Taxonomy, Natural History, and Ecology of Selected Herpetofaunal Species from the Sunda Islands and Adjacent Regions – Synergistic Effects of Fieldwork and Museum Collections for Biodiversity Research

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Illustration on the previous page:
Cyrtodactylus sp. from Com, Lautém District, Timor-Leste (S. Mecke).

Table of Contents

1 Summary

In this cumulative thesis (papers 1–13) I investigated the taxonomy, natural history, and ecology of selected species of amphibians and reptiles from the Sunda Islands and adjacent regions, and highlighted the importance of natural history collections for biodiversity research. Several Sundaic species provided unexpected challenges, primarily because of significant problems stemming from their taxonomic history. Only the synergy of fieldwork and collection-based studies, allowed me to resolve some of these issues, as outlined below.

Herpetological surveys in all districts of Timor-Leste (except the Oecusse exclave), including its offshore islands, contributed towards a comprehensive inventory of the amphibians and reptiles of this country at the southern border of the Wallacea Biodiversity Hotspot. New distribution records of amphibians and reptiles for 11 of the country's 12 contiguous districts, along with natural history data were presented. Results of the survey work increased the number of amphibian and reptile species known to occur in Timor-Leste to > 60, including > 20 candidate species. Many of the recorded species appear to be endemic to Timor Island, including the frog *Kaloula* sp. nov., several bent-toed gecko species of the genus *Cyrtodactylus*, and the agamid *Draco timoriensis*. Notable reptile discoveries included at least seven undescribed *Cyrtodactylus* species, a genus previously not recorded from Timor, the first records of the gecko *Hemidactylus garnotii* and of the gecko genus *Hemiphyllodactylus* for Timor-Leste, and several undescribed skinks (chapter 4, **papers 1 & 2**). Revisions of the genus *Cyrtodactylus*, and the skink genus *Eremiascincus* on Timor and adjacent islands, including the description of new species, are currently in preparation together with colleagues from the USA and the UK.

A revision of Timorese *Cyrtodactylus* is not possible without resolving the tangled taxonomy of some extralimital species. The taxonomy of selected non-Timorese *Cyrtodactylus* geckos was investigated accordingly, in three papers (chapter 5, **papers 3–5**). A new species of *Cyrtodactylus*, originally catalogued as *C. fumosus* in the herpetological collection of the Senckenberg Naturmuseum Frankfurt, Germany, was described from Klakah, Lumajang Regency, Jawa Timur Province, Indonesia. The new species differs from all other congeners by a combination of seven characters (**paper 3**). The *Cyrtodactylus* fauna of Java had been underestimated for centuries with four out of the five endemic species described as late as during the 2000s. *Cyrtodactylus fumosus*, hitherto considered widespread in the Sunda Archipelago, including the islands of Sumatra, Java, Bali, Sulawesi, and Halmahera, was redescribed and confirmed to possess a precloacal groove in males. Examination of the type specimen and additional vouchers from Rurukan and Mount Masarang, North Sulawesi Province, Indonesia, revealed that this population was distinct from other forms heretofore called '*fumosus*' by a combination of unique morphological characters. *Cyrtodactylus fumosus* was identified as the most distinctive species among the six bent-toed geckos recorded from Sulawesi, differing from Sulawesi congeners by four striking characters (**paper 5**). Since there was also much taxonomic confusion of *C. fumosus* with *C. marmoratus*, the type series of the latter taxon was described for the first time. I was able to demonstrate that the type series actually comprises two sets of specimens, and that examination of specimens from only one set or the other was responsible for some confusion surrounding these vouchers. Owing to the inconsistent naming and application of terms for some key characters (e.g., groove, sulcus, pit, hollow, depression) used in the diagnoses of *Cyrtodactylus* species, a set of novel and useful definitions was proposed. A comparative table for the bent-toad geckos of the Sunda Islands and Sulawesi was provided for the first time (**paper 4**). *Cyrtodactylus* throughout the Lesser Sundas, the Moluccas, and Sulawesi will be further investigated in future studies. Several museum vouchers will be described as new species.

The discovery of snakes of the genus *Cylindrophis* in Timor-Leste led to an investigation of the taxon *C. ruffus*, which is widely distributed in Maritime Southeast Asia. A new species of *Cylindrophis*, originally catalogued as *C. ruffus* in the herpetological collections of the Naturalis Biodiversity Center, Leiden, The Netherlands and the Naturhistorisches Museum Wien, Austria, was described from Grabag, Purworejo Regency, Jawa Tengah Province, Java, Indonesia. The new species can be distinguished from all congeners by several, distinct morphological features. A detailed account of the tangled taxonomic history of the similar and only putatively wide-ranging *C. ruffus* was provided, *Scytale scheuchzeri* (name referring to a colubroid taxon) was removed from the synonymy of *C. ruffus*, *C. rufa* var. *javanica* (a taxon originally described from Borneo) was listed as *species inquirenda*, and the recently described *C. mirzae* was synonymized with *C. ruffus*. Evidence was provided that the type locality of *C. ruffus* is Java. The discovery of *C. subocularis* and the bent-toed gecko *Cyrtodacytlus klakahensis* on Java highlights how little we know about the diversity of an island, on which herpetological research in Indonesia began two centuries ago (**paper 6**). The systematic relationships within *Cylindrophis* are being investigated in an ongoing study utilizing both molecular and morphological methods.

Based on specimens discovered in the collection of The Natural History Museum, London, UK, a new distribution record for the skink *Sphenomorphus oligolepis* was

made for Seram Island, Maluku Province, Indonesia. The find constituted the westernmost record for this species and extended the distribution of this Papuan lizard well into Wallacea (**paper 7**).

The Asian toad, *Duttaphrynus melanostictus*, which was recently introduced to Madagascar (**paper 8**), is the main research focus of chapter 6. During field work in Timor-Leste, an Asian toad that had consumed a brahminy blindsnake, *Indotyphlops braminus*, was discovered. This indicated that indiscriminate foraging by this recently introduced toad species could endanger small vertebrates (**paper 9**). Timor shows an exceptionally high level of endemism in a wide range of faunal groups, and concerns that *D. melanostictus* may have a negative impact on this diversity, including vertebrates, through direct predation, had been raised by scientists. To evaluate the potential impact the feeding by *D. melanostictus* might have on the local fauna, gut contents of > 80 preserved toad specimens from five habitat types in Timor-Leste were examined and almost 6000 prey items identified. All prey items were invertebrates, with small eusocial insects comprising the major component of the diet. The wide prey spectrum demonstrated that *D. melanostictus* is a generalist invertebrate feeder. Although the Asian toad seems to not generally prey on vertebrates, vertebrate species that are morphologically similar to invertebrates in their overall appearance (worm-like gestalt) may be consumed. Data on intestinal parasites occuring in *D. melanostictus* were presented alongside the food spectrum analysis (**paper 11**).

Whereas information on the diet and internal parasites of anurans based on internal examinations have been published by numerous researchers, details of the incision method used to open the abdominal cavity of preserved specimens are rarely explained. An optimal incision into the pleuroperitoneal cavity of liquid-preserved anuran specimens to gain access to and permit easy removal of parts of the digestive tract in preparation for food spectrum analyses was formally proposed. This U-shaped cut is easy to perform and teach, and it has already been adopted in lab manuals. It provides better access to the pleuroperitoneal cavity than a small ventrolateral incision, and is less destructive than the classic textbook medial “double T-incision” routinely listed in dissection protocols. This new method may encourage other researchers to use preserved anurans for the purpose of food spectrum analyses and other examinations of internal morphology (**paper 10**).

An instance of captive breeding in a species of Timorese night skink (genus *Eremiascincus*) was reported, and the taxon demonstrated to be viviparous. A summary of information pertaining to the reproductive biology of other members of the genus *Eremiascincus* was provided (**paper 12**). Increased knowledge on the reproductive biology of *Eremiascincus* taxa will contribute to revisions of the group carried out by morphological and molecular analyses.

The type of the skink *Anomalopus leuckartii* was rediscovered in the herpetological collection of the Museum für Tierkunde, Dresden, Germany, together with other specimens from the original collection of Karl Georg Friedrich Rudolf Leuckart, who was one of zoology's leading scientists during the second half of the 19th century and the founder of modern parasitology. This rediscovery serves as an excellent example to highlight the importance of maintaining natural history collections, not merely as static archives but rather as valuable dynamic and lively databases. This, in combination with optimal taxonomic expertise as a bedrock, guarantees an environment, in which new discoveries, like the ones presented in this dissertation, are actively promoted, thereby inevitably advancing modern biodiversity research (**paper 13**).

In a general conclusions section (chapter 8), the effects resulting from the combination and coordination of field work and collection-based studies are elaborated and illustrated in a diagram. The value of the studies presented in this thesis is primarily derived from specific interactions, synergistic effects, and an iterative process that connects them. Finally, the benefit for decision-makers dealing with conservation and species management is assessed.

1 Zusammenfassung

Im Rahmen der vorliegenden kumulativen Dissertation (Publikationen 1–13) stelle ich Studien zur Taxonomie, Naturgeschichte und Ökologie ausgewählter und überwiegend problematischer Amphibien- und Reptiliengruppen der Sunda Inseln und angrenzender Gebiete vor, wobei auf die Synergieeffekte zwischen Freilandarbeit und sammlungsbasierter Forschung und auf den damit erzielten Mehrwert der Forschung für die Biodiversitätsforschung eingegangen wird.

Die Bearbeitung der Herpetofauna in allen Distrikten von Timor-Leste (mit Ausnahme der Exklave Oecusse), inklusive der vorgelagerten Inseln, stellte einen konstruktiven Beitrag zur Arterfassung der Amphibien und Reptilien eines Landes dar, das an der südlichen Grenze des Wallacea-Hotspots liegt. Neue Verbreitungsnachweise für die Herpetofauna aus 11 der 12 aneinandergrenzenden Distrikte wurden, zusammen mit naturgeschichtlichen Daten, präsentiert. Als Ergebnis dieses Arteninventars stieg die Anzahl der ursprünglich aus Timor-Leste bekannten Amphibien und Reptilien auf über 60 Taxa, darunter mehr als 20 Kandidaten-Arten. Viele der nachgewiesenen Arten scheinen auf Timor endemisch zu sein. Zu diesen gehören der Ochsenfrosch *Kaloula* sp. nov., mehrere Bogenfingergeckos der Gattung *Cyrtodactylus* und die Agame *Draco timoriensis*. Zu den bemerkenswerten Entdeckungen unter den Reptilien zählen sowohl mindestens sieben unbeschriebene Arten von *Cyrtodactylus*, einer Gattung, die bislang nicht auf Timor nachgewiesen wurde, als auch die Erstnachweise der Gecko-Art *Hemidactylus garnotii* und der Gecko-Gattung *Hemiphyllodactylus* für Timor-Leste sowie zahlreiche unbeschriebene Skinke (Kapitel 4, **Publikationen 1 & 2**). Revisionen der Gattung *Cyrtodactylus* und der Skink-Gattungen *Eremiascincus* auf Timor und benachbarten Inseln, sowie die Beschreibung bisher unbekannter Arten, zusammen mit Kollegen aus den USA und Großbritannien, sind gegenwärtig in Vorbereitung.

Eine auf Timor beschränkte Revision der Gattung *Cyrtodactylus* war nicht möglich, ohne vorab die verworrene Taxonomie einiger Arten, die außerhalb von Timor vorkommen, zu klären. Die Taxonomie dieser in angrenzenden Gebieten vorkommenden *Cyrtodactylus*-Arten wurde in drei Publikationen näher untersucht (Kapitel 5, **Publikationen 3–5**). Eine neue *Cyrtodactylus*-Art, die in der herpetologischen Sammlung des Senckenberg Naturmuseums Frankfurt, Deutschland, ursprünglich als *C. fumosus* katalogisiert worden war, wurde beschrieben; sie stammt aus Klakah, Lumajang, Ostjava, Indonesien. Die neue Art unterscheidet sich von allen Vertretern der Gattung durch eine Kombination von sieben Merkmalen (**Publikation 3**). Die Diversität der *Cyrtodactylus*-Fauna von Java wurde, ähnlich derer auf Timor, lange

Zeit unterschätzt, und erst in diesem Jahrtausend wurden vier der fünf auf dieser Insel endemischen Arten beschrieben. *Cyrtodactylus fumosus*, eine Art, die bisher im südostasiatischen Archipel – mit Nachweisen aus Sumatra, Java, Bali, Sulawesi und Halmahera – als weitverbreitet galt, wurde neu definiert. Es konnte bestätigt werden, dass Männchen dieser Art eine präkloakale Furche aufweisen. Die Untersuchung des Holotypus und weiteren Belegmaterials aus Rurukan und vom Mount Masarang (Nord Sulawesi, Indonesien) ergab, dass diese Population von anderen Formen, die bisher als „*fumosus*" bezeichnet wurden, durch eine Kombination einzigartiger Merkmale unterscheidbar ist. *Cyrtodactylus fumosus* konnte auf Grund seiner Merkmale als die auffallendste Art der sechs auf Sulawesi vorkommenden Bogenfingergeckos identifiziert werden (**Publikation 5**). Weil bislang große taxonomische Verwirrung zwischen *C. fumosus* und *C. marmoratus* herrschte, wurde die Typusserie des letzteren Taxons zum ersten Mal komplett beschrieben. Ich konnte zeigen, dass die Typusserie historisch bedingt in zwei Gruppen (mit unterschiedlichen, aber ähnlichen Seriennummern) aufgeteilt wurde, und dass die Untersuchung von Exemplaren aus nur jeweils einer der beiden Gruppen für Wirren um diese Belege verantwortlich war. Aufgrund der inkonsistenten Terminologie und Anwendung von Begriffen für Schlüsselmerkmale, die bei der Diagnose von Bogenfinger-Geckos Verwendung finden (z.B. Furche, Sulcus, Grube, Mulde, Vertiefung), wurde eine Reihe neuer und nützlicher Definitionen vorgeschlagen. Eine Vergleichstabelle für die Bogenfinger-Geckos der Sunda Inseln und Sulawesis wurde zum ersten Mal bereitgestellt (**Publikation 4**). Die *Cyrtodactylus*-Fauna der Kleinen Sundainseln, der Molukken und Sulawesis soll künftig weiter untersucht werden. Zahlreiche Museumsexemplare werden als Basis für die Beschreibung neuer Arten dienen.

Die Entdeckung einer Walzenschlange der Gattung *Cylindrophis* in Timor-Leste führte zu einer umfassenden Untersuchung des im maritimen Südostasien weit verbreiteten Taxons *C. ruffus*. Eine neue Art, die in den Sammlungen des Naturalis Biodiversity Centers, Leiden, Niederlande, und der Naturhistorischen Museums Wien, Österreich, ursprünglich als *C. ruffus* katalogisiert worden war, konnte beschrieben werden. Die bekannten Exemplare stammen aus Grabag, Purworejo, Zentraljava, Indonesien. Die neue Art unterscheidet sich von allen anderen Gattungsangehörigen durch zahlreiche, auffällige morphologische Merkmale. Des Weiteren liegt nun eine detaillierte Beschreibung der Taxonomie-Geschichte der ähnlichen und nur vermeintlich weitverbreiteten *C. ruffus* vor. *Scytale scheuchzeri* (der Name bezieht sich auf die Beschreibung einer colubroiden Schlange) wurde aus der Synonymie von *C. ruffus* entfernt, *C. rufa* var. *javanica* (ein Taxon, das ursprünglich aus Borneo beschrieben worden war) als „species inquirenda“ eingestuft und die erst kürzlich beschriebene *C. mirzae* mit *C. ruffus* synonymisiert worden. Belege zur Untermauerung der Typuslokalität von *C. ruffus* als „Java“ wurden erbracht. Die Entdeckungen von *C. subocularis* und des Bogenfingergeckos *Cyrtodactylus klakahensis* aus Java zeigen, wie wenig wir eigentlich über die Artenvielfalt einer Insel wissen, auf der die herpetologische Erforschung Indonesiens immerhin schon vor zwei Jahrhunderten begann (**Publikation 6**). Die Verwandtschaftsverhältnisse innerhalb der Gattung *Cylindrophis* werden in einer laufenden Studie überprüft, bei der sowohl morphologische als auch molekularbiologische Methoden zum Einsatz kommen.

Basierend auf Exemplaren, die ich in der Sammlung des Naturhistorischen Museums in London, UK, entdeckte, konnte ein neuer Verbreitungsnachweis für den Skink *Sphenomorphus oligolepis* für die Molukkeninsel Seram (Indonesien) erbracht werden. Es handelt sich um das westlichste Vorkommen dieser papuanischen Echse und dehnt ihr Verbreitungsgebiet weit in die Wallacea-Region aus (**Publikation 7**).

