with moderate current. The tadpoles cling to rocks with their sucker mouth; however, they seem to avoid strong currents or cascades.

REPRODUCTION
Mating pairs have been observed perching 2–6 m above a stream. Small foam nests are produced and attached to overhanging vegetation. After initial development, tadpoles hatch from the nest and drop into the stream below. The number of eggs in the nest has not been reported.

COLORATION
The general background color is dark brown on the head and trunk and a beige for the muscular part of the tail. Body finely stippled with bright iridophores over dark background. Dark brown pigmentation extends from trunk to the muscular part of tail. Gills and heart visible trough the translucent ventral skin. A patch of iridophores covers the heart and the skin of the gill areas is stippled with iridophores. Abdomen opaque silver right and left, with a transparent streak in the mid-line. Gut coils only visible through the transparent streak. Tail fins mostly clear with scattered melanophores and iridophores. Major lateral tail vein and some myosepta discernible.

LITERATURE

Das, I., Haas, A. (2005) A new species of *Rhacophorus* (Anura: Rhacophoridae) from Gunung Gading, Sarawak. The Raffles Bulletin of Zoology 53: 257–263.

Leptomantis gauni (Inger, 1966)

Short-nosed Tree Frog

SNOUT
Expanded and broadly rounded, viewed from above. Snout profile sloping in a convex curve in general, however, the elevation of the nostrils gives the snout a distinctive angular profile in side view.

ORAL DISC
Ventral and wide (ca. 80% of max. body width). Sucker without emargination between upper and lower lip. Lips bear multiple rows of papillae.

Marginal row consists of fine papillae. Papillae towards mouth blunt and gradually shorter. Labial Tooth Row Formula (LTRF) 4(3–4)/3(1). Outer upper and lower lip keratodont rows long and spanning most of oral disc width. Relative to the disc, jaws small yet strongly built, black. Jaws V-shaped and subequal in width. Jaw edges bear coarse and blunt serrations.

ECOMORPH
Lotic, exotrophic, adherent–suctorial.

NOSTRILS & EYES
Nostril approximately midway between eye and snout. Eyes dorsolateral in position, relatively close to body outline in dorsal view but not reaching or projecting beyond body contour. Iris with black background that is mostly covered by a narrow golden ring around the pupil and dense golden stippling peripherally. Eyeball outside iris densely stippled with iridocytes, denser below than above.

BODY
Streamlined. In dorsal view, body contour oval to rectangular. Dorsoventrally depressed. Head broader than trunk; widest at level posterior to eyes. Spiracle sinistral and low, well below mid-body axis in lateral view. Spiracular orifice free, not fused to body wall. Spiracle points posteriorly.

TAIL
Strongly muscular, long, approximately 66–68% of total length. Tail base almost as deep as trunk at their junction. Dorsal fin starts at 10-16% of tail length posterior to trunk-tail junction. Dorsal fin slightly exceeds lower fin in height, both fins moderately high. Maximum tail height at about mid-tail position. Fin contours shallowly convex. Tail fins taper gradually and end in a moderately narrow rounded tip.

SIMILAR SPECIES
See comments for *L. gadingensis*.

Leptomantis gauni *tadpoles live in lowland and hilly terrain rocky streams of Sabah and northeast Sarawak. The body shape alone is clearly indicative of a stream adapted tadpole.*

HABITAT & ECOLOGY
The tadpoles of this species have been found in lowland primary and good secondary forests. The tadpoles are adapted to clear rocky streams. They live on and among rocks and pebble in moderate current. We also found them in riffle sections of streams. The tadpoles adhere to rocks in the current with their sucker mouth. Tadpoles seem to avoid fast currents or cascades.

REPRODUCTION
Frogs perch up to 8 m above a stream to seek a mate. Small foam nests are produced and attached to vegetation overhanging a stream. Tadpoles hatch from the nest and fall into the stream below.

COLORATION
The general background color is dark brown on the head and trunk and a beige to brown for the muscular part of the tail. Body finely stippled with bright iridophores over dark background. Dark brown pigmentation extends from the trunk to the muscular part of the tail where it is arranged in a approximately a dozen diffuse dark blotches on the tail. Red gills and heart faintly visible trough the translucent ventral skin. A patch of iridophores covers the heart. Skin below gills stippled with iridophores. Abdomen opaque silver with a distinct streak in the mid-line. Gut coils covered by silvery iridocyte sheath ventrally. Tail fins mostly clear with scattered melanophores and iridophores. Major lateral tail vein and some myosepta are discernible.

LITERATURE

Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series. 26: 1–89.

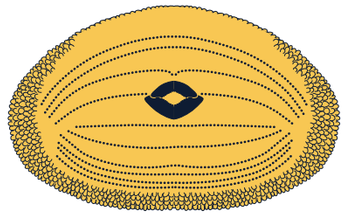
Inger, R.F., Tan, F.L. (1990) Recently discovered and newly assigned frog larvae (Ranidae and Rhacophoridae) from Borneo. The Raffles Bulletin of Zoology, 38: 3–9.

Leptomantis penanorum (Dehling, 2008)

Penan Flying Frog

SNOUT
Expanded, broadly rounded. Profile smoothly convex and sloping in lateral view.

ORAL DISC
Ventral and, in adhesion state, wider than snout. Sucker without emargination between upper and lower lip.



Lower and side parts of lip bear multiple rows of marginal and submarginal papillae, reduced on the upper lip. LTRF ranges from 4(4)/6 to 4(4)/7 (in the latter, row seven can be incomplete). Third upper row with an indentation, but no gap in keratodonts in the specimen examined. Upper and lower lip keratodont rows long and spanning most of oral disc. Relative to disc, jaws small yet strongly built, black. Keratinized black part of upper jaw less wide than lower jaw. Jaw edges equipped with coarse and blunt serrations.

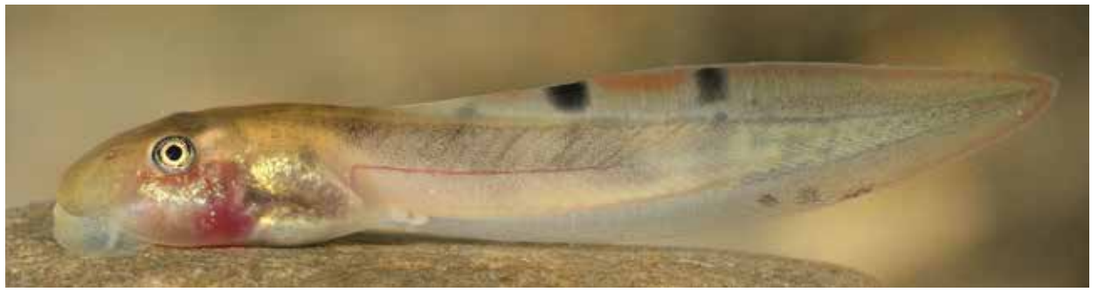
NOSTRILS & EYES
The nostril is approximately midway between the eye and the snout and slightly elevated. The eyes are dorsolateral in position and do not reach or project beyond the body contour. The iris and eyeball outside the iris are densely stippled with pale golden iridocytes on a black background. Towards the pupil the pigments merge into a solid golden ring.

BODY
Streamlined. In dorsal view, the body contour is inverted dropletshaped or pear-shaped, i.e., the head is wider than the trunk. Body dorsoventrally depressed. Head widest posterior to eyes, followed by a soft constriction at the transition from head to trunk. Spiracle sinistral and low, below mid-body axis in lateral view. Spiracular orifice free, not fused to body wall, directed posteriorly.

TAIL
Strongly muscular, long (approx. 64% of total length). Tail base almost as deep as trunk at their junction. Dorsal fin starts at trunk-tail junction. Dorsal fin exceeds the lower fin in height. Maximum tail height at about mid-tail position. Fin contours shallowly convex. Tail fins taper gradually and end in a moderately narrow rounded tip.

ECOMORPH
Lotic, exotrophic, adherent–suctorial, rheophilous.

SIMILAR SPECIES
Leptomantis penanorum tadpoles are distinct in their morphological features but can potentially be confused with *L. angulirostris* tadpoles. Distinguishing features have not been established by large samples. Dorsal coloration and tail fin coloration seem to separate *L. penanorum* from *L. angulirostris* samples, as well as a relatively longer snout, flatter slope of it, longer tail, reduced marginal papillae on upper lip, and one more rows of keratodonts on the lower lip in *L. penanorum*. Among Bornean *Leptomantis*, only these two species have been reported to possess the conspicuous black spots on their tail fins.

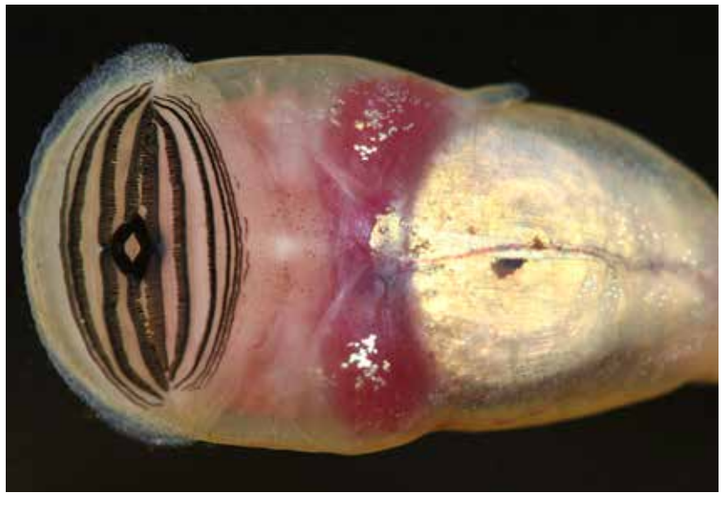


Tadpoles of Leptomantis penanorum *are restricted to high elevation, clear, rocky mountain streams. Their body shape is typical for rheophilous tadpoles.*

HABITAT & ECOLOGY
The known exemplars were recorded from approximately 1650 m elevation at Gunung Mulu in primary forest. Another population has been encountered at Gunung Hose at approximately 1000 m. The elevation range and the details of the ecological needs are mostly unknown. The tadpoles are adapted to a life in clear mountain streams. Only few tadpoles have been documented, limiting our knowledge about the species' variability. The tadpoles were found in small shallow stony pools with moderate current, which are interconnected by steep, narrow channels on bedrock. Tadpoles seemed to avoid channels with high water velocity.

REPRODUCTION
Dehling (2008) reported that males call at irregular intervals between 30 secs and 1 min. The call was described as a very short trill, without a significant frequency modulation within the notes of a single call. The dominant frequency spectrum of the notes was 3900–4600 Hz. Males present themselves bright green at night.

COLORATION
Generally pale amber above, with some dark brown dusting on the trunk and the muscular part of the tail. A patch of scattered golden pigment cells covers the top of the head between the eyes and behind. More golden pigment is located below the eye and at the flanks. Red gills visible through the cheek's skin. Gills and heart visible through the translucent ventral skin. Each of the gill areas and the heart bear a spot of silvery shining pigment cells. Abdomen opaque silver with a median longitudinal streak (Vena abdominalis). Gut coils obscured by iridocyte layer. Few clear round black spots are present on the otherwise clear tail fins. Edge of upper fin and edge of the posterior lower fin tinted orange. Major lateral tail vein and some myosepta discernible.



LITERATURE

Dehling, M. (2008) A new treefrog (Anura: Rhacophoridae: *Rhacophorus*) from Gunung Mulu, Borneo. Salamandra 44: 193–205.

Haas, A., Hertwig, S.T., Krings, W., Braskamp, E., Dehling, J.M., Min, P.Y., Jankowsky, A., Das, I. (2012) Description of three *Rhacophorus* tadpoles (Lissamphibia: Anura: Rhacophoridae) from Sarawak, Malaysia (Borneo). Zootaxa 3328: 1–19.

STAGNANT WATER BODIES

Stagnant waters have tadpole fauna distinct from flowing water communities. Highly efficient suspension-feeding tadpoles play an important role in stagnant water communities.

PONDS, POOLS, PUDDLES, WALLOWS
Pond here refers to any isolated body of water on the ground that is at least 5 m² in area. Smaller (< 5 m²), shallow, temporary bodies may be called puddles. Both are essentially water-filled depressions on the forest floor, often with silty bottoms that prevent drainage. Vast pools can form in riparian forests after heavy rainfall. Pigs create wallows, that are frequently used by some frog species for reproduction. Stagnant waters often have frog assemblages that are completely different from those encountered in flowing waters.

PHYTOTELMATA
A phytotelma refers to a stagnant body of water contained within a plant. Examples include tree holes, pitchers of *Nepenthes*, cavities in fallen logs and fruits, bamboo internodes, buttress anastomoses, and leave axils. The volume of fluid contained in such bodies can range from a few centiliters to several liters.

ISOLATED STREAM POOLS
Pot holes and other isolated pools on stream banks, or on the rocky stream bed, qualify as stagnant water bodies, as long as they have no connection with the water current, and attract species that avoid the stream itself. There seems to be a transition from quiet side-pools with connection to the stream to completely isolated pools. Only few species use both stagnant and flowing water bodies for their larval phase.

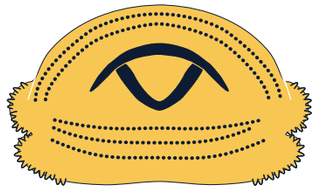
The famous Frog Pond at Kubah National Park has a rich amphibian fauna. Among others, year-round breeding colonies of *Rhacophorus pardalis*, *Polypedates otilophus*, *Polypedates macrotis*, *Chalcorana raniceps*, and *Microhyla malang* may be encountered. Such large bodies of standing water are rare in hilly terrain, their levels fluctuating with rainfall.

Duttaphrynus melanostictus (Schneider, 1799)

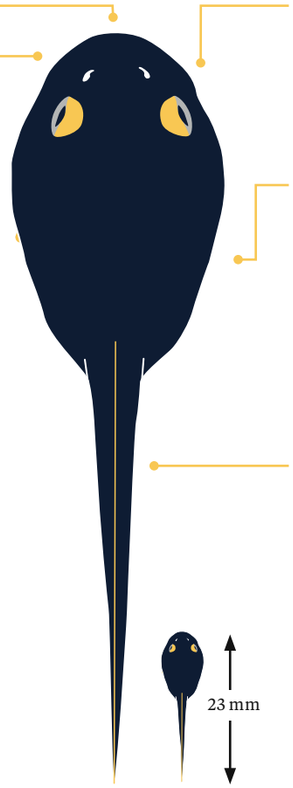
Asian Common Toad

SNOUT
In dorsal view, snout slightly tapering, yet broadly rounded. Profile rounded, steep and short.

ORAL DISC
Ventral in orientation. Papillation on both lips only in their lateral parts. Clear lateral indentation between upper and lower lip.
Two undivided labial tooth rows on



upper, three on lower lip (LTRF 2/3). Upper and lower beaks undivided. Beaks moderately strong. Upper beak braodly arching. Lower jaw V- to U-shaped



NOSTRILS & EYES
Nostril moderately large. Medial rim with soft bulge. Nostril closer to eye than to tip of snout. Eyes dorsolateral. Iris black with scattered iridophores around pupil edge of iris.

BODY
Ovoid in lateral view. Weakly rhomboid in dorsal view without distinct constriction at head-trunk transition. Wider than high, i.e., slightly depressed dorsoventrally. Widest point of body silhouette behind level eyes. Spiracle sinistral and attached to body wall, below mid-body axis in lateral view.

TAIL
Short, approximately 58% of total length. Muscular part moderate to narrow. Fins start at trunk-tail junction. Fins rise moderately high, shallowly convex in contour. Upper and lower fin ending in a blunt, rounded tip. Lateral tail vein invisible.

ECOMORPH
Lentic, benthic, exotrophic.

SIMILAR SPECIES
Near rhomboidal body shape with widest point behind the eyes in combination with a rather short tail, modest swimming performance, unpapillated gaps in upper, and lower lips, and LTRF 2/3 are typical for many toads (see *Ansonia* for exceptions). On Borneo, *D. melanostictus* may potentially be confused with *Ingerophrynus divergens* or *I. quadriporcatus* in some cases, but can be distinguished by deep black color (dorsal and ventral) and habitat choice. Tadpoles of *Kurixalus chaseni* (Rhacophoridae) are similar in size and general body shape at first glance. They live in forest ponds and puddles; however, they are distinguished from *D. melanostictus*, *I. divergens*, *I. quadriporcatus*, and *Rentapia hosii* by fully papillated lower lip and keratodont arrangement, as well as coloration (see there).

Duttaphrynus melanostictus *is a common toad all over Southeast Asia. It inhabits open country and rural areas. On the island of Borneo this species is usually found in cities, villages, along roads, and in agricultural areas.*

HABITAT & ECOLOGY
The small black larvae of *D. melanostictus* live in temporary to semi-permanent roadside ditches, flooded lawns, puddles and ponds with silty bottom in agricultural areas, or even in temporarily flooded parking lots. Tadpoles may occur in association with the few other species that will easily tolerate anthropogenic alterations of landscape: *Kaloula pulchra* and *Fejervarya limnocharis*. When present, tadpoles of *D. melanostictus* occur in large numbers. They stay on the bottom of the pool and feed at bottom particles, such as algae, silt with associated microbes.

REPRODUCTION
Males clasp females around the armpits (axillary amplexus). 1.000–40.000 eggs per female spawning have been reported. Eggs are laid in strings. In sun exposed ponds, develop of eggs and tadpoles is rapid.

COLORATION
Body black; scattered tiny white pigment cells can be seen in high magnification close-up. Muscular part of tail dark brown to black, dorsal tail fin with scattered dark melanocytes, ventral tail fin mostly unpigmented. Viscera darkly-pigmented, faintly visible. A closer look reveals that much of the dark pigmentation is not in the skin itself but at deeper body layers, giving the tadpole a sort of double silhouette in dorsal or ventral views. Evenly distributed moderately dense silver iridocytes contrast with the black background coloration at higher magnification.

LITERATURE

Leong T. M, Chou L. M. (1999) Larval diversity and development in the Singapore Anura (Amphibia). The Raffles Bulletin of Zoology 47: 81–137.

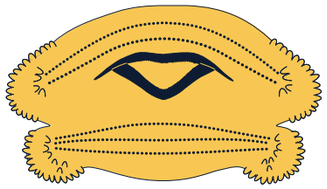
Chou, W., Lin, J. (1997) Tadpoles of Taiwan. Special Publication National Museum of Natural Science, 7: 1–98.

Ingerophrynus quadriporcatus (Boulenger, 1887)

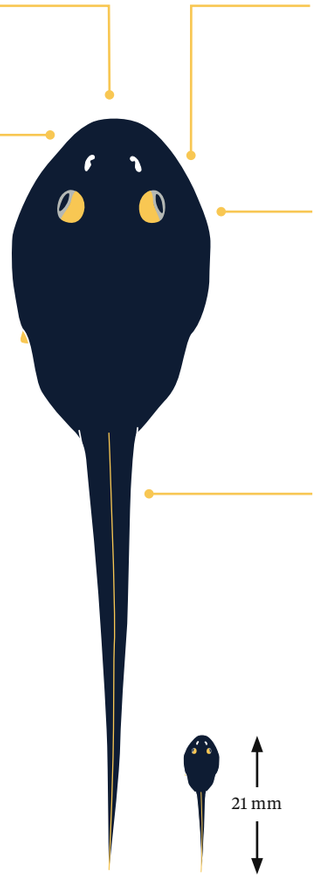
Swamp Toad

SNOUT
Tapering but rounded in dorsal view. Moderately long and smoothly rounded in lateral view.

ORAL DISC
Ventral to anteroventral in orientation, much narrower than maximum width of body. Marginal papillae on both lips only in their lateral parts. Marginal papillae small. 0–5 submarginal papillae may be present at areas where keratodont rows end.



A clear lateral indentation separates upper and lower lip. Two undivided labial tooth rows on upper, three on lower lip (LTRF 2/3). Upper and lower beaks undivided. Beaks narrow. Beak edges bear very fine serration. Upper beaks weakly swung and slightly M-shaped, lower beak a wide open V.



NOSTRILS & EYES
Nostrils conspicuously large. Medial rim with triangular process. Nostrils closer to eyes than to tip of snout. Eyes dorsolateral. Iris black with scattered iridophores around pupil edge of iris.

BODY
Ovoid in lateral view. Wider than high, slightly depressed dorsoventrally. Near rhomboidal in dorsal view with slight constriction at head-trunk transition. Widest point of head-body silhouette is behind the eyes. Spiracle attached to body wall, below mid-body axis in lateral view.

TAIL
Short, approximately 60% of total length. Muscular part moderate to narrow. Fins start at trunk-tail junction but upper fin keeps low for a short distance before it arches up. Fins become relatively high and end in a blunt, rounded tip. The overall shape of the tail fin resembles a spear blade.

ECOMORPH
Lentic, benthic, exotrophic.

SIMILAR SPECIES
The tadpole is similar to that of *Ingerophrynus divergens*. The latter possesses a dark blotch in the upper flank behind gill region. Although based on limited samples, the snout seems slightly more expanded, the mouth more anteroventral, and the dorsal tail fin more convexly arched in *I. quadriporcatus* than in *I. divergens*. *Duttaphrynus melanostictus* is similar in body silhouette but deep black in color above and below with fine white dotting. Ecology separates the species further: larvae of *I. quadriporcatus* are found in peat swamp habitats, whereas, *I. divergens* is a lowland dipterocarp and alluvial forest inhabitant, *D. melanostictus* is only found in human-modified habitats, and *Rentapia hosii* exclusively along mid-sized, clear, lowland streams in primary or secondary forests..

Ingerophrynus quadriporcatus *is a medium-sized toad of lowland peat swamp areas. The tadpoles are typical bufonid tadpoles in several features.*

HABITAT & ECOLOGY
We found tadpoles of this species in pools in flooded terrain of coastal forests. The pools were peaty and contained leaf litter. The tadpoles were observed to be bottom dwellers that feed on the various small particles at the bottom of the pools in which they live.

COLORATION
Dark brown above. Braincase (between and behind eyes) pigmented black. Brown pigmentation extends onto tail but fades towards tail tip. Tail fins mostly clear. Unpigmented below, inner organs visible.

REPRODUCTION
No pertinent details on reproduction are available for this species.

LITERATURE

Leong, T.M., Chou, L.M. (1999) Larval diversity and development in the Singapore Anura (Amphibia). The Raffles Bulletin of Zoology 47: 81–137.

Pelophryne misera (Mocquard, 1890)

Kinabalu Dwarf Toad

Tadpoles of species in the genus Pelophryne *are mostly unknown,* P. signata *and* P. misera *being the only exceptions*

TADPOLE DESCRIPTION

Malkmus (1996a, b) and Malkmus et al. (2002) published photos of eggs, a tadpole, and a metamorph. They described the tadpole as follows: Head-body of tadpole ovoid; eyes dorsolateral; oral disc ventral and subterminal; one row of keratodonts on upper lip (LTRF 1/0); beaks weak; spiracle not tubular; body and caudal muscle blackish brown, fins lighter; max. length 13 mm; 5.8 mm after metamorphosis.

HABITAT, ECOLOGY & REPRODUCTION

The species is endemic to the Gunung Kinabalu area, above 1400 m a.s.l. *Pelophryne misera* lives in the leaf litter of mossy forests and uses small accumulations of water for reproduction. Males are commonly encountered calling from low vegetation. Only one clutch has ever been reported in a water-filled leaf on the ground. It contained 10 pale eggs, each measuring 2.8 mm in diameter.

SIMILAR SPECIES

The tadpoles of *P. misera* seem similar to those of *P. signata* (see there), but are unlikely to be confused in the field due to separation by habitat and altitude in these two species. Possibly *P. misera* could be confused with tadpoles of the sympatric *Kalophrynus baluensis*. Although the tadpoles of the latter have not been described, it is likely that they are endotrophic as well (see *Kalophrynus*, pp. 216, 218).

ECOMORPH

Exotrophic, phytotelma specialist.

LITERATURE

Malkmus, R. (1996a): Voortplanting van de Dwergpad *Pelophryne misera*- Lacerta, 54: 129-133.

Malkmus, R. (1996b): Herpetologische Beobachtungen am Mt. Kinabalu, Nord-Borneo V - Mitteilungen des Zoologischen Museums, Berlin; 72: 277- 295.

Malkmus, R., Manthey, U., Vogel, G., Hoffmann, P., Kosuch, J. (2002) Amphibians & Reptiles of Mount Kinabalu (North Borneo). Koeltz Scientific Books, Königstein. 424 pp.

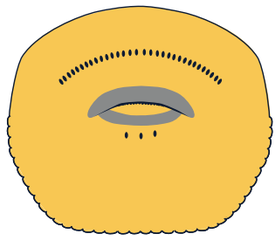
Mist in the forest of Gunung Kinabalu, Park HQ.

Pelophryne signata (Boulenger, 1895)

Lowland Dwarf Toad

SNOUT
Short, bluntly rounded to truncated in dorsal view; rounded in lateral view.

ORAL DISC
Ventral, small (< 50% head width). Near-circular shape. No marginal papillae on upper lip.



Papillae on lower lip very reduced giving the lip a wavy contour. A single labial tooth row is present on the upper and lower lip (LTRF 1/1). Keratodonts widely spaced, especially on lower lip row. Jaw sheaths distinct but unkeratinized or thinly keratinized along their margins.

NOSTRILS & EYES
Nostrils closer to snout than to eye, oriented laterally. Eyes lateral, cornea protruding beyond body contour. Eyes relatively large. Iris black.

BODY
Slightly depressed dorsoventrally. Oval in dorsal view (bulging elbows in advanced stages). Spiracle sinistral, well below head-body mid axis.

TAIL
Long, approximately 67% of total length. Muscular part moderately strong. Dorsal tail fin starts slightly anterior to trunk-tail junction. It mostly lacks convexity and is relatively flat in contour, approximately parallel to ventral tail fin. Both fins are moderately high. Tail tip broadly rounded.

ECOMORPH
Phytotelma specialist, endotrophic.

SIMILAR SPECIES
Other tadpoles that live in small phytotelmata, such as tree holes or *Nepenthes* pitchers, are *Kalophrynus* larvae, *Metaphrynella sundana* and tadpoles of at least two species of *Microhyla* and one *Philautus*. *Philautus nepenthophilus* lacks mouthparts. The microhylids have median spiracles, terminal mouth openings, lack oral discs, lack keratinized mouth structures, and, in *M. nepenthicola*, have tail shapes clearly different from *Pelophryne* tadpoles. The spiracular opening is difficult to see in these very small phytotelma-inhabiting tadpoles and requires optical instruments for magnification. However, the oral disc in *P. signata* is a distinguishing feature potentially applicable in the field. The published larval description of *P. misera* (see there) is similar to the description of *P. signata*. Their shared features may be shared by other *Pelophryne* species as well. Due to similarity and lack of data, *Pelophryne* tadpoles might be indistinguishable morphologically at this time. Presence of adults in the habitat, ecology of the species, and DNA matching need to be considered for identification of tadpoles within the genus.

Pelophryne signata *is widely distributed in primary and old secondary forest in lowland and hilly regions. Adults are encountered in many areas, usually in low numbers, and tadpoles are difficult to find.*

HABITAT & ECOLOGY
The tadpoles develop in small phytotelmata. Their mouthparts are somewhat reduced and the belly is filled with yolk; both suggests an endotrophic mode of development. Usually, development in endotrophic tadpoles is fast, however, data are not available for this species.

REPRODUCTION
Males call from vegetation near a suitable phytotelma. Current evidence suggests that the species utilizes very small phytotelmata for larval development. Thirteen tadpoles of the closely related *P. ingeri* were found in a small tree hole (3 cm diameter, 2 cm deep). The specimen presented here was discovered inside water-filled PVC pipes at the base of Gunung Santubong.

COLORATION
Dark grayish dorsally. Ventrally much less pigmentation, inner organs visible through translucent skin, especially the yolk rich, cream-colored gut. Body and tail are dusted with iridocytes. Some melanocytes along base of tail. Muscular part of tail pale whitish, tail fins relatively clear.

LITERATURE

Denzer, W. (1994) Tree hole breeding in the toad *Pelophryne brevipes* (Peters, 1867). Amphibia-Reptilia 15: 224–226.

Leong, T.M., Teo, S.C. (2009) Endotrophic tadpoles of the Saint Andrew's Cross Toadlet, *Pelophryne signata* (Amphibia: Anura: Bufonidae) in Singapore. Nature in Singapore 2: 21–25. [now recognized as *P. ingeri*]

Malkmus, R., Dehling, J.M. (2008) Anuran amphibians of Borneo as phytotelm-breeders - a synopsis. Herpetozoa 20: 165–172.

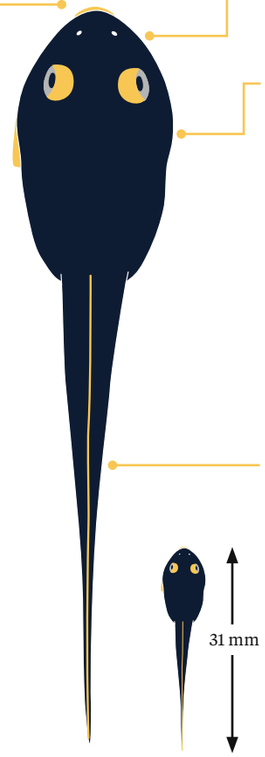
Fejervarya limnocharis (Gravenhorst, 1829)

Grass Frog

SNOUT
Smoothly triangular in dorsal view, slightly pointed. In lateral view, moderately long, distinctly arched at level of nostril, giving the snout a truncated appearance in profile. Oral disc slightly projects beyond snout in dorsal view.

ORAL DISC
Anteroventral, far anterior at snout so that upper lip usually projects beyond snout contour.

A clear emargination separates upper and lower lips. Blunt papillae present along margin, except for a broad gap in papillation medially in upper lip and a small medial gap in the lower lip. Submarginal papillae present in low numbers. LTRF 2(2)/3. Beaks moderately keratinized; jaw edges bear fine serrations. Upper beak broadly and shallowly arched and medially higher; lower beak widely V-shaped.



NOSTRILS & EYES
Eye dorsolateral with moderate interorbital space. Nostril with a smooth rim, closer to snout than to eye and oriented anterolaterally. Iris brass to gold. Iridocytes form a complete ring around pupil and are less dense in the anterior and posterior sector, both of which appear darker.

BODY
Oval in contour in dorsal view. Head wider than trunk, with a subtle constriction of contour between the two. Widest point of body at level of gill region. Shape of head a smooth triangle in dorsal view. Body dorsoventrally depressed. Spiracle sinistral, opening posteriorly or posterolaterally. Medial rim of spiracular orifice distinct. A short free spiracular tube located below mid-body level in lateral view. Lateral line organs visible on head and trunk.

TAIL
Moderately long, 62–63% of total length. Muscular part of tail moderately strong, over half of body height in lateral view, less than half of maximum trunk width in dorsal view. Upper fin starts at trunk-tail junction. Upper fin starts with a straight edge in first third of tail and forms a convexity at mid-tail where fin is highest. From there on, it slopes downwards with a straight contour line towards a narrowly rounded tip. Lower fin lower than upper fin and less arching. Lateral tail vein often masked by pigmentation. Tail myosepta indistinct.

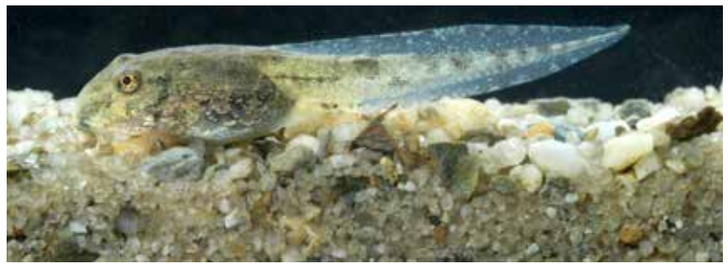
ECOMORPH
Lentic, benthic, exotrophic.

SIMILAR SPECIES
The tadpoles are relatively easy to identify by a combination of habitat, body color, oral disc features and unique belly color pattern (disappears in preservation). Tadpoles of *F. limnocharis* and *F. cancrivora* are similar and may be indistinguishable in a field situation; it may be necessary to take DNA samples or differentiate the tadpoles ecologically. *F. cancrivora* tolerates high salt content in the water. Such habitats (for example, coastal ponds, mangroves) will exclude *F. limnocharis*. Leong and Chou (1999) reported that *F. cancrivora* tadpoles grow larger (up to 36 mm). Both species share the same LTRF and general oral disc configuration (gaps in papillation, infralabial papillae); yet, it has been reported that the third keratodont row on the lower lip is relatively longer in *F. cancrivora* (>0.5 x second row). Schijsfma (1932) pointed out that the character is variable in *F. limnocharis*. Inger (1985) reported a more heavily pigmented posterior tail in *F. cancrivora*. Clearly, the full spectrum of intraspecific variation has not been explored and the potentially distinguishing features need more research.

Fejervarya limnocharis *is one of the few Bornean species that breed close to or within human settlements. The generalized pond-type tadpole can occur in large numbers in often man-created standing water bodies.*

HABITAT & ECOLOGY
Fejervarya limnocharis takes advantage of artificial modifications of the environment by humans. It needs open country and prefers shallow water bodies for reproduction. Tadpoles can be found in roadside ditches, rice fields, puddles, flooded lawns, sports fields or parking lots. These sun-exposed and shallow temporary pools of water will heat up to well above 30°C and tend to dry up quickly. The warmer the pool, the faster the tadpoles develop; it takes less than 3–4 weeks for the froglet to emerge from the pool. The tadpoles forage mostly at the bottom of the pools.

REPRODUCTION
Calling activity is stimulated by rainfall and males may congregate at flooded areas after heavy rainfall; their loud rasping chirps can be heard from far away. The small eggs are floating in a single-layer jelly mass on the water surface.



COLORATION
Tadpole generally brown, gray or olive above, with irregular pattern of diffuse darker and lighter areas. This mottling continues onto the sides of the body and tail. Often with diffuse darker bar between oral disc and eye and blurred short horizontal dark line posterior to eye. The abdominal skin is completely silver with at conspicuous mid-belly line. The gut is not visible through the venter. The gill, buccal, and gular region can either be clear (gills and heart clearly visible) or partly covered by large patches of silver. Few scattered melanocytes are present in the gular and lateral buccal region of the ventral skin. The lateral tail vein is masked by dark pigmentation and, thus, the root of the tail often bears a horizontal dark line laterally. The tail and its fins are mottled with patches of dark and light (iridophores) pigmentation; these dark flecks can be arranged such that a barred pattern arises on the mid and posterior tail.

LITERATURE
Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

Leong, T.M., Chou, L.M. (1999) Larval diversity and development in the Singapore Anura (Amphibia). The Raffles Bulletin of Zoology 47: 81–137.

Schijfsma, K. (1932) Notes on some tadpoles and frogs from Java. Truebia 14: 43–72.

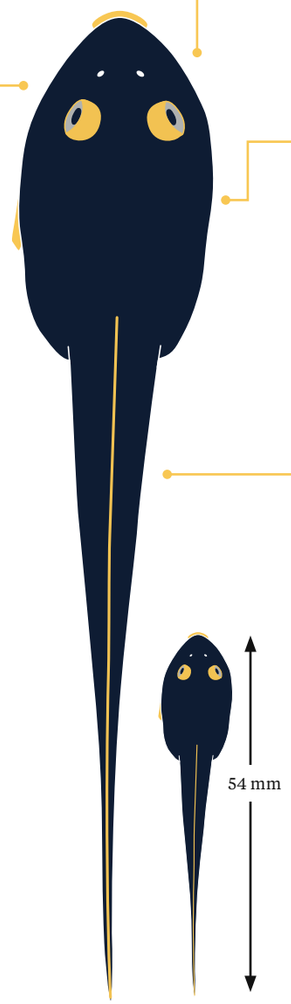
Hoplobatrachus rugulosus (Wiegmann, 1834)

Taiwanese Bullfrog

SNOUT
Smoothly triangular in dorsal view, slightly pointed. Snout long in lateral view, sloping downward from eyes forward with convex profile. Oral disc slightly projects beyond snout in dorsal view.

ORAL DISC
(Redrawn from Grosjean et al. 2004) moderately wide and located anteroventrally to terminally; upper lip projects beyond the snout contour. An emargination separates upper and lower lips.

Disc bears a continuous row of blunt and almost indistinct marginal papillae. Submarginal papillae absent. LTRF 4(3–4)/5(1–4). Keratodont ridges bear double rows of conical, needle-like keratodonts. Beaks strongly keratinized; upper jaw sheath with medial sharp, tooth-like projection, lower jaw sheath with two projections; additional spurs set back in the oral cavity.



NOSTRILS & EYES
Eyes positioned dorsolaterally with moderate interorbital space. Nostril slightly rimmed, closer to eye than to snout. Iris color brass to gold. Iridocytes form a complete ring around the pupil.