Die Schwarznarbenkröte, *Duttaphrynus melanostictus*, die kürzlich in Madagaskar eingeführt wurde (**Publikation 8**), ist das Hauptobjekt der Forschung, die in Kapitel 6 präsentiert wird. Während der Freilandarbeit in Timor-Leste wurde eine Schwarznarbenkröte entdeckt, die eine Blumentopfschlange, *Indotyphlops braminus*, gefressen hatte. Dies wies darauf hin, dass sich diese kürzlich auch nach Timor eingeführte Kröte möglicherweise durch Prädation bestandsgefährdend auf kleine Wirbeltiere auswirken könnte, die in Timor einen außergewöhnlich hohen Grad an Endemismus zeigen (**Publikation 9**). Um diese potentielle Auswirkung zu bewerten, wurde der Darminhalt von über 80 zuvor konservierten Kröten aus fünf verschiedenen Habitattypen innerhalb Timor-Lestes untersucht, wobei fast 6000 Beutetiere identifiziert werden konnten. Unter diesen befanden sich ausschließlich Invertebraten aus verschiedenen taxonomischen Gruppen. Kleine staatenbildende Insekten konnten als Hauptbestandteil der Nahrung von *D. melanostictus* identifiziert werden. Das breite Beutespektrum weist darauf hin, dass es sich bei *D. melanostictus* um einen generalistischen Invertebratenfresser handelt. Obgleich die Schwarznarbenkröte im Allgemeinen keine Vertebraten zu fressen scheint, ist nicht auszuschließen, dass Vertebraten die eine morphologische Ähnlichkeit mit Invertebraten aufweisen (Typ „Wurm“), ins Nahrungsspektrum dieser Kröte passen. Daten zu den Endoparasiten von *D. melanostictus* wurden zusammen mit der Nahrungsanalyse präsentiert (**Publikation 11**).

Obgleich von zahlreichen Forschern Informationen zur Nahrung und zu Endoparasiten von Froschlurchen auf der Grundlage von Untersuchungen des Gastrointestinaltraktes publiziert worden sind, wurde nie im Detail auf die Schnittführung eingegangen, die benutzt wird, um die Leibeshöhle von konservierten Exemplaren zu öffnen. Eine optimale Schnittführung, die den Zugang und das einfache Entfernen von Teilen des Verdauungstraktes bei in Flüssigkeiten fixierten Froschlurchen erlaubt, wurde vorgestellt. Dieser U-förmige Schnitt ist einfach durchzuführen und zu vermitteln und wurde bereits in Laborhandbüchern übernommen. Er ermöglicht einen besseren Zugang zu den relevanten Organen als ein kleiner ventrolateral durchgeführter Schnitt und hat eine weniger zerstörende Wirkung als der in Lehrbüchern routinemäßig aufgeführte mediane Schnitt in Form einer römischen I. Diese neue schonende Methode könnte andere Forscher dazu ermutigen, konservierte Froschlurche für Nahrungsanalysen und andere innere Untersuchungen zu nutzen und damit den wissenschaftlichen Gebrauch von Sammlungsexemplaren fördern.

Für einen auf Timor vorkommenden Nachtskink (Gattung *Eremiascincus*) gelang zum ersten Mal die Zucht in Gefangenschaft, wobei sich zeigte, dass die Tiere lebendgebärend sind. Die Informationen zur Reproduktionsbiologie der Gattung *Eremiascincus* werden zusammengefasst bereitgestellt (**Publikation 12**). Dieses Wissen wird bei laufenden morphologischen und molekularbiologischen Revisionen ergänzend zum Einsatz kommen.

Der Typus des Skinks *Anomalopus leuckartii* wurde in der herpetologischen Sammlung des Museums für Tierkunde Dresden, Deutschland, wiederentdeckt. Er gehört, zusammen mit anderen Exemplaren, zum Bestand der ehemaligen Sammlung von Karl Georg Friedrich Rudolf Leuckart, der einer der führenden Zoologen der zweiten Hälfte des 19. Jahrhunderts war und als Begründer der modernen Parasitologie gilt. Diese Wiederentdeckung ist ein Paradebeispiel, das aufzeigt, wie wichtig es ist, naturkundliche Sammlungen zu erhalten und zwar nicht als statische Archive sondern als aktiv zu nutzende, wertvolle Datenbanken. Die Arbeit in und an Sammlungen, in Kombination mit der bestmöglichen taxonomischen Sachkenntnis, schafft ein produktives Umfeld, das Entdeckungen, wie sie in dieser Arbeit vorgestellten werden, maßgeblich fördert und damit unweigerlich auch die moderne Biodiversitätsforschung bereichert (**Publikation 13**).

In einer „General Conclusions“ (Kapitel 8) werden die Effekte, die sich aus der Kombination bzw. Koordination von Freiland- und sammlungsbasierter Forschung ergeben, herausgearbeitet und in einer Übersichtsgrafik veranschaulicht. Sich zum Teil ergänzende Wechselwirkungen, Synergieeffekte und ein die Einzelarbeiten verbindender iterativer Prozess, sind die Kenngrößen, mit denen sich der Mehrwert der vorgelegten Arbeit beschreiben lässt. Abschließend wird der Nutzen für die Entscheidungsträger in Natur- und Artenschutz aufgezeigt.

3 General Introduction

Geographically situated east of the Indian subcontinent, south of China, west of Papua New Guinea, and north of Australia, Southeast Asia has one of the world's most diverse amphibian and reptile faunas (e.g., Das & Van Dijk 2013; Das 2016). The part of Southeast Asia located in the Malay Archipelago (Fig. 1), including the countries of Brunei, Malaysia (East Malaysia: Sabah, Sarawak, Labuan), Indonesia, the Philippines, Singapore, and Timor-Leste, is certainly no exception. Indonesia alone, whose islands make up most of the world-famous Wallacea Biodiversity Hotspot[1], is home to > 15% of the world's herpetofauna species (Iskandar & Erdelen 2006), with new taxa continuing to be discovered every year. During the period 2010–2017 alone, ~ 50 new reptile (Uetz *et al*. 2018) and ~ 130 new amphibian species (Frost 2018) were described from Indonesian islands, indicating that there is a high number of species of this regional herpetofauna still unknown or unrecognized by science. Alas, due to the environmental pressures from human activity, this incredible diversity is being threatened; and some species may become extinct even before they are discovered. At the same time, the taxonomy of many herpetofaunal groups in this geologically and environmentally complex archipelago has largely remained unchanged (see Appendix: Mecke 2017) since the last comprehensive taxonomic reviews for these islands were published by Van Kampen (1923: amphibians) and De Rooij (1915, 1917: reptiles). This is particularly true for taxa that appear to be widely distributed. Therefore, basic biodiversity research on the herpetofauna of the Malay Archipelago is urgently needed.

The process of identifying and classifying biological groups is probably as old as mankind itself (see Mayr 1975), and the scientific disciplines of taxonomy and systematics date back as far as antiquity (e.g., Kullmann 2007; Storch *et al*. 2013). Hence, taxonomy has been called 'man's oldest profession' (Hedgpeth 1961), and it certainly represents an important fundamental discipline for many other biological disciplines (Wilson 2004).

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[1] The Wallacea Biodiversity Hotspot (WBH) is a biogeographic region delimited by Wallace's Line to the west (marking the edge of the Asian or Oriental region), Lydekker's Line in the east (separating the eastern edge of Wallacea from the Australian region), and the Timor Sea to the south (*fide* Bellwood 2007; see Fig. 1). It is named after the 19th-century British naturalist Alfred Russel Wallace (1823–1913), who spent some eight years travelling 22,500 km and collecting 125,000 specimens of animals within the Indonesian Archipelago, and who identified the region now known as Wallacea as a bio-transitional zone between Asia and Australia (Wallace 1889). With a total land area of 33,494 km^2, the relatively small WBH harbors ~ 270 different amphibian and reptile species, ~ 130 of which are endemic; the degree of endemism exceeds 40% in both groups (Critical Ecosystem Partnership Fund, CEPF 2014). One of the endemics is the world's largest lizard, the Komodo dragon (*Varanus komodoensis* Ouwens, 1912), which is restricted to only a few small islands along the southern edge of the WBH.

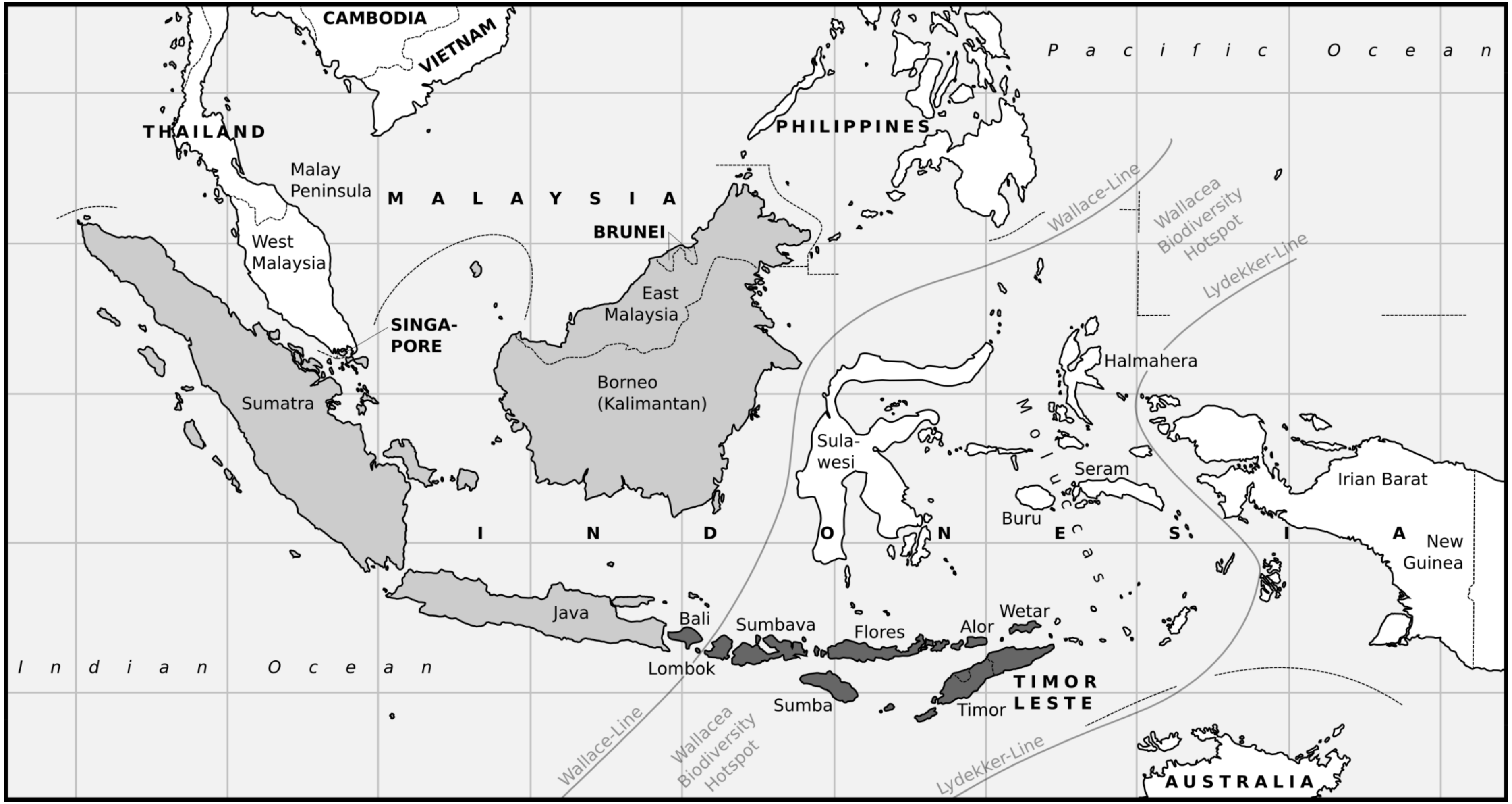

Fig. 1. Map of the region covered by this thesis – the Malay Archipelago and adjacent regions. Light grey – Greater Sunda Islands; dark grey – Lesser Sunda Islands. Map prepared by Heike Worth.

The history of taxonomy is closely linked to the development of collections, which originated as private 'cabinets of curiosities' or 'cabinets of wonders' in the 16th and 17th centuries. Nowadays, natural history collections have become transformed into modern tools of scientific research and public education, whose initial aim of storing biological specimens brought back by explorers made them comprehensive resources for taxonomic studies. Unfortunately, even though the disciplines of taxonomy and systematics, as well as collection-based studies, can provide unrivaled insights into organismic biology, they are often thought of as 'unfashionable,' 'old-fashioned' or 'out of date' (see Hewitt *et al*. 1990; Sivarajan & Robson 1991; Wheeler 2008; Hamilton 2014). Even worse, taxonomy is sometimes considered as having achieved its goals and no longer being needed as an active research field. This would relegate collections to the position of static archives merely needing maintenance and conservation (see Hewitt *et al*. 1990). Taxonomy, however, remains the cornerstone of all biological research in the life sciences (e.g., Wägele *et al*. 2011; Briggs & Walters 2016). Results of faunistic surveys and ecological or other biological studies are futile if they cannot be attributed to a specific taxonomic entity (usually a species). Research findings can also be distorted if they are erroneously derived from several similar looking species, or from a single, long-recognized 'species' under whose name additional species-level diversity is hidden. Furthermore, studies on the diversity within certain animal groups and their relationships to each other, can serve as more than mere taxonomic accounts: they help elucidate and corroborate biogeographic patterns, past geological events, or evolutionary processes. Examples for these include several recent studies on Southeast Asian herpetofaunal groups (e.g., Grismer *et al*. 2016; Ihlow *et al*. 2016; Amarasinghe *et al*. 2017; Quah *et al*. 2017; Siler *et al*. 2017).

A well-established discipline of taxonomy is also the basis for efficient conservation biology (e.g., McNeely 2002*;* Gutiérrez & Helgen 2013; Tahseen 2014). Unresolved species diversity can easily result in neglecting or underestimating of a species' threat status and concomitant negligence in protecting it. For amphibians and reptiles in Southeast Asia – many of which are forest-dwellers – habitat loss appears to be the one of foremost importance (e.g., Rowley *et al*. 2010; Koch *et al*. 2013). In Indonesia, which occupies most of the area of the Malay Archipelago, the loss of primary forest between 2000 and 2012 was more than 6 million hectares (Arunarwati Margono *et al*. 2014) – an area half the size of England. Therefore, basic taxonomic research should primarily focus on Southeast Asian taxa with a putatively wide distribution and a largely unresolved taxonomy, and/or geographic regions that have not yet been sufficiently explored by scientists but are suspected to hold a high number of endemic and/or potentially threatened species. Since herpetological survey work in many parts of Southeast Asia poses logistical challenges due to rugged terrain and/or a lack of infrastructure, and is dependent on the current political situation and system of research regulations, existing collections – as all-encompassing databases – should certainly be used extensively to study herpetological diversity in this region as well.

The Sunda Islands are a series of stepping-stones between the Malay Peninsula and the Moluccas, comprising the Greater Sunda Islands (Borneo, Java, Sumatra, and, depending on the source, Sulawesi) that are located on the Sunda Shelf, and the oceanic Lesser Sunda Islands (approx. 40 islands, including Bali, Flores, Lombok, Sumba, Sumbawa, and Timor) (Brown 2009; Fig. 1). Politically, these islands are part of Brunei and Malaysia (the northern parts of Borneo), Timor-Leste (the eastern half of Timor), and Indonesia (the remaining, larger part of the region). The region's herpetofauna (with the exception of northern Borneo; see e.g., Inger 1966; Inger & Lian 1996; Malkmus *et al*. 2011; Stuebing *et al*. 2014) did not receive much attention from taxonomists for several decades, either based on the assumption that certain islands were relatively well studied (e.g., Teynié *et al*. 2010: Java) or inhabited by relatively few species (e.g., Smith 1927: Timor). The species richness of the Sunda Islands, however, has recently been shown to be much higher than assumed (e.g., Riyanto *et al*. 2014, 2015: Java - Harvey *et al*. 2014, 2015, 2017: Sumatra - Kaiser, H. *et al*. 2011a; Kathriner *et al*. 2014: Timor), although a comprehensive, updated checklist akin to those presented by Van Kampen (1923) and De Rooij (1915, 1917) has yet to be prepared (but see Outlook). In this cumulative thesis I present my investigations into the taxonomy, natural history, and ecology of selected herpetofaunal species from the Sunda Islands, with a regional focus on Timor/Timor-Leste and Java.