BODY
Oval in dorsal view. Head wider than the trunk. Widest point of body at level gill region of the head. Shape of head a smooth triangle in dorsal view. Body dorsoventrally depressed. Spiracle sinistral, opening posteriorly or posterolaterally, below body axis in lateral view. Medial rim of the spiracular orifice distinct; it forms a short free tube. Lateral line organs indistinct.

TAIL
65% of the total length. Muscular part of the tail strong, more than half of body height in lateral view, approximately half of the maximum trunk width in dorsal view. Upper fin starts at trunk-tail junction or even slightly anterior to it. Upper fin forms a convex arch of moderate height. Lower fin more straight than upper fin and less high. Tail tip narrowly rounded. Lateral tail vein and myoseptal vessels in first quarter of tail accentuated by melanocytes.

ECOMORPH
Lentic-benthic, exotrophic, carnivorous.

SIMILAR SPECIES
The mouthparts of *H. rugulosus* are unique among Bornean tadpoles: strong jaw sheaths with tooth-like projections, keratinized spurs in the oral cavity, and double labial tooth rows. These features allow unequivocal identification. Apart from the mouthparts, the overall body shape and coloration is somewhat reminiscent of *F. limnocharis* or *F. cancrivora*, which occur in similar open or disturbed habitats; however, *H. rugulosus* tadpoles grow almost twice as large as *Fejervarya* species.

Tadpoles of the invasive Hoplobatrachus rugulosus *grow large and can be predators of smaller tadpoles. For that purpose, the mouth is oriented more forward than in most other dicroglossid tadpoles. Records for Borneo have been mostly from Sabah. Parts of the description follows Grosjean et al. (2004).*

HABITAT & ECOLOGY
Hoplobatrachus rugulosus has been introduced to Borneo most likely in the 1960s as a source of food. The species occurs in agricultural or urban settings. Tadpoles live in temporary pools, flooded depressions, pools at construction sites, or rice paddies. With their massive jaws, they are able to prey on smaller tadpoles that occur in the same disturbed habitats.

REPRODUCTION
The call consists of a series of up to 20 raspy, guttural notes.

LITERATURE
Grosjean, S., Vences, M., Dubois, A. (2004) Evolutionary significance of oral morphology in the carnivorous tadpoles of tiger frogs, genus *Hoplobatrachus* (Ranidae). Biological Journal Linnean Society 81: 171–181

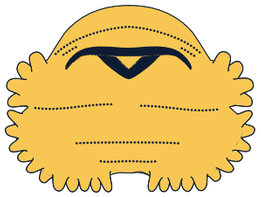
COLORATION
Generally brown, gray or olive above, with irregular pattern of diffuse darker and lighter areas. The mottling continues onto the sides of the body and upper muscular part of tail. At the side of the body is a sharp transition to the silver-white color of the venter. Belly opaque, gut coil is not visible, gills are mostly concealed. Upper fin is with some pigmentation, lower fin is mostly clear.

Limnonectes finchi (Inger, 1966)

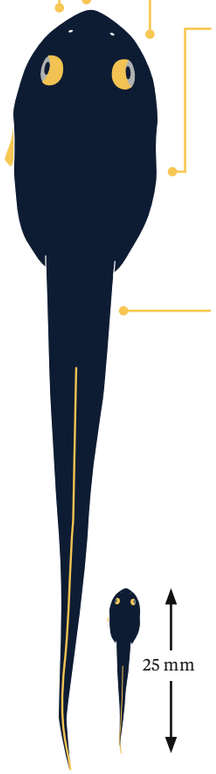
Rough Guardian Frog

SNOUT
Smoothly triangular in dorsal view, with a small protruding, slightly truncated part medially. Snout moderately long; its contour tapering to a narrowly rounded tip in lateral view. Oral disc may project laterally from under the snout in dorsal view.

ORAL DISC
Small (one fourth of head width or less), ventral. It reaches snout contour but does not project beyond it in dorsal view. A clear emargination separates upper and lower lips. Blunt papillae along their margins, except for a broad gap in papillation medially in upper lip and a narrow medial gap in lower lip.



Marginal papillae relatively thick and low in number, arranged in a staggered single row on the lower lip, so that they may appear as if standing in a double-row. Submarginal papillae absent. LTRF 2(2)/3(1). Beaks moderately strong, well keratinized but thin; their edges bear fine serrations. Upper beak almost straight medially and arched laterally; the lower jaw sheath is in the shape of a wide V.



NOSTRILS & EYES
Eyes dorsolateral. Nostrils closer to snout than to eye, oriented anterolaterally. Nostril moderate in size, rim smooth. Iris dotted with brass to gold iridocytes. Iris iridocytes form a solid ring around the pupil and are less dense in the anterior and posterior sectors; in some individuals, there may also be narrow areas devoid of iridocytes in the upper and lower sector, forming vertical black streaks.

BODY
Small to medium-sized. In dorsal view, the general body contour is oval. Head as wide as trunk. Widest point of body is the level of gill region. Head shape smoothly triangular in dorsal view. Body dorsoventrally depressed. Spiracle sinistral, opening posteriorly. Medial rim of spiracular orifice attached to body wall. Spiracular orifice below the mid-body level in lateral view. Lateral line organs indistinct.

TAIL
Approximately 67% of total length. Muscular part strong, almost as high as trunk in lateral view; half of the maximum trunk width in dorsal view. Origin of upper fin far posterior at approximately 20% of tail length. Upper fin is higher and more convex in contour than lower fin; however, the arching is relatively shallow. Upper fin starts with a flat section and then abruptly rises up. In the posterior fifth, the fins converge into a narrowly rounded tip with slight concavity in the contour lines of the fins so that the tail tip is weakly cuspidate. Maximum tail height at mid-tail level or slightly posterior. Lateral tail vein and tail myosepta indistinct.

ECOMORPH
Lentic, benthic, exotrophic.

SIMILAR SPECIES
Limnonectes finchi tadpoles can be diagnosed from many other Bornean tadpoles of other genera by their LTRF 2(2)/3(1). However, body shape, relatively small oral disc, low count of keratodont rows, benthic habits of *Limnonectes finchi* tadpoles are features that are similar to other *Limnonectes* species. The bodies of *Limnonectes finchi* and *L. palavanensis* appear more dorsoventrally depressed than those of Creek Frog tadpoles (that is, members of the "*L. kuhlii*" complex). Creek Frog tadpoles also have a more bluntly rounded, less tapering, snout in lateral view. *Limnonectes ingeri*, *L. leporinus*, *L. malesianus* and *L. paramacrodon* can be excluded by their respective LTRF (only one upper lip keratodont row). *Limnonectes finchi* and *L. palavanensis* stand out among *Limnonectes* by the contour of the tail fins and relatively low fins.

The tadpoles of Limnonectes finchi *are carried by the male to standing bodies of water, such as ponds, and slow moving small streams. Tadpoles are small to medium-sized, and inconspicuous at the bottom of the pool. When disturbed, they hide in the fine mud layer.*

HABITAT & ECOLOGY
Limnonectes finchi tadpoles have been observed in shallow muddy forest pools, pig wallows, muddy stagnant sections of small forest streams. The tadpoles are benthic. They stay close to the bottom when foraging. The composition of their diet has not been analyzed in detail; most likely they feed opportunistically on small items of organic matter such as algae, decaying plant material and microscopic organisms.

REPRODUCTION
The male calls to attract the female to a suitable nest site. The egg clutch is laid on land, under leaf litter. The male guards the clutch. When the tadpoles hatch from the eggs, they climb the back of the male, which then carries the tadpoles to the nearest suitable body of water, where the tadpoles disperse and develop independently.

COLORATION
Mostly brown to olive brown above. Head and trunk lack a well-defined pattern; rather, they have diffuse darker and lighter areas, dotted with black scattered melanocytes. In lateral view, the lower face of the head and the lower flanks may have irregular dark markings; on top of that background there are lots of horizontally oriented dashes of silver iridocytes. Ventral skin transparent, with only a few scattered iridocytes; gills and gut coil visible. The body's background color continues onto the dorsal tail. Clusters of well-defined black dots (round melanocytes) form irregular flecks along the sides of tail, including the fins (less so in the proximal lower fin); the pattern may be accentuated in the posterior third of the tail. At high magnification, vermiculate melanocytes can be seen, especially in the skin of the proximal upper fin. Tail and tail fins also bear scattered clusters of pale, shiny iridocytes.

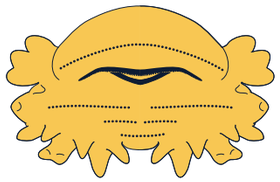
LITERATURE
Inger RF (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series. 26: 1–89.

Limnonectes ingeri (Kiew, 1978)

Inger's River Frog

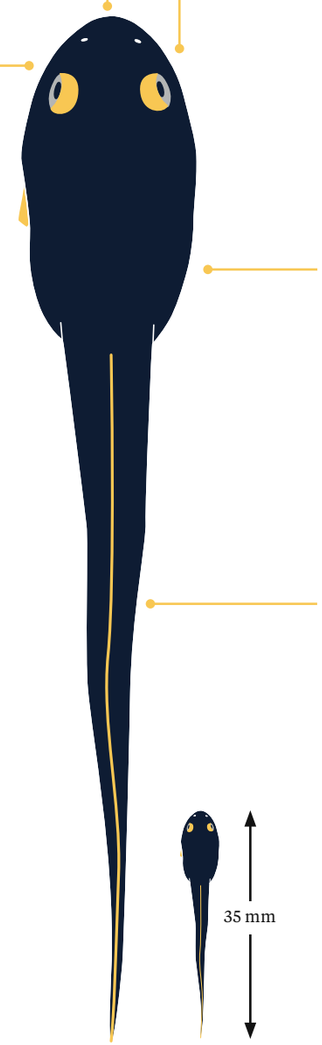
SNOUT
Smoothly arched in dorsal view, contour bluntly rounded, not distinctly tapering. Snout moderately long. Oral disc does not project beyond the snout in dorsal view.

ORAL DISC
Moderately large, approximately 30% of head width, anteroventral in orientation, not projecting beyond snout contour in dorsal view. An emargination sets the upper lip apart from the lower lip.



Oral disc with papillae along its margin, except for a wide gap in the upper lip and a narrower gap in the lower lip. Marginal papillae are large and low in number, arranged in a staggered way on the lower lip so that they seem to stand in a double-row. Submarginal papillae are absent. LTRF 1/3(1–2) or 1/3(1). Beaks thin, highly keratinized but not high; their edges bear fine serrations. Upper beak very shallowly convex medially and concavely arched laterally; lower jaw sheath in the shape of a flat wide V.

ECOMORPH
Lentic (possibly tolerating slight current), benthic, exotrophic.

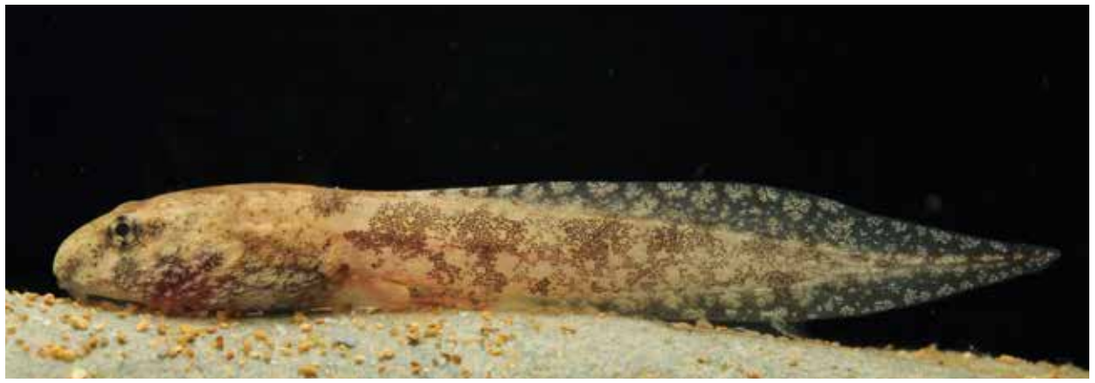


NOSTRILS & EYES
Eyes dorsolateral, spaced relatively widely apart. Nostril anterolaterally oriented, closer to snout than to eye, well-developed but difficult to see. Nostril rim without distinct projection. Iris dotted with gold iridocytes on black background. Iridocytes form an almost complete ring around the pupil (small gaps dorsally and ventrally); less dense stippling in the anterior, posterior, upper and lower sectors generates a radial iris pattern.

BODY
Head wider than trunk. Widest point of body at gill region of head. Anterior head contour smoothly rounded in dorsal view. Body dorsoventrally depressed. Spiracle sinistral, opening posteriorly. Medial rim of spiracular orifice free from body wall; spiracle forms a short free tube. Spiracle located at the mid-body level in lateral view. Lateral line organs indistinct.

TAIL
Long, up to 70% of total length. Muscular part of tail moderately strong. In dorsal view, tail muscle less than half of the maximum trunk width, and slightly less high than trunk in lateral view. Upper fin originates slightly posterior to trunk-tail junction, at 5-7% of tail length. Upper fin is higher than lower fin and arches moderately. In posterior fourth of tail, fins converge into an acute tip. Overall, tail elegantly lancet shaped. Maximum tail height at mid-tail level or slightly posterior. Lateral tail vein masked by pigmentation, tail myosepta indistinct.

SIMILAR SPECIES
The tadpole of *L. ingeri* is most similar to those of *L. malesianus* and *L. paramacrodon*. All have distinct blotches along the tail, radial iris patterns, dense rosette patterns on tail, and similar fin shape. *Limnonectes malesianus*, *L. paramacrodon*, *L. leporinus,* and *L. ingeri* have only one keratodont row on the upper lip. *L. leporinus* possesses a black stripe restricted to the base of the tail rather than a series of blotches along the tail as in *L. ingeri*. The color pattern of *L. malesianus* is richer in contrast than in *L. ingeri*. the few *L. paramacrodon* ever examined had distinctive iris color. See comments on the other River Frog species.



Limnonectes ingeri *tadpoles live in riparian settings; however, we found them in very quiet side pools or isolated pools on river banks. The tadpoles are similar to those of other* Limnonectes *and, at this point, it is unclear which of the described differences are reliable for diagnostics. DNA sampling is recommended.*

HABITAT & ECOLOGY
Limnonectes ingeri tadpoles live in quiet side pools, in water-filled potholes of stream beds, pools on river banks of lowland streams or quiet sections of forest streams. The tadpoles are benthic and stay close to the bottom. Their color pattern lets them blend in well with color background of the pool substrate. Tadpoles are sometimes associated with *Rhacophorus pardalis*.

REPRODUCTION
Details of egg laying, nesting site and early development remain unknown for this species.

COLORATION
Sandy brown to mid brown above, with irregular blurred marbling; densely dusted with iridocytes above. At high magnification, vermiculate melanocytes can be seen dorsally. One or two dark blotches mark the trunk-tail junction dorsally. Flank darker than dorsum, marbled. Three fuzzy dark areas present on the sides of head: a dark streak from the eye to the oral disc, a dark patch below the eye, and one posterior to eye. In the lower head and lower flank, the dense iridocytes break up into irregular, cloudy patches. Skin of venter mostly unpigmented, transparent but bearing scattered iridocytes in the gill and abdominal regions; gills and gut coil visible. Body color, continues onto the dorsal tail and fades distally. A distinct series of more or less sharply defined dark blotches marks the lateral side of the muscular portion of the tail. Numerous distinct rosette-like white clusters of iridocytes cover the tail and tail fins.

LITERATURE

Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

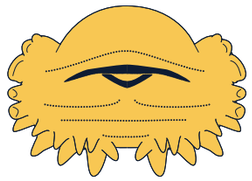
Inger, R.F. (2009) Contributions to the natural history of seven species of Bornean frogs. Fieldiana Zoology 116: 1–25.

Limnonectes malesianus (Kiew, 1984)

Malaysian River Frog

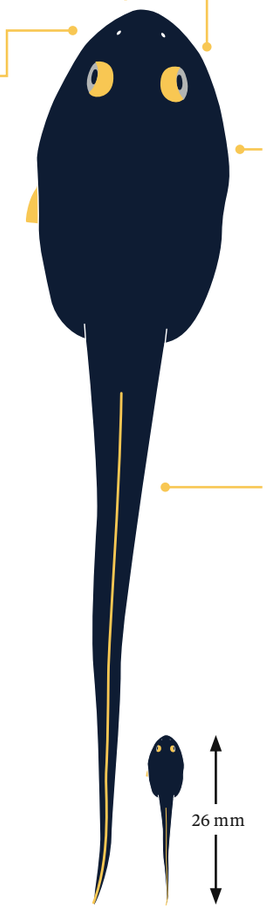
SNOUT
In dorsal view, a smooth broad, slightly tapering arch, with a subtle medial bulge, not distinctly tapering. Snout is moderately long. Oral disc not projecting beyond snout in dorsal view. Profile blunt and steep.

ORAL DISC
Moderately large, ~30% of head width, anteroventral in orientation; not projecting beyond snout contour in dorsal view.



Upper and lower lips demarcated only by a indistinct emargination between them. Marginal papillae present, except for a wide gap in upper lip and a narrow gap in lower lip. Marginal papillae thick and low in number. Some of the papillae flat and broad as if two or more papillae were fused. At medial part of lower lip, papillae arranged in a staggered way on the lower lip so that they may appear to stand in a double-row. Submarginal papillae absent. LTRF 1/3(1). Beaks well keratinized but thin; their edges bear fine serrations. Upper beak straight medially, shallowly arched laterally. Lower beak is V-shaped.

ECOMORPH
Lentic/lotic, benthic, exotrophic.

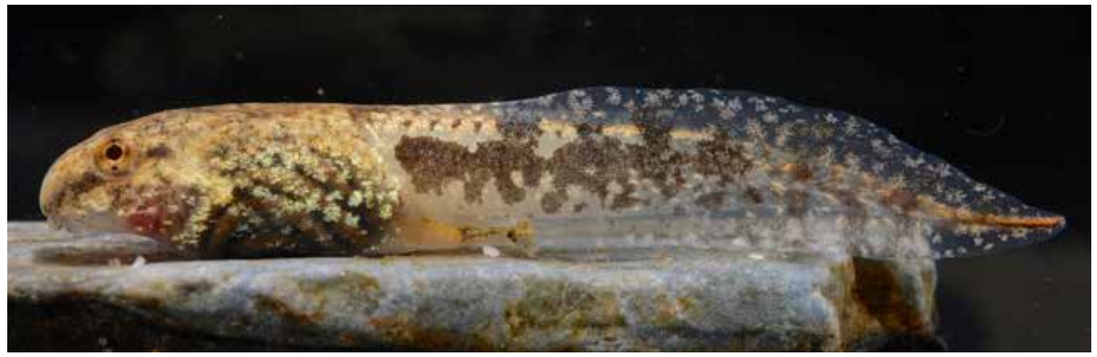


NOSTRILS & EYES
Eyes dorsolateral. Nostril oriented anterolaterally, closer to snout than to eye. Nostril rim without distinct projection. Iris densely dotted with brass or gold iridocytes, often with a reddish hue in the middle section. Iridocytes form an almost complete, solid ring around pupil with small gaps dorsally and ventrally. Iridocytes less dense in the anterior, posterior, upper, and lower sectors forming four dark radii.

BODY
Small to medium-sized. Body contour oval in dorsal view. Head equal to or slightly wider than trunk, widest at gill region. Head contour smoothly rounded, slightly tapering, in dorsal view. Body depressed dorsoventrally. Spiracle sinistral, opening posteriorly. Lateral face of spiracle extended further posteriorly relative to medial side. Spiracular orifice free from the body wall medially (short free tube). Spiracle located at mid-body level in lateral view. Lateral line organs indistinct.

TAIL
Up to 68% of total length. Muscular part of tail moderately strong. In dorsal view, the tail muscle is slightly less than half of the maximum trunk width; it is more than half trunk height in lateral view. Upper fin originates posterior to the trunk-tail junction, at ~ 5% of tail length. Upper fin is higher than lower fin and arches moderately. In posterior fourth of the tail, fins converge into an acute or narrowly rounded tip. Some individuals have a concavity in the contour of the upper fin close to the tip. In others, the tail is symmetrically lancet shaped. Maximum tail height at mid-tail level or slightly posterior. Lateral tail vein masked by pigmentation; tail myosepta indistinct.

SIMILAR SPECIES
The *Limnonectes malesianus* tadpole is most similar and likely to be confused with *L. leporinus*, *L. paramacrodon*, and *L. ingeri*. See descriptions and comments for these species. *L. malesianus* tadpoles do not grow as large as the other species mentioned; however, these differences become obvious in advanced stages only. We noted some morphological and color pattern differences between the above-mentioned River Frog species, but more samples from various areas are needed to corroborate these findings.



The tadpoles of Limnonectes malesianus *can be found in swampy areas or shallow pools in lowland forests. Tadpoles of this species are usually not found in large numbers.*

HABITAT & ECOLOGY
Limnonectes malesianus tadpoles live in swamp pools, flooded muddy forest depressions or stagnant, shallow slow-moving forest stream sections. They live at the bottom, where they feed on the organic matter that accumulates on the soft bottom layer. A particle suspension is generated by their movement and ingested.

REPRODUCTION
Inger et al. (2017) reported the breeding of a pair sitting in a stream in the middle of a circular depression in fine gravel, similar to breeding habits reported for *Limnonectes leporinus*.

COLORATION
Gold brown above, with irregular, indistinct marbling and scattered black dots; densely dusted with iridocytes above. A dark blotch marks the trunk-tail junction dorsally. Flank darker than dorsum, marbled. Three fuzzy dark areas present on the lateral face: a dark streak from the eye to the oral disc, a dark patch below the eye, and one posterior to eye; often another patch laterally at gill area. At the lower head and lower flank, the dense iridocyte layer dissolves into irregular light patches. Skin of venter is mostly unpigmented and transparent. Iridocytes and melanocytes are scattered in the gular, buccal, branchial, and anterior abdominal ventral skin areas. Body color continues onto the dorsal tail, becomes lighter there and fades distally. Distal fourth of the muscular part often with an orange or reddish tint. Tail laterally with several large irregular, partially fused polygonal blotches, mostly covering the muscular part but some reaching into the fin part. Numerous distinct rosette-like white clusters of iridocytes cover the tail and tail fins.

LITERATURE
Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

Leong, T.M., Chou, L.M. (1999) Larval diversity and development in the Singapore Anura (Amphibia). The Raffles Bulletin of Zoology 47: 81–137.

Limnonectes palavanensis (Boulenger, 1894)

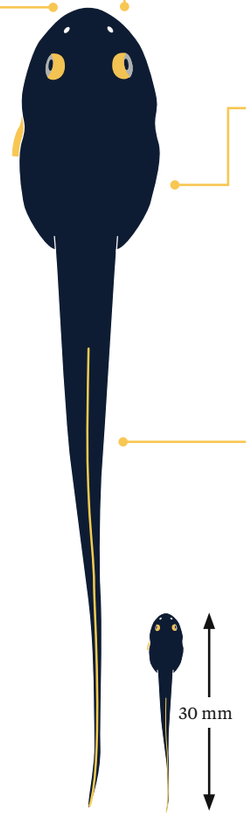
Smooth Guardian River Frog

SNOUT
In dorsal view, smooth wide arch, with only a subtle tapering towards tip. In lateral view, snout moderately long, slightly tapering into bluntly rounded tip overhanging oral disc.

ORAL DISC
Moderately large, ~30–35% of maximum head width, anteroventral in orientation, not projecting anteriorly beyond snout contour in dorsal view. An emargination between upper and lower lip is present but not deep.

Bluntly conical marginal papillae present with a wide gap medially in the upper lip and a narrow gap medially in the lower lip. Lower lip, papillae arranged in a single row, however, medially they are arranged in staggered fashion, as if arranged in a double-row. Submarginal papillae absent. LTRF 2(2)/3(1), with inner keratodont row of the upper lip very short. Beaks well-keratinized but not high; their edges bear fine serrations. Upper beak straight medially and concavely deflected distally. Lower beak is V-shaped.

ECOMORPH
Lotic/lentic, benthic, exotrophic.



NOSTRILS & EYES
Eyes dorsolateral, relatively widely spaced. Anterolaterally oriented nostril closer to the snout than to eye; nostril relatively large, rim without distinct projection. Iris and orbit dotted with gold iridocytes on a black background. Iridocytes form a solid ring around the pupil. Iridocytes less dense in the anterior, posterior, dorsal and ventral sectors, however, distinct radial pattern absent.

BODY
Medium in size. In dorsal view, general body contour oval; a constriction demarcates the transition from head to trunk. Body dorsoventrally depressed. Head as wide as trunk. Widest point of body at the gill region or at the anterior trunk. Head contour a broad and smooth arch in dorsal view. Spiracle sinistral, directed posteriorly, below mid-body line. Medial side of spiracle attached to body wall, lateral spiracular wall more extended posteriorly than the medial side. Lateral line organs indistinct.

TAIL
Long, 69–73% of total length. Muscular part of tail moderately strong. In dorsal view, tail muscle equals approximately half the maximum trunk width. Tail slightly less in height than trunk in lateral view. Upper fin originates far posterior to trunk-tail junction, at 15–20% of tail length. Both fins remain low, but the upper fin is slightly higher than the lower fin. Upper fin arches in a shallow convex curve. In the posterior fourth of tail, the fins converge into an acute or narrowly rounded tip. A shallow concavity in the contour of the upper fin close to the tip is often present. Maximum tail height at mid-third of tail. Lateral tail vein visible at proximal fifth of tail. Tail myosepta indistinct.

SIMILAR SPECIES
Limnonectes tadpoles can be distinguished from many other Bornean genera by their LTRF, with low keratodont row count ranging from 1/3(1) to 2(2)/3(1). *L. palavanensis* tadpoles may most likely be confused with *L. finchi* and less so with other tadpoles of the genus. Creek Frog tadpoles are less dorsoventrally depressed and have a more rounded, blunter snout. *L. ingeri*, *L. leporinus*, *L. malesianus*, and *L. paramacrodon* possess only one keratodont row on the upper lip (two in *L. palavanensis*), are more distinctly patterned at the lateral head (face), bear denser and clearer rosette-like iridocyte clusters all over the tail, and have a radial iris pattern. The upper fin contour of *L. finchi* and *L. palavanensis* rises in a distinct way well posterior to the trunk tail junction and larvae of these two species are smaller than *L. ibanorum*. See comments for other *Limnonectes* species.

Limnonectes palavanensis *likely encompasses several undescribed species. The morphological description of the tadpole herein is based on a population from the Matang Range.*

HABITAT & ECOLOGY
The tadpoles of western Sarawak *L. palavanensis* have been found in small, slow-moving, shallow forest streams, swampy areas, intermittent streams, as well as in roadside ditches of forest roads with some water current. We found tadpoles of populations in northeastern Sarawak to also utilize shallow ponds, silty puddles, muddy ephemeral flooded open areas, pig wallows or ditches at the forest edges for larval development. Tadpoles hide in the superficial layer of their soft-bottom habitat when disturbed.

REPRODUCTION
The calling male attracts the female to a suitable nesting site in the forest leaf litter. Up to 35–50 relatively large (2.6 mm) eggs are laid on the forest floor and guarded by the male after fertilization. As the tadpoles hatch, they climb onto the dorsum of the male, who subsequently carries them to a suitable body of water in the vicinity. Thereafter, the male leaves and the tadpoles develop independently.

COLORATION
Light to mid-brown above. Irregular and faint dark brown mottling above, with few scattered black dots. The body is dusted densely with iridocytes above. A dark blotch or saddle marking is present at the trunk-tail junction dorsally. Flanks darker than dorsum, marbled light and dark. Facial dark patches can be present at the lateral snout, below eye and lateral gill region, but are usually not distinct. In the lower head and lower flanks, iridocytes form a cloudy pattern of clusters. The ventral skin is mostly unpigmented, transparent. Scattered iridocytes are present at the anterior and lateral parts of the abdomen. The tail is similar to the trunk in dorsal color, but overall lighter and with more distinct markings. The tail (including fins) can be marbled to speckled. Numerous small clusters of iridocytes, cream to silver and reminiscent of rosettes, cover the tail and tail fins.

LITERATURE
Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

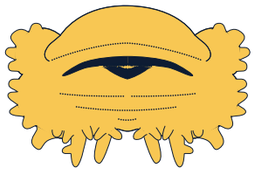
Malkmus, R., Manthey, U., Vogel, G., Hoffmann, P., Kosuch, J. (2002) Amphibians & Reptiles of Mount Kinabalu (North Borneo). Koeltz Scientific Books, Königstein. 424 pp.

Limnonectes paramacrodon (Inger 1966)

Lesser Swamp Frog

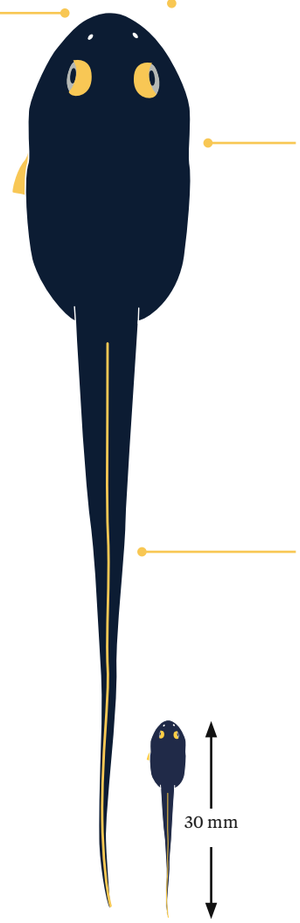
SNOUT
A smooth broad arch in dorsal view, with subtle tapering towards the tip. In lateral view, snout moderately long; contour blunt, slightly obtuse, rounded, not distinctly tapering. Snout hardly overhangs oral disc.

ORAL DISC
moderately large,~ 30% of head width. It is anteroventral in orientation. It does not project beyond the snout contour in dorsal view. Upper and lower lips are separated from each other by a indistinct emargination. Papillae along oral disc margin, except for two gaps: a wide gap on the upper lip and a very narrow gap on the lower lip.



The marginal papillae are low in number and heterogeneous in size. Usually there are 2–3 enlarged papillae per side on the lower lip, that bear shorter papillae on each side of their base in a staggered position (pseudo-double-row). The larger papillae may bear side branches. Submarginal papillae are absent. LTRF 1/3(1). Beaks moderately developed, well keratinized but not high; their edges bear fine serrations. Upper beak straight medially and slightly concave laterally; lower beak widely V-shaped.

ECOMORPH
Lentic/lotic, benthic, exotrophic.



NOSTRILS & EYES
Eyes dorsolateral. Nostril moderate in size and closer to snout than to eye, anterolaterally oriented. Nostril rim without distinct projection. Iris stippled with brass or gold iridocytes on black background and a reddish horizontal band across iris. Iridocytes form a complete ring around pupil. Iridocytes are less dense in the anterior, posterior, upper, and lower sectors, i.e., a radial pattern with four dark radii.

BODY
A medium size tadpole. In dorsal view, general body contour oval, with a mild constriction at head to trunk transition. Head equal to or slightly wider than trunk. Widest point of body at the gill region. Head contour smoothly rounded in dorsal view. Body depressed dorsoventrally. Spiracle sinistral and opening posteriorly. Medial side of spiracle attached to body wall and its lateral face extends more posteriorly than medial side. Spiracle at the mid-body level in lateral view. Lateral line organs indistinct.

TAIL
Long, approximately 68% of total length. Muscular part of tail is moderately strong. In dorsal view, tail muscle less than half of the maximum trunk width; it is clearly more than half trunk height in lateral view. Upper fin originates slightly posterior to trunk-tail junction, at approximately 5% of tail length. Upper fin higher than lower fin; both fins are similar in shape and present a shallowly convex contour line. In the posterior fourth of the tail, fins converge into an acute tip. Close to the tip, a concavity in the contour of the upper fin is present. Maximum tail height at mid-tail section. Lateral tail vein faintly visible at lateral tail root. Tail myosepta indistinct.

SIMILAR SPECIES
The species is similar to *Limnonectes malesianus*. The limited samples and specimens examined of *L. paramacrodon* had fewer blotches along the tail, less distinct facial markings, more reddish iris coloration, and different shape of the oral disc papillae. See comments for other *Limnonectes ingeri, L. malesianus,* and *L. leporinus*.

The tadpoles of Limnonectes paramacrodon *prefer low-level muddy sections of small to mid-sized forest streams and forest swamps. The sample that we describe here is from Tawau Hills. They were collected from a pool with leaf litter within an intermittent stream.*

HABITAT & ECOLOGY
Limnonectes paramacrodon tadpoles dwell in swampy side pools or stagnant sections of slow-moving, lowland forest streams in primary or selectively logged forests. Adults are also found in some coastal peat swamps. The tadpoles' habits and food might be similar to those of *L. malesianus* tadpoles and their relatively small mouth and oral disc suggest small particles as major food source. Tadpoles have rarely been found and not been documented before.

REPRODUCTION
Inger et al. (2017) presented a photograph of an amplecting pair in shallow water.

COLORATION
Ocher to dark brown above, with no distinct markings; densely dusted with gold and some silver iridocytes and scattered fine black dots above. Dorsal pattern dissolves into patches of pigment cells in the lower flank and head. Indistinct dark areas in the lateral face: a faint dark streak from the eye to the oral disc, a dark patch below the eye, a small one posterior to eye, and a patch laterally at gill area. Ventrally, there are few iridocytes and melanocytes scattered in the buccal/branchial region and the abdomen; otherwise the skin of venter is transparent. The background color of the body continues onto the dorsal tail along its muscular part; laterally on the tail, the background color is light. On the posterior half of the tail, the tail muscle is tinted orange-brown. The tail (including the fins) bears several large irregular blotches with diffuse edges particularly in the posterior half of the tail. Numerous distinct rosette-like white to brass clusters of iridocytes cover the tail and tail fins.

LITERATURE

Inger, R.F., Stuebing, R.B., Grafe, T.U., Dehling, J.M. (2017) A field guide to the frogs of Borneo. 3rd ed. Natural History Books, Kota Kinabalu. 228 pp.

Occidozyga baluensis (Boulenger, 1896)

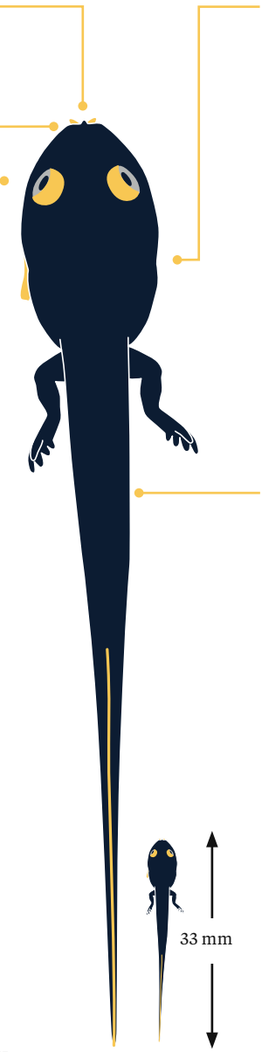
Seep Frog

SNOUT
Tapering in dorsal view, truncated anteriorly. A medial projection and slightly projecting oral structures generate three minute anterior projections in the silhouette of the snout in dorsal view. In lateral view, snout moderately long; contour tapering straight into obtuse tip.

ORAL DISC
Instead of an oral disc, a horseshoe-like short tube (open dorsally) is formed. Papillae and keratodont rows absent. LTRF (0/0). Oral orifice terminal. Jaws strongly developed and strongly keratinized but recessed far backward from external mouth orifice.

NOSTRILS & EYES
Eyes relatively large and positioned dorsolaterally, oriented anterolaterally, with a significant overlap in field of view anteriorly. Iris and orbit of eye beyond iris dotted with silver-brass iridocytes. Nostril opening absent for most of larval life; if present (in metamorphic stages), closer to eye than to snout.

ECOMORPH
Lentic, benthic, exotrophic, carnivorous.



BODY
A medium-size tadpole. In dorsal view, general body contour oval, yet head longer and wider than trunk. Body widest at level of the posterior region of the head. Head contour smoothly rounded in dorsal view, except for a truncation at snout. Body depressed dorsoventrally. Spiracle sinistral and opening posterolaterally. Because of the large head, the spiracle is located quite posterior relative to the body. Medial side of spiracle free, a short spiracular tube is present. Spiracle below the midbody level in lateral view. Lateral line organs indistinct. Hindlimbs developed precociously.

TAIL
Very long, approximately 75% of total length. Muscular part of tail strong. In dorsal view, tail muscle i more than half of maximum trunk width; nearly as high as trunk in lateral view. Upper fin originates far posterior to trunk-tail junction at approximately 40% of tail length. Upper fin higher than lower fin; both fins very low, with little convexity in the contour line. In the posterior fourth of tail, fins converge into an acute tip. Maximum tail height at approximately the beginning of the distal third of tail. Lateral tail vein and tail myosepta indistinct.

SIMILAR SPECIES
Occidozyga tadpoles have a number of unique features that distinguish them from other genera: a horseshoe-like terminal mouth, precocious hind limb development, long tail with low tail fin, and eye axis orientation more anteriorly. In combination, these features make it easy to identify them. The relationships within the genus have not been resolved, however. More *Occidozyga* species than previously known occur on the island, and until larger samples have been analyzed morphologically and diagnostic features have been established, the lineages within *Occidozyga* should be identified by genetic barcoding.

Tadpoles of Occidozyga baluensis *inhabit shallow water-filled depressions, in which clear water seeps in, especially at the base of slopes. With their distinctive features,* Occidozyga *tadpoles are unlikely to be confused with other Bornean genera.*

HABITAT & ECOLOGY
Occidozyga baluensis tadpoles are predatory and carnivorous. They feed on small invertebrates, such as insect larvae, but also have been observed to attack other tadpoles by nibbling their tails. Unlike others, they possess a large stomach-like structure in their digestive tract. The tadpoles can be seen perching motionless on leaf litter, often in the shallows, waiting in ambush. *Occidozyga* tadpoles show precocious hind limb development, and we have never encountered tadpoles without well-developed hind limbs. It is likely that hind limbs are associated with better balance, and perhaps produce thrust associated with prey capture.

REPRODUCTION
The details of reproduction are unknown. Male calls are a series of rasping notes in rather low sound pressure and low pitch.

COLORATION
Gold brown or sandy brown to mid brown above, with irregular small blurred darker flecks, particularly dark area on top of head and trunk-tail junction; head and trunk densely dusted with iridocytes; scattered dark melanocytes (dots), particularly at lateral face. Orbital space anterior to eye unpigmented. Flank darker than dorsum. Skin of venter is mostly unpigmented, transparent, except for scattered iridocytes at anterior abdominal and gill areas. Inner organs are visible through skin (large liver, often bright in color). The general color of the tail is similar to that of the body, but is lighter (with less dense pigment cells). Clusters of black dots are distributed along the tail, as well as clusters of whitish iridocytes; most of the tail's pigmentation is on the muscular part, but the fins are pigmented to some extent as well.

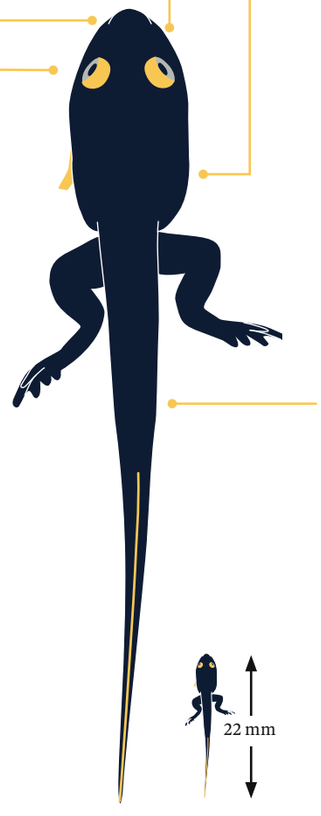
LITERATURE

Flury, J.M., Haas, A., Brown, R.M., Das, I., Pui, Y.M., Boon-Hee, K., Scheidt, U., Iskandar, D.T., Jankowski, A., Hertwig, S.T. (2021) Unexpectedly high levels of lineage diversity in Sundaland puddle frogs (Dicroglossidae: *Occidozyga* Kuhl and van Hasselt, 1822). Molecular Phylogenetics and Evolution 163: 107210.

Haas, A., Pohlmeyer, J., McLeod, D.S., Kleinteich, T., Hertwig, S.T., Das, I., Buchholz, D.R. (2014) Extreme tadpoles II: the highly derived larval anatomy of *Occidozyga baluensis* (Boulenger, 1896), an obligate carnivorous tadpole. Zoomorphology 133: 321–342.

Occidozyga berbeza Matsui, Nishikawa, Eto, Hamidy, Hossman, and Fukuyama 2021

Wrinkled Swamp Frog



NOSTRILS & EYES
Eyes relatively large and positioned dorsolaterally. Eye axis oriented anterolaterally, with a significant overlap in field of view of the two eyes, presumably producing a stereoscopic vision. Iris and orbit of eye beyond the iris are dotted with silver-brass iridocytes. Nostril opening absent for most of larval life.

SNOUT
In dorsal view, tapering towards a truncate tip; snout forms a medial bulge that overhangs the mouth tube. In lateral view, snout moderately long and contour tapers straight into an obtuse tip.

ORAL DISC
Mouth terminal in position; oral disc and lip flaps absent; a horseshoe-like short tube (open dorsally) is formed instead. This mouth structure is positioned in a recess of the snout, so that the mouthparts are not protruding the body silhouette in dorsal view. Papillae and keratodont rows absent. LTRF (0/0). Jaws well- developed and keratinized but recessed far backward from external mouth orifice.

ECOMORPH
Lentic, benthic, exotrophic, presumably carnivorous (unconfirmed).

BODY
Medium sized. In dorsal view, general body contour oblong oval, however, head slightly wider and longer than trunk and tapering anteriorly. Body widest at the level of posterior head region (gill region). Head contour smoothly rounded in dorsal view, except for the truncation at the snout. Body depressed dorsoventrally. Spiracle sinistral and opening posteriorly. Due to the large head, the spiracle is located in a posterior position. Medial side of spiracle not attached to body wall and spiracular orifice at the end of a long free tube. Spiracle below the mid-body level in lateral view. Lateral line organs indistinct. Hindlimbs developed precociously.

TAIL
Very long, up to 75% of total length. Muscular part of tail is strong. In dorsal view, tail muscle more than half the maximum trunk width, nearly as high as trunk in lateral view. Upper and lower fins both originate far posterior to the trunk-tail junction at approximately 40% of tail length. Upper fin is higher than the lower fin. Both fins very low, with little convexity in the contour line. In the posterior fourth of the tail, fins converge into an acute or narrowly rounded tip. Maximum tail height approximately at beginning of the distal third of the tail. Lateral tail vein and tail myosepta indistinct.

SIMILAR SPECIES
Tadpoles of the genus *Occidozyga* are easily recognized by their hind limbs, long tail, and peculiar mouthparts. Diagnostic characters that distinguish the three species described here have not been corroborated by larger samples. Additional undescribed species occur on the island of Borneo. However, the preliminary results presented here suggest that potential larval diagnostic features within the genus could be the mouthparts (recessed vs. protruding), the length of the snout, the shape of the snout in lateral view, the angle of eye axis (more anteriorly directed in *O. baluensis* and *O. berbeza* than in *O.* aff. *laevis*), and the position of the fin origins along the length of the tail.

Occidozyga berbeza *shows tadpole features typical of the genus, such as terminal mouth and early development of hind limbs.*

HABITAT & ECOLOGY
Occidozyga berbeza tadpoles share the general larval morphology with other *Occidozyga*. It is likely that *O. berbeza* tadpoles are obligate carnivores with an ecology similar to tadpoles of *O. baluensis* (see comments there). Tadpoles can live in a very shallow film of water.

REPRODUCTION
The frogs were found in shallow puddles and seepage areas where reproduction seems to occur.

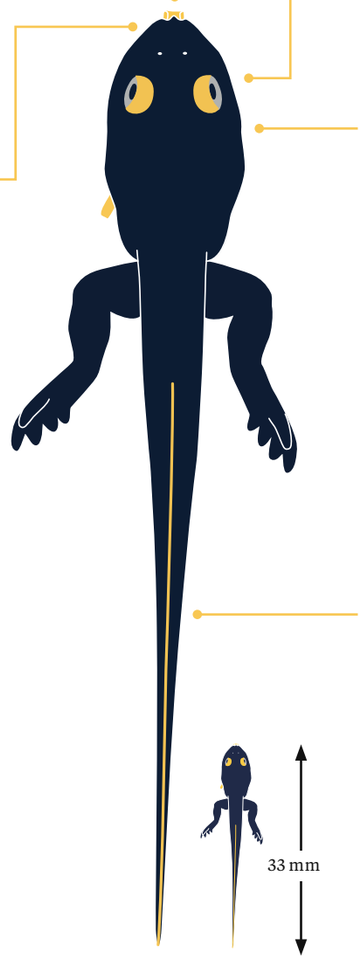
COLORATION
Brown above, with irregular blurred darker flecks on dorsum and dorsal tail. Large dark area between eyes and back to occipital region. A light cream patch dorsally on snout is bordered by darker areas laterally. Head and trunk densely dusted with iridocytes; scattered dark melanocytes (dots), particularly at the lateral face. Orbital space anterior to eye unpigmented. Flanks darker than dorsum. Skin of venter is mostly unpigmented, transparent, except for scattered iridocytes at anterior abdominal and gill areas. Inner organs visible through skin, especially a large orange liver and red gills. The general color of the tail is similar to that of the body, dark above and lighter on the sides. Black dots (melanocytes) are scattered over the tail with some cells congregating in many small clusters along the tail. Similarly, there are many small clusters of whitish to cream iridocytes distributed over the tail. Pigmentation of the tail extends onto tail fins.

LITERATURE
Flury, J.M., Haas, A., Brown, R.M., Das, I., Pui, Y.M., Boon-Hee, K., Scheidt, U., Iskandar, D.T., Jankowski, A., Hertwig, S.T. (2021) Unexpectedly high levels of lineage diversity in Sundaland puddle frogs (Dicroglossidae: *Occidozyga* Kuhl and van Hasselt, 1822). Molecular Phylogenetics and Evolution 163: 107210.

Matsui, M., Nishikawa, K., Eto, K., Hamidy, A., Hossman, Y., Fukuyama, I. (2021) A new *Occidozyga* from Sarawak, Malaysian Borneo (Anura: Dicroglossidae). Zootaxa 4926: 535–546.

Occidozyga aff. *laevis*

Puddle Frog



SNOUT
In dorsal view, tapering towards a truncated tip; at the tip, a mouth tube projects beyond the snout contour in dorsal and lateral views. In lateral view, snout long and angular; contour descends from the level of the eye more or less horizontally to the nostril, where it bends downward to continue to snout tip. Nostrils indistinct (closed).

ORAL DISC
Mouth opening terminal in position; oral disc and lip flaps absent; a horseshoe-like short tube (open dorsally) is formed instead, with a finger-like dorsal process of snout projecting into the open end of the horse-shoe (see *O. baluensis*); tube protrudes snout in dorsal view. Papillae and keratodont rows absent. LTRF (0/0). Jaws well developed and keratinized but recessed far backward from external mouth orifice.

ECOMORPH
Lentic, benthic, exotrophic, carnivorous.

NOSTRILS & EYES
Eyes dorsolateral. Eye axis more laterally than anteriorly oriented. Iris and orbit of eye beyond iris dotted with copper iridocytes with small gaps (black) in the periphery of the upper, lower, anterior, and posterior sectors. Nostril approximately midway between eye and snout.

BODY
Medium-sized. Depressed dorsoventrally. In dorsal view, general body contour a stretched oval. Head dominates the body and is larger than trunk part. Head slightly wider than trunk. Body widest at level of the posterior head region (gill area). Head contour tapering from eyes to snout in dorsal view. Spiracle sinistral and located relatively far posteriorly, due to the enlarged head. Spiracle opens posteriorly. Medial side of spiracle not attached to body wall; a long free tube present. Spiracle below mid-body level in lateral view. Lateral line organs indistinct. Hindlimbs developed precociously.

TAIL
Very long, up to 73% of total length. Muscular part of tail strong. In dorsal view, tail muscle more than half maximum trunk width; nearly as high as the trunk in lateral view. Upper and lower fins originate posterior to trunk-tail junction ~18% of tail length. Upper fin is higher than lower fin; both moderately low. Upper fin more convex in contour than lower fin. In posterior third of tail, fins converge straight into an acute tip. Upper fin contour slightly concave before it reaches the tip. Maximum tail height in the mid-tail region. Lateral tail vein partly obscured by pigmentation. Tail myosepta indistinct.

SIMILAR SPECIES
This tadpole can only be confused with other *Occidozyga* tadpoles. Body shape, precocious development of hind limbs and mouthparts are unambiguous characters for tadpoles of the genus. It is distinct from *O. baluensis* and *O. berbeza* by its long and angular snout; the eyes are less forward directed and the tail fins originate more proximally on the tail, compared to the other two species.

This Occidozyga *tadpole is distinctly different form* O. laevis and O. berbeza tadpoles. *The intrageneric relationships are under investigation and additional species other than the three species currently recognized are believed to exist on Borneo.*

HABITAT & ECOLOGY
The morphology suggests that this *Occidozyga* species is a carnivorous predator, as are the tadpoles of other species in the genus. They were observed at the banks of a black-water pond, in Gunung Mulu National Park, in shallow water, resting on leaf litter.

REPRODUCTION
unknown.

COLORATION
Homogeneously brown to chestnut brown above, without distinctive pattern; lighter in color, cream to sandy brown dorsally on snout. Head and trunk dusted with gold iridocytes; black dotting especially along the lateral face and flank. A dark streak runs from the eye along the temporal region. Orbital space anterior to eye pigmented. Flank darker than dorsum; lower head and lower flank with light patches of iridocyte in a cloudy pattern. The ventral skin bears scattered iridocytes and melanocytes. Particularly the anterior abdominal area has a high density of iridocytes and a closed silver sheet is formed. Inner organs visible through skin, but not as clear as in other species. Body color continues onto the tail. The tail and its fins are finely dusted with melanocytes. Clusters of melanocytes from several black small spots along the tail. A narrow black horizontal streak is formed at the root of the tail. Iridophores are scattered all over the tail but particularly form whitish flecks along both fin edges.

Glyphoglossus brooksii (Boulenger, 1904)

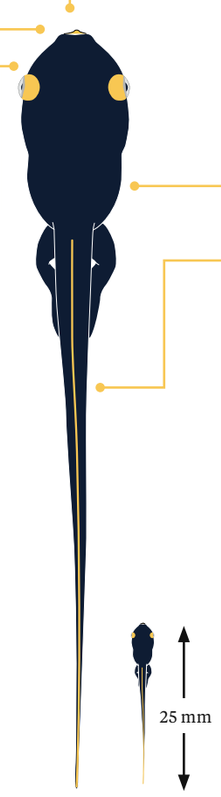
Brooks' Burrowing Frog

SNOUT
Short and bluntly rounded in dorsal view, except for a small truncation medially; blunt and rounded snout profile in lateral view.

ORAL DISC
absent except for tiny skin flaps below lower jaw. Mouth terminal, slightly upward directed. Keratinized jaw sheaths and keratodonts absent; LTRF (0/0).

NOSTRILS & EYES
Eyes positioned laterally; cornea protruding beyond body contour in dorsal and ventral views. Iris metallic shiny, with scattered golden iridocytes on black background above and more silver ones below; expect for an iridocyte-free, conspicuous black indentation in the ventral part of the iris. Nostril not perforated in larval stages and the position of the future nostril can be difficult to see (or presumed at the end of the orbitonasal streak); it is closer to the snout than to the eye.

ECOMORPH
Lentic, endotroph? (yellow thick gut coils).



BODY
Small. Head and trunk approximately as wide as deep, head somewhat flat above. In dorsal view, body composed of wider head and narrower trunk part. In lateral view, head bluntly rounded anteriorly. Body widest at gill region. Trunk much wider than the base of the tail. Spiracle ventral and in the medial plane. Spiracular orifice opens posteriorly at level of anterior abdomen. Rim of spiracular orifice smoothly square. Lateral line organs indistinct.

TAIL
Up to 74% of total length. Muscular part of tail moderately developed, much less high than body in lateral view. Upper fin rises at the trunk-tail junction; its contour is almost straight, with only slight convexity posteriorly. Lower fin more arched in shape than the upper fin and clearly higher than the latter. Both fins taper into a long flagellate tip. Skin glands absent. Lateral tail vein indistinct. Muscle myosepta slightly accentuated by pigmentation.

Top: Unidentified *Glyphoglossus* sp. from Batang Ai, in natural swimming position.

SIMILAR SPECIES
The body shape, lateral eyes, black indentation ventral in iris, vestigial oral disc, and tail fin shape (higher lower fin, flagellate tip) are unique in combination for *Glyphoglossus*; confusion with any other Bornean genus is unlikely. *Microhyla* species share some of these features but usually have a distinct color pattern on body or tail, absent in *Glyphoglossus brooksii*. For *Glyphoglossus* tadpoles see also Altig and Rowley (2014). For Borneo, tadpoles of the other *Glyphoglossus* species remain unknown, but see photo to the right.

Little information is available for Glyphoglossus brooksii. *We could observe the tadpoles only once in the field, at Kubah National Park, and matched them to adults by DNA.*

HABITAT & ECOLOGY
Like other, better known species of the genus *Glyphoglossus* (Altig and Rowley 2014), *G. brooksii* has free-living tadpoles. Advanced tadpole stages that we observed were small and had a yellow gut coil. This could indicate yolk deposits in the gut and endotrophic development of the tadpole. However, more research is needed to clarify that. We saw the tadpoles hovering in a pool of an intermittent forest stream. When in the water column, *Glyphoglossus* tadpoles orient their body head up at an angle to the surface, while the tail tip is constantly beating and holding the body in position or move it slowly. Upon disturbance, the tadpole will dart to the bottom of the pond with strong beats of its tail.

REPRODUCTION
The males respond strongly to rainfall with their calls. Calls have been reported during the day. The rather small size relative to stage of the tadpoles suggests that development might take only a few weeks.

COLORATION
Uniformly dark gray to black above, without distinct pattern, including the tail. The density of melanocytes declines along the flanks toward the ventral side. In high magnification, a fine light orbitonasal streak is discernible. The gut coil is visible in lateral and ventral views. Ventral gular and buccal regions are dusted with melanocytes, the abdomen less so. Loosely stippled with iridocytes above, along the proximal half of the tail and its fins, and some also on buccal region ventrally. Skin of ventral side is translucent. Heart and large blood vessels are visible in ventral view.

LITERATURE

Altig, R., Rowley, J. (2014) The breeding behavior of *Glyphoglossus molossus* and the tadpoles of *Glyphoglossus molossus* and *Calluella guttulata* (Microhylidae). Zootaxa 3811: 381–386.

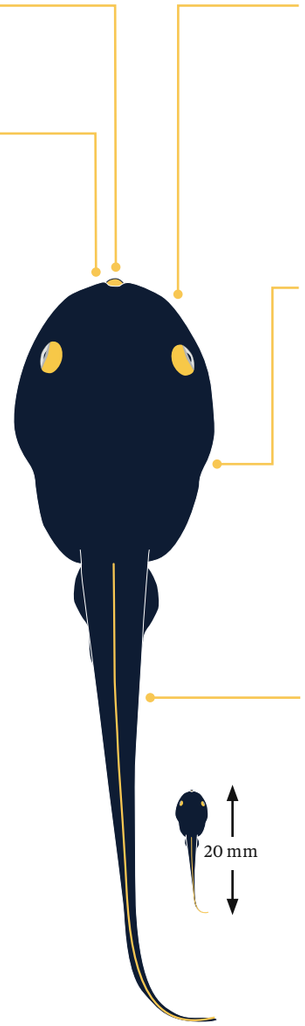
Chaperina fusca Mocquard, 1892

Saffron-bellied Frog

SNOUT
Tapering in straight line in lateral view; bluntly rounded in dorsal view with a small medial bay.

ORAL DISC
Terminal mouth; oral disc absent. Upper jaw straight medially and shallowly arched laterally. Lower jaw U-shaped, slightly protruding. Keratinized beaks and keratodonts absent; LTRF (0/0).

ECOMORPH
Phytotelma-dweller, exotrophic, suspension feeder.



NOSTRILS & EYES
Eyes dorsolateral, widely-spaced, cornea not protruding beyond body contour in dorsal view. Iris black with a silver-blue ring of iridocytes around the pupil. Beyond iris, eye ball stippled with silver iridocytes dorsally that produce a specular shine above. Nostril not perforated in larval stages.

BODY
Small in overall size. Head and trunk dorsoventrally depressed, head flat above. In dorsal view, the body is broadly inverse pear-shaped. Head significantly wider and longer than trunk, flat above. In lateral view, head and trunk are oblong ovoid with tapering snout profile. Trunk much wider than base of tail. Body widest at gill region. Spiracle ventral and medial. Spiracular orifice opens posteriorly at the mid-abdominal level, with crescentic edge. Lateral line organs invisible.

TAIL
Up to 67% of total length. Muscular part of tail relatively narrow, much less high than the body in lateral view. Upper fin rises at trunk-tail junction or slightly posterior to it; it forms a shallow convex arch toward posteriorly. Lower fin similar to upper fin in shape, slightly lower. Both fins taper with less convexity into a narrowly rounded tip. We observed some variation in fin shape among populations, the significance of which is unknown. Skin glands are absent. Lateral tail vein indistinct. Muscle myosepta indistinct.

SIMILAR SPECIES
The tadpoles of *C. fusca* are found in phytotelmata, rock pools, tins, buckets, or other small suitable bodies of water; however, the species seems to avoid ground puddles for reproduction. The easiest and most distinct feature in the field is the conspicuous reflecting specular spots on the eyes of this tadpole. The species is clearly distinguished by size and lack of oral disc from other phytotelma breeders, such as *Nyctixalus pictus*. It is distinguished by dorsoventrally depressed body shape and eyes not reaching body contour in dorsal view from tadpoles of *Microhyla* and *Nanohyla* (for example, *N. petrigena*) that potentially live in the same body of water.

The tadpoles of Chaperina fusca *can easily be overlooked, because they are small and dark-colored. Their coloration blends perfectly with dark tree holes or buttresses where these tadpoles live, except for their eyes, which reflect daylight with a specular silvery shine at the top.*

HABITAT & ECOLOGY
Chaperina fusca is widely distributed. Old secondary or primary forests from the lowlands to montane (1.500 m at Mt. Kinabalu) are suitable habitats for these frogs. Occasionally, disturbed habitats seem to be accepted as well. Tadpoles live in phytotelmata or in rock pools. We found tadpoles in buttress cavities, fallen logs containing water, but also in abandoned man-made receptacles, such as bottles, tins, toiletts and buckets. Tadpoles are obligate filter feeders. They hover quietly in the water and will rush to the detritus at the bottom of their phytotelma when alarmed.

REPRODUCTION
Malkmus et al. (2002) reported 6–10 gray eggs per clutch that were attached to the walls of the phytotelma or to submerged plant matter. Multiple females may deposit eggs in one given phytotelma. Males have been observed to be territorial and engage in combat at a breeding site.

COLORATION
Uniformly black above, without distinct pattern, however the trunk is darker than the head. The tail is darkly pigmented for most of its part, more lightly so posteriorly. The density of melanocytes declines along the flanks toward the ventral side. Gut coil usually visible in lateral and ventral views. Ventral gular and buccal region dusted with melanocytes, abdomen less so. Skin of venter translucent. Heart and large blood vessels visible in ventral and lateral views.

LITERATURE

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Inger, R.F., Stuebing, R.B., Grafe, T.U., 1, J.M. (2017) A field guide to the frogs of Borneo. 3rd ed. Natural History Books, Kota Kinabalu. 228 pp.

Malkmus, R., Dehling, J.M. (2008) Anuran amphibians of Borneo as phytotelm-breeders—a synopsis. Herpetozoa 20: 165–172.

Malkmus, R., Manthey, U., Vogel, G., Hoffmann, P., Kosuch, J. (2002) Amphibians & Reptiles of Mount Kinabalu (North Borneo). Koeltz Scientific Books, Königstein. 424 pp.

Kaloula baleata (Müller, 1836)

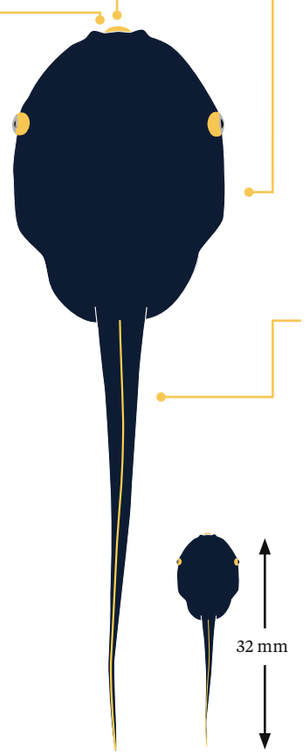
Brown Bullfrog

SNOUT
Long and wide. In dorsal view, it is very broadly rounded with an anterior embayment that harbors the mouthparts. Tip of the snout truncated in lateral view. Jaws slightly recessed.

ORAL DISC
Mouth terminal; oral disc with free lips absent. The mouth is located and recessed in a horizontal fold of the snout tip. Upper jaw flat medially, slightly arched laterally, corners slightly projecting. Lower jaw U-shaped. Jaw edges not darkly keratinized and keratodonts absent; LTRF (0/0).

NOSTRILS & EYES
Eyes lateral; the cornea protrudes beyond the body contour in dorsal and ventral views. Eyes small. Iris mostly black with a metallic golden ring around the pupil. Sclera dotted with silver iridophores dorsally. Nostril not perforated in larval stages.

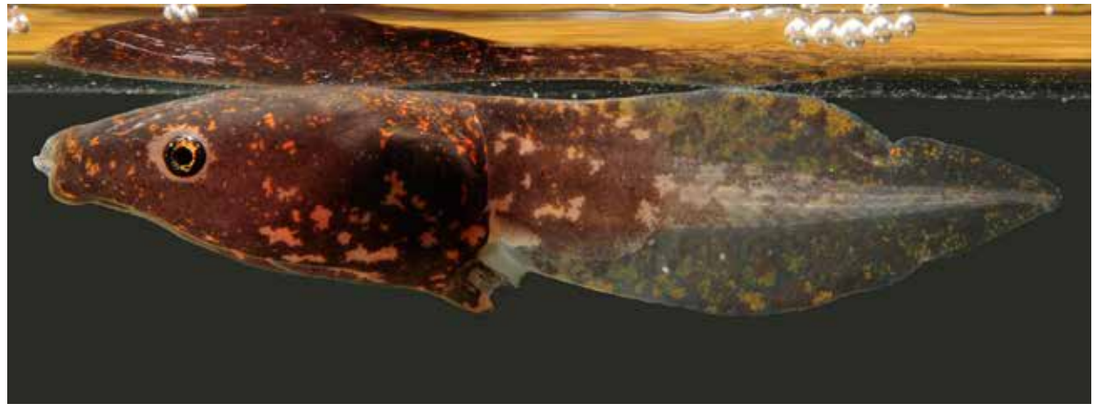
ECOMORPH
Lentic, exotrophic, suspension feeder.



BODY
Medium in overall size. Head and trunk depressed dorsoventrally, particularly the snout area; head flat above. In lateral view, body contour depressed ovoid, with a noticeable tapering of the head from level behind eyes forward to snout tip. Head enormously wide in relation to much narrower trunk region in dorsal view. Trunk broadly rounded posteriorly and much wider than base of tail. Body widest at gill region. Spiracle ventral and medial. Spiracle opens with a triangular funnel posteriorly. Spiracular orifice located posterior to trunk below tail root and vent. Lateral line organs indistinct.

TAIL
60–65% of total length. Tail moderately developed. Narrow in dorsal view for the size of the body, much narrower than trunk. Muscular part of tail much lower than body in lateral view. The upper fin originates at trunk-tail junction, rises straight up to form a convex arch at middle section of tail, where the tail is highest. Posteriorly, contour of upper fin runs straight, or slightly concave, down to a narrowly rounded tail tip. Lower fin similar in shape; however, slightly higher and reaches its maximum height slightly more anteriorly than the upper fin. At anterior 25% of tail, an opaque, heavily pigmented patch is present that covers muscular part of tail and parts of tail fins; patch longer than high, smoothly rounded posteriorly. Patch even more conspicuous in preserved tadpoles. Skin glands absent. Lateral tail vein invisible. Muscle myosepta visible only in magnification.

SIMILAR SPECIES
The dorsal view silhouette with its large wide head and feeble tail, clearly identifies tadpoles of *Kaloula* as microhylids and sets them apart from pond-type tadpoles of other frog families on Borneo. The larvae of *K. baleata* and *K. pulchra* are similar and diagnostic features have not been established with certainty. We could find an opaque patch (otherwise known from *Polypedates*) at the first third of the tail in *K. baleata* but not in *K. pulchra*, a possible distinguishing character. The sharp-edged orange-yellow flecks of *K. baleata* seem to be absent in *K. pulchra* tadpoles.



The tadpoles of Kaloula baleata *develop and grow in temporary forest ponds or forest edge ponds. They grow larger than most other microhylid tadpoles (except,* K. pulchra*) and can occur in large numbers.*

HABITAT & ECOLOGY
The tadpoles of *K. baleata* are pond-dwellers. Although *K. baleata* and microhylid tadpoles in general are suspension-feeding specialists, the tadpoles of *K. baleat*a not only hover in the water column or at the surface as other microhylids do but may also venture to the bottom layer of the pond for detritus intake. Filter efficiency in microhylid tadpoles is high. The anatomical structures associated with the feeding behavior (gill filters) are very large and therefore the head of these tadpoles is enormous compared to the trunk.

LITERATURE
Iskandar, D. T. 1998. The Amphibians of Java and Bali. Research and Development Centre for Biology– LIPI and GEF– Biodiversity Collections Project, Bogor. 117 pp + 26 pl.

REPRODUCTION
Adults congregate after heavy rainfalls at forest ponds but also at ponds at forest edges or clearings. Males usually call from hidden spots such as in vegetation or in hollow logs. The deep, forceful voice of the males gave them the name bullfrog. An amplecting pair can lay large numbers of eggs and, thus, a pond can be populated by large numbers of these tadpoles.

COLORATION
Dark brown above and below with scattered orange flecks of irregular shape. These flecks are smaller above and more blotched and cream colored at the flanks. The pattern extends from the trunk to the base of the tail without break. The yellow or cream flecks continue on the fins of the tail, whereas the melanocyte pattern is less dense in the distal parts of the tail. Ventral skin well pigmented, opaque, internal organs not visible.

Kaloula pulchra Gray, 1831

Banded Bullfrog

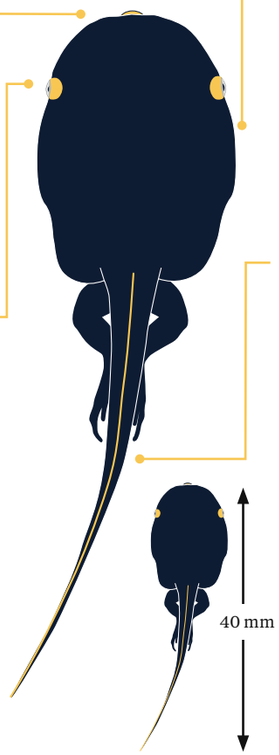
SNOUT
Relatively long and wide. In dorsal view, it is a very broad arch with an anterior truncation that harbors the mouthparts. Tip of snout appears truncated in lateral view as well. Jaws slightly recessed.

ORAL DISC
Mouth terminal; oral disc with free lips absent. Upper jaw flat medially, slightly arched laterally, corners slightly projecting. Lower jaw U-shaped. The mouth is located and recessed in a horizontal fold of the snout tip. Jaw edges without obvious keratinizations (beaks), keratodonts absent; LTRF (0/0).

NOSTRILS & EYES
Eyes small, widely spaced, and positioned laterally; cornea protruding beyond body contour in dorsal and ventral views. Iris mostly black with a metallic ring around pupil. Sclera dotted with silver iridophores dorsally. Nostril not perforated in larval stages; prospective position of nostril inconspicuous.

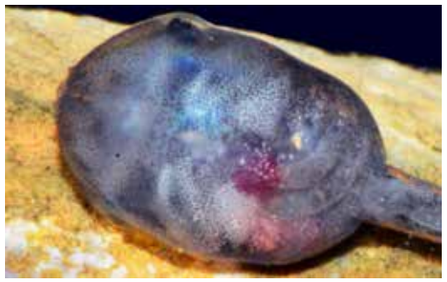
ECOMORPH
Lentic, exotrophic, suspension feeder.

SIMILAR SPECIES
Kaloula tadpoles are relatively easy to recognize: their head is large, the small eyes are widely spaced laterally and an oral disc and keratinized jaws sheaths are absent. Most of these features qualify other microhylids tadpoles as well, however, *Kaloula* tadpoles are larger than most other microhylid larvae and, unlike the other Bornean microhylids, the spiracle has shifted far posterior under the anal siphon at the base of the tail. The larvae of *K. baleata* and *K. pulchra* are similar and intraspecific variability is poorly known. Diagnostic features have not been established with certainty; however see comments for *K. baleata*.



BODY
Medium in overall size. Head and trunk depressed dorsoventrally, particularly snout area; head flat above. In dorsal view, head and trunk can be delimited by a soft constriction. In lateral view, body contour depressed ovoid, with a noticeable tapering of the head from the level behind the eyes forward to the snout tip. Head large in relation to smaller trunk region. Head wide in dorsal view. Trunk broadly rounded posteriorly and much wider than base of tail. Body widest at gill region. Spiracle ventral and medial. Spiracle opening with a triangular funnel posteriorly. Spiracular orifice located posterior to trunk below tail root and vent. Lateral line organs not visible.

TAIL
Approximately 62% of total length. Tail moderately developed; narrow in dorsal view for the size of the body. Tail much less wide than trunk in dorsal view. Muscular part of tail much lower than body in lateral view. Upper fin originates at trunk-tail junction, rises straight up to form a convex arch in the middle section of tail, where the tail is highest. Posteriorly, contour of upper fin runs straight, or even slightly concave, down to a narrowly rounded tail tip. upper and lower fin similar in shape. Lower fin as high as or slightly higher than the upper fin and reaches maximum height slightly more anteriorly than upper fin. Distinct opaque patch at root of tail absent. Skin glands absent. Lateral tail vein indistinct. Muscle myosepta are faintly visible in magnification.



Kaloula pulchra *tadpoles develop in any suitable body of standing water in or near human settlements, such as temporary roadside pools, golf course inundations, and agricultural ponds. The species is not native to Borneo and spreads with human activity to cities and villages; it does not enter deep into the forest.*

HABITAT & ECOLOGY
Kaloula pulchra needs stagnant bodies of water. The tadpoles are highly efficient suspension feeders but also actively seek other food sources, such as decaying animal, plant matter, or insects at the bottom. They commonly swim up and down in the water column or at the surface of a pond to feed, but can also be observed to visit the bottom of a pond to take up particles of detritus. In captivity, we observed congregations of tadpoles and schooling behavior. The internal gill filter structures occupy a large space in the head and therefore the head is substantially larger than the trunk in these larvae.

REPRODUCTION
Adults congregate after heavy rain at temporary ponds and floodings within or around human settlements. Males call while floating at the water surface. The call is deep and forceful. One amplecting pair can lay a thousand eggs. Densities of tadpoles in a pond can be high. Sun-exposed breeding ponds will heat up and accelerate growth and development. Metamorphosis is completed in less than four weeks.

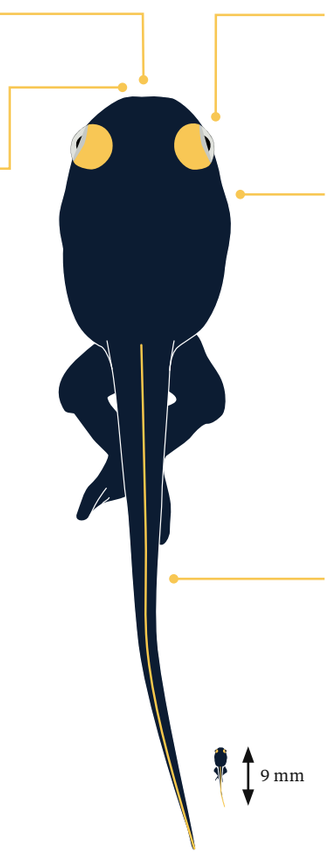
COLORATION
Dark brown or gray above, sometimes with diffuse brown to golden mottling above and laterally along the tail. Sometimes a fine orbitonasal streak is present. The dark background color extends seamlessly onto the tail. Ventral skin well pigmented but lighter than dorsal skin; abdomen semitransparent, internal organs visible at least in early stages, advanced stages more pigmented ventrally.

LITERATURE
Leong, T.M., Chou, L.M. (1999) Larval diversity and development in the Singapore Anura (Amphibia). The Raffles Bulletin of Zoology 47: 81–137.

Lalremsanga, H.T., Sailo, S., Hooroo, R.N.K. (2017) External morphology, oral structure and feeding behaviour of *Kaloula pulchra* TADPOLES Gray, 1831 (Amphibia: Anura: Microhylidae). Science & Technology Journal 5: 97–103.

Metaphrynella sundana (Peters, 1867)

Tree Hole Narrow-mouthed Frog



SNOUT
Very short, bluntly rounded with truncated tip in lateral view. In dorsal view, it is broadly rounded, medially truncated.

ORAL DISC
Mouth terminal; oral disc absent. Mouth small. with a shallowly arched upper jaw and a wide flat U-shaped lower jaw. Keratinized jaw sheaths and keratodonts absent; LTRF (0/0).