Approximately 34,000 km^2 in area, Timor is the largest of the Lesser Sunda Islands (Brown 2009) and positioned at the southern boundary of the Wallacea Biodiversity Hotspot (Fig. 1). The island is roughly divided in half, with the eastern part forming the sovereign state of Timor-Leste (nominally a former Portuguese colony from the 1520s) and the eastern part (West Timor) forming part of Indonesia's East Nusa Tenggara province (Brown 2009). Geologically, Timor is less than 4 million years old. It is one of the driest islands of the Lesser Sundas, and, as a result of slash-and-burn agriculture, largely covered by ruderal, savannah-like vegetation (Monk *et al*. 1997; Sandlund *et al*. 2001). Timor is part of the Timor and Wetar Deciduous Forests Ecoregion within the bioregion of Wallacea and possesses only highly fragmented natural habitat, which is itself threatened (Wikramanayake *et al*. 2002). A core of rugged hills and mountains with elevations of nearly 3000 m (Mount Ramelau, 2690 m) forms an intermittent east-west ridge that divides the northern and southern parts of the island, creating a rain shadow in the north that results in the observed aridity (Durand 2006). The country's topography generally favors the presence of a wide range of habitats (e.g., limestone forests, semi-evergreen rain forest, and tropical montane evergreen forest; Wikramanayake *et al*. 2002; Trainor *et al*., 2007, 2008). By the position of Timor at the crossroads of the Southeast Asian and Australo-Papuan biogeographic realms, the fauna of this island comprises an interesting mosaic[2] (Kaiser, H. *et al*. 2011a). Furthermore, the island harbors a remarkable variety and a high level of endemism among species (e.g., land snails, insects, frogs, lizards and snakes, birds – Trainor *et al*. 2008; Michaux 2010; Kaiser, H. *et al*. 2011a; Anderson *et al*. 2013; Köhler & Kessner 2014). Biodiversity research on Timor, however, is still in its infancy, and in Timor-Leste it has only just begun.

Most of our knowledge of the herpetofauna of Timor stems from explorations in West Timor from 1800–1830 and 1890–1930 (Kaiser, H. *et al*. 2011a). With the exception of a single expedition to West Timor in the 1990s, no further herpetological research was conducted in Timor until the first decade of the 21st century. The first comprehensive report of the herpetofauna of Timor-Leste (Kaiser, H. *et al*. 2011a) listed seven amphibian species, three of which were considered candidate species, and 30 reptile species, at least five of which were candidate species. Subsequent research yielded additional new country records and candidate species (Sanchez *et al*. 2012; O'Shea *et al*. 2012), indicating that Timor-Leste's amphibians and reptiles and their distribution within the country had not yet been adequately assessed. Despite the fact that herpetological fieldwork was conducted in Timor-Leste from 2009–2010 (published in Kaiser, H. *et al*. 2011a; Sanchez *et al*. 2012; O'Shea *et al*. 2012), the country is still poorly explored in comparison to other Southeast Asian nations, such as Malaysia, Singapore, or Thailand (see the detailed accounts by Cox *et al*., 1998; Chan-ard *et al*. 1999; Grismer 2011a, 2011b). The research results of three expeditions I participated in (19 January – 7 February 2012; 19 June – 10 July 2012; 19 June – 01 July 2013) are presented in chapter 7. The presented publications are a continuation of Kaiser, H. *et al*. (2011a), Sanchez *et al*. (2012), and O'Shea *et al*. (2012).

Candidate species discovered in Timor-Leste have yet to be officially described (Kaiser *et al*., in prep, Mecke *et al*., in prep.). Almost all of these belong to widely distributed genera or species groups with a complex taxonomy and taxonomic history. Of these, some key species were described or reported during historic times from Java, an island

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[2] The ancestors of Timor's fauna descended from Asia or Australia-New Guinea, since it is located in the transitional zone of the Wallacea Biodiversity Hotspot (see Fig. 1 and footnote 1).

with a history of commercial and strategic importance for Europe that reaches back ~ 500 years (e.g., De Lang 2017). The majority of Indonesian specimens available today were gathered by researchers on Dutch expeditions. Many were collected through the efforts of the Natuurkundige Commissie voor Nederlandsch-Indië (1820–1850), an organization that sent a group of naturalists (including Heinrich Boie, Johann Coenraad van Hasselt, Heinrich Kuhl, Heinrich Christian Macklot, and Salomon Müller) to the Dutch East Indies (today's Indonesia) to study and collect animals and plants for the Rijksmuseum van Natuurlijke Historie (now Naturalis Biodiversity Center; RMNH) in Leiden, The Netherlands and the Zoölogisch Museum, Universiteit van Amsterdam (ZMA) (e.g., Fransen *et al*. 1997; Gassó Miracle *et al*. 2007). Predictably for a collecting effort during this period, the greatest number of specimens came from Java (e.g., Amarasinghe *et al*. 2015). The growth of the collections from the Malay Archipelago in the RMNH and the ZMA (now a part of the RMNH), continued throughout the colonial period (until the Dutch recognition of Indonesian independence in 1949) rendering the present collection one of the most important in the world for studies of the Indonesian herpetofauna. Some other European collections (e.g., the Naturhistorisches Museum Basel, Switzerland, and the Senckenberg Naturmuseum Frankfurt, Germany) also received important specimens from Indonesia, especially from the region of Wallacea (e.g., Müller 1895; Mertens 1930; Koch 2012).

Some findings of the recent herpetological fieldwork conducted in Timor-Leste underlined the importance of investigating the taxonomy of problematic forms occurring on the Sunda Islands and well beyond, with the distribution of some taxa or species complexes spanning the entire Malay Archipelago and ranging into adjacent regions. At the forefront of this research have been (partly on-going) revisions of the Asian pipesnakes of the *Cylindrophis ruffus* (Laurenti, 1768) complex (initiated by the documentation of similar pipesnakes in Timor-Leste; see paper 1, chapter 4) and the resolution of the taxonomy of two bent-toed geckos of the genus *Cyrtodactylus*, *C. fumosus* Müller, 1895 and *C. marmoratus* Gray, 1831 that were repeatedly documented from the Lesser Sundas, including from Timor (e.g., McKay 2006; Das 2016: *C. fumosus* - Boettger 1892, 1900; Barbour 1912; Smith 1927; Mertens 1930: *C. marmoratus*). For this research, comprehensive use of museum specimens was made (> 700 vouchers examined) and 13 national and international collections were visited (see Appendix: Mecke 2017). The results, including the description of two new species, the redescription of another one, the description of important types, and new distributional records, are presented in chapter 5.

Currently, about 60 amphibian and reptile species, including many candidate species, have been reported from Timor (paper 1, herein). Potential threats for the amphibians were summarized by Kaiser *et al*. (2014), and some of these may also affect reptile populations. One distinct threat emanates from a toad species introduced to Timor (Trainor 2009) that was considered a potential predator of small frogs and lizards (e.g., Trainor 2009, Kaiser *et al*. 2014). Its ecological impact was sometimes compared to that of the cane toad, *Rhinella marina* (Linnaeus, 1758), one of the most successful invasive species worldwide (e.g., Kaiser *et al*. 2014; Kolby 2014). The toad introduced to Timor, however, is a member of the *Duttaphrynus melanostictus* (Schneider, 1799 in Schneider 1798–1801) complex (*sensu* Wogan *et al*. 2016), colloquially known simply as the Asian toad. This is an abundant anuran widely distributed throughout subtropical and tropical Asia, which was introduced to several localities outside its natural range, including the Maldives (Gardiner 1906), Bali (Church 1960), and Western New Guinea (Menzies & Tapilatu 2000). Aside from Timor, the Asian toad was recently introduced to Madagascar, and concerns that the taxon could have a negative impact on the native, largely endemic biodiversity were raised immediately (Kolby 2014), but, just as for Timor, scientific data that would prove that the toads were a threat were not provided. In chapter 6, I caution against making such simplified assertions and, at the same time, present an observation on a specimen of *Duttaphrynus melanostictus* that consumed a vertebrate species in Timor-Leste. This observation prompted a food spectrum analysis to evaluate the impact of the Asian toad on the local (vertebrate) fauna of Timor-Leste through direct predation. This analysis is based on toad specimens collected in the field during 19 June – 01 July 2013 and deposited in the collection of the Smithsonian Institution, National Museum of Natural History, Washington, D.C., USA (USNM). This study necessitated the development and presentation of an improved incision method in preserved anurans, which is provided alongside the food spectrum analysis. In chapter 6, which largely deals with ecological aspects, I also present a publication on the hitherto unreported reproductive biology of a little known skink species from Timor-Leste.

None of the research studies presented in this thesis would have been possible without the extensive usage of museum specimens. This is especially true for the description and redescription of several species that are so far known only from historic vouchers (see publications in chapter 5). While the synergistic effects of fieldwork and museum collections for biodiversity research are exemplified in chapters 5 and 6, the value of natural history collections is discussed in chapter 7. Based on a case example, the importance of reassessing and safeguarding these sources of biological data is highlighted. Although natural history collections are at the heart of chapter 7, studying vouchers and collections should be understood as an iterative process with strong interactions and feedback towards fieldwork (see General Conclusions).

In summary, the aims of this thesis are to (1) contribute towards a comprehensive inventory of the amphibians and reptiles of Timor-Leste, (2) assess the taxonomy of some challenging Southeast Asian reptile groups (e.g., *Cyrtodactylus fumosus*, *Cylindrophis ruffus*) by applying traditional methods of herpetological investigations when more modern analyses are unavailable or inappropriate, (3) provide ecological data and thereby create an opportunity to evaluate threats for the described fauna, and (4) demonstrate why natural history collections are, and will always remain, relevant for biodiversity research. The results are presented in four parts (chapters 4–7), all of which contain independent introductions and conclusions. All publications within the respective chapters have been published individually in peer-reviewed journals unless indicated otherwise.

4 The Herpetofauna of Timor-Leste (Fieldwork)

Cover page of *Asian Herpetological Research*, **6**(2) featuring *Cylindrophis boulengeri* Roux, 1911 and illustrating the work published in O'Shea *et al*. (2015): Herpetological Diversity of Timor-Leste: Updates and a Review of Species Distributions (paper 1, this chapter).

4.1 Introduction

The diversity and composition of the amphibian and reptile fauna of Timor-Leste is becoming better known (e.g., Kaiser, H. *et al*. 2009, 2010, 2011a; O'Shea *et al*. 2012; Sanchez *et al*. 2012; Kathriner *et al*. 2014). However, the geographic distribution and taxonomy of many herpetofaunal species, especially from the mountainous areas in central Timor-Leste and Timor-Leste's offshore islands (Jaco Island and Ataúro Island) are still largely unknown and in need of documentation. Mainland Timor-Leste's stratigraphy is diverse, including several distinctive, monolithic limestone formations (e.g., the Paitxau Mountains; Kaiser, H. *et al*. 2011a). Jaco Island (land area approx. 11 km^2) is located at the easternmost tip of this limestone landmass, separated by a narrow (< 1 km) and deep channel with fast-flowing currents (McCoy 2002). Ataúro (land area 141 km^2) is located 26 km north of Timor-Leste's capital Dili (McCoy 2002), and, although politically part of Timor-Leste, this island is geographically part of the Inner Banda Arc (e.g., Audley-Charles 1986; Monk *et al*. 1997; Kaiser, H. *et al*. 2011a). This arc is basically a volcanic extension of western Sumatra and Java (Michaux 1991). In contrast, the Outer Banda Arc, which includes Timor and Jaco Islands, is non-volcanic (Audley-Charles & Milsom 1974; Carter *et al*. 1976; Bowin *et al*. 1980; Monk *et al*. 1997) and dominated by sedimentary rocks, such as upraised limestone (e.g., Fortuin *et al*. 1997; Audley-Charles 2011; see Fig. 1 in paper 1, this chapter).

Timor-Leste can roughly be divided into the following major vegetation zones (Monk *et al*. 1997; see also Trainor *et al*. 2007 for a more detailed account): thorn forest (primarily along the dry coastal areas of the north), dry deciduous forest (in lower altitude habitats up to ~ 500 m), moist deciduous forest (especially on slopes), and evergreen rainforest (in a few pristine montane areas above 1,000 m). Secondary vegetation, including plantations, is found all across mainland Timor-Leste and Ataúro, but is especially dominant in the lowlands and along the coastline (see GEF Country Portfolio Study 2013: p. 14, for studies and data on loss of primary forest cover in Timor-Leste). Land areas around the beaches are often covered by a mosaic of tourist resorts and rural plots (pers. obs.). Jaco is a relatively flat, corallogenic island and also covered with tropical dry forest. In contrast to Timor and Ataúro, it has no permanent human population (Palmer & Do Amaral de Carvalho 2008).

Seven amphibian and ~ 35 reptile species were recently reported from mainland Timor-Leste (Kaiser, H. *et al*. 2011a; Sanchez *et al*. 2012; O'Shea *et al*. 2012), where 22 localities had been surveyed during 2009–2010. Further fieldwork in Timor-Leste during the years 2010–2013 was conducted in mainland Timor-Leste and – for the first time – on Jaco and Ataúro Islands. These surveys occurred both during the wet and dry seasons, with collections made during day and evening times. In mainland Timor-Leste, 21 new localities were sampled. Jaco was visited once during this period, and Ataúro twice, with 11 localities surveyed. Results of these surveys increased the number of amphibian and reptile species known to occur in Timor-Leste to > 60, including > 20 candidate species. More than ten reptile species but no amphibians were documented on Ataúro, an island with no permanent surface fresh water resources (Noske 1997; Trainor & Soares 2004).

In this chapter the results of the 2010–2013 surveys are presented in two publications. The first publication is an update of the herpetological diversity of Timor-Leste with a review of species distributions. Results of the survey to Jaco Island are included in this paper. The second publication is a first report of the herpetofauna of Ataúro Island. Both reports must be considered preliminary, since survey work is continuing, and revisions, including species descriptions, are in preparation (Kaiser *et al*. in prep.; Mecke *et al*., in prep.).

4.2 Paper 1

O’Shea, M., Sanchez, C., Kathriner, A., **Mecke, S.**, Carvalho, V.L., Ribeiro, A.V., Soares, Z.A., De Araujo, L.L. & Kaiser, H. (2015): Herpetological Diversity of Timor-Leste: Updates and a Review of Species Distribution. *Asian Herpetological Research*, **6**(2): 73–131.

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ORIGINAL ARTICLE

Herpetological Diversity of Timor-Leste: Updates and a Review of Species Distributions

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Abstract We report the results of five herpetological surveys during 2011–2013 that included visits to all districts of Timor-Leste (Aileu, Ainaro, Baucau, Bobonaro, Dili, Covalima, Ermera, Lautém, Liquiça, Manatuto, Manufahi, Viqueque) except the Oecusse exclave. Our fieldwork culminated in the discovery of one putative new frog species (genus *Kaloula*), at least five putative new lizard species (genera *Cyrtodactylus*, *Cryptoblepharus*, and *Sphenomorphus*), and two putative new snake species (genera *Stegonotus* and *Indotyphlops*). In addition, we present new distribution records of amphibians and reptiles for 11 of the country's 12 contiguous districts, along with additional natural history data. Results from our surveys increase the number of amphibian and reptiles known to occur in Timor-Leste from 22 species before our surveys began to over 60, including over 20 as yet undescribed species.

Keywords Timor-Leste, *Kaloula*, *Cyrtodactylus*, *Eremiascincus*, *Stegonotus*

1. Introduction

Timor-Leste (Figure 1) comprises four separate land areas, (1) the eastern half of Timor Island in the Outer Banda Arc of the Lesser Sunda Archipelago, with an area of approximately 14,480 km^2; (2) the small (12 km^2) uninhabited Jaco Island, a landmass of corallogenic origin lying ca. 750 m off the coast of Timor's easternmost point; (3) the much larger (105 km^2) inhabited Ataúro Island, a volcanogenic island geographically positioned in the Inner Banda Arc and situated ~25 km north of mainland Timor-Leste's northern coast at the capital city Dili; and (4) the Oecusse District, an exclave (810 km^2) on the northern coast of Timor, 53 km air-line distance west of contiguous Timor-Leste and surrounded on all landward sides by Indonesian West Timor. Timor-Leste's position at the southeastern edge of Wallacea makes the country an interesting area from a biogeographical perspective, as it is inhabited by a mosaic of faunal elements with either Southeast Asian or Australo-Papuan origin (see Monk *et al.*, 1997). Due to its turbulent history as the Portuguese colony farthest from the mother country (nominally since 1515; West, 2009) and because of a

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violent annexation by Indonesia between 1975 and 1999, the area could not be properly surveyed until after Timor-Leste regained independence in 2002. A summary of the geography, geology, and habitats of Timor-Leste and a history of herpetological collecting in the country since the early 19th Century, was presented by Trainor (2010) and Kaiser *et al*. (2011).

Timor-Leste is a country with very diverse habitats (Figure 2), ranging from beaches and rocky shores (Figure 2A) to montane meadows and mountains (e.g., Figure 2E). Much of the habitat has been altered by the presence of humans to a greater or lesser degree, ranging from active agricultural sites (e.g., Figure 2C) to patches of old-growth forest used by livestock (e.g., Figure 2D). The most pristine habitats include those demarcated by precipitous slopes (e.g., Figure 2E) or periodically inundated areas (e.g., Figure 2F), as well as those of particular cultural or religious significance where human alterations are prohibited (e.g., Figure 2G, H; pers. obs.). As we reported previously (Kaiser *et al*., 2011), it appears that the herpetofauna of Timor-Leste has shown some resilience to disturbance, and species diversity may be high locally despite low-level human disturbance, and even after the dramatic shift from primary tropical forest to coffee forest.