NOSTRILS & EYES
Eyes relatively large and positioned laterally; cornea protruding beyond body contour in dorsal and ventral views. Nostril not perforated in larval stages.

BODY
Very small in overall size. Head and trunk only slightly depressed dorsoventrally. In dorsal view, head smoothly confluent with trunk. In lateral view, head bluntly rounded anteriorly, snout very short. Trunk broadly rounded posteriorly and wider than base of tail. Body widest at head-trunk transition. Spiracle ventral and medial in a mid-belly position. Spiracular orifice opens posteriorly without flaps, a shallow arch.

TAIL
Approximately 67% of total length. Muscular part of tail moderately developed, approximately half of body height in lateral view and less than half or trunk width in dorsal view. Upper fin takes origin on the very posterior trunk part. It keeps low for a short distance and then rises to a shallow convex arch. Both fins subequal in height, symmetrical. Tail tip moderately to broadly rounded. Skin glands absent. Lateral tail vein indistinct. Muscle myosepta indistinct.

ECOMORPH
Phytotelma specialist, endotrophic.

SIMILAR SPECIES
Microhyla nepenthicola, species of *Kalophrynus*, species of *Pelophryne*, and *Metaphrynella sundana* all breed and develop in phytotelmata and have endotrophic tadpoles. In a given field situation, the three taxa can be confused due to their phytotelma habitat and miniature size. Among them, *Pelophryne* possesses a small oral disc with few keratodonts. *Microhyla nepenthicola* is diagnosed by its cuspidate tail tip. *Metaphrynella* and *Kalophrynus* are more difficult to differentiate. In fact, we cannot name a morphological feature that can be used to tell them apart until metamorphic stages, when broadly expanded toe and finger tips become apparent in *Metaphrynella* (not expanded in *Kalophrynus*). The tadpole of *Chaperina fusca* is also a relatively small phytotelma larva, however, it is twice as large as the aforementioned taxa, is exotrophic, and possesses a large head.

Metaphrynella sundana *has the smallest tadpoles in the Bornean frog fauna. They are difficult to find, although the species is not rare. Perhaps the development is so rapid that it is unlikely to find them during larval development. The photo depicts a preserved specimen.*

HABITAT & ECOLOGY
Metaphrynella sundana tadpoles live in phytotelmata such as tree holes or accessible bamboo internodes. The tadpoles do not feed but live off the yolk mass in their gut.

REPRODUCTION
Males call from phytotelmata, such as tree-holes or bamboo internodes, and exploit the resonance acoustic properties of the cavities by tuning the call pitch and duration to the resonance of the chamber for maximum resultant sound pressure. The call is a single pulse with little or no frequency modulation at 2–18 s intervals.

COLORATION
Uniformly brown above in preservation, without pattern, overall only lightly pigmented. Pigmentation of body continues onto tail and tail fins but quickly fades in the posterior and ventral parts of the tail. The density of melanocytes declines along the flanks ventrally. The ventral side is unpigmented and transparent. Gut coil and heart visible in ventral view.

LITERATURE

Lardner, B., bin Lakim, M. (2002) Tree-hole frogs exploit resonance effects. Nature 420: 475–475.

Matsui, M., Yong, H.-S., Araya, K., Hamid, A.A. (1996) Acoustic characteristics and systematic relationships of arboreal microhylid frogs of the genus *Metaphrynella* from Malaysia. Journal of Herpetology 30: 424–427.

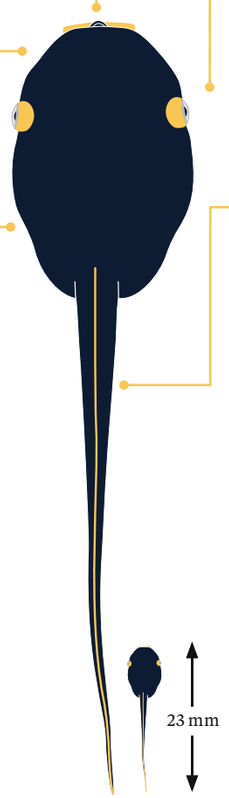
Microhyla berdmorei (Blyth, 1856)

Berdmore's Narrow-mouthed Frog

SNOUT
Snout moderately long, rounded. Tip of snout truncated in lateral view, with a bulging „chin".

ORAL DISC
Mouth is terminal. Oral disc present but reduced. Lower jaw present as distinct U-shaped arch. Jaw edges not keratinized noticeably (not black) and keratodonts absent; LTRF (0/0).

BODY
Small in overall size. Body broadly elliptical, flat above. Head dominates body and is longer and wider than trunk. Body widest at posterior gill region of head. Trunk rounded in cross-section. Spiracular orifice ventral and located medial, opening below the posterior abdomen. Spiracle opens posteriorly and bears a ventral, flap-like extension; edge of flap smoothly convex, not crenulated. Lateral line organs not visible.



NOSTRILS & EYES
The eyes are relatively large, widely spaced and positioned laterally; cornea protruding beyond body contour in dorsal and ventral views. Iris dusted with dense metallic pigmentation on a black background; scleral part of eyeball also covered with reflecting iridocytes. The nostril is not perforated in larval stages.

TAIL
Up to approximately 69% of total length. Tail muscle moderately developed, narrow; less than half the width of trunk in dorsal view. Muscular part of the tail s approximately half depth of body in lateral view. Upper fin originates slightly anterior to trunk-tail junction on trunk; upper fin contour line mostly straight with shallow convexity only in the middle third of tail. Lower fin similar in shape, higher than upper fin, particularly in proximal half of tail. In posterior fourth of tail, fins taper towards a narrowly rounded tip, without forming a distinct flagellum. Skin glands absent. Lateral tail vein invisible. Muscle myosepta faintly visible in magnification.

The larval account herein follows a detailed redescription of Microhyla berdmorei *tadpoles from the Malay Peninsula in Leong (2004). Unfortunately, no photographs of the larval stages of* M. berdmorei *were available for this book.*

SIMILAR SPECIES

Microhyla berdmorei tadpoles are easily diagnosable as microhylid tadpoles by their lack of keratinized mouthparts, reduced oral disc, terminal mouth, and ventromedian spiracle. In comparison, *Nanohyla petrigena, N. perparva, and Microhyla malang* have distinctive color pattern features, particularly on their tails, and are smaller in size than *M. berdmorei*. *Glyphoglossus* tadpoles differ from *M. berdmorei* by tail fin shape with higher lower fin relative to the upper.

LITERATURE

Lalremsanga, H. T., Hooroo, R. N. K. (2012) Remodeling of the intestine during metamorphosis of *Microhyla berdmorei* (Anura: Microhylidae). International Multidisciplinary Research Journal 2: 35–40.

Leong, T.M. (2004) Larval descriptions of some poorly known tadpoles from Peninsular Malaysia (Amphibia: Anura). The Raffles Bulletin of Zoology 52: 609–620.

Inger, R.F., Stuebing, R.B.., Grafe, T.U., Dehling, J.M. (2017) A field guide to the frogs of Borneo. 3rd ed. Natural History Books, Kota Kinabalu. 228 pp.

HABITAT & ECOLOGY
Microhyla berdmorei tadpoles inhabit temporary stagnant pools, drainages, or flooded areas where they filter the water for microscopic particles, often at mid-water level or at the surface. These larvae are highly efficient suspension feeders.

REPRODUCTION
Inger et al. (2017) reported the advertisement call as a short rasping pulse with dominant frequencies between 1500-1800 Hz.

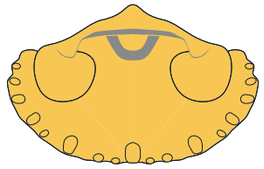
COLORATION
Overall mostly yellowish, body skin mostly transparent. Fins mostly clear. Transparent and unpigmented ventrally; inner organs visible.

Microhyla malang Matsui, 2011

Bornean Narrow-mouthed Frog

SNOUT
Moderately long, broadly rounded in dorsal view, with an anterior truncation in which the mouthparts are located; tip of snout truncated in lateral view, with a bulging „chin“. Jaws recessed.

ORAL DISC
Mouth terminal, slightly upward directed in lateral view. Upper oral disc reduced to a fold with triangular flap above upper jaw. Lower part of oral disc consists of a semi-circular lower lip with several knob-like papillae close to the edge.



Large knobs present left and right of mouth, surrounded by the lower lip. Particularly ventrally, snout bulges („chin“) so that mouthparts appear slightly recessed. Jaw edges not keratinized noticeably (not black) and keratodonts absent; LTRF (0/0).

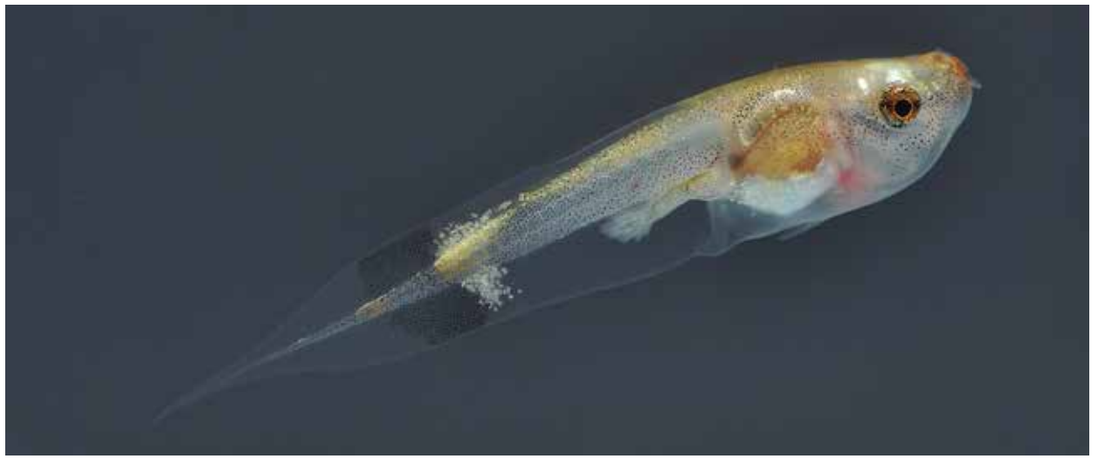
ECOMORPH
Lentic, endotroph, suspension-feeder.

NOSTRILS & EYES
Eyes large, widely spaced and positioned laterally. Cornea protruding beyond body contour in dorsal and ventral views. Iris dusted with dense metallic copper pigmentation on a black background with dark anterior and posterior iris sectors and sometimes a narrower ventral dark sector. Sclera covered with reflecting silvery or golden iridocytes. Nostril not perforated in larval stages.

BODY
Small. Head and trunk subtriangular in lateral view. Trunk about as wide as high. Head flat above in lateral view. In dorsal view, head and trunk oblong, parallel sided. The head is large relative to the trunk. Body widest at gill region of head. The trunk is broadly rounded posteriorly. The posterior trunk is significantly wider than the base of the tail. Spiracular orifice ventral and located medially, slightly posterior to the center of the abdomen. The spiracle opens posteriorly and bears a ventral, flap-like extension, smoothed V-shaped. Lateral line organs not visible.

TAIL
Up to ~73% of total length. Tail muscle moderately developed, approximately half the width of trunk in dorsal view. Muscular part of tail approximately half the depth of body in lateral view. Upper fin originates slightly posterior to trunk-tail junction. Upper fin contour line mostly straight with shallow convexity only in the distal third of the tail. Lower fin similar in shape, higher than the upper fin, particularly in the proximal half of tail. Tail tip long and flagellate. Skin glands absent. Lateral tail vein indistinct. Muscle myosepta faintly visible in magnification.

SIMILAR SPECIES
The terminal mouth and reduced oral disc, as well as the ventromedian spiracular opening clearly identifies *Microhyla malang* as a microhylid tadpole and separates it from all non-microhylid tadpoles. *M. malang* larvae may be most easily confused with *N. petrigena* or *N. perparva* tadpoles that also live in standing bodies of water. They are distinguished from both by its larger size, more parallel-sided body, longer flagellum and distinct color pattern, including conspicuous white elements. See comments of other *Microhyla* species.



The tadpoles of Microhyla malang *live in stagnant water, in puddles as well as in ponds. They will also breed in forest ponds with partially open canopy and even forest road ditches. The tadpoles can be observed suspension-feeding near the surface. Due to their small size, the hovering swimming behavior and their camouflage pattern, they may be difficult to spot against the leaf litter bottom of a pond.*

HABITAT & ECOLOGY
Microhyla malang tadpoles hold position almost motionless near the surface. They maintain that position by constantly beating their long flagellate tail tip. While doing so, the body is inclined at approximately 30° head up. The lungs are air-filled, shine silvery through the skin, and provide buoyancy. When disturbed, *M. malang* tadpoles are capable of bursts of swimming toward the bottom leaf litter. *Note*: The species has been referred to as „*M. borneensis*“ in the older literature until Matsui's (2011) description of *M. malang*. *M. borneensis* is now applied to another miniature species.

REPRODUCTION
Males call from the ground in the vicinity of permanent or temporary ponds. Pairs are formed on land. The male clasps the female at the shoulder. Eggs are small, black and float as a single layer on the water surface.

COLORATION
Head, trunk, and part of tail brown above. Sometimes a diffuse dark band runs from the mouth laterally across the eye to the flank. The muscular part of the tail may bear a black horizontal band for half of the tail length. A broad black vertical band runs across the tail in the distal half of the tail (at approximately 60% tail length). The black band is bordered anteriorly by a white band (iridocytes). The tail fins are otherwise unpigmented. Iridocytes are also scattered at some density along the dorsal side of the muscular part of the tail and dorsal trunk. Dense areas of iridocytes dorsally on the head near the eyes can appear as bright white spots in daylight. Mouth area often with orange or red tinge. Ventral skin transparent, devoid of pigment cells. Inner organs visible especially red heart and gills, gut silver from below, and silver lung (dorsal).

LITERATURE

Matsui M. (2011) Taxonomic revision of one of the Old World's smallest frogs, with description of a new Bornean *Microhyla* (Amphibia, Microhylidae). Zootaxa 2814: 33–49.

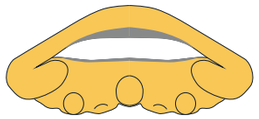
Leong, T.M., Chou, L.M. (1999) Larval diversity and development in the Singapore Anura (Amphibia). The Raffles Bulletin of Zoology 47: 81–137.

Microhyla nepenthicola Das and Haas, 2010

Matang Narrow-mouthed Frog

SNOUT
Very short, broadly rounded in dorsal view, with an anterior shallow bay that harbors the small mouthparts. Tip of snout appears truncated in lateral view as well, with a bulging „chin." Jaws slightly recessed.

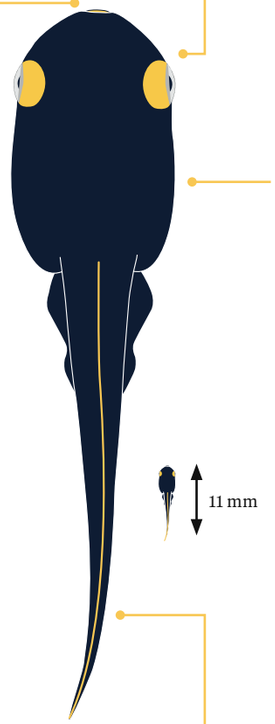
ORAL DISC
Mouth is terminal, slightly upward directed in lateral view.



Upper lip of oral disc almost completely reduced. Lower lip much reduced but present as a small flap; it bears few papillae each immediately inside the edge of the lip. Laterally, curved bulges are present at corners of mouth. Snout around mouth slightly bulges so that mouth appears recessed in a horizontal depression of snout tip. No black keratinization of jaw edges, keratodonts absent; LTRF (0/0).

ECOMORPH
Phytotelma specialist, endotrophic.

SIMILAR SPECIES
The combination of phytotelma habits, particularly association with *Nepenthes* pitchers, the small size even at advanced stages, swimming behavior, lack of color pattern, and the cuspidate tail fin make these tadpoles unique and not easy to confuse with any other tadpole in the field. *Microhyla malang* is a close relative on Borneo and differs from *M. nepenthicola* tadpoles in its larger size, long flagellate tail tip and more developed oral disc. A very similar species, *M. borneensis*, presumably has similar tadpoles, but this needs confirmation.



NOSTRILS & EYES
Eyes widely spaced and positioned laterally, large relative to the body. Cornea protruding beyond the body contour in dorsal and ventral views. Iris dusted with dense bronze pigmentation on a black background. Scleral part of eyeball covered with reflecting iridocytes. Depending on direction and intensity of light, iridocytes may appear silvery to golden. The nostril is not perforated in larval stages.

BODY
Very small in total length. Head and trunk not depressed noticeably. Trunk about as wide as high. Head rounded above in lateral view. In dorsal view, head and trunk smoothly oblong. Head not as dominant as in exotrophic microhylids. Head almost as wide as the trunk in dorsal view. Trunk broadly rounded posteriorly. Body widest at the trunk region and significantly wider than base of the tail. Spiracular orifice ventral and located medially, approximately at the middle of abdomen; it opens posteriorly. Ventral rim of spiracle bears a flap-like extension with the shape of a truncated V. Lateral line organs and lateral tail vein not visible.

TAIL
Approximately 67% of total length. Tail moderately developed, approximately half the width of trunk in dorsal view. Muscular part of tail lower than body in lateral view. Upper fin originates at trunk-tail junction. Upper fin contour line mostly straight with noticeable convexity only in the distal third of tail. Lower fin similar in shape, as high as or slightly higher than upper fin. Tail tip cuspidate (short flagellate). Skin glands absent. Lateral tail vein invisible. Muscle myosepta faintly visible in magnification.

The tadpoles of Microhyla nepenthicola *live in pitchers of* Nepenthes *plants, particularly* N. ampullaria. *The tadpoles are tiny. They do not feed but live from the yolk reserves stored in their gut.*

HABITAT & ECOLOGY
Microhyla nepenthicola tadpoles hover almost motionless in the small pool of water in a *Nepenthes* pitcher. Their short flagellate tail tip is constantly beating. The axis of the body oriented at ~35° head up. The tadpoles do not feed (endotrophic). We found up to 14 larvae in a single pitcher in different developmental stages. This indicates multiple egg depositions in one pitcher. When disturbed, tadpoles are capable of rapid swimming bursts and will hide among the accumulated debris at the bottom of pitchers.

REPRODUCTION
Males are found calling from the forest floor in the vicinity of pitcher plants. Amplecting pairs crawl into the pitcher and lay only a few large, yolk-rich eggs. Although pitcher plants are preferred, some other small phytotelmata near the forest floor may be used. Development is fast and culminates with a metamorphosis only two weeks after egg deposition. Despite their miniature size of only 3.5 mm, the metamorphosed froglets are powerful jumpers and manage to jump out of the pitcher.

COLORATION
Generally hues of gray or olive dominate above, on otherwise transparent skin; no pattern. Melanocytes scattered over top of head, trunk, flanks and muscular part of tail. Silver or golden iridophores scattered on the posterior trunk and the dorsal side of the tail musculature. Ventral skin transparent devoid of pigment cells, inner organs visible especially red heart, yellow gut, and silver lung (dorsal). Tail fins transparent.

LITERATURE

Das, I., Haas, A. (2010) New species of *Microhyla* from Sarawak: Old World's smallest frogs crawl out of miniature pitcher plants on Borneo (Amphibia: Anura: Microhylidae). Zootaxa 2571: 37–52.

Gorin, V.A., Solovyeva, E.N., Hasan, M., Okamiya, H., Karunarathna, D.M.S.S., Pawangkhanant, P., Silva, A. de, Juthong, W., Milto, K.D., Nguyen, L.T., Suwannapoom, C., Haas, A., Bickford, D.P., Das, I., Poyarkov, N.A. (2020) A little frog leaps a long way: compounded colonizations of the Indian Subcontinent discovered in the tiny Oriental frog genus *Microhyla* (Amphibia: Microhylidae). PeerJ 8, e9411-47.

Nanohyla perparva (Inger and Frogner, 1979)

Least Narrow-mouthed Frog

Flooded areas form after heavy rain in the forest. If the conditions are right, males of *Nanohyla perparva* congregate in the number of hundreds in temporary forest pools. Males float on the surface and call from their small territory that they defend against conspecific intruders. Note the concentric wave rings that calling males generate when calling. Gunung Mulu National Park.

The tadpoles of *Nanohyla perparva* are typical suspension-feeding microhylid tadpoles, with huge heads relative to the small trunk. As many pairs of adults may spawn at the same site, tadpoles can occur in large numbers. Tadpoles move very slowly through the water by constantly beating the flagellate tip of their tail. Only when disturbed will they rapidly accelerate forward in a short burst.

The tiny tadpoles of Nanohyla perparva *occur in flooded depressions or temporary ponds in the forest. Adults emerge after heavy rains and breed explosively in large numbers. Morphologically, the tadpole is similar to* Nanohyla petrigena*; diagnostic differences have not been established with certainty. See description of* N. petrigena.

HABITAT & ECOLOGY

The very small tadpoles of *Nanohyla perparva* are highly efficient, obligate suspension-feeders. Morphologically they are similar to those of *N. petrigena*. In fact, based on the limited samples examined, we could not establish any diagnostic feature between the two species at this point. Please refer to the description of *N. petrigena* for more details. Ecologically, however, both species are well separated. *Nanohyla perparva* tadpoles live in temporary forest ponds and floodings, whereas *N. petrigena* tadpoles can be found in rock pools and rock troughs along forest streams. Tadpoles of *N. perparva* hover in the water column, often close to the surface, while continuously pumping water through their highly efficient branchial filters. The tail end is constantly beating while the tadpole slowly maneuvers forward.

REPRODUCTION

After heavy rainfall, large numbers of *N. perparva* males congregate at flooded forest depressions. The calling males float at the surface of the water; they defend a small area (approximately 20–50 cm diameter) against competitors. We found one such congregation fully active at mid-day.

ECOMORPH

Lentic, exotrophic, obligate suspension-feeder.

SIMILAR SPECIES

Morphologically, the most similar tadpole on the island of Borneo is that of *N. petrigena*. The tadpoles of *N. perparva* and *N. petrigena* are similar in body shape and coloration. Both species are small but *N. petrigena* grows slightly larger. *N. parva* tadpoles are associated with forest ponds whereas *N. petrigena* tadpoles live in potholes and pools in or along rocky streams.

LITERATURE

Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

Inger, R.F., Stuebing, R.B., Grafe, T.U., Dehling, J.M. (2017) A field guide to the frogs of Borneo. 3rd ed. Natural History Books, Kota Kinabalu. 228 pp.

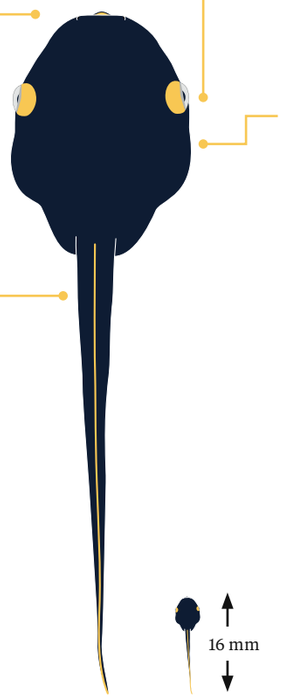
Nanohyla petrigena (Inger and Frogner, 1979)

Pothole Narrow-mouthed Frog

SNOUT
Moderately long, broadly rounded slightly truncated in dorsal view. In lateral view, moderately tapering and tip truncated, with a bulging „chin." Jaws recessed.

ORAL DISC
Mouth terminal. Oral disc absent. Upper jaw wide and straight, overhanging lower jaw substantially; lower jaw U-shaped and deeply recessed. Chin-like soft tissue bulge below mouth. Mouth opening recessed in a horizontal depression. No keratinization (beaks) on jawlines. Keratodonts absent; LTRF (0/0).

TAIL
up to 65-67% of total length. Tail musculature narrow, less than half the width of trunk in dorsal view and less than half the depth of body in lateral view. Upper fin originates at trunk-tail junction. Upper fin contour only shallowly convex (in the middle part of tail). Lower fin similar in shape and equal in height. Both fins taper in the posterior third of tail forming a narrowly rounded tip. Tip slightly flagellate, i.e, a mild concavity in contour present terminally. Skin glands absent. Lateral tail vein invisible. Muscle myosepta indistinct.



NOSTRILS & EYES
Eyes relatively large, widely spaced and positioned laterally. Eye cornea protruding beyond body contour in dorsal and ventral views. Iris black with scattered silver-gold iridophores dorsal and ventral of pupil. Scleral part of eyeball with scattered silver iridophores dorsally. Nostril not perforated in larval stages.

BODY
Small in overall size. Head very large in comparison to trunk. In dorsal view, head to trunk transition distinctly visible as a narrowing of the body. Head as broad as long in dorsal view; flat above. Body widest at the posterior end of gill region of head. Trunk short, broadly rounded posteriorly. Trunk significantly wider than base of tail in dorsal view. Spiracular orifice ventral and located medial, slightly posterior to center of abdomen. Spiracle opening posteriorly and extended by ventral flap; posterior edge of flap fringed with finger-like projections. Lateral line organs not visible.

ECOMORPH
Lentic, exotrophic, obligate suspension-feeder.

SIMILAR SPECIES
A combination of larval characters clearly diagnoses *Nanohyla petrigena* as microhylid and separates it from all other Bornean families: terminal mouth, reduced oral disc, and ventromedian spiracular opening. *N. petrigena* larvae can be confused with *Microhyla malang* or *N. perparva* tadpoles that also live in standing bodies of water. *N. petrigena* and *N. perparva* are distinguished from *M. malang* by smaller size, broader head, shorter flagellum, complete lack of oral disc, and lack of conspicuous white flecks above. Tadpoles of *N. petrigena* and *N. perparva* seem indistinguishable on the basis of the samples analyzed. The tail band seemed slightly more distal and the tail tip more abruptly flagellate in the few *N. perparva* we could compare to *N. petrigena*. This may, however, overlap with intraspecific variation or phenotypic plasticity in the two species. The two species are most clearly separated ecologically, in that *N. perparva* larvae populate temporary forest ponds and water-filled depressions of the forest floor, whereas *N. petrigena* is associated with rocky streams where the tadpoles live in rock pools.

Because of their small size, subtle movements and dark coloration, tadpoles of Nanohyla petrigena *may be difficult to spot against dark background. These tadpoles are delicate and need to be handled gently.*

HABITAT & ECOLOGY
The tadpoles of *Nanohyla petrigena* have exclusively been found in potholes or rock troughs in and along rocky streams. The tadpoles are obligate suspension-feeders; they filter microscopic particles from the water that they pump through their branchial filter system. They can be seen suspension-feeding near the water surface with slow swimming motions. As is typical for many suspension-feeders that feed at various levels in the water column, *N. petrigena* larvae maintain their position by constantly beating their tail tip.

REPRODUCTION
Males call from around suitable rock pools along the shores of clear, rocky forest streams. Eggs are small, black and float as a single layer in a perfectly transparent jelly mass on the water surface, usually sticking with one of the sides to a rock. Details of development have not been documented, but the larval period is suspected to be short.

COLORATION
Head, trunk, and proximal part of tail brown above. The muscular part of the tail is dark brown to black laterally for one third to half of the tail and fades distally. A broad black vertical band runs across the tail at approximately 66% of the tail length. Apart from the band, the tail fins are clear. Anterior to the black band, there are scattered iridophores along the dorsal and ventral edges of the muscular tail part. Scattered iridophores are furthermore present dorsally on the trunk and at the dorsal and lateral faces of the head. Ventral skin transparent, without pigmentation: The inner organs are visible, especially the gut.

LITERATURE

Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

Inger, R.F., Stuebing, R.B., Grafe, T.U., Dehling, J.M. (2017) A field guide to the frogs of Borneo. 3rd ed. Natural History Books, Kota Kinabalu. 228 pp.

Rock pool at a stream with freshly laid clutches of *N. petrigena* eggs floating as a single layered film on the surface of the water. Batang Ai National Park.

Kalophrynus intermedius Inger, 1966

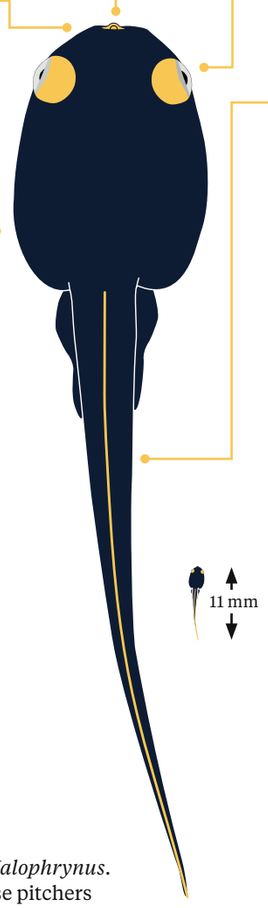
Sticky Frog

SNOUT
Very short and bluntly rounded in lateral view. In dorsal view, rounded, medially truncated or shallowly embayed

ORAL DISC
Mouth terminal; oral disc absent. Mouth small, recessed in a horizontal fold of snout tip. Mouth with a shallowly arched upper jaw and a wide U-shaped lower jaw. Keratinized jaw sheaths and keratodonts absent; LTRF (0/0).

BODY
Very small in overall size. Head and trunk slightly depressed dorsoventrally. In dorsal view, head not clearly separated from trunk, both relatively wide. Trunk broadly rounded posteriorly and much wider than base of tail. In lateral view, head bluntly rounded anteriorly, snout short. Body widest at the trunk region. Spiracle ventral and medial, in a mid-belly position. Spiracular orifice a simple shallow arch that opens posteriorly without flap.

ECOMORPH
Phytotelma specialist, endotrophic.



NOSTRILS & EYES
Eyes relatively large and positioned laterally, spaced widely. Cornea protruding beyond body contour in dorsal and ventral views. Iris mostly black, with a metallic golden ring around pupil. Beyond iris, eye ball dotted with silver iridophores. Nostril not perforated in larval stages.

TAIL
Long, 69% of total length. Muscular part of tail moderately developed, approximately half of body height in lateral view and less than half of trunk width in dorsal view. Upper fin takes origin at trunk-tail junction, keeps low for a short distance and then rises to a shallow convex arch. Upper fin relatively low. Both fins subequal in height. In the posterior half of tail, fins symmetrical and weakly taper to a moderately narrowly rounded tip. Overall tail fin shape lanceolate. Skin glands absent. Lateral tail vein indistinct. Muscle myosepta visible at high magnification, anteriorly slightly accentuated by pigmentation.

SIMILAR SPECIES
Larval stages have rarely been reported for *Kalophrynus*. It has been stated that *Kalophrynus* might use pitchers of *Nepenthes* for egg deposition. However, at least some of the reports may have confused *Microhyla nepenthicola* tadpoles with *Kalophrynus* tadpoles. In fact, the *Kalophrynus intermedius* larvae described here and *M. nepenthicola* tadpoles are similar superficially; however, they can be distinguished by tail tip shape (pointed cuspidate in *M. nepenthicola*). *Kalophrynus* tadpoles can be confused with *Metaphrynella* tadpoles. See comments for *Metaphrynella sundana*. Inger (1985) presented a description without photo of larval *K. meizon* (as *K. pleurostigma*).

LITERATURE

Inger, R.F. (1966) The systematics and zoogeography of the Amphibia of Borneo. Fieldiana Zoology 52: 1–402.

Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

Inger, R.F., Stuebing, R.B., Grafe, T.U., Dehling, J.M. (2017) A field guide to the frogs of Borneo. 3rd ed. Natural History Books, Kota Kinabalu. 228 pp.

Malkmus, R., Dehling, J.M. (2008) Anuran amphibians of Borneo as phytotelm-breeders - a synopsis. Herpetozoa 20: 165–172.

The tadpoles of Kalophrynus intermedius *are tiny, have a yellowish yolk-filled gut, and do not perform suspension-feeding movements of their gills when hovering in the water column as do other microhylids. This combination of features is indicative of an endotrophic mode of development.*

HABITAT & ECOLOGY
The *Kalophrynus* larvae depicted here were found in a partially water filled tin in disturbed vegetation at the forest edge. Adults that we identified as *Kalophrynus intermedius* (photo) were calling nearby. Larvae were tentatively assigned to that species. Only nine larvae were discovered in the tin. Body size was very small despite of advanced developmental stage in some (hind leg development) and all had cream-colored guts. This indicates an endotrophic lifestyle that does not require uptake of nutrients from the exterior.

REPRODUCTION
Phytotelmata or similarly small containers with water are used for egg deposition.

COLORATION
Uniformly dark brown above, without distinct pattern. Coloration of body continues onto tail and tail fins but quickly fades in the posterior and ventral parts of the tail. The density of melanocytes declines along the flanks toward the ventral side. Ventral side transparent. Gut coil visible in lateral and ventral views. Ventral gular and buccal region re slightly dusted with melanocytes. Heart and large blood vessels visible in ventral view.

Kalophrynus meizon Zug, 2015

Bornean Large Sticky Frog

The species has undergone taxonomic splitting (Zug 2015). Previously, K. meizon *was subsumed within* K. pleurostigma. *The latter species, however, is now considered restricted to Sumatra and the tadpole description of* K. pleurostigma *by Leong and Chou (1999) from Singapore is the extralimital (to Borneo) K. limbooliati.*

SIMILAR SPECIES

See *Kalophrynus intermedius*.

TADPOLE

We tentatively assign an early stage tadpole from Tawau Hills National Park (photo) to this species. It was recovered from a tank at a picnic area, associated with tadpoles of *Chaperina fusca*. At very early stage, with two adhesive glands present anteroventrally, this individual already had clearly developed hind limb buds and a very large belly. This could indicate endotrophic development. Due to the early developmental stages of the specimens examined, we do not present a formal larval description. Inger (1985) provided a description of larval stages, however, did not illustrate them. More research is needed.

HABITAT & ECOLOGY

Males call from the forest floor. Phytotelma breeder.

ECOMORPH

Phytotelma specialist, endotrophic.

LITERATURE

Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

Leong, T.M., Chou, L.M. (1999) Larval diversity and development in the Singapore Anura (Amphibia). The Raffles Bulletin of Zoology 47: 81–137. [described as *K. pleurostigma*]

Zug, G.R. (2015) Morphology and Systematics of *Kalophrynus interlineatus-pleurostigma* populations (Anura: Microhylidae: Kalphryninae) and a taxonomy of the genus *Kalophrynus* Tschudi, Asian Sticky Frogs. Proceedings of the California Academy of Sciences 62: 135–190.

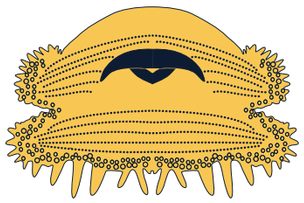
Maliau Basin

Abavorana luctuosa (Peters, 1871)

Mahogany Frog

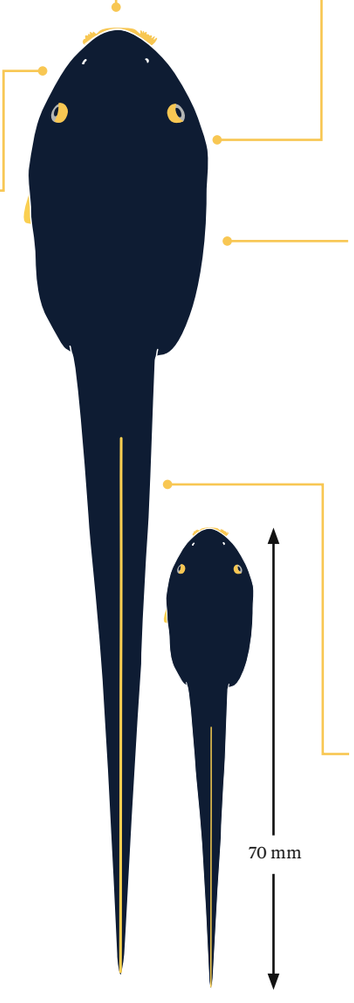
SNOUT
Narrowly rounded, both in dorsal and lateral views. In lateral view, snout long and sloping in a slight curve; this and the uprising ventral contour result in an overall pointed or wedged profile in lateral view. Oral disc may slightly project beyond snout in dorsal view.

ORAL DISC
Anteroventral. A clear emargination separates upper and lower lips. Lips with papillae along their margins, except for a broad gap in papillation medially in the upper lip.



Submarginal papillae present in 2–3 irregular, dense rows. Marginal papillae long in general but lower lip bears some exceptionally long, finger-like papillae. LTRF 6(5–6)/5 or 6(5–6)/5(1). In lateral parts of disc, irregular short stretches of accessory keratodont rows may be present. Beaks strongly keratinized and undivided; jaw edges bear serrations. Upper beak broadly and shallowly arched; lower beak widely V-shaped.

ECOMORPH
Lentic-benthic, exotrophic.



NOSTRILS & EYES
Eyes dorsolateral. Nostril smoothly rimmed and closer to snout than to eye, oriented anterolaterally. A distinct orbitonasal streak connects eye and nostril. Iris color variable, ranging from mostly black with only a narrow golden ring around the pupil to a much broader golden or coppery ring with silvery-golden stippling in the periphery.