Beginning with an initial survey in 2009, we have been conducting fieldwork in all 13 districts of Timor-Leste under the banner of the Victor Valley College Tropical Research Initiative. The present report on the field seasons of 2011–2013, with the addition of some more limited surveys conducted by AVR, LLA, and ZAS, supplements our reports for 2009 (Kaiser *et al*., 2011) and 2010 (O’Shea *et al*., 2012). Reports for the politically and geographically isolated Oecusse District (Sanchez *et al*., 2012) and Ataúro Island (Kaiser *et al*., 2013b) have been published elsewhere.

2. Methods

Surveys were conducted during both the wet season (Phase IV: 18 January–6 February 2011; Phase VI: 24 January–7 February 2012) and the dry season (Phase V:

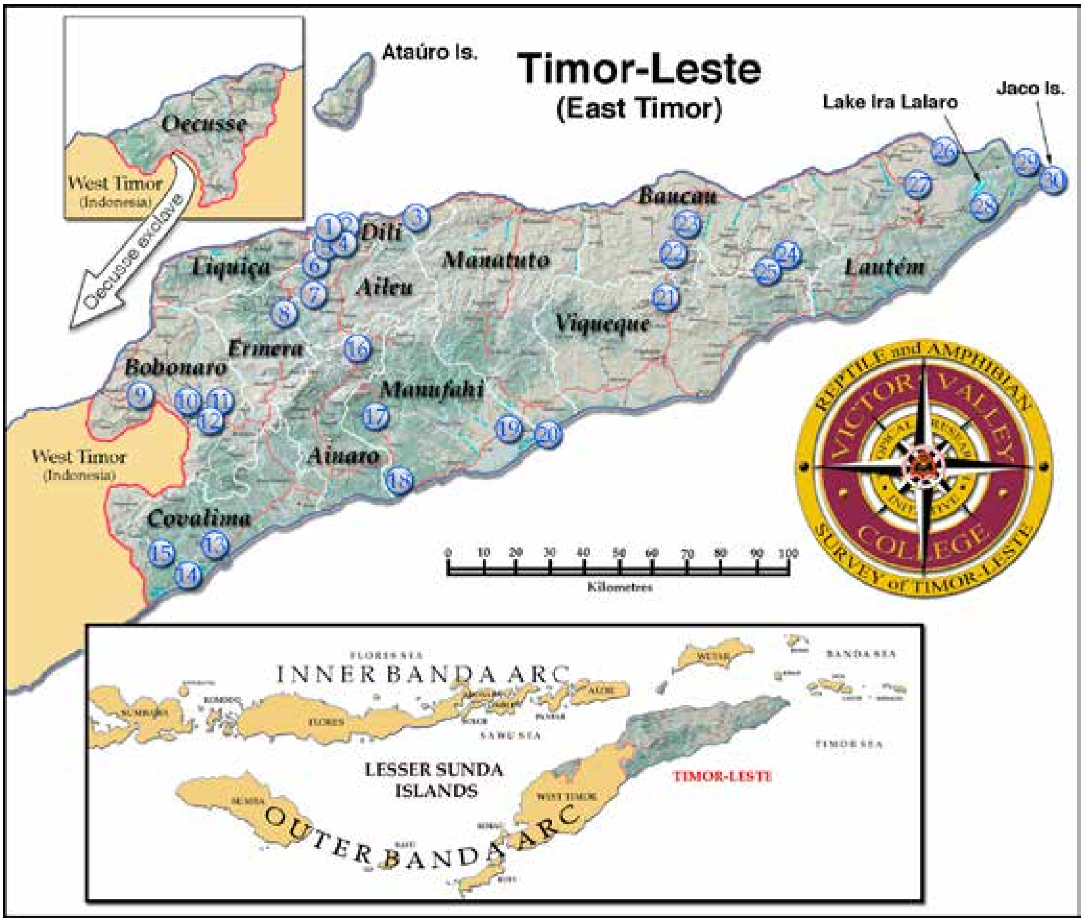

Figure 1 Map of Timor-Leste and its position in the Lesser Sunda Islands. Numbered localities are listed in Table 1.

19 June–5 July 2011; Phase VII: 21 June–10 July 2012; Phase VIII: 18 June–2 July 2013). Shorter wet season surveys were also conducted by ZAS, LLA, and AVR (11–14 October 2010, 10–12 November 2010, and 7 January 2011, respectively). During 2011–2013, fieldwork was carried out at 35 main localities (Table 1) with smaller sub-localities clustered around some of these. The general methods applied during fieldwork, the preparation of voucher specimens, and any associated scientific tasks, follow the protocols detailed by Kaiser *et al.* (2011). Most roadkills, depending on their state of decomposition, were skin- or scale-snipped to obtain tissue samples for molecular studies. All vouchered specimens have been deposited in the United States National

Table 1 List of localities surveyed by the Victor Valley College Herpetofaunal Survey of Timor-Leste during Phases IV–VIII (2011–2013). Each locality includes a superscripted Roman numeral to indicate during which phase they were surveyed (locations only visited during Phases I–III, on Ataúro Island, or in the Oecusse exclave are omitted (for these locations see Kaiser *et al.*, 2011, 2012; O'Shea *et al.*, 2012; Sanchez *et al.*, 2012).

Locality Number	District	Locality	Elevation (m)	GPS coordinates[1]
$1^{\text{I–VIII}}$	Dili	W Dili (Timor Lodge Hotel; Comoro; Tasi Tolu)	2–25	S 08°33' E 125°31'
2^{IV}	Dili	E Dili (Becora; Cristo Rei)	20	S 08°33' E 125°35'
$3^{\text{V–VI, VIII}}$	Dili	Metinaro mangrove swamp	1	S 08°31' E 125°47'
4^{VI}	Dili	S Dili (Dare)	545	S 08°36' E 125°32'
$5^{\text{III–IV}}$	Dili	Comoro River (Beduku)	60	S 08°35' E 125°32'
$6^{\text{V, VIII}}$	Dili, Liquiça, Aileu	Comoro River (confluence with Bemos River)[2]	115	S 08°37' E 125°32'
7^{VI}	Aileu	Lake Be Matin	1105	S 08°42' E 125°32'
$8^{\text{I–II, V–VII}}$	Ermera	Eraulo (Meleotegi River; Sta. Bakhita Mission)	1100–1250	S 08°47' E 125°27'
9^{VII}	Bobonaro	Balibo (Fiuren)	463	S 08°57' E 125°04'
10^{V}	Bobonaro	W Maliana (Ramaskora; Soto River)	196–230	S 08°59' E 125°12'
11^{VII}	Bobonaro	E Maliana (Maganuto, Mt. Leolaco)	1040–1063	S 08°59' E 125°16'
12^{V}	Bobonaro	E Maliana (Galosapulu swamp)	712	S 09°01' E 125°16'
$13^{\text{I, IV}}$	Covalima	Suai & surrounds (Castelo Fronteira Guest House)	30–53	S 09°19' E 125°15'
14^{IV}	Covalima	Kasabauk rice-paddies	9	S 09°24' E 125°09'
15^{IV}	Covalima	Tilomar (Tilomar Forest Reserve; Maubesi; Mt. Debululik)	260–900	S 09°20' E 125°06'
$16^{\text{I, IV}}$	Ainaro	Maubisse (Pousada Maubisse)	1495	S 08°50' E 125°36'
$17^{\text{I, IV}}$	Manufahi	Same (Ailelehun Guest House; Trilolo River; Ladiki; Mirbuti)	340–1200	S 09°00' E 125°39'
$18^{\text{IV–V}}$	Manufahi	Betano (Dry site; Wet site)	20–44	S 09°10' E 125°42'
$19^{\text{IV, VII}}$	Manufahi	Fatucahi (Convent of St Antony d'Lisboa; Lake Lenas)	36–38	S 09°02' E 125°59'
$20^{\text{IV, VII}}$	Manatuto	Nancuro, Natarbora, S Umaboco	3	S 09°02' E 126°04'
21^{VII}	Viqueque	N Ossa (Liamida; Mt. Mundo Perdido)	930–1160	S 08°44' E 126°22'
22^{VII}	Baucau	Venilale caves, N Venilale	675	S 08°37' E 126°23'
23^{VII}	Baucau	Uatubala, S. Afacaimau (*Carlia* spot)	370	S 08°33' E 126°26'
24^{VII}	Baucau	Baguia (Vila Rabilhi Guest House; Pousada de Baguia)	440	S 08°38' E 126°39'
25^{VII}	Baucau	Ossohuna (Ossohuna; Afaloicai)	938	S 08°41' E 126°37'
$26^{\text{V, VIII}}$	Lautém	Com (Com Beach Resort; Com wharf; Pousada de Com)	2–15	S 08°21' E 127°03'
$27^{\text{V, VIII}}$	Lautém	Raça caves & surrounds	400–553	S 08°26' E 126°59'
28^{V}	Lautém	Tutuala (Pousada de Tutuala)	373	S 08°24' E 127°15'
29^{V}	Lautém	Malahara (Mainina sinkhole; Lake Ira Lalaro)	336–424	S 08°29' E 127°11'
30^{V}	Lautém	Jaco Island	10–40	S 08°25' E 127°19'

[1] GPS coordinates are approximate to define the area in which the survey work was carried out. Exact localities are not provided to protect some of the unique and fragile habitats in Timor-Leste.

[2] The confluence of the Comoro and Bemos Rivers marks the border between Dili, Liquiça and Aileu Districts, with specimens collected on both banks in Liquiça and Aileu Districts.

Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM). Those specimens not yet accessioned have field tags of the USNM (USNM-FS). Photographs of road-killed specimens, CITES-protected species, and other unvouchered specimens have been deposited in the herpetological image collection of the USNM and are listed here with herpetological image numbers (accessioned as USNM-HI). Museum abbreviations are taken from Sabaj Pérez (2014).

In the species accounts, we provide information to aid in field identification of amphibians and reptiles, particularly for taxa not included in one of our earlier

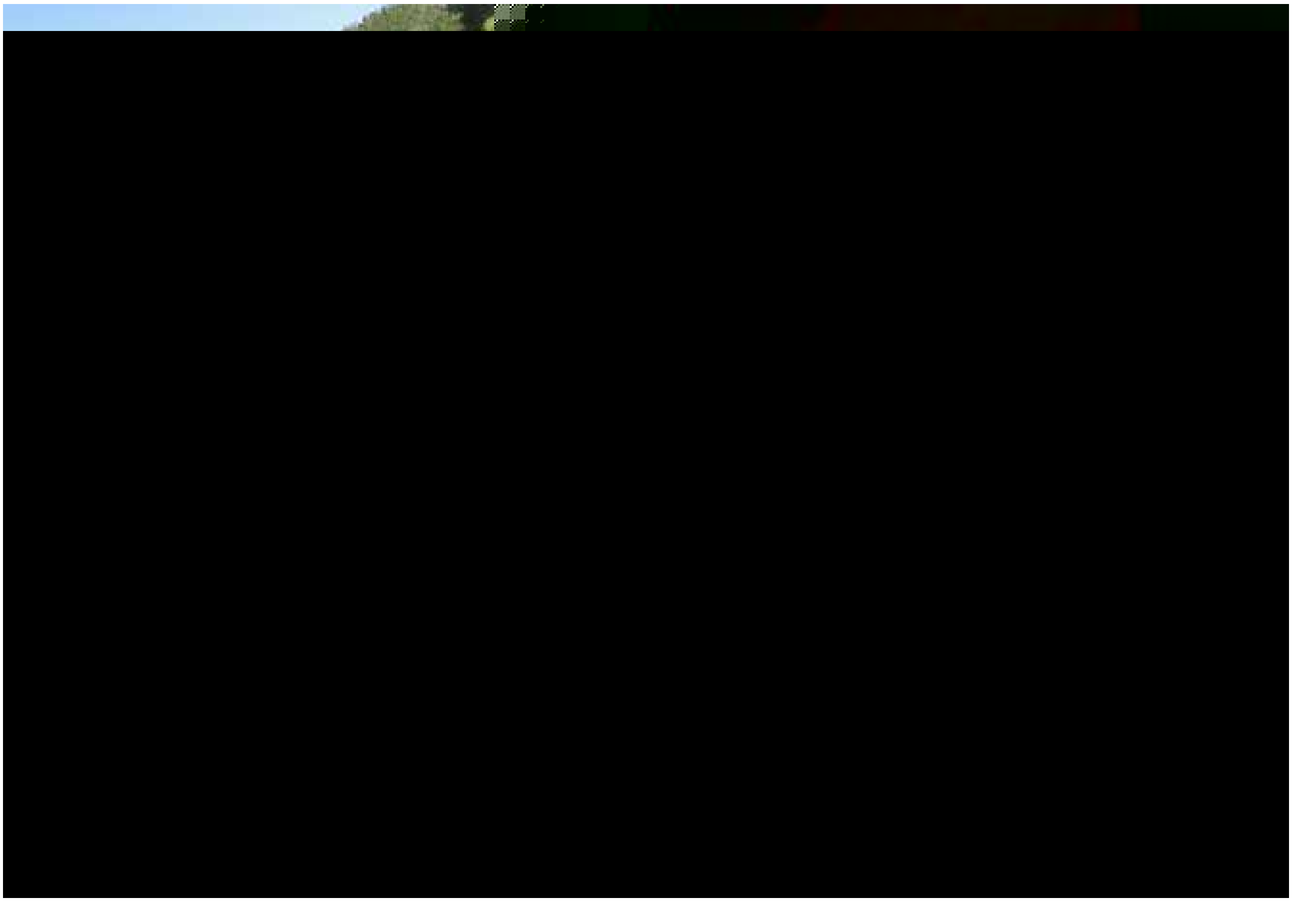

Figure 2 Sample habitat types surveyed in Timor-Leste during 2011–13. Localities are listed numerically (see Table 1). (A) Rocky shore at Cristo Rei Protected Area on the outskirts of Dili (Locality 2). The part of this habitat along the tidal and splash zones is a habitat of *Cryptoblepharus* cf. *schlegelianus* and *Laticauda colubrina*, whereas in the wooded area at higher elevation, sun skinks (*Eutropis* cf. *multifasciata*) and Timor monitors (*Varanus timorensis*) have been observed. (B) Montane habitat at Maganuto (Locality 11). This area has stands of tall bamboo in boulder-strewn areas, intermixed with a grassy meadow and a montane forest on the upper slopes. Whereas we found the forest to be unproductive in our search, the bamboo yielded *Hemidactylus* cf. *garnotii*, and in the grassy meadow we found a *Polypedates* cf. *leucomystax* under a flat rock some distance away from any vegetation. (C) The banana plantation at the confluence of the Bemos and Comoro Rivers (Locality 6; photo taken towards Aileu District) turned out to be an unexpectedly important site at which one of only two recent specimens of *Cylindrophis* cf. *boulengeri* was found. Other species recorded in this area include *Duttaphrynus melanostictus*, *Fejervarya* sp., *Polypedates* cf. *leucomystax*, sun skinks (*Eutropis* cf. *multifasciata*), and house geckos (e.g., *Hemidactylus frenatus*). (D) Disturbed forest at Fiuren (Locality 9). Overtly a nice patch of forest with an expansive growth of large trees, this area is beset by domestic pigs that scour the leaf litter and the root matter for food. We located *P.* cf. *leucomystax* and several gecko taxa (*Cyrtodactylus*, *Gekko*, *Gehyra*, *Hemidactylus*) in this area. (E) View of the mountains above our survey area near Baguia (Locality 25). A promising habitat with extreme topography, this is the only area in Timor-Leste where we have found individuals of *Hemiphyllodactylus* cf. *typus*. (F) The Mainina sinkhole (Locality 29) in Nino Konis Santana National Park. This locality is the only outflow of Lake Ira Lalaro, the largest lake in Timor-Leste. The area is seasonally inaccessible due to variations in the lake's water level, and it lies right at the foot of the steep-sided Paitxau Mountains karst formation. (G) The road passing through tropical wet forest in the Nancuro Protected Area (Locality 20). On either side of this road is dense, mixed coastal forest that includes some large trees. The ground is partially inundated after rains. This has been a very productive collection locality with a high diversity of herpetofauna, including *Kaloula*, *Cyrtodactylus*, *Sphenomorphus*, *Dendrelaphis*, *Stegonotus*, and *Trimeresurus*. (H) Dry coastal forest on Jaco Island (Locality 30). Even though this corallogenic island appears to be very dry, we have found species that we have more commonly encountered in moist habitats elsewhere in Timor-Leste, including *Cyrtodactylus*, *Eremiascincus*, and *Sphenomorphus*. Photos (A), (C), and (E)–(H) by Hinrich Kaiser, (B) and (D) by Mark O'Shea. (Continued on facing page).

reports (Kaiser *et al.*, 2011, 2013b; O'Shea *et al.*, 2012; Sanchez *et al.*, 2012), comment on new locality records for taxa previously recorded during Phases I–III (2009–2010), provide full accounts for taxa not previously recorded during our surveys, and discuss the natural history of the species and the manner in which they were encountered. The recording or collection of taxa during particular phases is indicated by the phase designation in bracketed superscripted Roman numerals, following taxon names. Thus, a species encountered in Phases IV and VII would carry the superscript [IV, VII].

Common names are provided in English (E), German (G) and the country's lingua franca, Tetun (T). We made a number of decisions with regards to the use or coining of common names in Tetun and the interested reader is referred to O'Shea *et al.* (2012) for a discussion of our arguments. Proposed common names for house geckos incorporate the commonly used Tetun name for small geckos and the scientific name or a descriptive term.

3. Results

Amphibia

Family Bufonidae — True Toads

Duttaphrynus melanostictus (Schneider, 1799) [IV–V, VII–VIII]

Common names. (E) Black-spined Toad, Common Asian Toad. (G) Schwarznarbenkröte. (T) Manduku Interfet (manduku = frog, INTERFET = International Force for East Timor).

Known distribution. *Duttaphrynus melanostictus* (Figure 3) has heretofore been reported from nine of Timor-Leste's 13 districts (Table 2): Aileu, Bobonaro, Covalima,

Figure 2 Continued.

Table 2 Amphibian records for the districts of Timor-Leste. Black dots indicate previously known records, red dots denote new records.

Taxon	District														References[*]
	Aileu	Ainaro	Baucau	Bobonaro	Covalima	Dili (Timor)	Dili (Ataúro)	Ermera	Lautém	Liquiça	Manatuto	Manufahi	Oecusse	Viqueque	
BUFONIDAE															
Duttaphrynus melanostictus	●		🔴	●	●	●		●		●	🔴	●	●	●	1–5
DICROGLOSSIDAE															
Fejervarya spp.	🔴		●	🔴	🔴	●		●	●	🔴	🔴	●	●	●	2–4
Limnonectes timorensis			🔴					●							2,5
HYLIDAE															
Litoria everetti								●							2,6
MICROHYLIDAE															
Kaloula sp.											🔴	🔴			5
RHACOPHORIDAE															
Polypedates cf. *leucomystax*		●	●	🔴	🔴	●		●	●	🔴	🔴	●	●	●	2–5

[*] References are identified numerically as follows: 1 = Trainor, 2009; 2 = Kaiser *et al*., 2011; 3 = O'Shea *et al*., 2012; 4 = Sanchez *et al*., 2012; 5 = this paper; 6 = Menzies, 2006.

Dili, Ermera, Liquiça, Manufahi, Oecusse, and Viqueque (Kaiser *et al.*, 2011; O'Shea *et al.*, 2012; Sanchez *et al.*, 2012; Trainor, 2009).

New localities. We collected additional specimens from the Comoro River valley (Localities 5 and 6; Table 1), which included a series of tadpoles from the confluence of the Comoro and Bemos Rivers, which occurs at the boundaries of Aileu, Dili, and Liquiça Districts. Tadpoles were captured in riverine kolks, where back eddies create a respite from rushing water, on the Aileu side (Locality 6). An adult was captured at Beduku Aldeia (Dili District; Locality 5). We vouchered single specimens from the Soto River (Bobonaro District; Locality 10) and the Franciscan Convent of St. Antony d'Lisboa (Manufahi District; Locality 19), and took voucher photographs for four other localities where we recorded this species: Sta. Bakhita Mission (Eraulo, Ermera District; Locality 8); Nancuro coastal forest (Natarbora, Manatuto District; Locality 20), Ossu (Baucau District; USNM-HI 2823), and Liamida (Viqueque District; Locality 21). The Manatuto and Baucau records constitute new district records and bring to a total of 11 (Table 2) the number of mainland districts that have been colonized by *D. melanostictus* since its arrival less than a decade ago. Based on our observations, the species has so far (mid-2013) not expanded into Lautém District, the country's easternmost and the site of Nino Konis Santana National Park, and it has not yet been documented from Ainaro District.

Natural history. This is an introduced species that is believed to have arrived in Timor-Leste with INTERFET peacekeeping troops. The first reports appear to have come from Oecusse District in 1999, a date that coincides with the arrival of South Korean INTERFET peacekeepers. From there the toad appears to have gradually spread eastwards, arriving in Dili District in 2007 (Trainor, 2009). We recorded it further southeast at Same (Manufahi District) in 2009 (Kaiser *et al.*, 2011), concurring with Trainor (2009), who also recorded it in the area during the same year, and on the south coast at Uma Boot (Viqueque District) in 2010 (O'Shea *et al.*, 2012).

Sanchez *et al.* (2012) reported this species from the Oecusse exclave. Our surveys so far have not revealed the presence of *D. melanostictus* or any other amphibian species on Ataúro Island (Kaiser *et al.*, 2013b). During 2011 and 2012 we were able to report a much wider range for the black-spined toad, across the contiguous districts of mainland Timor-Leste, from Bobonaro (Locality 10), in the extreme west near the border with West Timor, to Ossu Subdistrict of Viqueque District (Locality 21) in the east. We have now recorded *D. melanostictus* from nine of the 12 contiguous districts, plus Oecusse, from sea level to elevations of 930 m (Liamida, Viqueque District; Locality 21) and 1225 m (Sta. Bakhita Mission, Ermera District; Locality 8), in habitats ranging from anthropogenic (roadways, convent grounds) to coastal forests, rocky river beds, and upland boulder-strewn grasslands. Based on our observations this introduced toad species favors anthropogenically-modified habitats, where it can be found in great numbers; it appears to be absent in pristine habitats. In drainage ditches and rice paddies, *D. melanostictus* is frequently found in sympatry with frogs of the genus *Fejervarya*.

Our vouchers include adult toads and a series of tadpoles (USNM 581259–63) collected from muddy rivulets and pools alongside the Comoro riverbed. *Duttaphrynus melanostictus* was also found to be very common in the grounds of the Franciscan Convent of St. Antony d'Lisboa, Fatucahi (Manufahi District; Locality 19) but we vouchered only a single specimen (USNM 565895) that had predated and begun to pass a blindsnake (*Indotyphlops braminus*; O'Shea *et al.*, 2013). Another specimen was found sitting atop the 2.0 m stone convent wall, demonstrating the climbing ability of these terrestrial bufonids.

Although we initially did not collect voucher specimens of this non-Timorese amphibian, in our efforts to monitor its effects on native taxa, we collected 87 specimens in several districts in 2013 to be able to carry out a gut content analysis to study the diet of this exotic (Döring *et al.*, in prep.). Our most recent observations continue to confirm the absence from Timor-Leste of the much larger and elsewhere harmful cane toad (*Rhinella marina*), with which *D. melanostictus* has been confused by Timorese and expatriates alike.

Family Dicroglossidae — Fork-tongued Frogs

Genus *Fejervarya* [IV–VIII]

Common names. (E) Rice Paddy Frogs. (G) Reisfrösche. (T) Manduku natar (manduku = frog, natar = rice paddy).

Known distribution. Frogs of the genus *Fejervarya* (Figure 4) have been reported from seven of Timor-Leste's 13 districts (Table 2): Baucau, Dili, Ermera, Lautém, Manufahi, Oecusse, and Viqueque (Kaiser *et al.*, 2011; O'Shea *et al.*, 2012; Sanchez *et al.*, 2012).

New localities. For 2011, we report additional voucher specimens from the localities at the confluence of the Comoro and Bemos Rivers (see *D. melanostictus* account), from the Aileu bank (Locality 6). We also added vouchers from a roadside marsh at the junction of the Com–Bauro road with the North Coast Road (Com, Lautém District; Locality 26), and from the southern shore of Lake Ira Lalaro (Malahara village, Lautém District; Locality 28). We also provide the first records of *Fejervarya* spp. from southern Timor-Leste, namely for Manatuto District, from coastal forest (Locality 20); for Manufahi District from the grounds of the Franciscan Convent of St. Antony d'Lisboa and the southern shore of Lake Lenas (both near Fatucahi; Locality 19); and for Covalima District from the grounds of the Castelo Fronteira Guest House (Suai town; Locality 13) and the extensive rice-paddies at Kasabauk (Locality 14). The Aileu, Manatuto, and Covalima specimens represent new district records (Table 2). ZAS also provided our first records for Bobonaro District with vouchers from the Soto River and Ramaskora (Locality 10), and a single voucher from the Galosapulu swamp (Locality 12).

In 2012 we obtained additional vouchers from west of Dili town (Timor Lodge Hotel grounds, Dili District; Locality 1) and the Meleotegi River (Ermera District; Locality 8), and made collections in two new localities: Lake Be Matin (Aileu District; Locality 7), and the Afaloicai and Ossohuna rice paddies (Baucau District; Locality 25). *Fejervarya* spp. have now been reported from 11 of the 12 contiguous mainland districts in addition to Oecusse (Sanchez *et al.*, 2012), but they have not been recorded from Ainaro District; based on the limited environments suitable for *Fejervarya*, we do not anticipate their presence on Ataúro Island (Kaiser *et al.*, 2011; 2013b).

Natural history. Recorded widely on all previous phases, our additional collection confirms that rice-paddy frogs occupy a much broader variety of habitats than their common name indicates. Along the mostly dry Comoro riverbed (Locality 6), an adult (USNM 579397) was found under a rock right at the edge of the narrow flow, whereas a tadpole (USNM 581584) was collected from a nearby shallow pool shared with tadpoles of *Duttaphrynus melanostictus*. Near this locality, we observed a wolf spider (family Lycosidae) that appeared to follow the movements of *Fejervarya* tadpoles grazing near the surface (Figure 5), and we consider it likely that these spiders take tadpoles as prey. Lycosid spiders have already been documented as hunting in this way (Jara and Perotti, 2004).

Specimens were also vouchered from the Soto River (Locality 10; USNM 579287–92) and Meleotegi River (Locality 8; USNM 579710, 580466) during both the wet and the dry seasons. A population of rice paddy frogs from far-eastern Timor-Leste (Locality 26) was initially located based on their vocalizations along the edge of the road, where a leaking water pipe had created puddles. This population (USNM 579398–401) extended into a marshy area next to the road. In Bobonaro District, a single specimen was collected in a swamp at 712 m

Figure 3 *Duttaphrynus melanostictus* found in a streamside refugium along the Comoro River (Locality 1). This specimen was not vouchered. Photo by Mark O'Shea.

Figure 4 A female rice-paddy frog (genus *Fejervarya*) from active, inundated rice paddies near Baguia (Locality 25; USNM 580467). Photo by Mark O'Shea.

elevation (Locality 12; USNM 279297). Near Malahara village (Lautém District; Locality 28) several individuals were seen in the marshy area along the edge of Lake Ira Lalaro, and a single specimen was vouchered (USNM 579402).

Our south coast records for a *Fejervarya* species come from pristine wet coastal forest (Locality 20; USNM 579279); grassy areas of a residential compound (Locality 19; USNM 579276–77); the grassy edge of a small lake (Locality 19; USNM 579278); and an ornamental fountain in a residential compound (Locality 13; USNM 579280–81), where they occurred in the company of a large number of tadpoles (USNM 581264–77). As expected, *Fejervarya* were found to be especially common in rice paddy habitats, from near sea level at Kasabauk (9 m, Locality 14; USNM 759284–86) and medium elevations (e.g., 229 m at Ramaskora; Locality 10; USNM 279293–96) to higher elevations (e.g., 775 m at Afaloicai and Ossohuna (Locality 25; USNM 580468–72, 581287–93), and over 1105 m at Lake Be Matin (Locality 7; USNM 579706–09). Individuals were also encountered crossing or occupying rain puddles on the road (e.g., at Baucau District, between Localities 24 and 25; USNM 580467).

As during previous phases we found rice-paddy frogs to be extremely abundant where they occurred, and although numerous specimens were initially collected, only a few were selected as vouchers. The physiological plasticity of these species and their adaptability to anthropogenic habitats is discussed elsewhere (Kaiser *et al.*, 2011; O'Shea *et al.*, 2012) and will not be expanded upon further here.

***Limnonectes timorensis* (Smith, 1927)** [V, VII]

Common names. (E) Timor River Frog. (G) Timorfrosch (T) Manduku mota (manduku = frog, mota = river).

Known distribution. *Limnonectes timorensis* (Figure 6A) has heretofore been reported from only a single locality in Ermera District (Table 2; see Kaiser *et al.*, 2011)

Figure 5 Tadpole of *Fejervarya* sp. (arrow) with its potential predator, a wolf spider. The spider was observed in close proximity to tadpoles along a slow-flowing side arm of the Comoro River (Locality 1). Photo by Hinrich Kaiser.

New localities. Additional specimens were collected at the Meleotegi River location (Locality 8) during the dry seasons of 2011 and 2012, and a single voucher was obtained from the Afaloicai rice paddies near Baguia (Baucau District; Locality 24). This single voucher is a juvenile and its location at Afaloicai is over 130 km E of the Meleotegi River.

Natural history. Previously we had encountered this frog only along the Meleotegi River (near the Sta. Bakhita Mission (Eraulo, Ermera District; Locality 8), with only two vouchers collected during the dry season of 2009. During the dry season of 2011 we again encountered *L. timorensis* along the Meleotegi River, where several males (e.g., USNM 579403–07) were discovered sheltering under rocks at the water's edge. Two of these specimens (USNM 579404, 579407) contained parasitic cestodes (Platyhelminthes: Cestoda) in their leg muscles (Figure 6C, D), which likely constitute another host record for spargana (Goldberg *et al.*, 2010). A return to the same location, at the same time of year, in 2012 produced a series of nine tadpoles (Figure 6B) collected from a rock pool on a large mid-stream rock (USNM 581278–86). The tadpoles were euthanized and photographed at sequential stages of development over the following ten days.

All specimens of *L. timorensis* collected at the Meleotegi River (elev. 1175–1185 m) were found in close association with the river, albeit in the dry season, on rocks along its periphery. The single juvenile collected at Afaloicai, near the Baucau-Viqueque boundary at an elevation of 775 m (USNM 580371) was taken at night in the grass surrounding a rice-paddy.

Taxonomic comment. The generic status of some of the frogs in the genus *Limnonectes* is being re-evaluated, and it appears that both molecular evidence and some morphological characteristics align the Timor population with ranids in the genus *Hylarana* (Che *et al.*, 2007; Kaiser *et al.*, 2014). If this generic concept is confirmed, this species should be assigned to the genus *Hylarana* and transferred to the Ranidae.

Family Hylidae — Treefrogs

Litoria everetti (Boulenger, 1897) [V]

Common names. (E) Everett's Timor Treefrog. (G) Everett-Laubfrosch. (T) Manduku ai Timor (manduku = frog, ai = tree).

Known distribution. *Litoria everetti* (Figure 7) is reported from a single locality in Ermera District (Table 2; see Kaiser *et al.*, 2011).

New localities. None, but an additional specimen was collected at the known locality.