BODY
Oval in dorsal view and slightly depressed in lateral view. Snout narrowly rounded in dorsal as well as in lateral views. Widest part of body in dorsal view at the gill region, behind level of eyes. Spiracle sinistral, opening posteriorly or posterolaterally. Medial rim of the spiracular orifice is distinct, but no long, free tube is present. Spiracular orifice lies below the mid-body level in lateral view. In some specimens, lateral line organ discernible as distinct lines of dots on the head, trunk, and tail. In other specimens, these organs are indistinct. Many specimens bear scars on body or tail, probably from predator attacks.

TAIL
~63–66% of total length. Muscular part of tail strong and high, almost equal to body height. Upper fin starts posterior to trunk-tail junction (at ~10–13% of tail length), sloping up to the highest point, anterior to half-point of tail. Lower fin originates at a level with the upper fin, but remains low before it gains height more posteriorly. Skin of anterior half of tail opaque and distinct from the partially transparent posterior half. Posterior tail and its fins reminiscent of a pointed lancet in shape; however, in many specimens the tail tips are damaged or regenerated. In intact tails, the tip is narrowly rounded. Ventral and lateral tail veins indistinct.

SIMILAR SPECIES
Because of their size and distinct coloration, *Abavorana luctuosa* tadpoles cannot be confused with other species. *Polypedates macrotis* tadpoles, which can be present in the same pond, can be distinguished by color pattern, tail fin shape, fin extent, and oral disc features. Diagnostics to distinguish *A. luctuosa* from *A. decorata* tadpoles still need to be established.

Abavorana luctuosa *tadpoles are impressive and stand out amongst other tadpoles by their size and heavy body. Despite of that, it may be difficult to find them because they are wary and dash off to the muddy bottom of their habitat at the slightest disturbance. Recently a second taxon has been resurrected,* A. decorata *(Mocquard, 1890). The ecological separation of their larvae is unknown.*

HABITAT & ECOLOGY
Most *A. luctuosa* tadpoles live in rainforest pools, artificial pools, deep ditches along logging roads with soft bottom and leaf litter; deep pools > 30 cm are preferred. Occasionally, the tadpoles are found in deep sections of small, slow-moving forest streams or intermittent streams. During the day, they hide at the bottom of the pond, coming out to forage by night. They come to the surface to gulp air at intervals and return to the bottom quickly.

REPRODUCTION
Abavorana luctuosa males call from sheltered sites, such as under logs or cavities in the mud banks, close to the waterline, sometimes in small groups. The call is a single note rising in frequency.

COLORATION
Coloration variable between populations (see also p. 14). The general coloration of the body and tail is a dark brown background color above, sometimes with hues of olive. This is broken up by irregular mottling of a lighter color (light brown, cream or even slightly orange). Night and day coloration differ: at night, the body is paler than during daytime and the posterior half of the tail becomes black; the black posterior sections of the tail is far less distinct or disappears completely during daytime. In some populations, the mottling can change to a marbling pattern at the lower flanks and the proximal tail. Dorsally and laterally, there are no conspicuous clusters of iridocytes. The pigmentation of the trunk extends seamlessly onto the muscular part of the tail. The muscular part and tail fins are mottled dark (paler at daytime), in rare cases with an orange tint, often with irregular clusters of iridocytes. The ventral skin of the body is opaque white with dense stippling of small melanocytes; gills and gut not visible through the skin. The oral disc also bears some dark (melanocyte) stippling.

LITERATURE

Inger, R.F. (1966) The systematics and zoogeography of the Amphibia of Borneo. Fieldiana Zoology 52: 1–402.

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Quah, E.S.H., Grismer, L.L., Wood, P.L., Lim, K.K.P.L, Imbun, P.Y., Anuar, S. (2021) An investigation into the taxonomy of *Abavorana luctuosa* (Peters, 1871) (Anura, Ranidae) and the resurrection of *Rana decorata* Mocquard, 1890 from Borneo. Vertebrate Zoology 71: 75–99.

Chalcorana megalonesa (Inger, Stuart, and Iskandar, 2009)

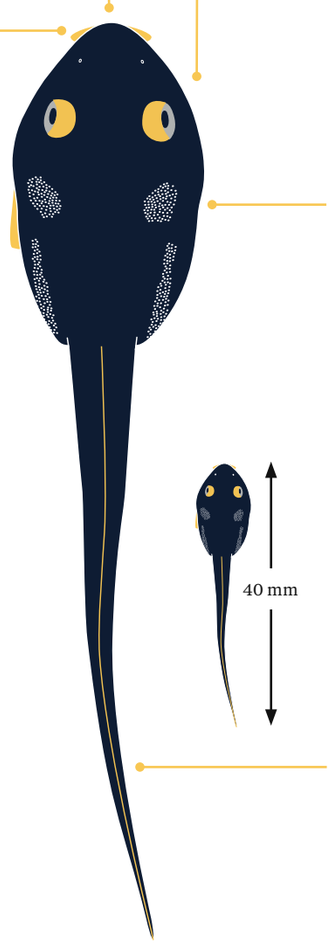
Large white-lipped Frog

SNOUT
Tapering and relatively narrowly rounded in dorsal view. In lateral view, snout moderately long and sloping downward in a slightly convex curvature. Area posterior to nostril forms a weak bump in profile.

ORAL DISC
Anteroventral. A clear emargination separates upper and lower lips. Papillae along oral disc margin present, except for a broad gap in papillation medially in upper lip. Submarginal papillae are present in two loose rows.

Marginal papillae short and rounded on upper lip. Lower lip bears long, finger-like marginal papillae. LTRF 3(2–3)/3 to 4(2–4)/3. Beaks well-keratinized but narrow in height, undivided; jaw edges with fine serrations. Upper beak broadly arched; lower jaw sheath V-shaped, weak.

ECOMORPH
Lentic, exotrophic, benthic-nektonic.



NOSTRILS & EYES
Eyes dorsolateral. Nostril small, closer to snout than to eye, oriented anterolaterally. Orbitonasal streak indistinct. A golden, sometimes coppery or orange ring borders the pupil. Iris periphery outside that ring black. Sclera stippled with silvery iridophores.

BODY
Rhomboid to oblong oval, with a slight constriction behind the gill region. Widest part of the body at level of gill region, posterior to eyes. Snout tapering. Body moderately depressed dorsoventrally. Spiracle sinistral, opening posteriorly into a short free tube, positioned below the mid-body axis in lateral view. Lateral line organs indistinct. Patches of skin glands located dorsally above the gill region (posterior to eyes) and at the upper trunk flanks. Lungs may be visible as stretch of several bubbles under the upper flank gland field. Very distinct oblong bands of glands present along the lateral abdomen; two round less distinct patches located at the buccal region (posterior to oral disc).

TAIL
~65% of total length. Muscular part moderately strong, and less than body in height. Upper fin starts slightly posterior to the trunk-tail junction. Both tail fins are moderately arched, upper fin higher than the lower. In posterior third of tail, fins taper into a narrowly rounded tip. Lateral tail vein visible in the anterior third of tail; myosepta visible in posterior part of tail musculature.

SIMILAR SPECIES
Chalcorana megalonesa is known from northern Sarawak, Sabah and Brunei. *C. raniceps* is morphologically similar. Color patterns have been observed to be variable between populations (presence/absence of dark markings) and reliable differences between *C. megalonesa* and *C. raniceps* tadpoles have yet to be established. In the field, it is important to identify the adults of the respective area. Both *Chalcorana* species can be confused with the tadpole of *Rhacophorus pardalis* that may live in the same water bodies and has similar size-range and body and tail shapes. The easiest distinguishing character is the presence of clusters of skin glands in *C. megalonesa* and *C. raniceps* (absent in R. *pardalis*). Furthermore, *R. pardalis* differs in its LTRF.

The tadpoles of Chalcorana megalonesa *dwell in stagnant waters and are of medium size. They are less shy than other species, and may be seen swimming in the open even by day. The contrast-rich head pattern and presence of fields of skin glands are key features of* Chalcorana *tadpoles, however, head color markings can be reduced in some populations.*

HABITAT & ECOLOGY
Larvae of this species are commonly seen around forest ponds, at clearing edges and along streams. They also breed in stagnant pools in the proximity of river banks. Little is known of their tadpole ecology and behavior. It is possible that their extensive skin glands deter predators. They seem active by day and night, and spend most of the time at the bottom of the water body, but may venture up along aquatic vegetation or twigs in the water to feed.

REPRODUCTION
Males of *C. megalonesa* gather around ponds or other suitable bodies of standing water and call from low vegetation, branches, or twigs.

COLORATION
General background coloration from ocher-yellowish to mid-brown above; darker by day and lighter at night. The trunk is usually darker than the head above. Dark markings typically include dark blotches or bands at the lateral face of head and trunk: below nostril, below eye and dorsoventrally over gill region and flank. Light areas between these markings give the tadpoles a distinct facial look. The nostril may be embedded in a small dark dot. Dark opposing V- or W-markings present between eyes. The dorsal clusters of skin glands may be embedded in darker pigments. All dark markings are typical, yet seemingly reduced in some populations. Iridocytes are dusted over parts of the cheek and flank. The pigmentation of the trunk extends onto the muscular part of the tail; the pigmentation lightens up towards the fins and the posterior parts of the tail. Tail without distinct dark markings. Ventral skin of body mostly translucent, but an opaque shining silvery layer may be present at the anterior abdomen. Buccal and gular skin populated with melanocytes but semi-transparent; gills and heart shine through in red, heart with a small patch of iridocytes. Oral disc is finely stippled with melanocytes; oral papillae pigmented at their tips.

LITERATURE
Inger, R.F., Stuart, B.L., Iskandar, D.T. (2009) Systematics of a widespread Southeast Asian frog, *Rana chalconota* (Amphibia: Anura: Ranidae). Zoological Journal of the Linnean Society 155: 123–147.

Chalcorana raniceps (Peters, 1871)

White-lipped Frog

SNOUT
Tapering and relatively narrowly rounded in dorsal view. In lateral view, moderately long and sloping downward with slight convex curvature. Area posterior to nostril forms a weak bump in profile.

ORAL DISC
Anteroventral. A clear emargination separates upper and lower lips. Oral disc margins with papillae, except for a broad gap in papillation medially in upper lip. Submarginal papillae present in two dense rows.

Marginal papillae short and rounded on the upper lip. Lower lip bears several long, spaced, finger-like marginal papillae, with a medial gap. LTRF 4(2–4)/3. Beaks well-keratinized but moderately thick, undivided; jaw edges bear fine serrations. Upper beak broadly and very shallowly arched, flat medially; lower jaw sheath shallowly V-shaped.

ECOMORPH
Lentic, exotrophic, benthic-nektonic.

SIMILAR SPECIES
see comments for *Chalcorana megalonesa*

NOSTRILS & EYES
Eyes dorsolateral. Nostril small, closer to snout than to eyes, oriented anterolaterally. Orbitonasal streak indistinct. A golden, sometimes coppery or orange ring present around pupil. Iris periphery black. Sclera stippled with silvery iridophores.

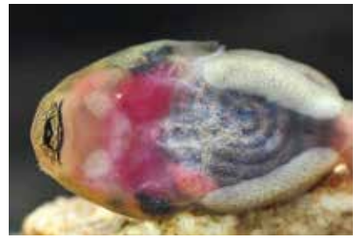
BODY
Oblong oval, with slight constriction behind the gill region in dorsal view. Widest part of body at level of gill region. Snout tapering. Body moderately depressed dorsoventrally. Spiracle sinistral. Spiracle opens posteriorly into a short, free tube. Vertical spiracular position below mid-body level in lateral view. Lateral line organs visible but usually indistinct. Patches of skin glands located dorsally above gill region and at upper trunk flank; both patches may be confluent. Lungs may be visible as stretch of several bubbles under that upper flank gland field. Conspicuous, oblong bands of glands present along lateral abdomen ventrally and two round patches located at buccal region.

TAIL
~65–67% of total length. Muscular part of tail moderately strong, less than body height. Upper fin starts slightly posterior to trunk-tail junction. Both tail fins moderately arched, upper fin higher than lower fin. In posterior third of tail, they taper into a narrowly rounded tip. Lateral tail vein visible in first third of tail. Myosepta visible in posterior part of tail musculature.

The medium-sized tadpoles of Chalcorana raniceps *tadpoles live in stagnant waters. The contrast rich head pattern (reduced in some populations) and presence of fields of skin glands are a key feature of* Chalcorana *tadpoles.*

HABITAT & ECOLOGY
This lowland species is frequently seen around forest ponds, at clearing edges and along streams where they may breed in stagnant pools on the river bank. Little is known about the ecology and behavior of the tadpoles. We observed that they tend to live in more exposed and less secretive spots than other species. It is possible that their extensive skin glands deter predators. They spend most of the time foraging at the bottom of the water body but may feed along aquatic vegetation or twigs upwards in the water column.

REPRODUCTION
Males call from low vegetation or twigs, close to or above the water, at ponds or other suitable bodies of standing water. Occasionally larger congregations have been recorded in some nights. Series of clicking notes are produced in rapid succession.



COLORATION
Body and tail ocher-yellow to mid-brown above; darker during daytime and lighter at night. Frequently, the trunk is much darker above than the head. Dark markings typically include blotches or bands at the lateral face of head and trunk: below the nostril, below the eye and dorsoventrally over the gill region and flank. The nostril may be embedded in a small dark spot. Dark opposing V- or W-markings present between eyes. The dorsal clusters of skin glands may be embedded in darker areas. These dark markings can be absent in some populations. Iridocytes are dusted over parts of the cheek and flank (inconspicuous). The pigmentation lightens up along the tail and towards the fins; tail is without distinct dark markings. The ventral skin of the body is mostly transparent. The anterior abdomen and the heart and gill regions may bear clusters of silvery iridocytes. The skin of the ventral head is translucent or semi-transparent, with fine melanocyte stippling; gills and heart shine through in red, heart with a small patch of iridocytes. The oral disc is finely stippled with melanocytes and oral papillae bear clusters of melanocytes.

LITERATURE

Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26, 1–89. [for *P. signata*].

Inger, R.F., Stuebing, R.B., Grafe, T.U., Dehling, J.M. (2017) A field guide to the frogs of Borneo. 3rd ed. Natural History Books, Kota Kinabalu. 228 pp.

Hylarana erythraea (Schlegel, 1837)

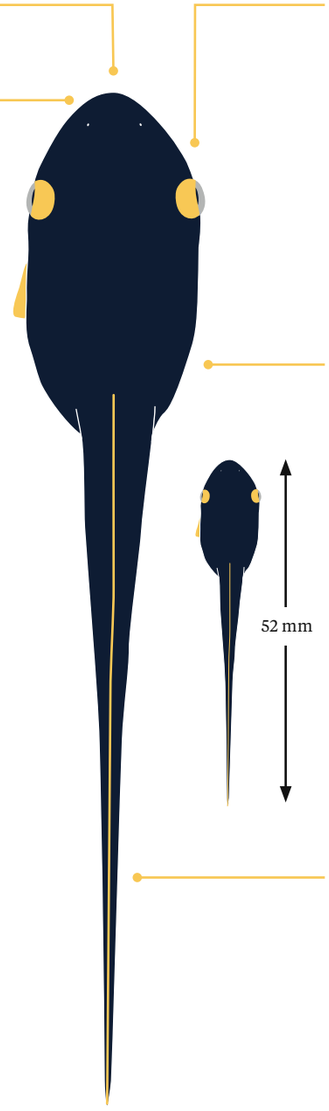
Green Paddy Frog

SNOUT
Tapering and tip rounded in dorsal view. In lateral view, long and sloping downward in weakly convex curvature. Nostrils not elevated.

ORAL DISC
Subterminal. A clear emargination separates upper and lower lips. Papillation along all of the oral disc margin, except for a broad upper lip gap medially. Papillae on the lateral parts of upper lip short.

Submarginal papillae are present in one loose row. Lower lip bears long, finger-like marginal papillae. LTRF 1/2. Beaks well-keratinized but moderate in height, undivided; jaw edges finely serrated. Upper beak mostly straight medially with a soft medial bulge and arched laterally; lower jaw sheath smooth, widely V-shaped.

SIMILAR SPECIES
Hylarana erythraea can be distinguished from other species by a combination of iris color, eye position, cheek color pattern, and habitat choice. *Indosylvirana nicobariensis* is likely to be associated with *H. erythraea* in many settings but differs from it in the dorsolateral position of the eyes and a radial pattern on the iris, among other distinguishing features in LTRF and color pattern.

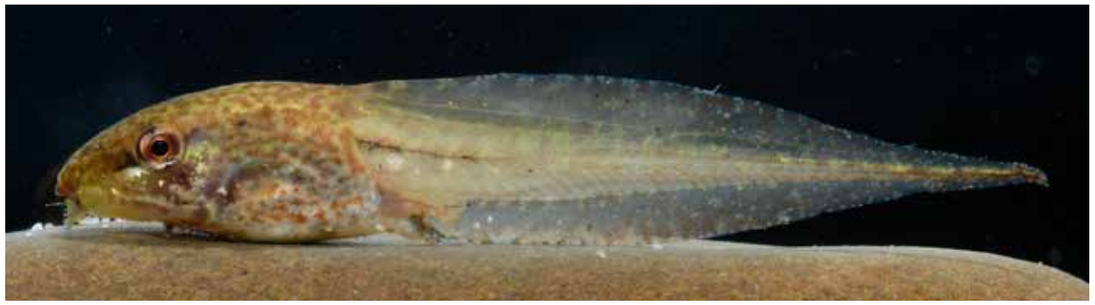


NOSTRILS & EYES
Eyes lateral, protruding beyond body contour in dorsal view. Nostril small, indistinct, much closer to the snout than to eye. Distinct orbitonasal streak absent. Iris densely stippled with iridophores on black background. Iris iridophore color reddish in the middle part and golden or silver in the upper and lower sectors. Sclera silver with some reddish or orange stippling in the upper sector.

BODY
Oblong oval, parallel-sided in dorsal view. Widest part of the body at level of gill region or at abdomen. Snout slightly tapering. Body not depressed dorsoventrally, rather smoothly square in cross-section. In lateral view, body shape smoothly triangular: the dorsal contour line slopes and curves softly and smoothly from trunk to snout (no nasal bumps or eye ball bumps); the ventral contour line is concave at the buccal region (at level below eye). Spiracle sinistral. Spiracle opening posterodorsally in a short free tube. Vertical spiracular position below mid-body level in lateral view. Lateral line organs indistinct.

TAIL
~69–70% of total length. Muscular part of tail moderately strong, less than body height in lateral view. Upper fin starts slightly anterior to trunk-tail junction. Both tail fins moderately arched and similar in height. Tail tip acuminate, with concave contour leading into a narrowly rounded tip. Lateral tail vein visible in proximal part of tail (lined with melanocytes). Myosepta indistinct.

ECOMORPH
Lentic, exotrophic, benthic-nektonic.



Hylarana erythraea *is a commensal frog species that takes advantage of human activities and is abundant in agricultural areas. The tadpoles can grow large and hide among aquatic vegetation.*

HABITAT & ECOLOGY
This lowland species is commonly seen around rural ponds, paddy fields, roadside ditches, open area swamps, park ponds, etc. The tadpoles hide among dense aquatic vegetation during the day and forage in more open areas of the pond during the night. They spend most of the time at the bottom of the water body, but may swim up and down in the water column to feed on organic matter.

REPRODUCTION
Males of *Hylarana erythraea* gather in ponds or other suitable bodies of standing water. They like to call from floating vegetation, such as lotus leaves.

COLORATION
From ocher to mid-brown above. Olive green hues and a faint vertebral streak are present in late tadpole stages. On the background color, a mottled pattern of dense dark brown or reddish-brown spots is present. The brown mottling continues from the trunk to the tail, including the fins, however, less dense and dark than on the trunk. This species bears conspicuous white markings: some white lines and iridophore blotches at the cheek and ventrally; a light line along the posterior two thirds of the tail musculature and a fainter one along the base of upper fin. Along the tail fin edges, iridophore clusters may alternate more or less clearly with dark pigmentation. Venter mostly shiny white. The buccal and gular regions are light brown semitransparent to dark brown mottled in early and advanced tadpoles, respectively. Gills, heart and gut coils are not clearly visible through the skin. The oral disc is finely stippled with melanocytes, particularly the oral papillae bear clusters melanocytes.

LITERATURE

Inger, R.F. (1966) The systematics and zoogeography of the Amphibia of Borneo. Fieldiana Zoology 52: 1–402.

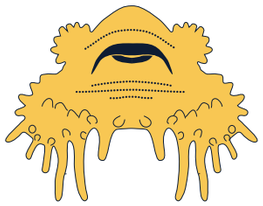
Leong, T.M., Chou, L.M. (1999) Larval diversity and development in the Singapore Anura (Amphibia). The Raffles Bulletin of Zoology 47: 81–137.

Indosylvirana nicobariensis (Stoliczka, 1870)

Cricket Frog

SNOUT
Rounded and slightly tapering in dorsal view. In lateral view, it is moderately long and sloping. This and the uprising ventral contour line creates a wedged, almost pointed profile in lateral view.

ORAL DISC
Anteroventral. A clear emargination separates upper and lower lips. Papillae present along oral disc margin, except for a broad gap in papillation medially in the upper lip. Submarginal papillae present in 1–2 irregular rows.



Marginal papillae are short and broadly rounded on the upper lip. Lower lip has several long marginal papillae, reminiscent of barbels. LTRF 1/3 to 1/3(1); if divided, gap in the first posterior row narrow, indistinct. Third posterior row short. Beaks well keratinized but thin, undivided; jaw edges finely serrated. Upper beak broadly arched, almost straight in the middle third. Lower jaw sheath a wide smooth arch.

ECOMORPH
Lentic, exotrophic, benthic-nektonic.

NOSTRILS & EYES
Eyes dorsolateral. Nostrils small, inconspicuous, closer to snout than to eye, and oriented anterolaterally. A orbitonasal streak is indistinct. Iris copperish red in color around pupil and golden at periphery. Iris periphery has four dark sectors: anterior, posterior, dorsal, and ventral, giving the eye a radial appearance.

BODY
Oblong to oval or ovoid in dorsal view; ovoid and tapering towards the anterior end in lateral view. Snout slightly tapering but not pointed in dorsal view. Widest part of the body at level of gill region or abdominal region, depending on feeding status. Spiracle sinistral, opening posteriorly. Medial rim of the spiracular orifice distinct, but there is no long, free tube. Vertical spiracular position at mid-body level in lateral view. Lateral line organs indistinct.

TAIL
~65–67% of total length. Muscular part of tail moderately strong, less than body height in lateral view. Upper fin starts slightly anterior to trunk-tail junction. Both tail fins moderately arched, upper fin higher than lower fin. In the posterior third of tail, they taper into a narrowly rounded or pointed tip. Lateral tail vein visible in the anterior third of tail.

SIMILAR SPECIES
Indosylvirana nicobariensis may co-occur in ponds with *Hylarana erythraea*, and occasionally with *Polypedates leucomystax* or *P. otilophus*, however, these latter species do not share the characteristic tail, eye, and facial color patterns of *I. nicobariensis* and differ in keratodont row formula and oral disc configuration.

LITERATURE
Inger, R.F. (1966) The systematics and zoogeography of the Amphibia of Borneo. Fieldiana Zoology 52: 1–402.

Inger, R.F., Stuebing, R.B., Grafe, T.U., Dehling, J.M. (2017) A field guide to the frogs of Borneo. 3rd ed. Natural History Books, Kota Kinabalu. 228 pp.

Indosylvirana nicobariensis *tadpoles are mid-sized to large pond-type larvae. Although the frog is omnipresent in rural areas and along roads, tadpoles may be difficult to encounter due to their wariness and escape behavior.*

HABITAT & ECOLOGY
Tadpoles live in stagnant water bodies with abundant aquatic vegetation such as ponds in open areas, roadside ditches, rural land and large forest clearings. The species does not enter the forest but depends on open country with grass and other low vegetation. Little is known about the ecology of the tadpoles. They seem to spend most of the time near the bottom of the pond. Their broad tail fin suggests that they swim up and down in the water column as well. These tadpoles are shy and will disappear among macrophytic vegetation at the slightest disturbance. The altitudinal distribution ranges from the lowlands up to at least 1000 m a.s.l.

REPRODUCTION
Males of *Indosylvirana nicobariensis* can be heard everywhere in rural settings but are not easily seen because they like to call from among dense grass. The call is a series of up to ten harsh „kek“ notes.

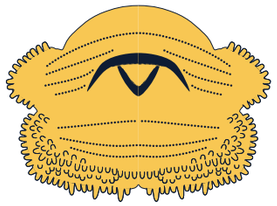
COLORATION
The general background coloration of the body and tail ranges from light to dark brown above, with fine mottling pattern. Pattern in the face is arranged in such a way that a blurred dark band runs from the eye forward to the snout and another one from the eye over the cheek, and one posterior to that. Small clusters of iridocytes are scattered over the head and trunk laterally. The pigmentation of the trunk extends onto the upper part of the tail. The upper muscular part and upper tail fin are mottled and finely dusted with melanocytes. The tail fins and posterior tail may present hues of orange. The alternating pattern of light and dark blotches along the edge of the upper and lower tail fin are characteristic for this species. The abdominal ventral skin is partially translucent, with stippling of small melanocytes and many clusters of iridocytes in the gular and abdominal regions. Thus, gut and gills are indistinct. A thin dark line is present medially on the abdomen. The oral disc also possesses melanocyte stippling. Tips of oral disc papillae pigmented.

Pulchrana glandulosa (Boulenger, 1882)

Rough-sided Frog

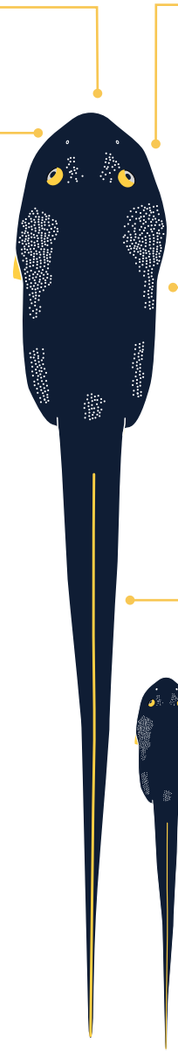
SNOUT
Rounded to narrowly rounded in dorsal and lateral views, moderately long.

ORAL DISC
Anteroventral, width slightly less than half body width. Emarginations present at lateral margin between upper and lower lips. Upper lip devoid of papillae across a wide medial area but with single row marginal papillae in the lateral parts.



One row of marginal papillae present along margin of lower lip with a small medial gap. Marginal papillae generally moderately long, except for few longer ones on lower lip. Staggered rows (one medially to four laterally) of submarginal papillae on the lower lip. LTRF 4(2–4)/3(1) or 5(2–5)/3(1). Division of first keratodont row on lower lip may be indistinct, without wide gap between ridges. Beaks highly keratinized, black, but only moderately thick; jaw edges bear very fine serrations. Upper beak broadly U-shaped, somewhat angled; lower beak smoothly V-shaped.

ECOMORPH
Lentic, exotrophic; leaf litter interstice specialist.



NOSTRILS & EYES
Eyes dorsolateral; eyes and nostrils relatively small. Nostrils slightly sunken in, without raised rim, and closer to snout than to eyes.

BODY
A medium to large-sized tadpole. In lateral view, body flat above and below, belly not bulging. Snout rounded, convex and not elongate. In dorsal view, the body contour is slender, oval to rectangular. Body widest at level of gills, posterior to eyes. Spiracle sinistral, spiracular tube opening posterodorsally and well below the longitudinal body axis in lateral view. Spiracular orifice attached to the body wall. Lateral line organs indistinct. Conspicuous fields with densely arranged glands present: between eyes, dorsal at body tail junction, along the upper flanks, laterally at the abdomen, and a large median cluster immediately behind the oral disc covering nearly all of buccal area ventrally.

TAIL
Two thirds of total length. Muscular part of tail strong and high, slightly less high than body in lateral view. Upper fin starts posterior to trunk-tail junction at ~10% tail length. It rises up, curves only slightly and tapers relatively straight to a narrowly rounded tip. Lower fin similar to upper fin in contour shape, but slightly less high; both fins relatively low. Maximum height of tail approximately at the mid-point of tail. Skin glands on tail or tail fins absent.

SIMILAR SPECIES
The number, arrangement and sizes of glandular fields present in *Pulchrana glandulosa* are unique among Bornean tadpoles. Species of *Chalcorana* also possess extensive glandular fields, somewhat different in arrangement, but are markedly different from *P. glandulosa* in body color pattern and body shape. The slender, black tadpoles of *P. signata* or *P. picturata* have less extensive gland fields on the body. Larvae of *Staurois* are somewhat similar in body shape but lack gland fields and are different in oral disc features and color pattern, the same applies to larvae of some *Leptobrachella* which are also fossorial leaf litter specialists.

In many forest swamp sites, Pulchrana glandulosa *is a common species, yet its larvae have escaped description for long (Inger, Stuebing and Stuart 2006). The reasons are that these tadpoles live in blackwater pools with deep leaf litter where they are hard to detect. They are alert and fast, quickly disappearing into the leaf litter at the slightest disturbance.*

HABITAT & ECOLOGY
Pulchrana glandulosa tadpoles live in stagnant pools in alluvial forest, blackwater swamps, flooded depressions near streams, or peat swamps. Typically these are lowland habitats (up to 700 m) and pools are often filled with thick layers of leaf litter. The tadpoles hide deep in the litter by day. At night, they emerge to feed among the superficial leaf layers in the pool. Body shape of the tadpoles and the circumstances under which they have been encountered suggest that they are leaf litter interstice specialists.

REPRODUCTION
Males call from twigs and branches near suitable pools. Although the loud barking sound of the males is well-known, details of the reproductive behavior have not been reported. Males have paired subgular vocal sacs and reach the same size as females. Egg diameter 1.5–2,0 mm.

COLORATION
Body and tail uniformly black above; markings absent; skin with bluish iridescence in life. Fins pigmented as well, dark gray. Skin of venter semi-transparent with bluish iridescence (not in preserved specimens). Oral disc pigmented; in particular, papillae bear groups of melanocytes. Buccal and branchial regions dusted with melanocytes. Buccal glandular field dark brown and covering most of the buccal region. Gills and heart not clearly visible in branchial region. The abdominal skin is also dusted with melanocytes, laterally covered with skin gland clusters (also pigmented). The gut is faintly visible through the skin between the glandular fields.

LITERATURE

Leong, T.M., Chou, L.M. (1999) Larval diversity and development in the Singapore Anura (Amphibia). The Raffles Bulletin of Zoology 47: 81–137.

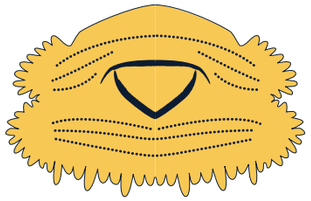
Inger, R.F., Stuebing, R.B., Stuart, B. L. (2006). The tadpole of *Rana glandulosa* Boulenger (Anura: Ranidae). The Raffles Bulletin of Zoology, 54: 465–467.

Pulchrana picturata (Boulenger, 1920)

Spotted Stream Frog

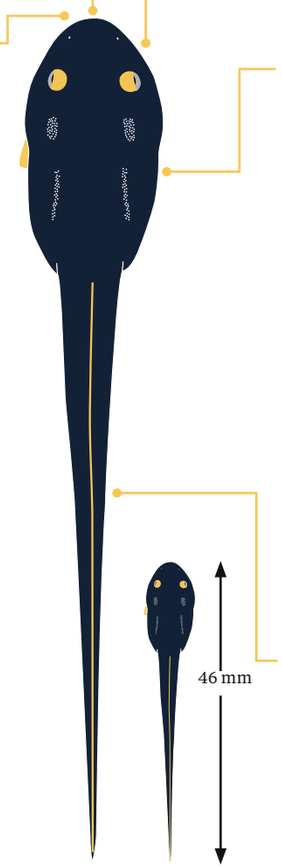
SNOUT
Rounded in dorsal view and slightly tapering; narrowly rounded in lateral view; moderately long.

ORAL DISC
Anteroventral; width less than half the width of body. Emarginations present at lateral margin between upper and lower lips. Upper lip devoid of papillae in broad middle part but bears a single row of marginal papillae in the lateral parts. One continuous row of marginal papillae present along margin of lower lip. Marginal papillae moderately long, except for few longer ones on lower lip. Submarginal papillae absent.



LTRF 3(2–3)/3(1) or 4(2–4)/3(1); the division of the first posterior keratodont row very narrow, indistinct. Beaks keratinized and black, thin. Jaw edges very finely serrated. Upper beak a broad smooth arch. Lower beak smoothly V-shaped.

ECOMORPH
Lentic to lotic, exotrophic; leaf litter interstice specialist.



NOSTRILS & EYES
Eyes dorsolateral. The iris is bright red around the pupil and black further peripherally. Nostril small, closer to snout than to eyes.

BODY
Elongate oval, medium to large. In lateral view, body depressed, smoothly convex above and below. Body widest at the level of the gills, posterior to eyes. Spiracle sinistral. Spiracular tube opens posteriorly and well below the longitudinal body axis in lateral view. Spiracular orifice free from the body wall; a short tube is formed. Lateral line organs present and visible. Extensive skin gland clusters are present: paired fields on dorsum approximately at level of posterior head, longitudinal dorsal fields above flanks; scattered glands dorsally between eyes; ventrally paired clusters at anterior buccal area, a single field in the posterior buccal region and scattered glands far lateral at abdomen (see photo; see also tail).

TAIL
long, two thirds or more of total length. Muscular part of tail strong and high, slightly less high than body in lateral view. Upper fin starts at or slightly posterior (~10% tail length) to trunk-tail junction. Both tail fins arch with slight convexities and are moderately high. Lower fin lower than the upper fin. Tail tip triangular, pointed. Maximum height of the tail anterior to mid-point of tail length. Tail fins each with many scattered tail glands.

SIMILAR SPECIES
Pulchrana picturata and *P. signata* tadpoles are similar and both have dark bodies in combination with red iris ring as a conspicuous character. Distinguishing characters have not been established yet. We saw some differences in our *picturata/signata* samples in the beginning point of the dorsal tail fin, skin gland densities, and upper lip keratodont rows. This could, however, fall into the range of intraspecific variation and needs further investigation. *P. picturata/signata* tadpoles can be distinguished from *Chalcorana* tadpoles (that have skin glands too) by their black color, less broad body, relatively longer tail and lower tail fins. *P. glandulosa* larvae are just as black as *P. picturata/signata* but have more elongate bodies, dense submarginal papillae, and grow larger than *picturata/signata* tadpoles. Tadpoles of *Staurois*, *Odorrana*, and *Pelobatrachus* may live in the same leaf litter with *P. picturata/signata*, but all differ in mouthparts, coloration, and absence of skin glands, especially in tail fins.

Pulchrana picturata *tadpoles are similar to those of the closely related* P. signata. *Distinguishing characters have not been established with certainty yet.*

HABITAT & ECOLOGY
Pulchrana picturata often prefers rocky streams, whereas we observed *P. signata* more regularly along soft bottom streams. However, it needs further research to determine possible ecological overlap. Tadpoles of *P. picturata* have been collected from rock troughs and side-pools that where partially or completely disconnected from the main stream and filled with leaf litter. Tadpoles are wary, shy away from daylight and hide deep under leaf litter. At night, they emerge to feed among the leaves. The species has been recorded up to 750 m a.s.l. and will accept disturbed forests.

REPRODUCTION
Males of *Pulchrana picturata* call from very near to the water (< 1 m). Often, they sit elevated on rocks, twigs or roots at the base of steep banks of small to medium-sized streams. Calls consist of several repeated low notes of decreasing intensity.

COLORATION
Body and tail appear uniformly black above in daylight; markings are absent. The dark color makes it difficult to see the skin glands. The skin has bluish iridescence in living specimens. Fins are darkly pigmented. Ventral skin of the body is semi-transparent with bluish iridescence (disappears in preservation). The oral disc is pigmented, in particular papillae bear groups of melanocytes near their tips. Buccal region dusted with melanocytes. Red gills and heart, as well as gut visible through skin. The abdominal wall with scattered melanocytes laterally.

LITERATURE
Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89. [*P. signata*].

Inger, R.F., Stuebing, R.B., Grafe, T.U., Dehling, J.M. (2017) A field guide to the frogs of Borneo. 3rd ed. Natural History Books, Kota Kinabalu. 228 pp.