Natural history. As with *Limnonectes timorensis* (see above), our previous encounters with this frog were in 2009, only on the Meleotegi River (Ermera District;

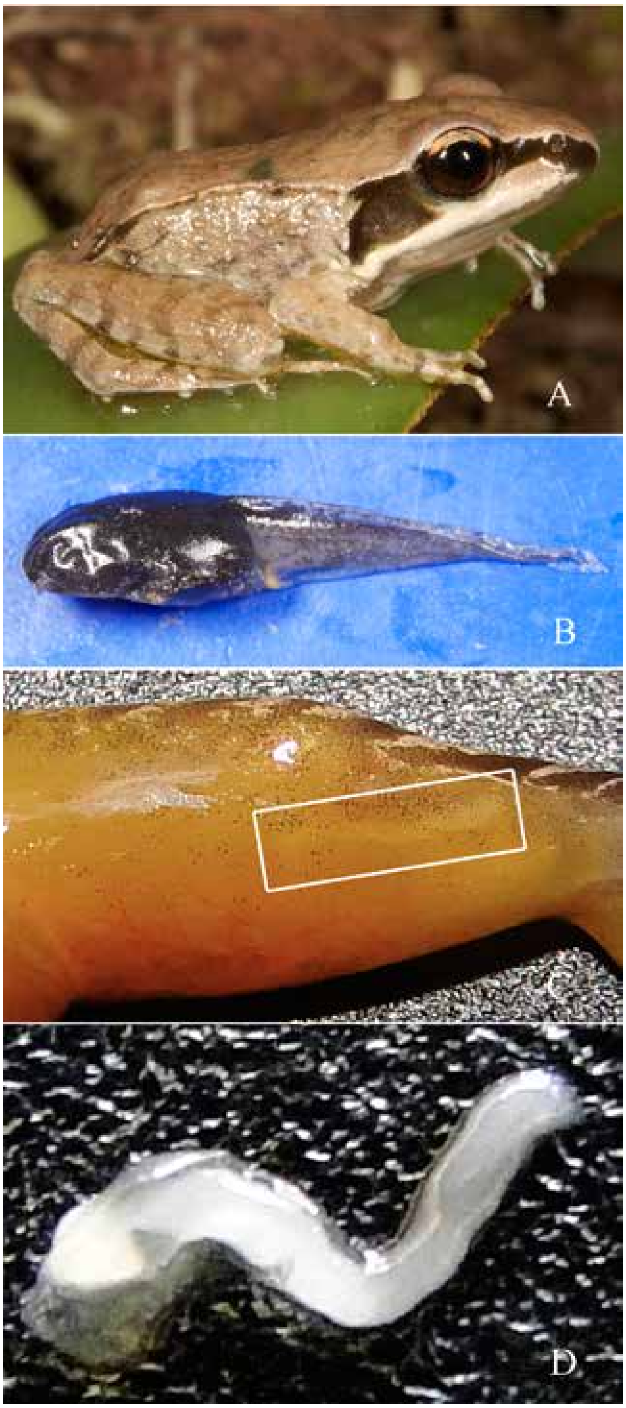

Figure 6 (A) Juvenile *Limnonectes timorensis* from a grassy patch at Afaloicai (USNM 580473, Locality 25). (B) Tadpole of *L. timorensis* from the Meleotegi River (USNM 581286; Locality 8). (C) Upper leg of an adult *L. timorensis* from the Meleotegi River (USNM 579404, Locality 8), showing an embedded parasite (box). (D) Tapeworm extracted from the animal in (C), presumably a sparganum that is part of the host-parasite interaction described by Goldberg *et al.* (2010). Photos (A) and (B) by Mark O'Shea, (C) and (D) by Hinrich Kaiser.

Locality 8), when we collected two specimens. During 2011 we collected a third specimen (USNM 579408) at the same location. This specimen was discovered underneath a rock on a small rocky island in midstream, and it attempted to escape by jumping into the flowing water. After this initial escape attempt, it remained motionless on the bottom of a slow-flowing portion of the river, where it was easily captured.

Family Microhylidae — Narrow-mouthed Toads

Kaloula sp. [IV, VII]

Common names. (E) Timor Pumpkin Bullfrog. (G) Timor-Ochsenfrosch. (T) Manduku lakeru (manduku = frog, lakeru = pumpkin).

Identification. *Kaloula* sp. is a small rotund frog with a blunt head and highly tuberculate dorsum (Figure 8A). The limbs are short, the toes unwebbed. Coloration consists of a mixture of olive green and light brown blotches. The only Timorese frogs with which this species could be confused are Asian black-spined toads (*Duttaphrynus melanostictus*), from which it can be separated by its smaller size, longer fingers and toes, discrete tympanum, the lack of cranial crests, parotoid glands, and black tipped tubercles.

Known distribution. There are no previous reports of this species from Timor Island or Timor-Leste.

New localities. Specimens collected in 2011, in southern Manufahi District (within the grounds of the Franciscan Convent of St. Antony d'Lisboa, Fatucahi; Locality 19) constitute the first records of this species, genus, and family for Timor Island. Two relatively juvenile specimens collected in 2012, in the wet coastal forest at Nancuro (Locality 20) represent the first records of the taxon from Manatuto District. These two localities are only 10 km apart.

Natural history. Within the grounds of the Franciscan Convent of St. Antony d'Lisboa we encountered four species of anurans, three of which (*Duttaphrynus melanostictus*, *Fejervarya* sp., *Polypedates* cf. *leucomystax*) are widespread in Timor-Leste. However, we also collected numerous specimens of *Kaloula* sp. at night in the vegetable gardens, on the rubbish dump, and around the convent wall. One specimen was found on a low tree axil approximately 45 cm from the ground, whereas all others were encountered at ground level, including under rocks together with *D. melanostictus*. A series of ten specimens was vouchered (USNM 579246–55).

The juvenile specimens collected at Nancuro (USNM 580464–65) were found on the forest floor in deep leaf litter. They demonstrated much more vivid markings than the adults from Fatucahi, in the form of a series of black-edged, bright orange flashes across the flanks anterior to the hind limbs, on the inner surfaces of the thighs, and on the proximal portions of the hind limbs (Figure 8B).

Figure 7 Female *Litoria everetti* found underneath a flat rock alongside the Meleotegi River, Ermera District (Locality 8; USNM 579394). Photo by Mark O'Shea.

Figure 8 (A) Adult female *Kaloula* sp. (USNM 579254) from the grounds of the Convent of St. Antony d'Lisboa near Fatucahi, Manufahi District (Locality 19). (B) Juvenile *Kaloula* sp. from wet forest in the Nancuro Protected Area (Locality 20; USNM 580464) showing the characteristic flash colors on the posterior part of the body in juveniles of this form. Photos by Mark O'Shea.

These markings were exposed when the frogs made short hops and presumably constitute aposematic eyespots to deter potential predators, as has been well-documented for frogs of the genus *Physalaemus* (Wells, 2010).

Taxonomic comments. There are no previous records of *Kaloula*, or any microhylid frog, from the island of Timor, but three species of *Kaloula* are reported to occur on other islands in Indonesia. *Kaloula pulchra* Gray, 1831 has been reported from Sumatra, Borneo, Sulawesi, and Flores (Barbour, 1912; Dunn, 1928; Mertens, 1930), and it is unclear whether these populations are native or introduced. The same problem exists for *K. baleata* (Müller, 1833), which occurs on Bali, Borneo, Java, Komodo, Sulawesi, Sumatra, and Sumba (Dunn, 1928; Iskandar, 1998; McKay, 2006); the Western Australian Museum holds specimens from Flores and Lembata (Paul Doughty, *pers. comm*.). A population listed as "*K. albotuberculata*" by Inger and Voris (2001) may represent an endemic taxon found exclusively in central Sulawesi; the listing of this name, based on a manuscript by Djoko Iskandar, has created a *nomen nudum*, which was referred to as "*Kaloula* sp. n." by Koch (2012). *Kaloula baleata*, as currently defined, is certainly a polymorphic taxon that contains at least three species in addition to the recently described *K. indochinensis* Chan *et al*., 2013 and *K. latidisca* Chan *et al*., 2014 (Rafe Brown, *pers. comm*.), and it seems likely that *K. pulchra* is a species complex as well. Specimens from the Lesser Sundas may well have been allocated to these two species without comparison to specimens from the type localities (Java for *K. baleata* and China for *K. pulchra*) and may therefore constitute undescribed species. Detailed examinations by one of us (HK) of the Timor specimens now housed in the USNM leads us to believe that they represent an undescribed species of *Kaloula*. True *K. baleata* and *K. pulchra* may be separated by the degree of toe webbing (webbing reaching the middle subarticular tubercle on the inner edge of the fourth toe in *K. baleata*, but not extending beyond the basal subarticular tubercle in *K. pulchra* (Inger, 1966), but the Timor material does not comply with either arrangement. The detailed morphological and morphometric information provided by Chan *et al*. (2013, 2014) to assist with delineating species boundaries in the *K. baleata* complex provides an excellent opportunity for determining the taxonomic status of the Timor population. On the basis of our discovery, and pending comparative examination of the Timor specimens with other Lesser Sunda and extralimital material of *K. baleata sensu lato*, we assign the specimens from Fatucahi and Nancuro to *Kaloula* sp.

Family Rhacophoridae — Afro-Asian Foam-nest Treefrogs

Polypedates cf. *leucomystax* [IV–VIII]

Common names. (E) Striped Treefrog, Four-lined Treefrog. (G) Weißbart-Ruderfrosch. (T) Manduku ai-riskadu (manduku = frog, ai = tree, riskadu = striped) or manduku loron (manduku = frog, loron = sunlight).

Known distribution. *Polypedates* cf. *leucomystax* (Figure 9) is so far known from eight of Timor-Leste's 13 districts (Table 2): Ainaro, Baucau, Dili, Ermera, Lautém, Manufahi, Oecusse, and Viqueque (Kaiser *et al.*, 2011; O'Shea *et al.*, 2012; Sanchez *et al.*, 2012).

New localities. In 2011 we collected specimens at the confluence of the Comoro and Bemos Rivers, along the Liquiça bank (see *Duttaphrynus melanostictus* account; Locality 6), on the south coast (grounds of the Franciscan Convent of St. Antony d'Lisboa, Fatucahi, Manufahi District; Locality 19), and in the Mt. Debululik area (north of Tilomar, Covalima District; Locality 15). The Liquiça and Covalima specimens represent new district records (Table 2).

Bobonaro specimens were collected by ZAS from all three of his study sites: the Soto River and Ramaskora rice paddies (Locality 10) and the Galosapulu swamp (Locality 12). These are our first records of *Polypedates* from Bobonaro District.

In 2012 we collected two specimens in the grounds of the Timor Lodge Hotel (Comoro, Dili District; Locality 1) and vouchered a series of specimens from near Baguia (Baucau District; Localities 24 and 25), near Balibo (Bobonaro District; Locality 9), and from the south coast in the wet coastal forest at Nancuro (Locality 20), this last record constituting a first record for Manatuto District. The only district without records of *Polypedates* cf. *leucomystax* is Aileu, and despite of our efforts on three collecting trips to Ataúro Island no frog vouchers were collected there (Kaiser *et al.*, 2013b).

Natural history. These treefrogs were found exclusively in microhabitats with some form of water storage capacity, sometimes in unexpected circumstances. For example, specimens found in village gardens along the Comoro River (Dili District; Locality 6; USNM 579395–96) were discovered by peeling back the stem leaves at the bases of banana plants (*Musa* sp.), where runoff water collects. These banana plots had recently undergone an agricultural slash-and-burn, yet several of the banana plant stems were found to harbor treefrogs. Striped treefrogs were also seen in the freshly mown grassy vegetation of the grounds of the Franciscan Convent (USNM 579256–62), where moisture is retained well and where disturbed insects provide abundant food. Treefrogs were also fairly abundant near upland rice paddies at Ossohuna and Afaloicai (Baucau District; Locality 25; USNM 580453) at an elevation of 712 m. Another of our highest-elevation specimens (elev. 706 m; USNM 579263) came from a rock pile in the Mt. Debululik area (Covalima District; Locality 15), while specimen found on the ground in bamboo litter at Ossohuna (Baucau District; Locality 25; USNM 580452) occurred at 938 m. The highest elevation recorded for *P.* cf. *leucomystax* was 1074 m for a specimen curiously found under a rock on an exposed step-cultivated grassy hillside above Maganuto village, almost midway between, but still a considerable distance from, a large stand of bamboo and a stunted elfin forest growing in the shadow of Mt. Leolaco, Bobonaro District (Locality 11; USNM 580457).

Striped treefrogs found in anthropogenic habitats included a small series (USNM 580458–63) collected in a significantly degraded forest at Fiuren village, Bobonaro District. Curiously, these frogs were found in leaf litter or buttress roots close to the forest floor, despite the entire area being drastically altered by a large population of domestic pigs. The presence of the pigs resulted in a low number of terrestrial reptiles encountered, yet the treefrogs endured. Another treefrog was found at night, perched on the branch of a tree growing within the ruins of an old school (Escola do Reino de Haudere) near Baguia (Baucau District; Locality 24; USNM 580451). In a more natural environment, our single Manatuto specimen (Locality 20; USNM 580456) was found inside a hollow log.

Taxonomic comments. The taxonomic status of *P.* cf. *leucomystax* is discussed in previous reports (Kaiser *et al.*, 2011; O'Shea *et al.*, 2012) and will not be elaborated upon here. The taxonomy of the *P. leucomystax* species complex is currently under investigation (Rafe Brown, *pers. comm.*; Hidetoshi Ota, *pers. comm.*). *Polypedates leucomystax* has generally been considered a widespread Asian species that also occurs on many islands across the Sunda Shelf. However, *P. leucomystax sensu stricto* may not extend further east than Bali, into the Lesser Sunda Archipelago, although molecular data for the Lesser Sundas is still lacking (Brown *et al.*, 2010; Kuraishi *et al.*, 2013; Kuraishi *et al.*, 2011). Specimens from Nusa Tenggara Province, including those from the island of Timor, could represent introduced populations originating in the Greater Sunda area, or they could be a regionally endemic, hitherto unrecognized Lesser Sunda species.

LIZARDS (ORDER LACERTILIA)

Family Agamidae—Agamas and Dragon Lizards

Draco timoriensis Kuhl, 1820 [IV–VI, VIII]

Common names. (E) Timor Flying Dragon, Timor Flying Lizard. (G) Timor-Flugdrache. (T) Teki liras (teki = gecko, liras = winged). In direct translation, the Tetun name more accurately describes the gekkonid genus *Ptychozoon*, which is not found east of Wallace's Line. We believe that the common name of *D. timoriensis* is not an indication that local residents are unable to tell a gecko from an agamid lizard. Instead, it may reflect the assumption that lizards of comparable size are likely geckos, an error culturally perpetuated by the lack of opportunities to catch more than a fleeting glance at an individual because of the *Draco* lifestyle.

Known distribution. *Draco timoriensis* (Figure 10) is currently reported from five of Timor-Leste's 13 districts (Table 3): Baucau, Lautém, Liquiça, Oecusse, and Viqueque (Kaiser *et al.*, 2011; O'Shea *et al.*, 2012; Sanchez *et al.*, 2012). There are no records of any *Draco* species from Ataúro Island (Kaiser *et al.*, 2013b), a location surrounded by islands where *Draco* have been recorded, but islanders are adamant that they do not occur there (O'Shea and Kaiser, 2013).

New localities. During 2011 and 2012 we obtained additional specimens from Lautém District, from Com (Locality 26) and Raça (Locality 27). New district records were established for Manufahi District through the collection of specimens in the Betano area on the south coast (Locality 18), and from several localities around Same (Locality 17): in the mountains, in the grounds of the Ailelehun Guest House, and at Ladiki village, 5 km NE of Same. Southern coastal records came from the Nancuro coastal forest (Manatuto District; Locality 20), the grounds of Castelo Fronteira Guest House in Suai (Covalima District; Locality 13), and two sites outside of Tilomar (Covalima District; Locality 15), namely the Tilomar Forest Reserve and just N of Maubesi. On the north side of Timor we obtained a single specimen from the Meleotegi River (Ermera District; Locality 8), as well as a specimen from Dare, in the hills above Dili (Dili District; locality 4). The vouchers from Manufahi, Manatuto, Covalima, Ermera, and Dili are first district records and this doubles the number of districts from which *Draco timoriensis* has been recorded to ten (Table 3).

Natural history. Although a relatively small and slender species, *Draco timoriensis* is a fairly conspicuous lizard. It is usually seen running up the trunks of coconut palms or smooth-barked eucalypts and if pursued will easily leap and glide gracefully to another tree. It clearly exhibits a wide distribution, both on the southern and

Figure 9 Adult *Polypedates* cf. *leucomystax* from a creek-side tree near Ossohuna (USNM 580454, Locality 25). Photo by Mark O'Shea.

Figure 10 Adult female *Draco timoriensis* from a tree at Dare (USNM 579711, Locality 4). Photo by Mark O'Shea.

northern coasts, including the Oecusse exclave (Sanchez *et al.*, 2012), and it is relatively common at elevations only marginally above sea level (e.g., at 3 m in the Nancuro wet coastal forest, Manatuto District; Locality 20; USNM 579298; at 3 m on a tree opposite the wharf at Com, Lautém District; Locality 26; USNM 579491). We also obtained specimens at significantly higher elevations, on the upland limestone plateaus and central mountains of Timor-Leste (e.g., at 412 m elevation on trees around Raça village, Lautém District; Locality 27; USNM 579310–12, 579490; on forest trees at 442 m elevation near Tilomar, Covalima District; Locality 15; USNM 579302–04; and at 600 m elevation on a large tree, opposite the war memorial at Dare, Dili District; Locality 14; USNM 579711). The Meleotegi River specimen (Ermera District; Locality 8; USNM 579492) was collected at 1177 m, and constitutes the highest elevation record for *D. timoriensis* we have observed on Timor Island.

Family Gekkonidae —True Geckos

Cyrtodactylus spp. [IV–VIII]

Common names. (E) Bent-toed Geckos, Bow-fingered Geckos. (G) Bogenfinger-Geckos. (T) Teki ain-fuan kleuk (Teki = small gecko, kluek = bent, ain-fuan = toe).

Known distribution. During our initial survey in 2009 we collected two geckos of the genus *Cyrtodactylus* in Timor-Leste (see Taxonomic comment below). This population, currently referred to as *Cyrtodactylus* sp. 'Trilolo River,' was collected 4 km north of Same (Manufahi District; Locality 17; Kaiser *et al.*, 2011). In 2010 we collected a single specimen of *Cyrtodactylus* sp. 'Manucoco' on the northwestern slopes of Mt. Manucoco on Ataúro Island (Kaiser *et al.*, 2013b), and a series of ten vouchers of a third population, *Cyrtodactylus* sp. 'Abanat River,' in the Oecusse exclave (Sanchez *et al.*, 2012). Populations of *Cyrtodactylus* are therefore known from two mainland districts (Manufahi, Oecusse) and from Ataúro Island (Dili District) so far (Table 3).

New localities. During 2011 we discovered further populations of *Cyrtodactylus* (Figure 11) over a wide area of Timor-Leste. Specimens collected at sea level on Ataúro Island (USNM 579712–25) are being treated as *Cyrtodactylus* sp. 'Ataúro coast' (Kaiser *et al.*, 2013b). Additionally, we located two more populations in Lautém District, along the north coast at Com (Figure 11B; Locality 26; USNM 579411–23) and on the adjacent limestone plateau, at Raça (Figure 11A; Locality 27; USNM 579313, 579408–09), and near the Mainina sinkhole (Locality 29; USNM 579410, 579424) (see Taxonomic comment below).

During 2012 four further populations of *Cyrtodactylus* were discovered and sampled: from a network of man-made tunnels at Venilale, Baucau District (Figure 11C; Locality 22; USNM 580474–84); in the coastal forest at Nancuro, Manatuto District (Figure 11D; Locality 20; USNM 580485–86); near Maganuto village, in the mountains surrounding Maliana, Bobonaro District (Figure 11E; Locality 11; USNM 580457), and in Fiuren village, near Balibo, Bobonaro District (Figure 11F; Locality 9; USNM 580488). At an altitude of 1036 m, the Maganuto locality is the highest record for these geckos in Timor-Leste.

In the summer of 2013, we discovered yet another population of bent-toed geckos in the vicinity of Com (Locality 26; USNM 581153–54), one clearly distinct from the small-bodied form we found in 2011. *Cyrtodactylus* spp. have now been recorded from six mainland districts and Ataúro Island (Table 3).

Natural history. The only general habitat requirement

Table 3 Records of lizard species for the districts of Timor-Leste. Black circles indicate previously known records, red circles denote new records. The black open circle refers to a literature record only. Records listed in grey denote literature records from West Timor, with open circles representing known museum specimens.

Taxon	District															References[*]
	Aileu	Ainaro	Baucau	Bobonaro	Covalima	Dili (Timor)	Dili (Ataúro)	Ermera	Lautém	Liquiça	Manatuto	Manufahi	Oecusse	Viqueque	W.Timor	
AGAMIDAE																
Draco timoriensis			●		🔴	🔴		🔴	●	●	🔴	🔴	●	●		1–4
GEKKONIDAE																
Cyrtodactylus sp. 'Trilolo River'												●				1
Cyrtodactylus sp. 'Manucoco'							●									5
Cyrtodactylus sp. 'Ataúro coast'							●									5
Cyrtodactylus sp. 'Abanat River'													●			3
Cyrtodactylus sp. 'Plateau'									🔴							4
Cyrtodactylus sp. 'Com small'									🔴							4
Cyrtodactylus sp. 'Com large'									🔴							4
Cyrtodactylus celatus															○	6
Cyrtodactylus sp. *incertae sedis*			🔴	🔴							🔴					4
Gehyra mutilata			🔴	🔴			●		●	🔴	🔴					1,4
Gekko gecko			🔴	🔴		🔴	●		●	●	🔴	●	●	●		1–5
Hemidactylus frenatus			●		🔴	●	●			●	●	🔴	●	●		1–5
Hemidactylus cf. *garnotii*				🔴												4
Hemidactylus platyurus					🔴	●			●	●	●		●	●		1–4
Hemidactylus tenkatei						🔴			🔴	●			●			1–4
Hemiphyllodactylus cf. *typus*			🔴													4
SCINCIDAE																
Carlia peronii															○	7
Carlia spinauris															○	7,8
Carlia sp. 'Maubisse'		●														1
Carlia sp. 'Meleotegi River'								●								1,2
Carlia sp. 'South Coast'									●		🔴	🔴		●		1,2,4
Carlia sp. 'Baucau'			●													1,2
Carlia sp. 'Abanat River'													●			3
Carlia sp. *incertae sedis*												🔴				4
Cryptoblepharus leschenault			●				●		●		🔴					1,2,4,5
Cryptoblepharus sp. 'Bakhita'								●								2
Cryptoblepharus cf. *schlegelianus*						🔴			🔴						○	4,9
Eremiascincus antoniorum															○	10
Eremiascincus cf. *timorensis*								🔴							○	4,10
Eremiascincus sp. 'Ermera'								🔴								4
Eremiascincus sp. 'Montane'		●										●				1,2
Eremiascincus sp. 'Lautém'									●							1,2
Eremiascincus sp. 'Jaco'									●							4
Eremiascincus sp. 'Ataúro'							●									5
Eutropis cf. *multifasciata*							●	●	●		🔴	🔴	●			1–5
Lamprolepis smaragdina cf. *elberti*			●	🔴	🔴		●		●		🔴	🔴	●	●		1–5
Sphenomorphus cf. *melanopogon*									●		🔴					1,2,4
Sphenomorphus sp. 'Highland large'								●								1,2
Sphenomorphus sp. *incertae sedis*		●	🔴						🔴		🔴	●				1,2,4
VARANIDAE																
Varanus timorensis			🔴		🔴	🔴			●	○	●					1,2,4,11
Varanus cf. *salvator*							●									5

[1] References are identified numerically as follows: 1 = Kaiser *et al*., 2011; 2 = O'Shea *et al*., 2012; 3 = Sanchez *et al*., 2012; 4 = this paper; 5 = Kaiser *et al*., 2013b; 6 = Kathriner *et al*., 2014; 7 = Zug, 2010; 8 = Smith, 1927; 9 = Brongersma, 1942; 10 = Aplin *et al*., 1993; 11 = Bethencourt Ferreira, 1898.

for representatives of this versatile gecko genus on Timor appears to be the availability of hiding places. Beyond this, we have encountered representatives of putative, undescribed species in habitats ranging from the wall of a cave in limestone karst (Raça, Locality 27) to the vertical walls of man-made tunnels (Venilale, Locality 22), and from wet lowland forest (Nancuro, Locality 20) to dry montane forest (Maganuto, Locality 11). Having had all of these encounters, it appears obvious to us that members of *Cyrtodactylus* on Timor display a considerable ecological plasticity when it comes to colonizing new habitats and adapting.

On Ataúro Island, the lowland population appears to occur in most sampled habitats from near-coastal cliffs to disturbed localities, such as plantations or residential areas. Whereas the majority of our specimens came from areas near a source of water (e.g., in proximity to a riverbed, a shallow ravine with water run-off), some were found under rocks in Barry's Place Ecoresort, or by rolling palm logs and pulling apart palm leaf piles in a plantation.

Some of the microhabitats where we discovered

Figure 11 Species of *Cyrtodactylus* in Timor-Leste. These six individuals represent populations of bent-toed geckos we consider distinct at the species level (Kathriner *et al*., in prep.). We refer to them here by their localities. (A) Adult specimen (sex not determined, SVL = 60 mm) of the 'Plateau' population from the wall of a limestone karst cave near Raça (USNM 579408, Locality 27). (B) Adult male (SVL = 42 mm) of the small north coast bent-toed gecko from the ruin of the Portuguese pousada at Com (USNM 579412, Locality 26). (C) Adult male (SVL = 55 mm) from a wall in the man-made tunnels at Venilale (USNM 580474, Locality 22). (D) Adult female (SVL = 41 mm) from inside a rotten log in the coastal wet forest at Nancuro (USNM 580486, Locality 20). (E) Adult individual (sex not determined, SVL = 44 mm) from a dry rotting tree in the alpine habitat at Maganuto (USNM 580487, Locality 11). (F) Adult male (SVL = 40 mm) from a fallen log in disturbed dry forest at Fiuren (USNM 580488, Locality 9).

Cyrtodactylus include oddities. For example, our highest elevation specimen (1036 m, Maganuto; Locality 11) was recovered from the inside of a decaying tree that stood isolated in an alpine meadow surrounded by very little vegetation. Our search there was focused on *H. garnotii* (see below), individuals of which we had found nearby in decaying bamboo microhabitat, and when breaking apart the decaying wood, a single *Cyrtodactylus* was discovered. A second unusual locality was the rather disturbed forest habitat in Fiuren (Locality 9) that appeared to endure regular disturbance from the foraging activity of a group of free-roaming domestic pigs. The most unusual locality, however, were the roadside tunnels at Venilale (Locality 22). These tunnels were dug by forced labor during the Japanese occupation of Timor in the 1940s, and upon our first visit to the locality in 2009 we did not even consider conducting a careful search for reptiles there. While showing this locality to some of our team members in 2012, however, we chanced upon a gecko at head height on the surface of a vertical tunnel wall. Our subsequent, careful search revealed several additional specimens distributed throughout the tunnel system, including all tunnel surfaces (sides, floor, and ceiling), and in both exposed positions as well as underneath rocky debris. There was no evidence of standing or running water in the tunnels, although the air was cool and the humidity high.

Taxonomic comments. *Cyrtodactylus* is the largest genus in the Gekkonidae, indeed the most speciose in the entire Gekkota, a highly diverse group that comprises seven families, over 100 genera, and around 1400 species. *Cyrtodactylus* currently comprises one eighth of that diversity (199 species; Uetz and Hošek, 2014; Wood *et al.*, 2012), distributed from Tibet, China and India to northern Australia (Western Australia, Queensland) and east across the Indonesian island chain and New Guinea into the Solomon Islands, with new species being described at considerable frequency. Despite the geographic position of Timor near the center of this range, the only previous record of the genus from the territory of what is now Timor-Leste was a single specimen of '*Gymnodactylus timorensis*' listed by Duméril and Bibron (1836). However, this specimen is neither a member of the genus *Cyrtodactylus*, nor did it originate from anywhere close to the island of Timor (L. L. Grismer, in prep.; HK, unpubl. data). Therefore, prior to the initiation of this project, Timor-Leste was considered devoid of any representatives of the genus *Cyrtodactylus*.

Our fieldwork soon proved this not to be the case as the first six populations sampled during the project were found to represent six different species, from at least two different larger clades (AK, unpubl. data). The Ataúro coastal population has similarities to the regionally endemic *C. darmandvillei* (Weber, 1890) but some morphological characteristics lead us to consider this population as a potentially new species, here called 'Ataúro coast' (*Cyrtodactylus* sp. 2 of Kaiser *et al.*, 2013b). We only possess a single specimen of the montane *Cyrtodactylus* sp. 'Manucoco' but it clearly represents a different taxon from its lowland neighbor based on both morphological and molecular data (AK, unpubl. data). The five mainland populations also represent distinct and separate species, which currently lack names and are therefore documented here as *Cyrtodactylus* sp. 'Trilolo River,' *Cyrtodactylus* sp. 'Abanat River,' *Cyrtodactylus* sp. 'Plateau' (Figure 11A), *Cyrtodactylus* sp. 'Com small' (Figure 11B), and *Cyrtodactylus* sp. 'Com large.' The taxonomic status of the four more recently sampled populations, from Venilale (Baucau District; Figure 11C), Nancuro (Manatuto District; Figure 11D), and Maganuto and Fiuren (both Bobobaro District; Figs. 11E and 11F, respectively) has yet to be determined, and we list them here as populations *incertae sedis*. In addition Kathriner *et al.* (2014b) described *C. celatus* from near Kupang, West Timor, from a single specimen collected in 1924 by M. A. Smith, and deposited, then essentially forgotten, in the Natural History Museum, London, United Kingdom.

Three of the populations we discovered stand out by their body size (up to 75 mm SVL), including the highland karst dwellers at Raça and Mainina (Localities 27 and 29, respectively), the lowland coastal limestone form at Com (Locality 26), and the lowland form on Ataúro. A preliminary analysis of molecular data (Kathriner *et al.*, unpubl. data) indicates that the larger mainland populations likely constitute a separate radiation from the small-bodied forms (up to 46 mm SVL). While it is too early to determine their exact phylogenetic affinities or the vector by which they arrived on Timor, there appears to have been sufficient time elapsed for the two major radiations to adapt to diverse niches and to diversify into an unexpectedly rich bent-toed gecko fauna.

Gehyra mutilata (Wiegmann, 1834) [IV–VII]

Common names. (E) Mutilated Gecko. (G) Vierklauen-Gecko. (T) Teki kulit kanek (Teki = small gecko, kulit = skin, kanek = injured).

Known distribution. *Gehyra mutilata* (Figure 12) has so far been reported from only two districts (Table 3), from Dili and Lautém, as well as on Mt. Manucoco, Ataúro Island, Dili District (Kaiser *et al.*, 2011, 2013b).

New localities. During the last four surveys additional specimens were obtained from sea level to an elevation of 572 m on Ataúro Island (Kaiser *et al.*, 2013b), and in Lautém District from sea level habitats at Com (Locality 26) to the elevated central limestone plateau at Raça (elevation > 400 m; Locality 27). Additional lowland records from Phases IV–VII on the mainland came from the confluence of the Comoro and Bemos Rivers (8 km S of the Comoro River bridge, Liquiça District; Locality 6; USNM 579425), and the wet coastal forest at Nancuro (Natarbora, 8 km S Umaboco, Manatuto District; Locality 20; USNM 581759), while upland localities include the ruins of Escola do Reino de Haudere, Baguia (Baucau District; Locality 24; USNM 580489), and the grazed forest at Fiuren, near Balibo (Bobonaro District; Locality 9; USNM 580490–91). On the mainland *Gehyra mutilata* has now been recorded from five districts, on both the northern and southern coastal lowlands, at altitudes > 400 m in the central massif of Timor and > 570 m on Ataúro Island (Table 3).

Natural history. Specimens of *G. mutilata* have been recovered from the standard set of microhabitats typically frequented by house geckos (see natural history comments on the species of the genus *Hemidactylus* below). Most frequently, these geckos were found associated with dry wooden structures, such as the loose bark on decaying trees, in dry leaf litter, or in the building materials used to make traditional huts. They were also collected from the walls of houses. Occasionally, a specimen was retrieved from underneath dry rocks (such as in a rock pile) or by rolling rocks in dry habitats.

***Gekko gecko* (Linnaeus, 1758)** [IV–VII]

Common names. (E) Tokay Gecko. (G) Tokeh, Tokee, Panthergecko. (T) Toke.

Known distribution. *Gekko gecko* (Figure 13) has so far been reported from five of Timor-Leste's 13 districts (Lautém, Liquiça, Manufahi, Oecusse, and Viqueque; Kaiser *et al.*, 2011; O'Shea *et al.*, 2012; Sanchez *et al.*, 2012) and from Ataúro Island, Dili District (Kaiser *et al.*, 2013b) at elevations from near sea level to over 500 m (Table 3).

New localities. During 2011 and 2012 four more mainland districts were documented as part of the range for *Gekko gecko* in Timor-Leste (Baucau, Bobonaro, Dili, Manatuto). Since this is an introduced species and there are no arguments regarding its identity or taxonomy, we collected only few voucher specimens whenever it was encountered; some of our records therefore comprise a voucher photograph rather than a specimen. In addition, this is the most vocal member of the Gekkonidae on the island of Timor, and it possesses a characteristic, eponymous vocalization. Individuals issuing the onomatopoeic "toh-kay" call are frequently heard in forests, on rocky outcrops or buildings, both by night and day.

Voucher specimens were collected along the Comoro River (Dili District; Locality 1; USNM 579314), at Betano 'dry site' (Manufahi District; Locality 18; USNM 579315), and near Raça (Lautém District; Locality 27; USNM 579316–17). Voucher photographs were contributed for the wet coastal forest at Nancuro (Natarbora, 8 km S Umaboco, Manatuto District; Locality 20; USNM-HI 2824), Com village (Lautém District; Locality 26; USNM-HI 2764), the ruins of Escola do Reino de Haudere (Baguia, Baucau District; Locality 24; USNM-HI 2759–60), and from the grazed forest at Fiuren (Bobobaro District; Locality 9; USNM-HI 2762). Aural observations were made in the forest on Jaco Island (Lautém District; Locality 30) and along a rocky outcrop at Maganuto (Bobonaro District; Locality 11) for specimens that could be heard but not seen. *Gekko gecko* is now known from ten districts, including Ataúro Island (Table 3).

Natural history. *Gekko gecko* is the largest member of the Gekkonidae in the Lesser Sunda Archipelago, and one of the most visible elements of the gecko fauna anywhere. As a predator of significant size (we encountered adult specimens with SVL in excess of 22 cm), this is not a species that needs to hide itself but tends to threaten when disturbed. Our relatively frequent encounters with this species have happened during both day and night and we have seen adults, juveniles, and eggs containing developing embryos (but destroyed by local children as sport) during both wet and dry season surveys. This species is familiar to the local population throughout the country, and we believe its range encompasses all of Timor.