Feihyla inexpectata (Matsui, Shimada, and Sudin, 2014)

Bornean Opposite-fingered Tree Frog

Originally described as Chiromantis inexpectatus, *the species has been recorded in primary lowland and hilly forests up to 1050 m a.s.l. It has been known scientifically for only a short time and therefore information on the species is scarce. Specimens from Gunung Mulu (right) and Maliau Basin (left), respectively.*

TADPOLE

We encountered the larvae of this species in only two localities (Maliau, Mulu). Each time, it was only a single specimen. The Mulu specimen (top left), photographed in a plastic bag, died during expedition transport and the small Maliau specimen (top right) was damaged during vigorous netting. Due to these circumstances and lack of sufficient samples, we cannot present all larval details. The photographic evidence, however, shows that this tadpole is unique in color pattern: the tip of the snout bears a bright white patch. More vertically elongated patches are located at the body sides, at the transition from the gill region to the flank. The color pattern of the specimens from those locations was very similar. It remains open, whether this unique color pattern changes during ontogenesis. The Maliau individual was 15 mm in total length, with the damaged tail representing 60.7% of total length. Body shape in dorsal view resembles a smoothly rounded rectangle. Eyes lateral in position, cornea extends beyond body contour in dorsal view.

HABITAT & ECOLOGY

The species has been described from the type locality at Nepenthes Camp, Maliau Basin. We recorded tadpoles and adults from there and from lowland primary forest at Gunung Mulu. Furthermore, sightings from Danum Valley have been reported to us. This anecdotal evidence suggests that this species may have a wide distribution in northeast Borneo. The tadpoles live in swampy forest pools. We found the tadpole in association with *Abavorana luctuosa* and *Rhacophorus pardalis* tadpoles. Note that the tadpoles of its congener, *Feihyla kajau* (p. 154), are ecologically different and live in slow moving, small streams.

REPRODUCTION

Individuals perched 1–3 m high on vegetation close to the breeding pool. Males were observed to call from above as well as from under leaves.

SIMILAR SPECIES

The unique color pattern of these tadpoles make misidentification unlikely. The tadpole of the related *F. kajau* has a different pattern and has been reported from almost stagnant sections of small streams; *F. kajau* does not use forest ponds for reproduction.

LITERATURE

Matsui, M., Shimada, T., Sudin, A. (2014) First record of the tree-frog genus *Chiromantis* from Borneo with the description of a new species (Amphibia: Rhacophoridae). Zoological Science 31: 45–51.

Haas, A., Boon-Hee, K., Joseph, A., bin Asri, M., Das, I., Hagmann, R., Schwander, L., Hertwig, S.T. (2018) An updated checklist of the amphibian diversity of Maliau Basin Conservation Area, Sabah, Malaysia. Evolutionary Systematics 2: 89–114.

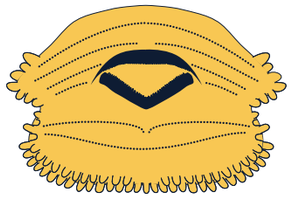
Breeding habitat of *Feihyla inexpectata*; Maliau Basin, 1050 m a.s.l.

Kurixalus chaseni (Smith, 1924)

Frilled Tree Frog

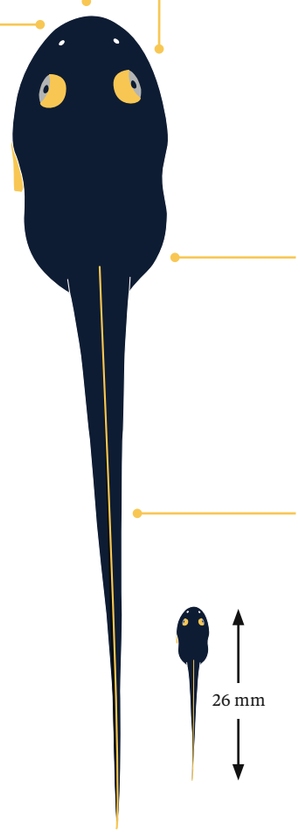
SNOUT
Sloping in lateral view, rounded but slightly tapering in dorsal view.

ORAL DISC
Oriented anteroventrally. Marginal papillation with broad gap on the upper lip, no gap on the lower lip. Marginal papillae arranged in a single row on the lateral upper lip, in double rows in lower lip, except for a narrow medial part with single row.



Marginal papillae moderately long, blunt. Lateral oral disc indentations present. Labial ridges bear uniserial keratodont rows. LTRF 4(2–4)/3(1) or 3(2–3)/3(1). Jaws well-keratinized, moderately strong. Upper jaw broadly and shallowly arched, lower jaw widely V-shaped. Beak edges finely serrated.

ECOMORPH
Lentic, exotrophic.



NOSTRILS & EYES
Nostril round, directed anterolaterally. Nostril slightly elevated and at about equal distance to eye and snout in lateral view. Eyes moderately large, positioned and facing dorsolaterally. Iris densely dusted with coppery iridophores (sometimes gold) on black background. Sclera densely covered with coppery and golden shiny iridophores.

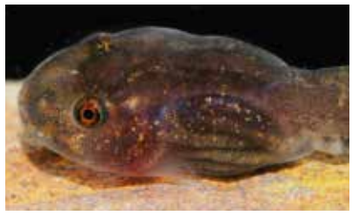
BODY
Rhomboid to inverse pear-shaped in dorsal view. Gill region wider than trunk. Body dorsoventrally depressed. Spiracle sinistral. Spiracular tube fused to body and directed posterolaterally. Spiracular opening very low, well below the longitudinal body axis in lateral view.

TAIL
~66–68% of total length. Upper tail fin rises from body-tail junction. Tail fins arched shallowly and tapering gradually towards a narrowly rounded tip. Fin shape can vary, however, lanceolate fin shapes are most common. Upper and lower fin subequal in height. Maximum height of tail at approximately 35% of tail length. Lateral tail vein visible but indistinct. Tail myosepta discernible in distal part of tail.

SIMILAR SPECIES
Kurixalus chaseni shares small size, stagnant water preferences, and body shape with some bufonids. However, it is easily diagnosed from any superficially similar bufonid (for example, *Ingerophrynus divergens* or *Duttaphrynus melanostictus*) by 3-4 upper lip keratodont rows (as opposed to two in bufonids).

The Bornean Kurixalus chaseni, *formerly subsumed under* Rhacophorus appendiculatus, *is a common frog in lowland primary and secondary habitats. The tadpoles are small and inconspicuous, resembling those of certain bufonids in general body shape and small size.*

HABITAT & ECOLOGY
The species occurs from lowland primary and secondary forests up to at least 1060 m a.s.l. Larvae live in swampy areas. They can be encountered in stagnant, water-filled muddy depressions in the forest or at forest edges. Sometimes pigs use the same muddy depressions as wallows, however, an association with pig activities does not seem mandatory for this species to reproduce. Water depth of breeding pools typically is <50 cm. If a gap in the canopy allows for sunspots, the shallow water heats up and development of the tadpoles will be fast.



REPRODUCTION
Males call from low to moderately high vegetation (1–4 m) above a pool. Males commonly aggregate in calling groups. These groups seem fairly stationary as calling males can be found frequently at pools that have dried up temporarily, awaiting the next rainfalls. The call is complex, starting with raspy clicks, followed by longer notes. Eggs are deposited in a foams nests attached to twigs or leaves above the water.

LITERATURE

As *Rhacophorus appendiculatus* in:

Inger RF (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

Leong, T.M. (2004) Larval descriptions of some poorly known tadpoles from Peninsular Malaysia (Amphibia: Anura). The Raffles Bulletin of Zoology 52: 609–620.

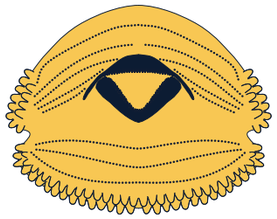
COLORATION
Brown dorsally. In close-up, dark brown and yellow marbling is discernible. Scattered bronze pigment cells can be present at the cheek, the lateral gill region and lateral trunk. At the flanks, dark pigmentation fades towards the venter; the ventral skin is transparent. Gills, heart and gut coils are clearly visible. The muscular tail is marbled in dark brown, sometimes with yellow pigment cells along the proximal, dorsal tail muscle. The marbling extends somewhat onto the tail fins, more so onto the upper fin than the lower fin; the latter is mostly clear. In the proximal half of the tail, usually the lateral vein is visible. Metamorphosing specimens develop beige spots at knees and angles.

Leptomantis fasciatus (Boulenger, 1895)

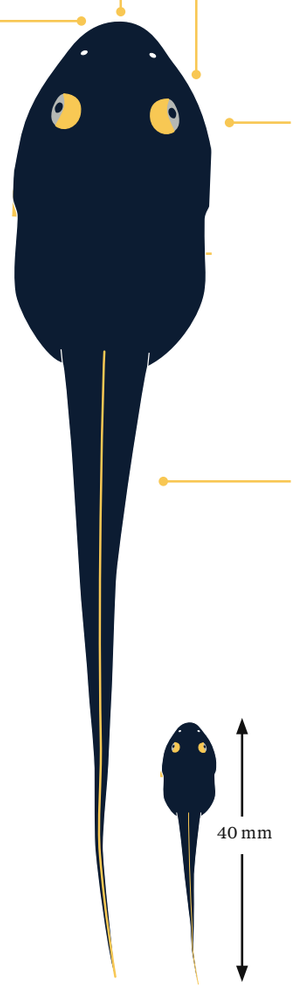
Banded Tree Frog

SNOUT
From above, snout tapering, narrowly rounded. Viewed from the side, snout relatively long and profile slightly angled due to the somewhat elevated position of nostrils.

ORAL DISC
Anteroventral. Marginal papillation present on lower lip and lateral parts of the upper lip. Upper lip with a broad gap in papillation, no gap in lower lip papillae rows.



Marginal papillae arranged bi-serially on lower lip. Lateral part of upper lip bears a row of marginal papillae plus a row of submarginal papillae. Papillae short and blunt. Emarginations are present between upper and lower lips. LTRF 5(2–5)/3. Peripheral keratodont rows long, spanning most of upper and lower lips. Beaks well keratinized but moderately strong; jaw edges bear sharp serrations. Upper beak broadly and shallowly arched. Lower jaw more V-shaped, edge mildly convex laterally.



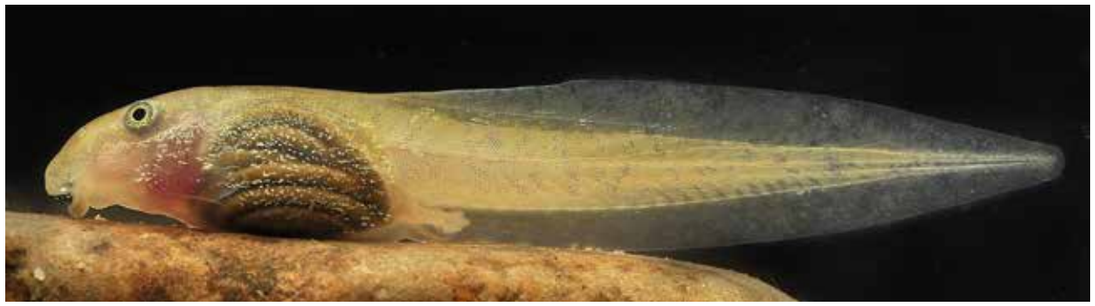
NOSTRILS & EYES
Eyes dorsolateral. In dorsal view, nostril closer to snout than to eye, oriented anterolaterally, and slightly elevated. Iris densely stippled with golden pigment cells, merging into a golden ring towards pupil. Sclera black in background color and stippled with silver/gold iridocytes.

BODY
Depressed ovoid in lateral view, i.e., the trunk is deeper than the head part. In dorsal view, body contour broadly oval with a slight constriction between head and trunk. Body widest at the gill region in dorsal view. Spiracle sinistral. Spiracular tube opens posterolaterally and low, below longitudinal body axis in lateral view. Medial part of spiracular orifice free from the abdominal wall; short free spiracular tube present.

TAIL
Moderately strong, long, approximately 67% of total length. Upper fin rises from level of trunk-tail junction. In lateral view, upper tail fin not arching much in profile. Edges of upper and lower fins gradually converge with fairly straight contours into a narrowly rounded tail tip. Upper fin slightly higher than lower fin. Maximum height of tail reached at mid-tail. Lateral tail vein present but indistinct. Myosepta discernible distally but indistinct.

ECOMORPH
Lentic, exotrophic, benthic.

SIMILAR SPECIES
Leptomantis fasciatus tadpoles could be confused with *Rhacophorus pardalis*, because of similar size, general body color, and habitat. *L. fasciatus* lacks the conspicuous cheek color pattern of most (but not all!) *R. pardalis* populations and has 1-2 keratodont rows less on the upper lip than *R. pardalis*. Inger (1985) described "*Rhacophorus* sp. D" that, he reasoned, may represent *L. fasciatus*. The tadpole of the closely related *L. rufipes* is similar in general body shape and LTRF. *L. fasciatus* tadpoles seem to grow larger, are more in the light brown color range (vs. dark gray), have conspicuous iridocyte patterns laterally (absent in *L. rufipes*) and a more tapering snout in dorsal view. More research is needed to demonstrate that these differences do not overlap with intraspecific variation.



The taxonomy and distribution of Leptomantis fasciatus *is poorly understood. Assignment of the tadpoles in this description are based on a population of western Sarawak (Gunung Penrissen). Tadpoles of this species are mid-sized pond dwellers, that prefer the bottom layer of the water column.*

HABITAT & ECOLOGY
Tadpoles have been found in ponds at forest edges. As reports on the species' breeding habits are scarce, it is possible that the species is not restricted to forest edges or clearing situations for breeding, but may also use ponds inside the forest. Preliminary observations suggest that the tadpoles are mostly active at the bottom of the ponds. Adults live high up in trees and descend only for reproduction.

REPRODUCTION
Observations on active breedings groups have rarely been documented. We detected adult frogs, some in amplexus, in low vegetation around a breeding pond. Details on nest building have hitherto not been recorded. Calls consist of a click, followed by a raspy trill.

COLORATION
Light brown to gray above. The trunk is darker than the head and tail. The brain case is darkly pigmented; it is visible as a dark polygonal shape between the eyes. On top of the general background color, the flanks are stippled with iridophores. The dorsal trunk is devoid of such stippling but has iridophores arranged into some golden patches above the spine of the trunk and the root of the tail. The body pigmentation continues onto the tail where it fades distally. The tail fins are slightly pigmented with scattered groups of melanocytes, mostly clear. The ventral side of the body is mostly transparent and without much pigmentation, except for scattered melanocytes in the gular and buccal areas. Inner organs are visible through the skin. The anterior abdomen (gut coil) may be marked by a stippling of iridocytes medially. Oral disc unpigmented.

LITERATURE

Inger R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89; [Inger described "*Rhacophorus sp. D*" that, he reasoned, may represent *L. fasciatus*].

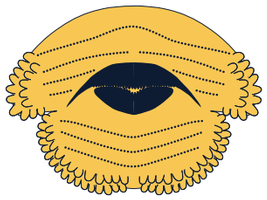
Inger, R.F., Stuebing, R.B., Grafe, T.U., Dehling, J.M. (2017) A field guide to the frogs of Borneo. 3rd ed. Natural History Books, Kota Kinabalu. 228 pp.

Leptomantis harrissoni (Inger and Haile, 1959)

Brown Tree Frog

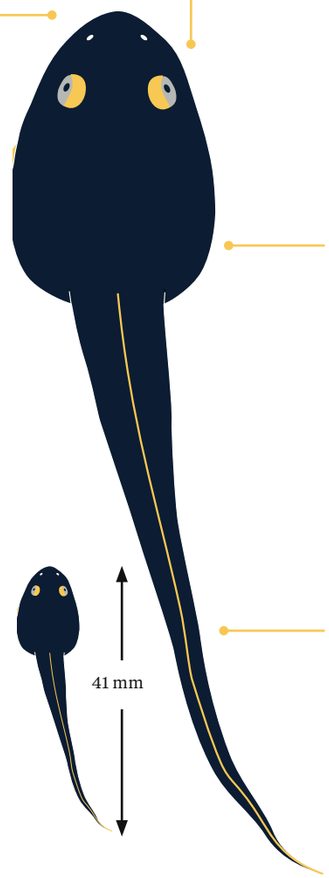
SNOUT
Tapering and rounded in dorsal view. Moderately long and sloping with convex contour in lateral view.

ORAL DISC
Anteroventral. Marginal papillation present on lower lip and lateral parts. Upper lip bears a broad gap in papillation, gap in lower lip may be so narrow that it appears gap-less. Marginal papillae arranged bi-serially on lower lip.



Lateral part of upper lip bears a row of marginal papillae plus a row of submarginal papillae. Papillae short and blunt. Emarginations are present between upper and lower lip. LTRF 4(2–4)/3 or 5(2–5)/3. Peripheral keratodont rows span most of the upper and lower lips, respectively. Beaks strong and well-keratinized; jaw edges with sharp serrations. Upper beak broadly arched. Lower jaw flat V-shaped.

ECOMORPH
Lentic, phytotelma specialist, exotrophic, facultative (?) oophagous.



NOSTRILS & EYES
Eyes dorsolateral. Nostril moderately sized. In dorsal view, nostril closer to snout than to eyes, oriented anterolaterally, rimmed, and slightly sunken in. Iris background color black, covered with loosely scattered golden or coppery pigment cells. Around pupil, iridocytes arranged in a narrow, broken, golden ring. Remaining eye bulb is also black in background color and stippled with silver/gold iridocytes.

BODY
Depressed ovoid in lateral view, tapering to the snout. In dorsal view, body contour ovoid (depending on feeding status), with hardly any constriction between head and trunk. Body widest at gill region in dorsal view. Spiracle sinistral. Spiracular tube opens posterolaterally, positioned low, well below longitudinal body axis in lateral view. Medial part of the spiracular orifice free from abdominal wall. Free spiracular tube short.

TAIL
Strong and long, approximately 69–71% of total length. Upper fin rises from the level of trunk-tail junction. In lateral view, upper tail fin not arching much in profile, rather with rather straight edge. Curving at about 75% of the tail, edges of upper and lower fins converge with fairly straight lines into a narrowly rounded tail tip. Muscular part of tail strong and high. Maximum height of tail reached at or posterior to middle portion of tail. Lateral tail vein indistinct or invisible due to heavy pigmentation.

SIMILAR SPECIES
Leptomantis harrissoni tadpoles are hard to confuse with any other species considering the phytotelma habitat, size, and dark uniform body color. In the field, it will be necessary to check against *Nyctixalus pictus* which can live in similar phytotelmata but differs distinctly in body shape and tail fin shape.

The tadpoles of Leptomantis harrissoni *are phytotelma specialist. They have been exclusively reported from tree holes.*

HABITAT & ECOLOGY
Tree holes or other pocket structures in tree trunks, anastomosing buttresses, and branches are the natural habitat for *Leptomantis harrissoni* tadpoles (p. 37). They have been reported from tree phytotelmata at 0.15–4 m above ground. Possibly, they breed higher up in the canopy, but this has not been confirmed yet. A phytotelma of 1–2 liter volume can hold a fairly large number of tadpoles, possibly more than such phytotelmata could provide food for. This and the presence of ingested eggs in some tadpoles suggests, that the tadpoles are at least facultative egg-eaters (oophagous).

REPRODUCTION
The mating pair builds a foam nest immediately above the water at the phytotelma. The foam nest is attached to the tree's trunk. The tadpoles hatch from the nest and glide into the water of the phytotelma. Females have been seen around phytotelmata that already held a swarm of tadpoles, suggesting that the tadpoles were fed with eggs produced by the female from time to time. More research is needed to elucidate details of this behavior.

COLORATION
Uniformly light brown to dark brown or black above, the more advanced the tadpole the darker. The body is darker than the tail. Markings are absent. The body pigmentation continues onto the tail where it lightens up distally. The tail fins are well-pigmented and brown as well. The ventral side of the body is well-pigmented but much less so than the dorsal side of the body. Inner organs are still faintly visible through the skin. Particularly in ventral view, in extreme close-up, the thin and long melanocytes show a conspicuous cross-hatching pattern. This mixes with irregular dot-like melanocytes. As in other rhacophorid tadpoles, the anterior abdomen (gut coil) may bear a patch of iridocytes, however, it may not be obvious in advanced tadpoles due to dense melanocytes. Oral disc bears melanocytes at its base.

LITERATURE
Inger RF (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

Inger, R.F., Stuebing, R.B., Grafe, T.U., Dehling, J.M. (2017) A field guide to the frogs of Borneo. 3rd ed. Natural History Books, Kota Kinabalu. 228 pp.

Leptomantis rufipes (Inger, 1966)

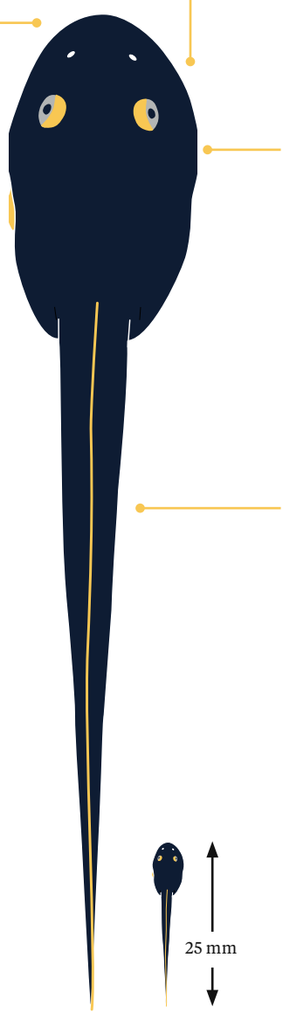
Red-legged Tree Frog

SNOUT
Rounded and slightly tapering viewed from above. Viewed laterally, snout relatively long, rounded in a smooth convex curve.

ORAL DISC
Subterminal. Marginal papillation of oral disc present on lower lip and lateral parts of upper lip.

A wide area of upper lip is devoid of papillae. Marginal papillae arranged bi-serially on lower lip. Lateral part of upper lip bears a uniserial row of marginal papillae plus a short row of submarginal papillae. Papillae short, blunt and adjoining. Emarginations between upper and lower lip present. LTRF 4(2–4)/3 or 5(2–5)/3. If present, fifth row on upper lip very short. Peripheral keratodont rows long and extend far laterally on both lips. Beaks well-keratinized, moderately strong. Jaw edges bear sharp serrations. Upper beak broadly and smoothly arched, whereas lower jaw sheath very robust and bluntly V-shaped.

SIMILAR SPECIES
Leptomantis rufipes tadpoles superficially resemble *Rhacophorus pardalis* or *R. borneensis* in body shape, but differ in coloration and size and oral disc features. *L. rufipes* tadpoles are rarely encountered; presence of adults at a given site warrants a closer look at nearby pools where tadpoles might live. See comment for *L. fasciatus*.



NOSTRILS & EYES
Eyes dorsolateral. Nostrils closer to snout than to eyes, oriented anterolaterally. Iris background color black covered with densely scattered golden and coppery pigment cells. Around pupil, iridocytes fused to form a narrow ring.

BODY
Depressed ovoid in lateral view, tapering towards snout. In dorsal view, body contour oval to slightly inverse pear-shaped with shallow constriction behind gill region. Body widest at gill region (posterior to eyes) in dorsal view. Spiracle sinistral. Spiracular tube opens posterolaterally and lies below the longitudinal body axis in lateral view. Medial part of spiracular orifice attached to abdominal wall.

TAIL
Moderately strong, approximately two thirds of total length. Tail shape moderately arched in lateral view. Tail fins taper in posterior two thirds with straight edges to a narrow, pointed tip; no flagellum is formed. Muscular part of tail moderately high, approximately half of body height. Upper fin starts at trunk-tail junction, lower fin connects broadly to the trunk. Maximum height of tail at a level anterior to mid-point of tail.

ECOMORPH
Lentic, exotrophic, benthic-nektonic.

Leptomantis rufipes *is known from lowland habitats in primary forests. The tadpoles have rarely been reported. The body shape of this tadpole is suggestive of a pond tadpole with a generalist life-style.*

HABITAT & ECOLOGY
We observed *Leptomantis rufipes* tadpoles in *kerangas* forests (heath forests) in a small pool of water created by an uprooted tree. Tadpoles were sighted hovering at the surface of the pool at night. The water was tea-colored and peaty. Leaf litter and a thick layer of decomposing plant matter formed the bottom of the pool.

REPRODUCTION
Occasionally small groups of males have been seen gathering 1–3 m high on vegetation around breeding ponds. The species seems to have unpredictable bursts of breeding activity. Mating pairs produce foam nests attached to leaves overhanging water. The call consists of two short clicks, often followed by a short much lower trill.

LITERATURE

Haas, A, Hertwig, S.T., Krings, W., Braskamp, E., Dehling, J.M., Pui, Y.M., Das, I. (2012) Description of three *Rhacophorus* tadpoles (Lissamphibia: Anura: Rhacophoridae) from Sarawak, Malaysia (Borneo). Zootaxa 3328: 1–19.

Inger, R.F., Stuebing, R.B., Grafe, T.U., Dehling, J.M. (2017) A field guide to the frogs of Borneo. 3rd ed. Natural History Books, Kota Kinabalu. 228 pp.

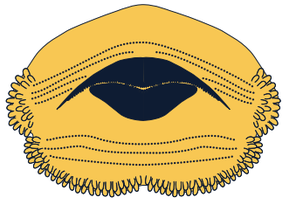
COLORATIONS
Gray above. The pigmentation is diffuse, and there are no sharply defined spots or blotches. The gray background color is modified with a slight tint of olive on the head and trunk dorsally. In dorsal and lateral views, the coloration is darkest along the abdominal cavity. The red gills are visible through the skin in lateral and ventral views. There are only few iridocytes that appear in light blue or gold; they are located in small scattered patches between the eye and the spiracle, along the spiracular tube, on the lower cheek, and on the snout close to the oral disc. The pigmentation of the trunk extends seamlessly onto the muscular part of the tail. The tail fins are clear without pigmentation, except for the base of the upper fin and the distal base of the lower fin. The ventral body skin is mostly transparent and slightly iridescent. The dark gut coil, red heart, and red gills are clearly visible in ventral view. A small silvery iridophore area may be present posterior to the heart at the level of the anterior gut.

Nyctixalus pictus (Peters, 1871)

Cinnamon Frog

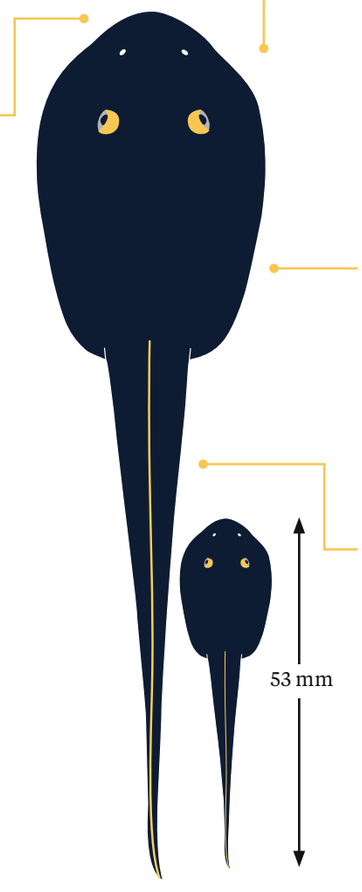
SNOUT
Extended and sloping in lateral view, with lateral cheek bulges. Broadly rounded in dorsal view, weakly set off from bulging cheeks.

ORAL DISC
Subterminal. Marginal papillation with broad gap on upper lip, gap absent on lower lip. Marginal papillae arranged in a single row on the upper lip, but approximately one dozen submarginal papillae present at lateral upper lip. Lower lip with papillae in double or triple rows.



Marginal papillae moderately long, blunt. Lateral oral disc indentations present. LTRF 4(2–4)/3. Very robust jaw sheaths. Upper beak with soft median convexity. Beaks bear fine, sharp, pointed serrations.

ECOMORPH
Lentic, exotrophic, phytotelma specialist.



NOSTRILS & EYES
External nostrils oval and moderately large, directed anterolaterally, slightly sunken in. Nostril closer to snout than to eyes. Eyes very small, positioned dorsolaterally, sunken in. Distance between eyes much smaller than head width at eye level. Iris black with some iridophores scattered around the pupil. Scleral part of eye all black.

BODY
In dorsal view, body inverse ovoid, i.e. broader end anteriorly. Cheeks bulging conspicuously. Body very wide, widest at eye level, dorsoventrally depressed. Spiracle sinistral. Spiracular tube fused to body and directed posterolaterally. Spiracular opening low, well below longitudinal body axis in lateral view.

TAIL
Approximately 62-64% of total length. Muscular part strong, more than half of body height in lateral view. Upper tail fin rises from body-tail junction. Tail fins hardly arched, tapering slightly toward a broadly rounded tip. Tail fin height only moderate. Upper and lower fins subequal in height. Maximum height of tail is approximately at 35% of tail length.

SIMILAR SPECIES
Nyctixalus pictus tadpoles are unique in the combination of body shape, size, tail shape, and black color. They are easily distinguishable from tadpoles that may also live in similar phytotelmata, for example, *Leptomantis harrissoni*. Tadpoles of the closely related *Theloderma* species could potentially occur in similar phytotelmata and are most likely very similar in morphology to Nyctixalus tadpoles. However, *Theloderma* tadpoles have to our knowledge not been sampled on Borneo.

Fallen log with a leaf filled phytotelma inside. Habitat for *Nyctixalus pictus* tadpoles. Kubah National Park.

Nyctixalus pictus *is a common phytotelma breeder in primary or secondary forests from sea level up to 1650 m. Tadpoles live in tree holes and other suitable phytotelmata, usually in small numbers. Genetic analyses indicated that this species could be a species complex of several morphologically very similar species.*

HABITAT & ECOLOGY
The species breed in phytotelmata such as fallen, water-filled, hollow logs (photo), tree holes etc., or even in oil barrels or plastic containers. Phytotelmata with tadpoles commonly are well above the ground (>0.7 m). Typically, they hold from 0.5 to several liters of water. Little is know about the tadpole ecology. The jaws are particularly strong, and jaw and hyoid musculature are massive, raising questions about their food items. More research is needed to elucidate if tadpole numbers correlate with available volume of water; we commonly found 1–20 per phytotelma.

REPRODUCTION
Males call nearby suitable phytotelmata. Although we occasionally encountered 2–4 males in proximity around a phytotelma, breeding congregations are not formed and, therefore, these frogs may be difficult to find in the field unless one is familiar with their soft, whistling, bird-like call.

COLORATION
Uniformly black in color above. The deep black pigmentation of the head and the trunk extends onto the tail and fades along the tail only in the distal half. Ventrally, the gular region bears dense black pigmentation, but less so the ventral skin at the gill and abdominal regions, where the skin is transparent. Gills, heart and gut coils are discernible. Tail venation is indistinct.

LITERATURE

Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

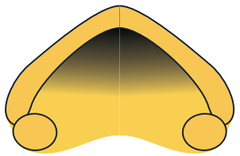
Leong, T.M., Chou, L.M. (1999) Larval diversity and development in the Singapore Anura (Amphibia). The Raffles Bulletin of Zoology 47: 81–137.

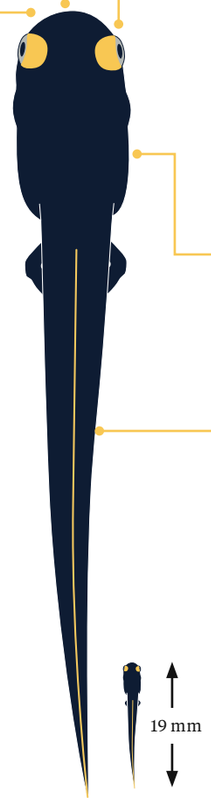
Philautus macroscelis (Boulenger, 1896)

Mossy Bush Frog

SNOUT
Very short snout, bluntly rounded in dorsal and ventral views.

ORAL DISC
Mouth present as a tiny, barely visible, ventral opening. Oral orifice crescentic. Oral disc highly reduced, except for one lateral papilla on each side of the mouth. Keratinized structures absent.





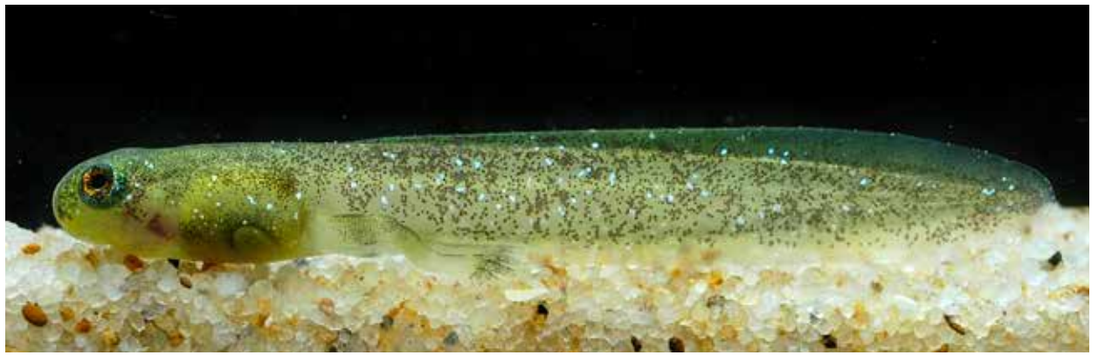
NOSTRILS & EYES
Eyes positioned laterally and very large in relation to head. Sclera black in background color with silver-blue iridocytes. Iridocytes dense ventrally and scattered dorsally on the eye ball. Iris background color black dusted with dense coppery spots, which partially fuse along the pupil. Nostrils in a unique ventral(!) position.

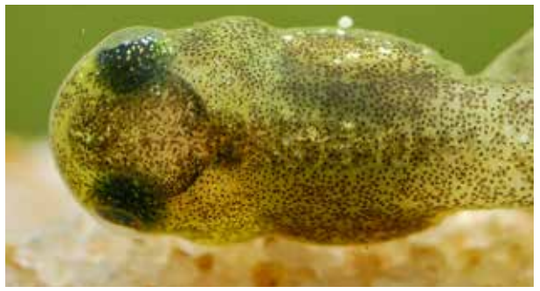
BODY
A small tadpole. Body rounded rectangular in dorsal view. Body moderately depressed, longer than wide and only slightly wider than high, approximately cylindrical.

TAIL
Relatively strong and very long (75% total length). Tail dominated by its muscular part, upper and lower tail fins low. Upper tail fin rises slightly posterior to body–tail junction. Tail fin contours nearly parallel in the proximal half of the tail, not profoundly different in height in any transverse plane along the length of the tail. Maximum tail height at about 60% of tail length. Fins weakly converge in the posterior 25% of the tail. Tail tip broadly rounded.

ECOMORPH
Endotrophic, nidicolous?

SIMILAR SPECIES
Large eyes, short snout, white-blueish iridophores, very long tail, and highly reduced mouth and mouthparts are unique among Bornean tadpoles. A very similar specimen was described by Leong (2004, fig. 3) and assigned to *Limnonectes laticeps,* however, without DNA barcoding; we doubt the species identification of that larva. Some features are shared with *Philautus nepenthophilus*, which, however, features a unique posteroventral skin flap.





The tadpoles of Philautus macroscelis *are difficult to find. These photos document the only specimen that has, to our knowledge, ever been collected. Its unique features suggest a nidicolous mode of larval development. The identitiy of the single know tadpole was confirmed by DNA barcoding.*

HABITAT & ECOLOGY
The ecology of this tadpole is unknown, however, there are other tadpoles in the world with similar body features. These convergent cases suggest that the tadpole of *P. macroscelis* might develop in a nidicolous mode, in which the tadpole stays in the egg deposition place for some time to finalize development without feeding (endotrophic). If so, the nest is probably terrestrial, but close to a small stream. We caught our specimen at the edge of a very small stream. It may have been washed into the stream from a nearby location. The intestine is thick and yellowish indicating rich content of yolk. This, the very small mouth, and the absence of jaw sheaths and keratodonts suggests a non-feeding mode of larval life.

REPRODUCTION
Males call with a long rattling note along small streams in cool highland primary forest (1100–1800 a.s.l.). This is where reproduction takes place. No further details have been reported.

LITERATURE

Leong, T.M. (2004) Larval descriptions of some poorly known tadpoles from Peninsular Malaysia (Amphibia: Anura).The Raffles Bulletin of Zoology 52: 609–620.

Hertwig, S.T., Das, I., Schweizer, M., Brown, R., Haas, A. (2011) Phylogenetic relationships of the *Rhacophorus everetti*-group and implications for the evolution of reproductive modes in *Philautus* (Amphibia: Anura: Rhacophoridae). Zoologica Scripta 41: 29–46.

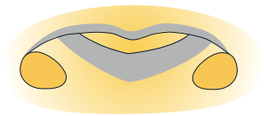
COLORATION
Olive above, pigmentation moderate. Melanocytes mainly on dorsal and lateral body skin. Ventral side mostly unpigmented and translucent, except for some scattered melanocyte clusters on the anterior abdominal region and at gill region. Heart, fore limbs (if present), and intestine discernible in ventral view. Braincase and vertebral column with dark pigmentation. Pigmentation of body continues onto the muscular part of the tail and upper tail fin. Pigmentation of fins fading towards fin margins. Conspicuous silver-blue iridophores are scattered along body and tail; they start behind the eye and continue along the flanks and the muscular part of the tail, few of them reach the upper fin.

Philautus nepenthophilus Etter, Haas, Lee, Pui, Das, and Hertwig, 2020

Nepenthes Bush Frog

SNOUT
Very short, truncated in dorsal view, except for a medial protruding bulge. In lateral view, snout bluntly rounded.

ORAL DISC
Mouth ventral. Oral disc highly reduced and keratodonts absent. Structures that might represent remnants of an oral structures are papilla on each side of the mouth.



Mouth and its surrounding structures positioned in a circular depression in the ventral gular region. Depression possibly works as a sucker. LTRF 0/0. Reduced keratinization of jaw sheaths: thin dark lines along jaw edges seen under high magnification. Oral orifice very small and difficult so see without proper magnification.

TAIL
Moderately strong. 66–68% of total length. Upper and lower fins begin at the body-tail junction. Fins do not arch but are mostly parallel and straight along most of tail. Tail tip broadly rounded. Upper and lower fins equal in height. Maximum height of tail at approximately one third of tail length.

NOSTRILS & EYES
Eyes dorsolateral. Cornea does not reach the head contour in dorsal view. Orientation of eye axis anterolaterally. Nostril much closer to the snout than to eye, positioned almost terminally on the snout in lateral view; nostril facing anterolaterally, smoothly rimmed, sunken in. Orbitonasal streak present. Sclera and iris possess black backgrounds with dense iridophores scattered on them. Iris iridophores shine golden, pupil framed by a narrow silver ring. Iridophores on sclera mostly silvery to blueish. Orbital cavity includes an unpigmented area at the origin of the orbitonasal streak.

BODY
In dorsal view, body of advanced stages broadly inverse pear-shaped. Trunk slightly narrower than head. A constriction marks the head-trunk transition in dorsal view. Maximum body width anterior to that constriction (where elbows are). Body dorsoventrally depressed. Spiracle sinistral. Medial spiracular orifice fused to body wall, free tube absent. Spiracle directed posteriorly. Spiracular position well ventral to mid-body axis. A peculiar large, transparent circular skin flap is present that extends from the abdomen posteriorly under part of tail. It is confluent with the ventral tail fin dorsally. It underlies the developing posterior limbs.

ECOMORPH
Endotrophic, phytotelma breeder and *Nepenthes* pitcher specialist.

SIMILAR SPECIES
The morphological features of this tadpole, especially the short snout, the small ventral oral orifice with two pairs of lateral oral papillae are unique among Bornean species, except for tadpoles of the congeneric *Philautus macroscelis* (Hertwig et al. 2011). The latter differs most notably from *Philautus nepenthophilus* in coloration (conspicuous scattered white-bluish iridophores), the position of the nostrils (ventral), the relative size of the eyes (larger), relative body width (less broad), and absence of a posteroventral skin flap.

Philautus nepenthophilus *has only been reported from Gunung Murud. Tadpoles are endotrophic and develop in* Nepenthes *pitchers.*

HABITAT & ECOLOGY
The tadpoles were discovered in pitchers of *Nepenthes mollis*, 2–4 m above the ground. They seemed inactive in the pitcher, resting among bottom debris that had accumulated in the pitcher or at the pitcher wall. Tadpoles were able to hold position vertically at the pitcher wall suggesting some sort of adhesive mechanism. In one pitcher, we observed two markedly different stage groups letting us assume that successive spawings may utilize the same pitcher. All larvae present a large yellowish gut, indicative of an endotrophic mode of development.

REPRODUCTION
Males perch on *Nepenthes* pitchers several meters above the ground. The advertisement call is short, fast and rattling, consisting of three notes with 6–7 pulses each, average note duration is 36.33 ms and the dominant frequency 2812.5 Hz.

COLORATION
Dark brown to dark gray dorsally. Although there are slightly darker (brain case) and lighter areas (branchial), there is no clear patterning or any markings. The dark brown of the upper sides rapidly dissolves towards the ventral side of the head, trunk, legs, and tail. The trunk coloration continues onto the upper half of the tail, where it fades posteriorly and ventrally. The pigmentation extends to the base of the upper fin, whereas the ventral muscular part and lower fin are devoid of melanophores. The ventral skin (including oral field and posteroventral flap) is transparent, only finely pigmented in the peripheral ventral oral and gular regions. Inner organs are visible through the ventral skin.

LITERATURE

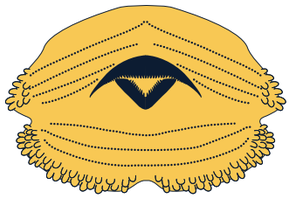
Etter, L., Haas, A., Lee, C., Pui, Y.M., Das, I., Hertwig, S.T. (2021) Out of the trap: A new phytothelm-breeding species of *Philautus* and an updated phylogeny of Bornean bush frogs (Anura: Rhacophoridae). Journal of Zoological Systematics and Evolutionary Research 59: 1064–1096.

Polypedates colletti (Boulenger, 1890)

Collett's Tree Frog

SNOUT
Tapering and rounded in dorsal view, sloping and rounded in lateral view, not angled.

ORAL DISC
Anteroventral. Marginal papillation with a broad gap on upper lip and a narrow gap on lower lip. Lateral indentations present. Upper lip with a medial notch, through which first keratodont row passes.



Marginal papillae arranged in double to triple rows. Some submarginal papillae located in lateral areas of the disc. Marginal papillae short and blunt. LTRF 4(2–4)/3. Upper and lower beaks undivided, well developed, black, and serrated along their edges. Lower beak V-shaped, upper beak broadly arched.

ECOMORPH
Lentic, exotrophic, benthic-nektonic.

NOSTRILS & EYES
Eyes lateral. Cornea protrudes beyond the body contour. Nostril closer to snout than to eye. Orbitonasal streak present. Iris distinct: black background with dusted brown pigment in upper parts, silver-white pigment in ventral sector, and a narrow copper-red ring around pupil. Beyond iris, iridocyte pattern continues onto the sclera. Sclera brown dorsally, silver-white ventrally.

BODY
Oblong parallel-sided to weakly rhomboid in dorsal view. In lateral view, depth of body increases from head to trunk. Body only slightly depressed or as wide as deep, i.e., cylindrical. In lateral view, gular region slightly concave. Spiracle sinistral. Posterior spiracular orifice fused to body. Spiracle directed posteriorly. Spiracular position well ventral to mid-body axis. Lateral line organs indistinct.

TAIL
Long, approximately 65–69% of total length. Muscular part moderately strong, more than half of body height in lateral view. The dorsal tail fin begins at the body-tail junction. A patch of semi-opaque tissue (sometimes indistinct) covers the first third of the tail and extends there into the upper and lower fins. The dorsal tail fin is moderately arched. Fins taper posteriorly with slightly concave contours into acuminate tip forming a flagellum. Upper and lower fins approximately of the same height. Maximum height of tail in the anterior half of tail length.

SIMILAR SPECIES
The combination of coloration features, especially the spot pattern on flank and iris color, body and tail fin shape make it easy to identify this tadpole. The early stages of other *Polypedates* species, however, show similar morphology but a great deal of variation in coloration. *P. colletti* tadpoles are smaller and their trunk is less deep than that of the other *Polypedates* species in Sarawak and Sabah.

Pools with black water are the home of Polypedates colletti *tadpoles. They hover quietly in the water column when feeding and will dart to the leaf litter covered bottom of the pool when disturbed.*

HABITAT & ECOLOGY
The species occurs in lowland forests up to 650 m a.s.l. in scattered populations. Tadpoles have not been reported very often. We observed them hovering quietly in black-water pools, holding position by constantly beating their flagellate tail. Their hovering behavior suggests that they rely on filtering small food items from the water. The tadpoles hide in or close to dense leave litter during the day and will mostly be active at night. The species seems to prefer water rich in humic acids for tadpole development such as pools in peat swamp and *kerangas* forests.

REPRODUCTION
Breeding groups gather around forest pools and swampy areas. Males often perch and call in horizontal position on vertical branches or trunks 1–4 m above the ground. The call consists of a series of crackling notes, often preceded by numerous low-pitched, broad-band notes. Eggs are laid into a foam nest above the water, which male and female build during mating amplexus.

COLORATION
Generally dark brown dorsally. In closer view, the body bears dark brown mottling, indistinct spots on a lighter brown background. On the flanks, the pattern can to some extend reverse to light spots on dark background in a distinct high contrast pattern; variable between populations. Ventrally, the pattern transforms in a narrow gradient to the whitish venter coloration. Ventral side white to silver in abdominal trunk region but finely pigmented in the ventral gill and gular region. Dotted pattern of flanks may continue ventrally at the anterior abdomen. Oral disc mostly without pigmentation. Viscera are covered, neither the gut coils nor the gills are clearly visible through the skin. The marbling of the trunk continues onto the tail, with decreasing contrast and intensity. Spots are mostly on the muscular part of the tail but extend onto the fins proximally. Lower fin clearer than upper fin. Caudal blood vessels inconspicuous.

LITERATURE

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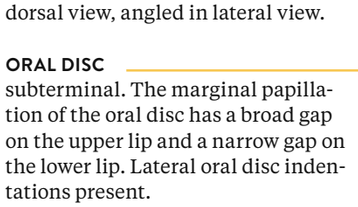
Polypedates leucomystax (Gravenhorst, 1829)

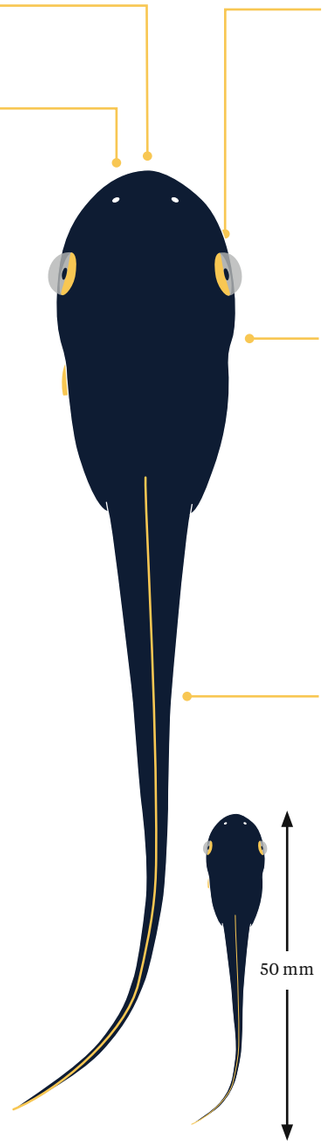
Four-lined Tree Frog

SNOUT
Rounded and slightly tapering in dorsal view, angled in lateral view.

ORAL DISC
subterminal. The marginal papillation of the oral disc has a broad gap on the upper lip and a narrow gap on the lower lip. Lateral oral disc indentations present.

Oral disc marginal papillae arranged in single row. Few submarginal papillae are located in lateral areas of the upper lip. Marginal papillae short and blunt laterally, but elongate and pointed along most of the margin of lower lip. Labial Tooth Row Formula (LTRF): 4(3–4)/3. Upper and lower beaks are undivided, robust, black, and serrated along their edges.





NOSTRILS & EYES
The eyes are positioned laterally, protruding beyond the head contour. The nostril is closer to the snout than to the eye. A well-developed orbitonasal streak is present. Iris golden with some black in the anterior and posterior sector. Beyond the iris, the sclera is dusted with silvery or golden pigment cells above and fully silvery in the anterior, ventral, and posterior sectors.

BODY
Rhomboid in dorsal view; widest point of body at eye level. In lateral view, depth of body increases from head to trunk. Trunk approximately as wide as deep, not depressed. In lateral view, there is a moderate concavity in the gular-buccal region. Spiracle sinistral; posterior spiracular orifice fused to the body. Spiracle directed posteriorly; spiracular position well ventral to mid-body axis.

TAIL
Moderately strong, long, approximately 67% of total length. Dorsal tail fin begins at the body-tail junction. A patch of semi-opaque tissue (sometimes indistinct) is located at the first third of tail and extends there into the upper and lower fins. Dorsal tail fin arched. Fins taper posteriorly with slightly concave contours into a narrow tip. Lower fin slightly higher than upper fin. Maximum height of tail at approximately one third of tail length.

ECOMORPH
Lentic, exotrophic, benthic-nektonic, suspension rasper.

SIMILAR SPECIES
Polypedates leucomystax resembles *P. otilophus* and *P. macrotis*, but can be distinguished from them by pigmentation details (streaks, abrupt lateral transition), smaller size, generally lower tail fins, and a less distinct opaque tissue patch at the proximal part of the tail. Identification at early stages is more difficult. Note that *P. leucomystax* also differs from the other two species in LTRF (difficult to verify in the field).

Polypedates leucomystax *prefers open areas and forest edges and is present in agricultural areas, disturbed habitats along roads or at clearings, rather than in habitats in the forest. Tadpoles most commonly live in sun-exposed puddles and ponds.*

HABITAT & ECOLOGY
Polypedates leucomystax tadpoles live in puddles and ponds in open or semi-open situations, often in rural areas or even in city parks. The tadpoles feed on organic matter at the bottom layers but can also venture into the water column to filter-feed on small particles.

REPRODUCTION
Males scatter around the breeding pond and call from the ground. The call is a low-pitched loud quack. During mating, a foam nest is produced by the amplecting pair at the edge of the pond, floating on the surface of the water and attached to vegetation. Tadpoles hatch from the foam and develop quickly.

COLORATION
General appearance brown, gray or olive dorsally, sometimes with diffuse scattered spots. A light spot is located medially on the snout, and two dark spots between nostrils. The flanks bear an abrupt transition from the dark pigmentation above to the white-silvery ventral side; the edge of this color change runs horizontally below the eye but above the spiracle. Ventral side white to silver, gills, heart, and gut coils not visible. The dark pigmentation of the trunk continues caudally onto the tail. Very often streaks are formed in the proximal half of the tail: dark above and dark along the mid-axis and reduced pigmentation (light streak) between these dark areas and below. Fin pigmentation variable. Diffuse pigmentation particularly in proximal upper fin, melanocyte dusting or reticulation and iridophore groups may occur in fins at middle section of tail. Lateral tail vein visible in first third of tail. Oral disc and papillae unpigmented.

LITERATURE

Inger RF (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

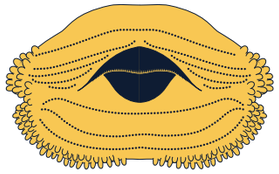
Leong TM, Chou L. (1999) Larval diversity and development in the Singapore Anura (Amphibia). The Raffles Bulletin of Zoology 47: 81–137.

Polypedates macrotis (Boulenger, 1891)

Dark-eared Tree Frog

SNOUT
Tapering and rounded in dorsal view, moderately angled in lateral view.

ORAL DISC
Subterminal. Marginal papillation with a broad gap on upper lip and a narrow gap on lower lip. Lateral oral disc indentations present. Upper lip marginal papillae arranged in single row on upper lip, but submarginal papillae are close.



Lower lip marginal papillae mostly arranged in double rows, but in a single row towards the narrow medial gap. Several submarginal papillae located in lateral areas of the lower disc, giving a triple row impression. Marginal papillae moderately long and blunt. LTRF 5(2–5)/3, 5(2–5)/3(1) or 6(2-6)/3. If present at all, the break in the innermost lower lip keratodont row may be very narrow and indistinct. Upper and lower beaks undivided, robust, black, and serrated along their edges. Upper beak weakly convex medially.

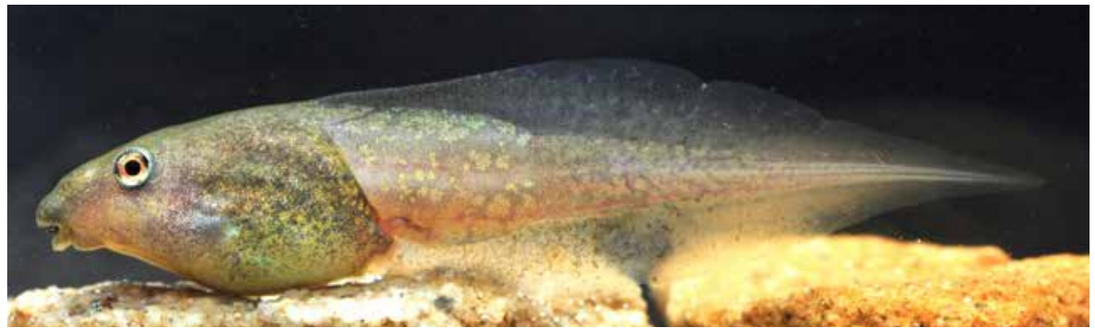
ECOMORPH
Lentic, exotrophic, benthic-nektonic, suspension rasper.

SIMILAR SPECIES
In general body shape, *Polypedates macrotis* resembles *P. otilophus* and *P. leucomystax*. *P. leucomystax* does not grow as large and differs in LTRF and color pattern. The differences to *P. otilophus* are more subtle (see. comments for *P. otilophus*).

NOSTRILS & EYES
Eyes lateral, protruding beyond head contour. Nostril closer to snout than to eye. A well-developed orbitonasal streak is present. Black iris background color densely dusted with golden or coppery pigment cells. In the anterior, upper, and posterior iris sectors black and gold mix irregularly. In the ventral iris, sector golden pigments almost completely cover the black background. Sclera stippled with silvery or golden pigment cells above and fully silvery in ventral sector.

BODY
Slightly rhomboid in dorsal view; widest point of body at eye level. In lateral view, trunk much deeper than head. Body flat above. Trunk as wide as deep, not depressed. In lateral view, moderate concavity present in the gular-buccal region. Spiracle sinistral well below mid-body axis in lateral view. Posterior spiracular orifice fused to the body wall. Spiracle directed posterolaterally.

TAIL
Moderately strong, long, approximately 68–70% of total length. Upper tail fin begins at the body-tail junction. A patch of semi-opaque tissue located at first third of tail and extending slightly into the upper and lower fins. Upper tail fin well-arched. Fins taper posteriorly with slightly concave contours into acuminate, narrow tip. Fins vary with habitat. We found some in which the upper fin was slightly higher than the ventral and others in which it was the opposite. Maximum height of tail reached at approximately one third of tail length. Lateral tail vein visible but often indistinct.



Polypedates macrotis *is widely distributed in primary and secondary forests. It occurs at forest edges, clearings, roadside forest, and sometimes forest edges along agricultural land and villages. The tadpoles grow large and are variable in coloration.*

HABITAT & ECOLOGY
The tadpoles live in turbid ponds, often in open or semi-open situations, such as clearings, farm land or forest edges. The body shape indicates that the tadpoles feed on organic matter at the bottom of the pond as well as on small particles obtained by filter-feeding in the water column.

REPRODUCTION
Males assemble around the breeding pond. They prefer to perch on dead wood, on or in hollow logs, occasionally also on low vegetation. The call is a drawn out chuckle. Foam nests are built during mating. They are attached to logs or branches above the water. Tadpoles hatch from their foam nest and drop into the water below.

COLORATION
General appearance variable: brown, gray or greenish dorsally, sometimes (in at least one population) hues of orange or with scattered black spots. The flanks gradually go from the dark pigmentation above to light color below. Ventral head and belly are opaque white in background color, but finely stippled with melanophores and sometimes also yellow pigments. The dark pigmentation of the trunk continues caudally onto the tail where light spots (sometimes yellow) or blotches add to the pattern. Diffuse pigmentation particularly in proximal upper fin, melanocyte dusting or reticulation may occur in fins predominantly in the proximal part of the tail. Lateral tail vein visble but often indistinct. Oral disc and papillae stippled with melanocytes (advanced stages).

LITERATURE

Inger, R.F. (1966) The systematics and zoogeography of the Amphibia of Borneo. Fieldiana Zoology 52: 1–402.

Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89. 1

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Polypedates otilophus (Boulenger, 1893)

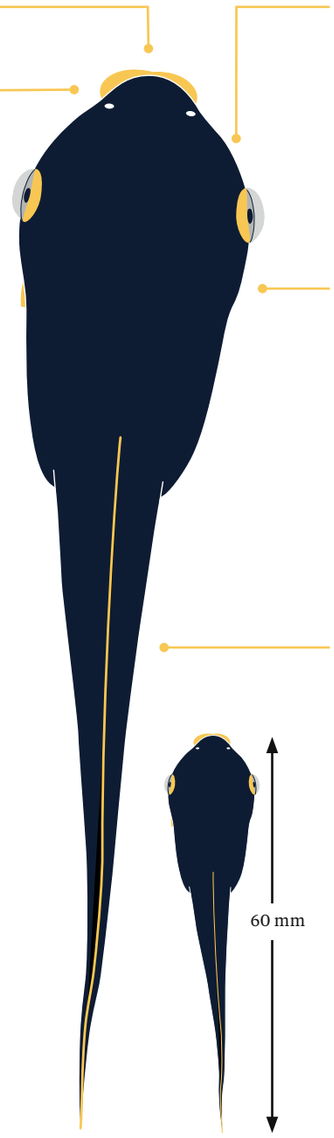
File-eared Tree Frog

SNOUT
In dorsal view and between eyes and mouth, snout first tapering in a rather straight line to terminate bluntly rounded. Snout long, profile slightly angled in lateral view.

ORAL DISC
Subterminal to terminal. Upper lip bears papillae only in lateral parts. Lateral oral disc indentations present and delimiting upper and lower lip.

Upper lip marginal papillae arranged in a single row, but additional submarginal papillae present giving a double or triple row impression. On lower lip, marginal papillae mostly arranged in double rows, fading into a single row medially. Small gap in lower lip papillation present medially. Marginal papillae moderate in length, blunt. LTRF 4(2–4)/3 or 5(2–5)/3. Upper and lower beaks undivided, robust, black, and serrated along their edges. Upper beak weakly convex medially.

ECOMORPH
Lentic, exotrophic, benthic-nektonic, suspension rasper.



NOSTRILS & EYES
Eyes lateral, protruding beyond head contour. Nostril closer to snout than to eye. Orbitonasal streak present and distinct. Iris silver with some coppery hue or pale golden. Peripherally, iris stippled in black. Sclera silvery, often with a slight blueish sheen below and gradually increased black stippling above.

BODY
Rhomboid in dorsal view; widest point of body at eye level. In lateral view, trunk much deeper than head. Head flat above. Trunk as high as wide or higher than wide. In lateral view, moderate concavity present in gular region (from snout to abdomen). Spiracle sinistral, orifice large, located well below mid-body axis in lateral view. Posterior spiracular orifice fused to the body. Spiracle is directed posterolaterally.

TAIL
Moderately strong to strong, approximately 65–68% of total length. Upper tail fin begins anterior to or at body-tail junction. Level of upper tail fin start variable, tail fin arching, and tail fin height depending on stage of development and size. A patch of opaque tissue is located at first third of tail and extends slightly into the upper and lower fins; patch bright and conspicuous. Upper tail fin is well-arched. Fins taper posteriorly with slightly concave contours into a narrow tip. Tail generally high but variable in height. Maximum height of tail at approximately 30–50% of tail length. Lateral tail vein visible but often indistinct. Myosepta visible.

SIMILAR SPECIES
In body shape, *Polypedates otilophus*, *P. macrotis*, and *P. leucomystax* are similar superficially. *P. leucomystax* does not grow as large and differs in color pattern and lower lip papillae. *P. macrotis* and *P. otilophus* tadpoles are more difficult to distinguish. Although the differences have not been worked out with large samples, preliminary observations suggest that *P. otilophus* differs from *P. macrotis* in its greenish coloration, longer snout, lighter belly, more expansive and more conspicuous opaque patch on proximal tail. Mouthparts are very similar in both species. Inger (1966) reported that *P. otilophus* commonly has 4(2–4 divided) rows of keratodonts on the upper lip, *P. macrotis* 5 (2–5 divided); however, variants of *P. otilophus* with 5(2–5) may be common.

Polypedates otilophus *is an arboreal species. It inhabits primary and secondary forests, forest edges, and clearings from sea level to beyond 1000 m a.s.l. The tadpoles grow large. Many specimens loose their tail tips, presumably due to dragonfly nymph attacks.*

HABITAT & ECOLOGY
Polypedates otilophus tadpoles live in turbid forest ponds, at clearings or forest edges. The tadpoles normally hide in the depth of the pond but occasionally rush to the surface to exhale and refill their lungs. As in other *Polypedates* tadpoles, they feed on organic matter at the bottom of the pond or filter-feed small particles from the water column. Often, this species occurs in association with *Polypedates macrotis* and *Rhacophorus pardalis*.

REPRODUCTION
Males descend from the canopy at night and perch on trunks and twigs around the breeding pond. Mating pairs in amplexus produce a foam nest. Several males may attempt to mate during foam-nesting. Nests are attached to logs or branches 1-3 m above the water. Tadpoles hatch from their foam nest and drop from the bottom of the nest into the pond below.

COLORATION
General appearance yellow-greenish above. On the flanks, the coloration gradually transforms from the greenish pigmentation above to white below. The ventral side is opaque white, but finely stippled with melanophores, more so in the gular (throat) region; sometimes also yellow pigments are present ventrally. The yellow-greenish pigmentation of the trunk continues caudally onto the tail, even on the tail fins in the first 30–50% of the tail. In the distal 50–70% of the tail, upper and lower fins are translucent. Lateral tail vein visible, sometimes indistinct. Oral disc and papillae lightly stippled with melanocytes in advanced stages.

LITERATURE

Inger R.F. (1966) The systematics and zoogeography of the Amphibia of Borneo. Fieldiana Zoology 52: 1–402.

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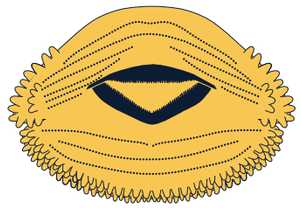
Inger, R.F., Stuebing, R.B., Grafe, T.U., Dehling, J.M. (2017) A field guide to the frogs of Borneo. 3rd ed. Natural History Books, Kota Kinabalu. 228 pp.

Rhacophorus baluensis Inger, 1954

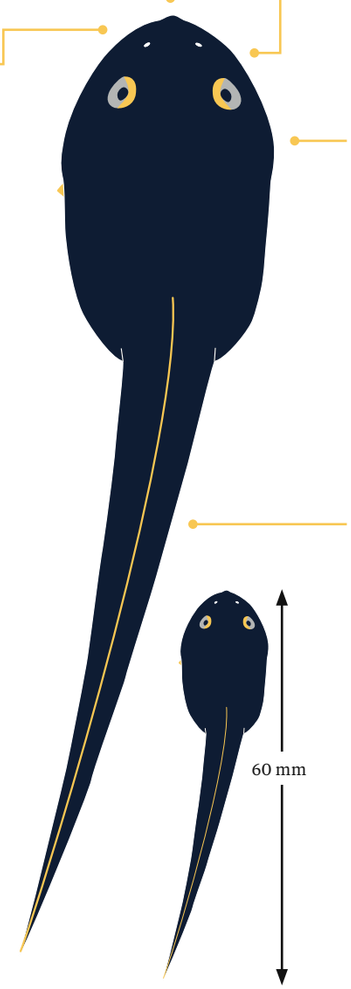
Kinabalu Tree Frog

SNOUT
Viewed from above, snout rounded and slightly tapering, terminating in a small medial bulge. In lateral view, snout relatively long and profile slightly angled at level of nostrils.

ORAL DISC
Anteroventral. Marginal papillation present on lower lip and lateral parts of upper lip. Upper lip possesses a broad medial gap in papillation; no medial gap in lower lip papillation. Marginal papillae arranged in 2–3 rows on lower lip and one row on upper lip. On upper lip, however, additional short rows of submarginal papillae present laterally.



Papillae moderately long and blunt. Emarginations present between upper and lower lips. LTRF 7(3–7)/3(1), 6(2–6)/3(1), or 6(2–6)/3; division of the first row on lower lip, if present, may be indistinct. Peripheral keratodont rows span most of the upper and lower lips. Beaks well keratinized but narrow. Jaw edges bear serrations. Upper beak relatively flat, only shallowly arched, without noticeable medial convexity. Lower jaw resembles a very wide and flat V.



NOSTRILS & EYES
Eyes dorsolateral. Iris stippled with golden iridocytes on a black background. Towards the pupil, stippling fuses to form a bronze or coppery ring. Sclera stippled with iridocytes on black background. In dorsal view, nostrils closer to snout than to eyes, opening anterolaterally.

BODY
Depressed, flat above. In dorsal view, body contour broadly oval to smoothly rectangular. Body widest at gill region in dorsal view. Spiracle sinistral. Spiracular tube opens posterolaterally. Spiracular orifice relatively large, round and very low, well-below the longitudinal body axis in lateral view. Medial part of spiracular orifice rimmed but attached to abdominal wall. Orbitonasal streak indistinct. On the dark body, lateral line pores visible.

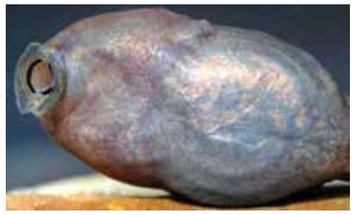
TAIL
Muscular part of tail strong and high (>50% body height). Tail long, approximately 68–69% of total length. Upper fin rises anterior to level of trunk-tail junction. In lateral view, the upper tail fin is only slightly arched, mostly straight. In posterior third of tail, edges of the upper and lower fins converge in straight lines toward a narrowly rounded tip (often broadly rounded in regenerated tail tips). Upper and lower fins are only moderately high and subequal in height. Maximum height of tail reached beyond half tail length. Lateral tail vein invisible. Myosepta indistinct.

ECOMORPH
Lentic, exotrophic, benthic.

SIMILAR SPECIES
Because of their large size, stout body, and homogeneous brown to dark brown coloration, it is unlikely that tadpoles of *Rhacophorus baluensis* tadpoles could be confused with other species. They may resemble *Abavorana luctuosa* tadpoles, but the latter differ in pattern, oral disc features, and tail shape. Tadpoles of *R. nigropalmatus* and *R. borneensis* are lighter in color and have posteriorly black tails (night coloration).

Rhacophorus baluensis *tadpoles grow large and are robustly built. In these pond-type tadpoles, tail tips will be found damaged in many individuals, probably due to predator attacks. Thus, tips may be regenerated and the shape of the tip may be altered.*

HABITAT & ECOLOGY
Because the range of the species is restricted to higher elevations in western Sabah and northeastern Sarawak and not many observations were published, data about its larval ecology are scarce. The tadpoles live in temporary or permanent forest pools or pools in clearings. They will also accept very slow moving sections of streams. The tadpoles are bottom dwellers. We encountered them in black-water habitats rich in humic acid and >30 cm in depth.



REPRODUCTION
Similar to other rhacophorid tree frogs, *R. baluensis* is most likely seen in the vicinity of a suitable breeding pond. The species breeding ecology needs further investigation.

COLORATION
Body and tail generally mid to dark brown, without markings. There are inconspicuous irregular spots of bronze iridocytes at the flanks. The skin is opaque and lungs and gut coils are not visible in lateral view. The brown coloration also covers much of the tail and fades only towards the terminal 20% of the tail and towards the fin margins. Clusters of iridocytes are scattered along the tail and tail fins. The ventral side of the body is mostly brown in the gular and buccal region and grayish at the abdominal part. Bronze or coppery iridophores are scattered over the ventral side, but may be indistinct. The ventral skin is opaque (in larger specimens at least) and inner organs, not visible through the skin. Oral disc and papillae with melanocyte pigmentation. Heavy pigmentation conceals myosepta and tail veins.

LITERATURE

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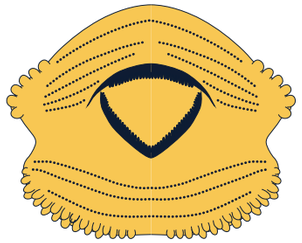
Inger, R.F., Tan, F. L. (1990) Recently discovered and newly assigned frog larvae (Ranidae and Rhacophoridae) from Borneo. The Raffles Bulletin of Zoology 38: 3–9.

Rhacophorus borneensis Matsui, Shimada, and Sudin, 2013

Bornean Flying Frog

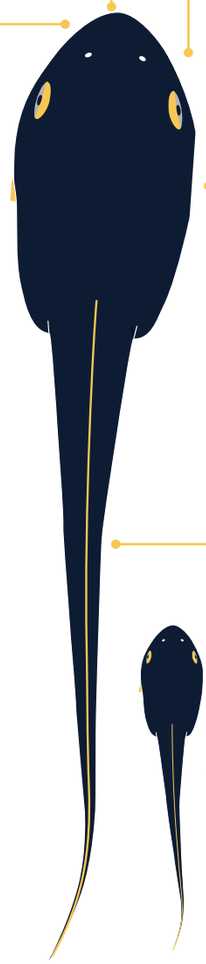
SNOUT
From above, tapering and narrowly rounded at tip. In lateral view, snout relatively long and profile slightly angled at level of nostrils.

ORAL DISC
Subterminal. Marginal papillae of oral disc present on the lower lip and lateral parts of the upper lip. Upper lip with a broad medial section devoid of papillae. Lower lip bears a narrow but distinct gap in papillation medially.



Marginal papillae arranged mostly bi-serially on lower lip and uniserially on the upper lip. Papillae moderately long and blunt. Emarginations present between upper and lower lips. LTRF 5(2–5)/3. Peripheral keratodont rows span most of the upper and lower lips. Beaks well keratinized but narrow. Jaw edges sharply serrated. Upper beak broadly and shallowly arched, without noticeable medial convexity. Lower jaw V-shaped.

ECOMORPH
Lentic, exotrophic, benthic.



NOSTRILS & EYES
Eyes dorsolateral. Iris stippled with golden iridocytes on black background. Around pupil, iris stippling fuses to form a closed ring. Sclera stippled with silver/gold iridocytes on black background as well. In dorsal view, nostrils closer to snout than to eyes; opening anteriorly. Orbitonasal streak weak, indistinct.

BODY
Medium to large; depressed ovoid in lateral view; trunk higher than head part. In dorsal view, body contour broadly oval. Body widest at gill region in dorsal view. Spiracle sinistral. Spiracular tube opens both posterolaterally and upward. It is relatively large, oval and low, well-below the longitudinal body axis in lateral view. Medial part of the spiracular orifice attached to the abdominal wall. Lateral line organ visible.

TAIL
Muscular part moderately strong, long, approximately 64–70% of total length. Upper fin rises from the trunk, at or slightly anterior to trunk tail junction. In lateral view, dorsal tail fin arching. Edges of upper and lower fins converge gradually into a narrowly rounded, acute tail tip. Upper fin high, higher than lower fin. Maximum height of tail reached at approximately 45% of tail length. Lateral tail vein present but sometimes indistinct; the same applies to the myosepta.

SIMILAR SPECIES
Rhacophorus borneensis tadpoles could be confused with *R. nigropalmatus*. We found the description of. *R. nigropalmatus* tadpoles in Inger 1985 resembles our *R. borneensis* tadpoles samples. *R. nigropalmatus* is distinguished from *R. borneensis* by larger size, bulkier body (makes eyes appear conspicuously small), dorsal tail fin reaching further anterior, and differences in LTRF and papillation pattern. *R. pardalis* can be similar in general body color. Most (but not all) *R. pardalis* tadpoles, however, have high contrast cheek markings. A distinctly black distal part of the tail, abruptly set off against the lighter tail base, is absent in *R. pardalis* and *R. nigropalmatus*.

Rhacophorus borneensis *is a species of the forest canopy. Adults will climb down to suitable forest ponds only for reproduction. Tadpoles grow large.*

HABITAT & ECOLOGY
Rhacophorus borneenis is arguably the most beautiful frog of Borneo, however, little is know about its tadpoles. Adults spend their lives high up in the trees; males occasionally can be heard calling >10 m above the ground. Only at the breeding pond, there is a chance to encounter this frog. Tadpoles live in forest ponds of variable depths. Stagnant pools in intermittent streams might be used as well. We observed tadpoles in forest ponds of <60 cm depth. Tadpoles stay close to the bottom.

REPRODUCTION
Males call from trees around forest ponds. The call is a rapid wooden knock, reminiscent of a woodpecker. We have observed males come gliding down from a tree and plunging into a pond. Mating *Rhacophorus borneensis* produce a foam nest on low vegetation overhanging the pond. Pre-feeding development of the tadpoles takes place in the nest. Finally they make their way out through the bottom of the nest and drop into the pond below where they begin to feed.

COLORATION
Body and tail beige to uniformly gray or olive above, without spots. The braincase and vertebral column may be marked darker (as in some other species). The lower flanks are dusted with iridophores. Flank and abdominal skin semi-opaque; lungs and gut coils not clearly discernible. The tail is black in the distal two thirds (night color). The black distal part often begins abruptly with a nearly vertical line. However, tail coloration is subject to variation. The black posterior tail part lightens up during the day (contracted melanocytes) and scattered groups of iridophores become visible in the distal parts of tail fins. The ventral side of the body is mostly pigmented by silvery, golden or coppery iridophores and covered by a milky, semi-opaque skin. A medial silver streak is present at the anterior abdomen. Inner organs (red heart and gills, gut) are only diffusely visible through the skin.

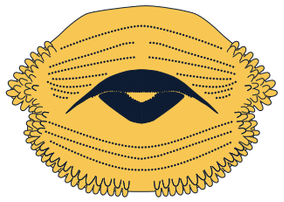
LITERATURE
Inger RF (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

Rhacophorus nigropalmatus Boulenger, 1895

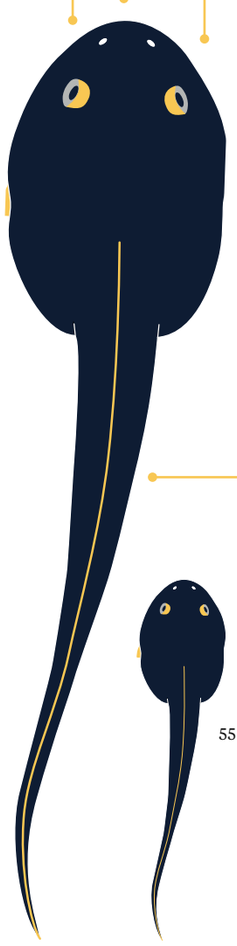
Wallace's Flying Frog

SNOUT
Only slightly tapering in dorsal view, rounded. In lateral view, snout relatively long and profile slightly angled at the position of the nostrils.

ORAL DISC
Subterminal. Marginal papillation present on lower lip and lateral parts of upper lip. Upper lip mostly free of papillation, except for lateral forths. Lower lip possesses a narrow but distinct gap in papillation medially.



Marginal papillae arranged bi-serially on lower lip. Lateral part of the upper lip bears a row of marginal papillae plus one or two shorter rows of submarginal papillae. Lower lip equipped with a short submarginal row in the lateral parts as well (i.e., three rows laterally). Papillae moderately long and blunt. Emarginations present between upper and lower lips. LTRF 7(2–7)/3. Peripheral keratodont rows span most of upper and lower lips. Beaks well keratinized but moderately strong. Jaw edges bear sharp serrations. Upper beak broadly and shallowly arched, without distinct medial convexity. Lower jaw V-shaped.



NOSTRILS & EYES
Eyes positioned dorsolaterally. Iris mostly solid golden, but stippled golden on black background in its periphery. Eye outside the iris (sclera) stippled with silver/gold iridocytes on black background as well. Eyes appear small in relation to the large body and sit high in lateral view. In dorsal view, nostril closer to snout than to eye. Nostril opening anteriorly.

BODY
In lateral view, body shape ovoid. Trunk deeper than head part. In dorsal view, body contour broadly oval. Body widest at mid-body region in dorsal view. Spiracle sinistral. Spiracular tube opens posterolaterally and also upward. Spiracular orifice relatively large, oval and low, below longitudinal body axis in lateral view. Medial part of the spiracular orifice attached to abdominal wall.

TAIL
Moderately strong, long, approximately 67% of total length. Upper fin rises from the trunk, well anterior of trunk tail junction. In lateral view, upper tail fin moderately arching. Edges of upper and lower fins gradually converge into a narrowly rounded tail tip. Upper fin slightly higher than lower fin. Maximum height of tail reached slightly before mid of tail length. Lateral tail vein present but indistinct. Myosepta indistinct.

ECOMORPH
Lentic, exotrophic, benthic-nektonic.

SIMILAR SPECIES
Rhacophorus nigropalmatus tadpoles could be confused with *R. borneensis* or *R. pardalis* because of similar general body color. *R. pardalis*, however, is distinguished by smaller size, less bulky body, and (usually) contrast-rich markings on the cheeks. Furthermore, it differs in LTRF and lip papillation. *R. borneensis* differs from *R. nigropalmatus* in reduced lip papillae, narrower jaw sheath, ventral coloration, and LTRF. *R. borneensis* has a distinct black posterior tail (night coloration) with sharp border to the lighter anterior part of the tail. We did not find such sharp borders in our samples of R. *nigropalmatus*.

Rhacophorus nigropalmatus *tadpoles have often been reported from pig wallows, puddles, and ponds in the forest but also along forest edges, logging roads, and clearings. These benthic tadpoles grow large.*

HABITAT & ECOLOGY
The largest and most impressive flying frog spends most of its time high up in the trees. Adults are not frequently encountered, and if they are seen, it is most likely at a breeding site, such as ponds at forest edges, ditches along forest roads or pig wallows. Wallace's Flying Frogs seem to prefer ponds for reproduction that are visited or created by mammals. Because of the disturbance by mammals, theses breeding habitats typically have turbid water. Tadpole will be difficult to see. *R. nigropalmatus* tadpoles are mostly active at the bottom of the ponds. They hide in the superficial mud layer during the day. They venture to the surface during the night for filter feeding and gulping air. The juvenile froglets do not resemble the adults in coloration and skin color. Juveniles are rough-skinned, brown to reddish brown with light spots.

REPRODUCTION
Like other members of the genus *Rhacophorus*, *R. nigropalmatus* mating pairs create foam nests, approximately 1–3 m above the breeding puddle or pig wallow.

COLORATION
Beige to gray above sometimes with dark irregular spots on the posterior trunk. The lower flanks are dusted with iridophores. In the upper part of the flanks, the lung is visible through the skin as a line of silvery bubbles on each side. Gut coils are faintly visible in lateral view as well. The body pigmentation, particularly the dark spots, continues onto the tail. At night, the tail (including fins) is spotted in the first (proximal) third and more solid black in the distal two thirds. These black markings are lighter in color during daytime (contracted melanocytes) and scattered groups of iridophores become visible in the distal parts of tail fins. The ventral side of the body is mostly clear and transparent, except for scattered golden or coppery iridophores at the anterior region of the abdomen. Inner organs are visible through the skin.

LITERATURE

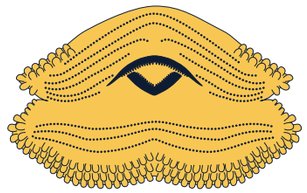
Inger RF (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

Rhacophorus pardalis Günther, 1858

Harlequin Treefrog

SNOUT
Rounded, yet slightly tapering when viewed from above. In lateral view, snout moderately long, smooth convex curve of profile slightly angled at level of nostril.

ORAL DISC
Anteroventral. Marginal papillation present on lower lip and lateral parts of upper lip; a wide area of upper lip devoid of papillae.



Marginal papillae arranged bi- or tri-serially on lower lip. Lateral part of upper lip bears a row of marginal papillae plus a row of submarginal papillae. Papillae generally short and blunt. Emarginations present between upper and lower lip. LTRF 6(3–6)/3 or 7(3–6)/3 (gap in third upper row may be indistinct). Peripheral keratodont rows long and extending far laterally on both upper and lower lips. Beaks well-keratinized, only moderately strong. Jaw edges bear fine, sharp serrations. Upper beak broadly arched, lower jaw V-shaped.

NOSTRILS & EYES
Eyes dorsolateral. In dorsal view, nostril are closer to snout than to eye, oriented anterolaterally, slightly sunken in. Orbitonasal streak present. Iris background color black covered with densely scattered golden or coppery pigment cells, merged into a thin ring around pupil. Sclera silvery below and stippled silver/gold on a black background above.

BODY
Body shape depressed ovoid in lateral view, tapering to the snout. In dorsal view, body contour oval with head broader than trunk. Body widest at gill region (posterior to eyes) in dorsal view. Spiracle sinistral. Spiracular tube opens posterolaterally positioned very low, well below the longitudinal body axis in lateral view. Medial part of spiracular orifice attached to abdominal wall. Lateral line organs visible in darker specimens.

TAIL
Moderately strong, long, approximately 66–71% of total length. Tail fin contours moderately arched in lateral view, more so in upper fin. Fins taper in the posterior two thirds with straight edges into a narrow, pointed tip. A true flagellum is not formed. Upper fin rises from trunk-tail junction. Maximum height of tail before mid of tail.

ECOMORPH
Lentic, exotrophic, benthic-nektonic.

SIMILAR SPECIES
Rhacophorus pardalis tadpoles superficially resemble *R. rufipes* or *R. borneensis* in body shape, but differ in coloration. The contrast-rich area below the eye (if present) distinguishes *R. pardalis* from both, as well as LTRF.

Specimens of *R. pardalis* with high contrast color pattern can be confused with *Chalcorana raniceps*. The latter, however, is clearly distinguished by its extensive gland field on belly, trunk, and head.

The medium-sized tadpoles of Rhacophorus pardalis *inhabit many different lentic habitats and settings. The coloration of the tadpoles is variable.*

HABITAT & ECOLOGY
Despite being a lentic tadpole, the species occurs along rivers as well, where it reproduces in pools on river banks or in isolated rock pools. During the day, tadpoles stay close to the bottom and hide under leaves. At night they are more active and less restricted to the bottom.

REPRODUCTION
Males and females are commonly seen 1–3 m high on vegetation around breeding pools. The mating pair builds a foam nest above the water, into which the eggs are laid. The tadpoles hatch from the nest and drip into the water below, where they start feeding.

COLORATION
Light brown to chocolate brown above, usually with dark markings above and on the flanks. Most markings are diffuse. The trunk is darker than the head. On the top of the head, two opposing chevron markings embrace the braincase anteriorly and posteriorly; the posterior marking is extended into a black streak along the vertebral column. Very often a light area exists below the eye that possesses one or two dark spots. The body pigmentation continues onto the tail where it very much fades after half of the tail. The tail fins are mostly clear but are dusted with melanophores and a few iridophores. The ventral side commonly is transparent or slightly milky. Red gills and gut are visible through the skin. The heart and the anterior third of the abdominal space are covered by a silvery sheath of iridophores. In the ventral mid-line sometimes a longitudinal silver streak (lining Vena abdominalis) is present. As variants from the general color scheme, both paler and very dark, or less contrast-rich tadpoles of this species have been recorded.

LITERATURE

Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89.

Zhangixalus dulitensis (Boulenger, 1892)

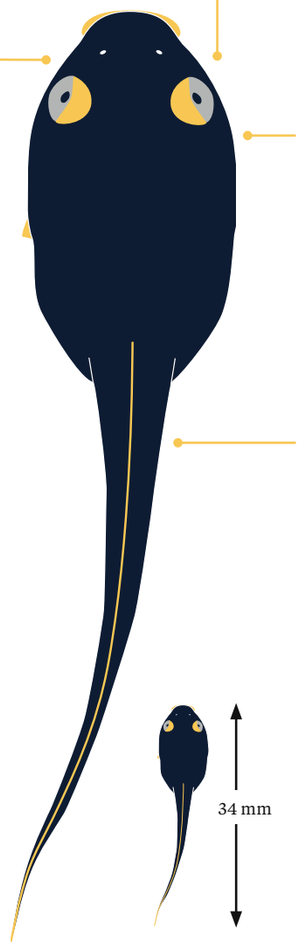
Jade Tree Frog

SNOUT
Slightly narrowed, viewed from above. In lateral view, snout short, sloping in steep convex curve. An elevated position of the nostrils and a bulge at the tip give the snout a characteristic profile.

ORAL DISC
Anteroventral. Width approximately half of max. body width or slightly less. Papillation present along margin of lower lip and lateral parts of upper lip. Wide medial area of upper lip devoid of papillae.

Marginal papillae arranged mostly bi-serially. Papillae short and rounded. LTRF 5(2–5)/3 to 6(2–6)/3. Beaks well keratinized but narrow. Beaks equipped with fine, sharp serrations along edges. Upper beak broadly arched. Lower jaw sheath flat V-shaped.

ECOMORPH
Lentic, exotrophic, benthic.



NOSTRILS & EYES
Eyes dorsolateral, high in position in lateral view. Pale nostril sits elevated, closer to snout than to eye, oriented anterolaterally. Eyes black with scattered golden pigmentation, increasingly dense toward iris, forming a golden ring around pupil.

BODY
Depressed dorsoventrally. In dorsal view, body contour oval to ovoid. Body widest at level of gill region. Spiracle sinistral and low, well below mid-body axis in lateral view. Spiracular tube points posterodorsally, yet the opening is laterally. Its inner wall attached to body wall. Spiracular orifice completely rimmed but a clearly free tube is not formed.

TAIL
Tail fin rises abruptly at trunk-tail junction. Tail contributes 60% of the total length. Upper fin originates at the same level as the tail muscles, at trunk-tail junction. Height of tail increases gradually, achieving maximal extent at level of mid-tail. Posteriorly, tail tapers gradually and terminates with flattened curvature in a narrowly rounded tip. Muscular part of tail moderately high (50% of body height).

SIMILAR SPECIES
Zhangixalus dulitensis tadpoles look very indistinct at first glance (size, shape, color). Superficially, they can be confused with *Kurixalus chaseni* or early stage *Rhacophorus pardalis* tadpoles, both may occur in the same pond and *R. pardalis* often has similar dark markings around the braincase. However, particularly the peculiar snout profile in lateral view identifies *Z. dulitensis* reliably against the others. *Chalcorana* tadpoles are readily separated from *Z. dulitensis* by their distinct gland fields. The description of *Z. dulitensis* tadpoles in Inger et al. (2017) is erroneous and may have been confused with *R. borneensis*. Our samples described here were verified by DNA barcoding.

The tadpoles of Zhangixalus dulitensis *are generalists that inhabit ponds. This species can be encountered in lowland primary forest. Adults are arboreal and live in the canopy.*

HABITAT & ECOLOGY
We observed *Zhangixalus dulitensis* tadpoles in partially sun-exposed, shallow (<50 cm) ponds at clearings or forest edges, where their presences seemed to be rather intermittent. The ponds had muddy bottoms. The tadpoles were more active at night and tended to hide during the day. Occasionally, tadpoles were seen aggregating in schools that wander around and feed on bottom particles and algal overgrowth of plants and leaves.

REPRODUCTION
Adults come down from the canopy and gather on vegetation around the pond. The moment when congregations form seems unpredictable. Small foam nests are produced and attached to vegetation overhanging the water. After initial development, tadpoles hatch from the nest and drop into the pond below. Calls of males have been described as a weak cricket-like trill.

COLORATION
Ocher or buff brown above overlain by dark, diffuse pigmentation. In dorsal view, there is a rhomboid figure of melanocytes above the braincase, starting anterior the eyes and reaching the posterior end of the head where it transforms into a band posteriorly and terminating at the end of the trunk. In lateral view, the pigmentation of the trunk slightly decreases from above to below. Some individuals may also have a diffuse dark band from the anteroventral corner of the eye to the snout, passing below to the nostril. The lungs are discernible through the skin as an arched line of spherical shiny bubbles dorsal to the gut coils. The ventral skin is only lightly pigmented and mostly transparent. The inner organs are visible through the skin in ventral view. Iridocytes form a medial silvery patch right posterior to the heart region on the gut. The muscular part of the tail is dusted with melanocytes fading in the first half towards the distal end of the tail. Fins are mostly clear, except at their proximal bases. Sometimes 2–3 small, dark circles (glands?) are present at the lateral tail base. Tail venation and myosepta indistinct.

LITERATURE

Haas, A., Hertwig, S.T., Krings, W., Braskamp, E., Dehling, J.M., Pui, Y.M., Das, I. (2012) Description of three *Rhacophorus* tadpoles (Lissamphibia: Anura: rhacophoridae) from Sarawak, Malaysia (Borneo). Zootaxa 3328: 1–19.

Inger, R.F. (1985) Tadpoles of the forested regions of Borneo. Fieldiana Zoology new series 26: 1–89. [as *Rhacophorus dulitensis*]

Inger, R.F., Stuebing, R.B., Grafe, T.U. Dehling, J.M. (2017) A field guide to the frogs of Borneo. 3rd ed. Natural History Books, Kota Kinabalu. 228 pp.

TERRESTRIAL SITES —DIRECT DEVELOPMENT

Direct development implies that development is completed in the egg and no free-swimming tadpole is part of the ontogenetic development. Thus, direct development does not require water bodies for development. Species, however, that do have terrestrial eggs but develop free swimming tadpoles, are dealt with in the section on stagnant and flowing water bodies, respectively.

EGGS OF SPECIES WITH DIRECT DEVELOPMENT
Eggs are typically laid at moist sites under leaves or moss. Development is completed in the egg jelly. A free swimming stage is not formed, rather, a froglet hatches from the egg. This mode of development has been postulated for species of Bornean *Philautus*. However, evidence is available for only some of the *Philautus* species. Furthermore, *P. macroscelis* and *P. nepenthophilus* possess free-swimming larvae and are not direct-developers.

Forest trail, Gunung Murud

Philautus acutus Dring, 1987

Sharp Bush Frog

HABITAT & ECOLOGY

Philautus acutus is an endemic species with a restricted distribution on the island of Borneo. It is a small tree frog (SVL of males 23.4–27.1 mm), characterized by a short, rounded snout and a smooth skin with few small tubercles on snout, upper eyelid and occipital region. The dorsum shows a broad dark brown bifurcate pattern on a pale tan to clay-brown ground color. The species is known from the higher elevations of Gunung Mulu National Park, where it inhabits primary upper montane forests at about 1200–1300 m a.s.l.. Three egg capsules were found incidentally on the forest floor within montane forest. One egg capsule was empty, the other two contained one froglet each. The eggs had been deposited between wet, rotting leaf litter, beneath a dead branch of a tree. The jelly capsules measured 13 mm in diameter.

SIMILAR SPECIES

In the vast majority of Bornean *Philautus* species, the effective breeding behavior has never been confirmed by direct observations, by captive breeding or via genetic matching (barcoding) of developmental stages to adults. This lack of basic knowledge hampers both the understanding of their ecology, as well as the reconstruction of the evolution of their reproductive strategies. It remains unclear whether aerial direct development has evolved once or several times independently within different lineages of *Philautus*. Our sample of *P. acutus* was verified by DNA barcoding. Aerial direct development in Sundaland *Philautus* has only been recorded positively in *P. acutus*, and *P. saueri*. In *Philautus kerangae*, *P. mjobergi*, and *P. saueri*, deposition and incubation of the eggs in pitchers of *Nepenthes* have been reported. In some of the anecdotal reports, the species' identity of the eggs or developmental stages in the pitcher was not confirmed unequivocally and needs further investigation. A confirmed case of development with free-living larvae in *Nepenthes* pitchers is *Philautus nepenthophilus*.

Philautus tectus. The developmental mode of this common species is still unknown. Although direct development has been assumed, evidence has not been published yet.

Philautus bunitus. A group of eggs was discovered in nest fern on a low branch and was tentatively assigned to the species. However, the identity of the eggs could not be verified genetically and further research is needed to confirm that this species deposits eggs on epiphytic fern.

LITERATURE

Etter, L., Haas, A., Lee, C.C., Pui, Y.M., Das, I., Hertwig. S.T. (2021) Out of the trap: A new species of bush frog (Anura: Rhacophoridae: *Philautus*) from Borneo, with an updated phylogeny of *Philautus*. Journal Zoological Systematics Evolutionary Research 59: 1064–1096.

Hertwig, S.T., Lilje, K.E., MIN, P.Y., Haas, A., Das, I. (2012) Molecular evidence for direct development in the rhacophorid frog, *Philautus acutus* (Rhacophoridae, Anura) from Borneo. The Raffles Bulletin of Zoology 60: 559–567.

Malkmus, R., Dehling, J.M. (2008) Anuran amphibians of Borneo as phytotelm-breeders—a synopsis. Herpetozoa 20: 165–172.

Malkmus, R., Manthey, U., Vogel, G., Hoffmann, P., Kosuch, J. (2002) Amphibians & Reptiles of Mount Kinabalu (North Borneo). Koeltz Scientific Books, Königstein. 424 pp.

ABDOMEN/ABDOMINAL
Belly or referring to the belly. The abdominal space contains the gut and associated organs as well as gonads and kidneys. In tadpoles, the abdomen begins posterior to the gill region or branchial chamber.

ADHERENT
Here: tadpole ecomorph in flowing water that has an oral disc commonly with complete ring of marginal papillae. The oral disc is used to hold on to the substrate and maintain position in moderate current.

ALLOPATRY
Occurrence of species in non-overlapping distributional ranges, isolated from each other.

AMPLEXUS
Situation during breeding when the male clasps the female with his forearms and rides on the back of the female, prior and during spawning in many species.

ANAL SIPHON
The tubular vent of tadpoles, usually embedded in the lower fin of the tail and opening medially, right, or left to the fin.

ANTERIOR
At or towards the front end of the body or body part; the antero-posterior axis of an animal refers to the body axis from head to tail. If „A is more anterior than B“ then A is located more toward the snout than B. (vs. posterior).

ANURA
The taxonomic group of amphibians that include frogs and toads. “Anura” literally means “without tail.”

ANURAN
Referring to the taxonomic group of frogs (including toads).

BEAK
see > jaw sheath.

BENTHIC
Here: tadpole ecomorph that prefers to stay at the bottom of water bodies, where they rasp food from submerged surfaces. Benthic tadpoles have somewhat dorsally oriented eyes and fully developed tail fins..

BIOGEOGRAPHY
Studies the distribution and geographic history of life on earth.

BRANCHIAL
Referring to the gills or gill region.

BUCCAL
Referring to a region in between mouth and gill area of the head of a tadpole. See also *gula*.

CLASPING
Tadpole ecomorph of very slow to moderate current in lotic waters, oral disc with gap in papillation; oral disc used to prevent animal from being drifted away in slow current, but plays a minor role in maintaining the animal‘s position.

DEXTRAL
On the right hand side of the body (vs. sinistral)

DIRECT DEVELOPMENT
In the egg, embryos develop directly into a froglet that finally hatches from the egg jelly capsule, omitting the tadpole stage. Eggs of species with direct development are laid on a terrestrial site (under or on leaves, in moss, etc.); example: some *Philautus* species

DISPERSAL
Spread of a species from one region to another causing a change in distributional range.

DISTAL
Further from the body center, relative to some other body part; example: the wrist is more distal than the elbow along the arm.

DORSAL
At or towards the upper part (back) of the body or body part (vs. ventral)

DORSUM
Back of the body.

ECOMORPH
A group of organisms with a certain similar body shape (morphology) that relates to habitats and habits (ecology). Similar ecomorphs are not necessarily related to each other phylogenetically.

EMARGINATION
Indentation or notch, for example between upper and lower lip of the larval oral disc.

ENDEMIC
Occurring exclusively in a defined area, for example “endemic to Borneo”, “endemic to Gunung Mulu” etc. If the area is quite small, species are called micro-endemics.

ENDOTROPHIC
Endotrophic tadpoles do not feed but grow and develop from the yolk that the female frog provided in the egg; as the embryo develops, the yolk mass is internalized and stored in gut tissue for further resorption.

EPHEMERAL POND/PUDDLE
A stagnant water body that exists for a short time.

EXOTROPHIC
Taking up nutrients by feeding on external resources to grow and develop; see > endotrophic.

FLAGELLUM
Here: narrow, long tail tip, set off from fins by section of concave contour.

FOSSORIAL
Burrowing, living below the substrate. Fossorial tadpoles live in the interstices of gravel (for example, *Leptobrachella)* or deep in stacks of leaf litter.

GASTROMYZOPHOROUS
Tadpoles with abdominal (belly) sucker adjacent to the oral disc (genera *Meristogenys* and *Huia*).

GULA/GULAR
Throat / located at the throat. In tadpoles, the region immediately posterior to the oral disc. The gula cannot be separated from the buccal area of the ventral skin that follows posteriorly to it (see p. 61).

HYOBRANCHIAL APPARATUS
Structure belonging to the head and composed of skeletal elements of the gill arches and other elements of visceral head structures. The function of the hyobranchial apparatus is feeding and pumping water through the gills.

INTERMITTENT STREAM
A stream that ceases to flow in dry periods of the year. Often isolated pools persist for a while even if no water is flowing. Such pools may be used by amphibians to reproduce.

IRIDOPHORE/IRIDOCYTE
Cell that produces silvery or golden, reflective iridescence by light diffraction at purine crystals. For example, at the iris of the eye or the belly of some tadpoles. Only visible in living animals. Iridophores rapidly loose their color in preserved specimens.

JAW SHEATH
Or beak. A hard, brown or black keratinous coverings of jaws in tadpoles. Often with serrated edges and suitable to bite off matter.

KERATODONT
Small keratin structures, often spoon-like with serrated edges. Keratodonts are commonly arranged in lines (=keratodont rows) of many tadpoles’ oral discs, visible as black lines. Keratodonts are sometimes called “larval teeth”, however, they have no relation to true teeth and are of different material and origin.

LATERAL
Position to the side of the body or body part, or at least more so in relation to another part. in comparison. (vs. medial).

LENTIC
Any stagnant water system.

LOTIC
Any flowing water system.

LTRF
Labial Tooth Row Formula, a formula that expresses the number and arrangement of labial “teeth” (= keratodonts) in simple form, see text for details.

MACROPHAGOUS
Ability to take up large food items; for example, tadpoles of *Occidozyga*.

MARGINAL PAPILLAE
In many tadpoles, papillae are aligned along the margins of the lips (oral disc) and probably have mechanical and sensory functions.

MEDIAL
At or towards the middle plane of the body, or more so related to some other body part in comparison. (vs. lateral).

MELANOPHORE/MELANOCYTE
Pigment cell with brown to black pigment (melanin).

MORPHOLOGY
The science of form and structure; often adopted as synonym for “structure” or “shape”.

NEKTONIC
Tadpoles that swim up and down while foraging in the water column in lentic or quiet parts of lotic waters; not restricted to bottom of water habitat. Rasping jaws, more lateral eyes, tail fins high, tail tip pointed. Example: *Polypedates*.

NEUSTONIC
Tadpoles that filter particles from the water at or near the surface in lotic or lentic environments. Long tail, terminal mouth with terminal or upturned mouthparts. Example: *Megophrys*, *Pelobatrachus*, some *Microhyla*.

NIDICOLOUS
Here, tadpoles are nidicolous if they spend time of their development in some kind of terrestrial nest.

NOSTRIL
External opening of the nasal passage.

ONTOGENY/ONTOGENETIC
The development during the lifespan of an organism. Ontogenetic changes can involve physical, physiological, or other features of the organism.

ORAL DISC
Extended, thin lips of a tadpole, surrounding the mouth orifice often forming a disc-shaped structure. Features of the oral disc, such as orientation, size, the number of keratodont rows, presence or absence of marginal or submarginal papillae, are important taxonomic characters.

ORBIT/ORBITAL
Eye region or related to it.

ORBITONASAL STREAK
In some tadpoles present as fine line (with reduced pigmentation) between the anterior corner of the eye and the nostril (see p. 61).

PAPILLAE
Here: papillae of the oral disc that are specifically formed protuberances of the skin and underlying tissue of a certain shape and size. At the margin of the oral disc, papillae are arranged in dense rows in many species.

PHYTOTELMA
Isolated pocket of water provided by plants, such as leaf axils, tree holes, buttress holes, bamboo internodes, *Nepenthes* pitchers etc. Phytotelmata can range from a few milliliters to several liters of water. Sometimes the term is restricted to living plants; however, the distinction of phytotelmata in living vs. dead plants is not meaningful here because some species use both for reproduction. Therefore, we use the term liberally in this book.

POSTERIOR
At or towards the hind end of the body or body part; the antero-posterior axis of an animal refers to the body axis from head to tail. If „B is more posterior than A" then B is located more toward the hind end than A.

PROXIMAL
Closer to the body center relative to some other item; example: the upper arm is more proximal to the trunk than the wrist.

RHEOPHILOUS
Preference for living in the flowing water; literally "current-loving".

ROSTRAL
Position towards the snout.

SCLERA
Part of the eye outside iris. In humans it represents the white of the eye. In tadpoles, it is pigmented, often slightly different from the iris pigmentation.

SINISTRAL
On the left hand side. (vs. dextral)

SNOUT
Part of the head anterior to the eyes.

SPIRACLE
Opening of the gill chamber, through which water flows out from the gills. The position of the spiracle is used in classification and taxonomy. Bornean tadpoles have a singular spiracular opening: medially in microhylids, sinistral in all other tadpoles.

SUBMARGINAL PAPILLAE
Papillae set in from the margin on the oral disc most commonly on the lower lip.

SUCTORIAL
Guild of tadpoles in fast lotic waters with a strong sucker mouth not only used to permanently hold onto the substrate against the current to maintain position of the animal, but also used to feed in the current and move about by action of the jaws and oral disc. Examples: many *Ansonia*.

SUSPENSION FEEDER
Guild of tadpoles in lentic waters that are specialized in highly efficient suspension feeding (filtering) of smallest food particles (down to the size of bacteria) suspended in the water. These tadpoles remain quiescent in the water column where they constantly pump water through their filter apparatus (hyobranchial apparatus). Eyes lateral, no keratinized mouthparts. Example: *Microhyla*.

SUSPENSION RASPERS
Nektonic tadpoles of lentic waters that can filter feed suspended particles but also rasp food from submerged surfaces and possess keratinized mouthparts for that purpose, but also rely heavily on filtering small particle from the water by pumping water constantly from varying positions within the water column. Examples: some *Polypedates*.

SYMPATRIC
Living of species in overlapping distributional ranges.

SYNTOPIC
Occurring in the same habitat at the same time.

SYSTEMATICS
Science of studying the relationships between organisms in the light of phylogeny and evolution.

TAXON
Plural: taxa. An operational entity of organisms in taxonomy. This entity can be a species, or a genus, a class, etc., depending on context.

TAXONOMY
Science of the classification of organisms in a hierarchical system. Taxonomy includes identification, description, and delimitation of species as well as forming higher groups such as genera, families etc. according to international rules.

VENTER
Belly, abdomen.

VENTRAL
At or towards the lower part of the body, absolutely or relative to some other body parts in comparison. (vs. dorsal).

VERMICULATE
Here referring to the shape of narrow, elongated, and slightly wavy melanocytes in the skin of some tadpoles. Latin *vermis* = worm.

VICARIANCE
Split of a species,' or generally taxon's, distributional range into sub-areas due to development of geological barriers, such as rivers, mountain ranges, breakup and drifting of tectonic plates etc.

Gunung Murud, mossy forest

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From left to right: *Leptobrachium abbotti*, *Meristogenys orphnocnemis*, *Limnonectes palavanensis*, *M. kinabaluensis*, 3x natural size.

Abavorana luctuosa 220
Ansonia echinata 70
Ansonia guibei 70
Ansonia hanitschi 74
Ansonia kanak 76
Ansonia leptopus 78
Ansonia longidigita 80
Ansonia minuta 82
Ansonia spinulifer 84
Chalcorana megalonesa 220
Chalcorana raniceps 224
Chaperina fusca 198
Duttaphrynus melanostictus 168
Feihyla inexpectata 234
Feihyla kajau 154
Fejervarya limnocharis 176
Glyphoglossus brooksii 196
Hoplobatrachus rugulosus 178
Huia cavitympanum 128
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Indosylvirana nicobariensis 228
Ingerophrynus divergens 168
Ingerophrynus quadriporcatus 170
Kalophrynus intermedius 216
Kalophrynus meizon 218
Kaloula baleata 200
Kaloula pulchra 202
Kurixalus chaseni 236
Leptobrachella baluensis 100
Leptobrachella dringi 102
Leptobrachella fritinniens 104
Leptobrachella gracilis 106
Leptobrachella itiokai 110
Leptobrachella juliandringi 112
Leptobrachella mjobergi 108
Leptobrachium abbotti 114
Leptobrachium gunungense 116
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Leptobrachium montanum 120
Leptomantis angulirostris 156
Leptomantis cyanopunctatus 158
Leptomantis fasciatus 238
Leptomantis gadingensis 160
Leptomantis gauni 162
Leptomantis harrissoni 240
Leptomantis penanorum 164
Leptomantis rufipes 242
Leptophryne borbonica 88
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Limnonectes finchi 180
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Limnonectes palavanensis 186
Limnonectes paramacrodon 188
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Meristogenys amoropalamus 130
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Meristogenys jerboa 134
Meristogenys kinabaluensis 136
Meristogenys maryatiae 138
Meristogenys orphnocnemis 140
Meristogenys penrissenensis 142
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Microhyla berdmorei 206
Microhyla malang 208
Microhyla nepenthicola 210
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Pelobatrachus nasutus 126
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Pelophryne signata 174
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Philautus macroscelis 246
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Polypedates otilophus 256
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Pulchrana picturata 232
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Rhacophorus borneensis 260
Rhacophorus nigropalmatus 262
Rhacophorus pardalis 264
Staurois guttatus 148
Staurois parvus 150
Staurois tuberilinguis 153
Zhangixalus dulitensis 266

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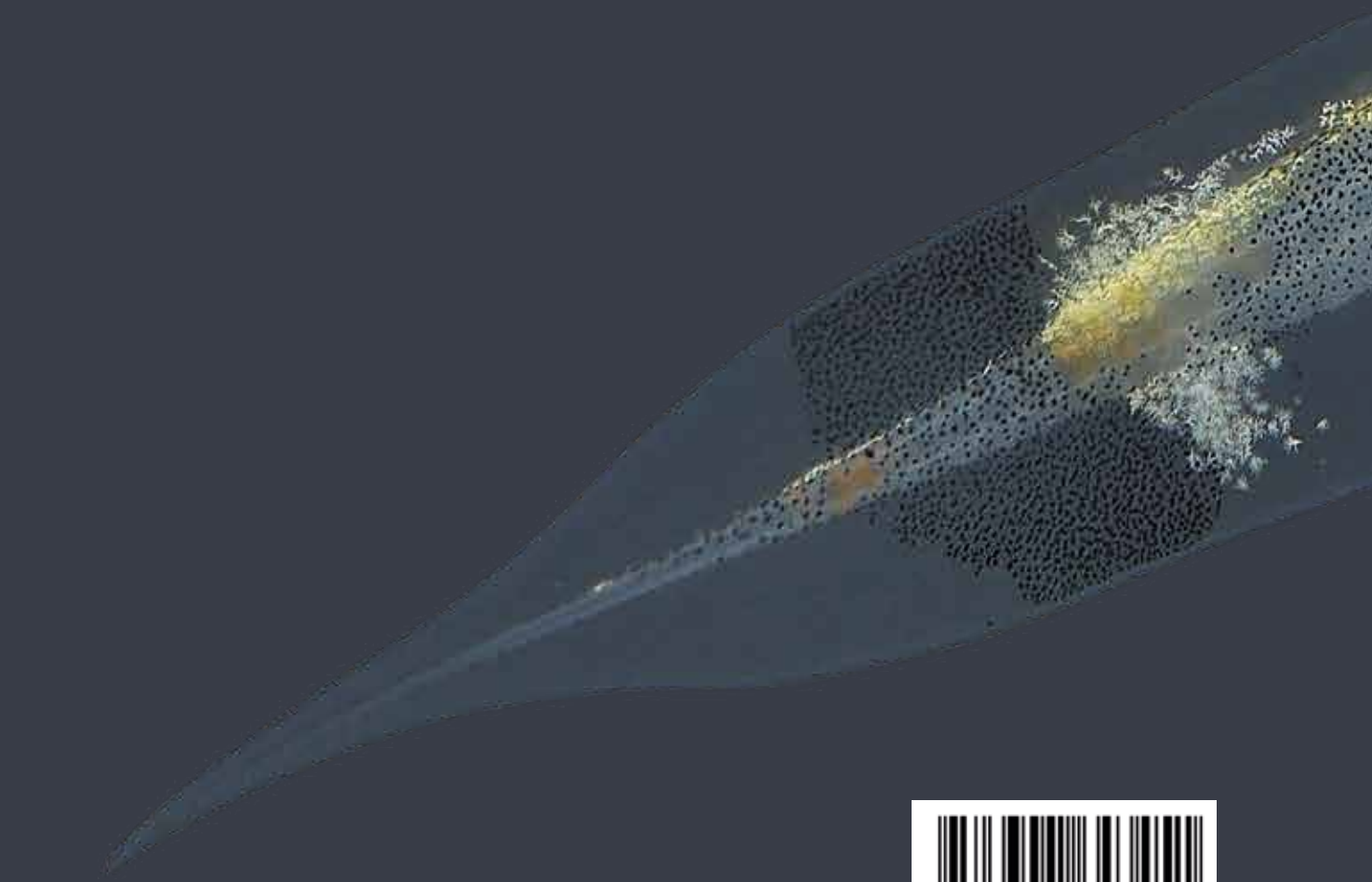
Tadpoles are an important, albeit often neglected, part of the life-cycle of frogs. These larval forms play a critical role in the ecology of aquatic habitats. Their morphological and ecological diversity is remarkable, although comprehensive inventories and descriptions of the tadpole fauna are unavailable for most regions of the world.

This book presents tadpole descriptions for 99 species from the southeast Asian island of Borneo, covering all species commonly found, as well as representatives of the more cryptic ones. These are typically depicted from life with color photographs, mostly for the first time. The aims of this book are to allow a broad audience an easy access to the tadpole fauna of Borneo, increase awareness of these life stages, document their diversity, and provide insights into their fascinating biology.



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