***Hemidactylus frenatus* Schlegel, 1836** [IV–VIII]

Common names. (E) Common House Gecko. (G) Asiatischer Hausgecko. (T) Teki uma baibain frenatus (teki = small gecko, uma = house, baibain = common).

Known distribution. *Hemidactylus frenatus* (Figure 14) has so far been reported from seven of Timor-Leste's 13 districts (Baucau, Dili, Lautém, Liquiça, Manatuto, Oecusse, and Viqueque; Kaiser *et al.*, 2011; O'Shea *et al.*, 2012; Sanchez *et al.*, 2012) and from Ataúro Island, Dili District (Kaiser *et al.*, 2013b) (Table 3).

New localities. We here report additional voucher specimens from mainland Dili District on the shoreline at Tasi Tolu, the grounds of the Timor Lodge Hotel, the mangrove swamp at Metinaro, and from the Comoro

Figure 12 Adult male *Gehyra mutilata* from a fallen log at Fiuren (USNM 580490, Locality 9). Photo by Mark O'Shea.

Figure 13 Subadult *Gekko gecko* still showing the distinct juvenile tail pattern. This specimen was not vouchered. Photo by Mark O'Shea.

Figure 14 Adult *Hemidactylus frenatus* (sex not determined) from the tidal rocks at Tasi Tolu, near Dili (USNM 580494, Locality 1). This individual is a good example of the habitat plasticity displayed by house geckos, as it was discovered in an area near the tidal splash zone that it shared with individuals of *Cryptoblepharus* cf. *schlegelianus*. Photo by Mark O'Shea.

River (Localities 1, 3 and 5; USNM 579726, 579731–32, 579736, 580494, 581746). Vouchers were also taken at the confluence of the Comoro and Bemos Rivers, on the Liquiça bank (Locality 6; USNM 579425, 579431). Further specimens were obtained from Lautém District, from Com at sea level, and from Raça on the central limestone plateau (Localities 26 and 27; USNM 579428–40, 581755–56). Other low-lying locations sampled during 2011 and 2012 produced vouchers from both the 'wet site' and 'dry site' at Betano (Manufahi District; Locality 18; USNM 581753–54), and the grounds of the Castelo Fronteira Guest House, Suai (Covalima District; Locality 13; USNM 581747). Vouchers were also obtained from upland localities, such as the ruins of the Escola do Reino de Haldere, Baguia (Baucau District; Locality 24; USNM 580492–93). The Covalima and Manufahi District records constitute first records for these districts, elevating the number of districts where *H. frenatus* has been recorded to nine (Table 3). We believe that this species is likely found associated with human disturbances almost anywhere on Timor Island, certainly at elevations between sea level and 600 m (see Natural history for *H.* cf. *garnotii*).

Natural history. Throughout all of our surveys, this species is clearly the most frequently encountered gecko. Due to its perianthropic lifestyle, it is encountered on the walls of almost any human habitations. These geckos are able to colonize even new construction rapidly and indiscriminately, and they appear to live in clean hotel rooms just as well as in natural vegetation, rock piles, or even trash. We have not encountered them in pristine habitats, with the exception of healthy-looking forest areas experiencing some minor form of human impact, such as those adjacent to coffee plantations. We believe that the species exists in all of Timor-Leste's districts, and we believe its arrival on the island and its dispersal throughout the country may be correlated with historic and current local trade patterns.

Hemidactylus cf. *garnotii* [VII]

Common names. (E) Indo-Pacific House Gecko. (G) Indopazifischer Halbfinger-Gecko, Jungfern-Halbfinger-Gecko. (T) Teki uma baibain garnotii (teki = small gecko, uma = house, baibain = common).

Identification. *Hemidactylus* cf. *garnotii* (Figure 15) is the fourth house gecko species (genus *Hemidactylus*) recorded from Timor-Leste, and especially in preservative it is one easily confused with the more common species (e.g., *H. frenatus*, *H. tenkatei*). Specimens encountered in Bobonaro were dark brown when collected, with several longitudinal rows or dark-edged light spots on the dorsum and a prominent ventrolateral series of white spines along the edge of the tail. The dorsal color paled in captivity but the light spots and white caudal spines were still in evidence. *Hemidactylus* cf. *garnotii* can be distinguished from *H. platyurus* by a tail that is not dorsoventrally flattened and by the absence of skin webbing and fringing associated with tail, digits, limbs, and flanks; from *H. tenkatei* by the absence of that species' distinctive longitudinal rows of raised dorsal tubercles, and from *H. frenatus* by a series of small scales that separate the 2nd pair of postmental scales from the infralabials (both pairs of postmentals are in contact with the infralabials in *H. frenatus*). *Hemidactylus frenatus* also has four longitudinal rows of elevated spines on its original tail, whereas in *H.* cf. *garnotii* the character of tubercle rows is limited to two lateral rows. *Hemidactylus* cf. *garnotii* is easily distinguished from *Gehyra mutilata* by its longer and flatter snout and the pattern of chin scales. Several of our specimens had symmetrical calcium deposits in the neck area (Figure 15B), which is something we never observed in the other house gecko species found in Timor-Leste.

Known distribution. There were no previous records of this species for Timor-Leste.

New localities. *Hemidactylus* cf. *garnotii* was encountered only during the survey in 2012 (Phase VII) when seven vouchers were collected in the bamboo forest above Maganuto, near Maliana (Bobonaro District; Locality 11; USNM 580495–501) and a single voucher obtained from the degraded, grazed forest at Fiuren, near Balibo (Bobonaro District; Locality 9; USNM 580502). The Fiuren specimen came from an elevation of 463 m but the Maganuto specimens were collected at 1041–1063 m on the slopes of Mt. Leolaco at an altitude far above that recorded for any other *Hemidactylus* species in Timor-Leste.

Natural history. The seven specimens collected in the bamboo forest above Maganuto were mostly sheltering at the bases of bamboo leaf-axils or in termite-inhabited dead bamboo stalks, but one specimen was found under a rock and another behind the bark of a tree in close proximity to the bamboo. Several specimens had regenerated tails, and one (USNM 580498) had lost both its left fore- and hind limbs but had healed and survived the trauma. The Fiuren specimen, containing two eggs, was also found inside a clump of bamboo.

Hemidactylus garnotii Duméril and Bibron, 1836 is an all-female parthenogenetic species and should be considered a good colonizer: only a single adult female is needed to produce eggs to establish a new colony. It is therefore somewhat surprising that its reproductive ability has not made this species more prevalent in Timor-Leste. We believe that it may be its reduced genetic variability, inherent in clonally reproducing organisms, that gives this species only few options to successfully compete with aggressive bisexual species, such as *H. frenatus* or *H. tenkatei*. If it is difficult for *H. garnotii* to live in sympatry with other house geckos, unlike *Gehyra mutilata* or *H. platyurus,* its presence and apparent success on the slopes of Mt. Leolaco at elevations above 1000 m might be explained by the fact that no other house geckos have yet been found above 563 m in mainland Timor-Leste.

Taxonomic comments. *Hemidactylus garnotii* is a colonizing species, which we would most expect to encounter in coastal lowland beachheads. Whilst the Fiuren record came from a locality which was at an intermediate elevation (463 m) and heavily influenced by human activities, both being common factors associated with colonizing species, the majority of our specimens were collected at Maganuto, on the slopes of Mt Leolaco at an elevation considerably above that documented for any other Timor *Hemidactylus* (1041–1063 m), in a habitat that seemed to us incompatible with a colonizing species such as *H. garnotii* due to its remoteness and high elevation. This leads us to wonder if this taxon is an undescribed species of *garnotii*-like *Hemidactylus*, but in the absence of any males we cannot as yet differentiate it morphologically from true *H. garnotii.* We therefore refer to it as *Hemidactylus* cf. *garnotii*.

Hemidactylus platyurus (Schneider, 1792) [IV–V]

Common names. (E) Common Flat-tailed Gecko. (G) Saumschwanz-Hausgecko. (T) Teki ikun belar (teki = small gecko, belar = flat, ikun = tail).

Known distribution. *Hemidactylus platyurus* (Figure 16) has so far been reported from six of Timor-Leste's 13 districts (Dili, Lautém, Liquiça, Manatuto, Oecusse, and Viqueque; see Kaiser *et al.*, 2011; O'Shea *et al.*, 2012; Sanchez *et al.*, 2012). It has not been recorded on Ataúro Island (Table 3; see Kaiser *et al.*, 2013b).

New localities. Additional specimens were collected in 2011 in Lautém District, near sea level on the north coast at Com (Locality 26; USNM 579445–47) and at 520 m elevation, 5 km N of Maubesi (Tilomar, Covalima District, Locality 15; USNM 581757–58). This is a little lower than our elevation record for *H. platyurus* at 545 m near Dare, Dili District (Locality 4; USNM 579112) during Phase III. Covalima is the seventh district from which we have recorded *H. platyurus* (Table 3).

Natural history. This is another of the perianthropic house gecko species, though it is seen around human

Figure 15 Adult *Hemidactylus* cf. *garnotii* from a bamboo stand above Maganuto (USNM 580502, Locality 11). This individual shows the presence of mature eggs and gular calcium deposits. Photo by Mark O'Shea.

habitations in considerably lower numbers than either *H. frenatus* or *H. tenkatei*. In each of the new localities, other house geckos were present, although not all cohabiting gecko species were vouchered. The two Maubesi specimens were found on a roadside tree that initially caught our attention because of the presence of a monitor lizard (*Varanus*; see below). After capturing the monitor lizard, we managed to obtain both specimens from a height of ca. 5 m above ground level. Both of the specimens caught in Com were found along with individuals of *H. frenatus* and *H. tenkatei* in the rafters of the cabins at Com Beach Resort and on stone walls surrounding the compound.

Hemidactylus tenkatei van Lidth de Jeude, 1895 [IV–VII]

Common names. (E) Roti House Gecko. (G) Roti-Hausgecko. (T) Teki uma baibain Roti (teki = small gecko, uma = house, baibain = common).

Identification. *Hemidactylus tenkatei* (Figure 17) can be distinguished from *H. frenatus* by the presence of 16–20 longitudinal rows of large, strongly keeled tubercles, as opposed to the numerous scattered, small conical tubercles of its more common congener. It also lacks the broad, flattened, filamentous-edged tail and strongly webbed toes of *H. platyurus*. *Hemidactylus tenkatei* may be distinguished from *Gehyra mutilata* by its chin shields, which are arranged to form a smoothly arched posterior border in the latter species, and from *H. garnotii* by the presence of enlarged keeled tubercles on its dorsum.

Figure 16 Adult *Hemidactylus platyurus* (sex not determined) from the wall of a building at the Com Beach Resort (USNM 579447, Locality 26). Photo by Mark O'Shea.

Known distribution. *Hemidactylus tenkatei* had previously only been recorded from Liquiça and Oecusse Districts (Table 3; see O'Shea *et al.*, 2012; Sanchez *et al.*, 2012).

New localities. We here report new district records for *H. tenkatei* from Dili District at Timor Lodge Hotel, Dili (Locality 1; USNM 579728–30) and Metinaro mangrove swamp (Locality 3; USNM 579733), and from Lautém District at Com Beach Resort (Locality 26; USNM 579417, 579430, 579441–44), elevating the number of districts from which this introduced species has been recorded to four. All records are from elevations below 25 m and from northern coastal locations, indicative of an invading species establishing bridgeheads. The lack of any specimens of *H. tenkatei* further inland could be a result of its recent arrival, its inability to compete with the already established *H. frenatus*, *H. platyurus*, or *Gehyra mutilata*, or its adaptation to a microhabitat that currently remains undiscovered. At our accommodation in Dili, the Timor Lodge Hotel, we have noticed an increase in the abundance of *H. tenkatei* relative to *H. frenatus* over the five-year period of our survey work, but this observation will require further verification.

Figure 17 Adult *Hemidactylus tenkatei* (sex not determined) from a wall in the grounds of the Timor Lodge Hotel in Dili (USNM 581158, Locality 1). Photo by Mark O'Shea.

Natural history. We collected six specimens of what we initially believed to be *H. frenatus* from trees and rocks in the center of a seasonally dry riverbed, west of Maubara (Liquiça District: locality 3) on 6 February 2010 (Phase II). Upon later examination, one of these (USNM 579064) was re-identified as *H.* cf. *tenkatei* (A. M. Bauer, *pers. comm.*), the first specimen of the perianthropic *H. brookii* complex recorded from Timor-Leste. With a distribution of this species complex ranging from Pakistan and Indian Ocean islands to the Philippines and south into the Lesser Sunda archipelago (Bauer *et al.*, 2010), ancestors of Timorese *H. tenkatei* may have found their way onto Roti Island, the type locality of *H. tenkatei*, and later on to Timor Island by stowing away with neolithic human migrants and their chattels.

Taxonomic comments. Geckos called *Hemidactylus brookii* exist in museum collections from throughout South and Southeast Asia, and the broad distribution and the likely influence of historical human trading and colonization patterns has led to an inconsistent use of names for these forms. Recently, Bauer *et al.* (2010) completed a molecular analysis, in which they restricted the distribution of true *H. brookii* to Borneo, Peninsular Malaysia, Burma, and Karnataka State in India. However, their analysis conspicuously excluded data from islands of the Indonesian Archipelago, notated with a centrally placed question mark in their distribution map (Figure 1 in Bauer *et al.*, 2010).

The species *H. tenkatei* was described by van Lidth de Jeude (1895) based on three specimens from Roti, a small (1200 km^2) island off the extreme southwestern corner of Timor. Two decades later, de Rooij (1915) placed the species into the synonymy of *H. brookii* after a limited study of specimens from Flores and Wetar, presumably with literature accounts then available, but without the presentation of data. In two recent revisions of the *H. brookii* group, of which *H. tenkatei* is a member, Rösler and Glaw (2010) and Mahony (2011) removed *H. tenkatei* from the synonymy of *H. brookii*, but did not examine the relevant type material. Addition of these important specimens to the analysis, along with the Bornean type material of *H. brookii* and molecular data for specimens from Timor-Leste to the data set of Bauer *et al.* (2010), shows that *H. tenkatei* is a species distinct from *H. brookii* and that Timorese populations are indeed identical to those on Roti (Kathriner *et al.*, 2014a). Furthermore, it appears that the species *H. tenkatei* is a widespread and successful colonizer found not only in the Lesser Sundas but also in Sarawak, Borneo, and Penang Island, Malaysia (Kathriner *et al.*, 2014a), and that these populations can therefore all be referred to *H. tenkatei.*

Hemiphyllodactylus cf. *typus* [VII]

Common names. (E) Dwarf Tree Gecko. (G) Zigeunergecko, Gewöhnlicher Halbblattfinger-Gecko. (T) Teki ai isin lotuk (teki = gecko, ai = tree, isin lotuk = very small body).

Identification. *Hemiphyllodactylus* cf. *typus* (Figure 18) is the smallest gecko in the region and easily overlooked, as it had been during six previous phases of our survey. This is an extremely slender, etiolated gecko, its body so elongated that the adpressed limbs do not overlap or even come into contact. It can be distinguished from *Hemidactylus* spp. by its clawless 1st digit, a characteristic it only shares with members of the genus *Lepidodactylus*, a taxon as yet unrecorded from Timor, and the complete lack of any enlarged postmental scales in the chin region. In *L. lugubris* the clawless 1st digit is otherwise well developed, being at least two-thirds the length of the 2nd digit, whereas in *H.* cf. *typus* the 1st digit is much reduced in size.

Known distribution. There were no previous records of this genus from Timor-Leste.

New localities. Two specimens of *Hemiphyllodactylus* cf. *typus* were collected at Ossohuna, near Baguia (Baucau District; Locality 25) during Phase VIII, the first record of the taxon from Timor Island.

Natural history. The only two specimens of *H.* cf. *typus* (USNM 580503–04) found in Timor-Leste so far were collected in a clump of bamboo in a dry river gorge, sheltering behind the leaf-like culm sheaths that protect the base of the bamboo shoots. Their movements, when uncovered, were slow, meaning they did not 'scamper' as do many species of *Hemidactylus*.

Taxonomic comments. The Indo-Pacific genus *Hemiphyllodactylus* contains as many as 20 species although most exhibit fairly or extremely localized distributions (Zug, 2010b; Grismer *et al.*, 2013, 2014). The one widespread species is the parthenogenetic *H. typus* Bleeker, 1860, which is found from southern Myanmar and Taiwan of China to New Guinea and across the South Pacific to Fiji and Tonga, with established but isolated populations in Sri Lanka, the Mascarene Islands,

Figure 18 Adult *Hemiphyllodactylus* cf. *typus* from a bamboo stand near Ossohuna (USNM 580503, Locality 25). Photo by Mark O'Shea.

and the Hawaiian Islands (Zug, 2010b, 2013). This is a colonizing species that often goes undetected due to its small size and secretive nature, so its true distribution is incompletely documented (Zug, 2010b). Small beachhead populations of parthenogenetic geckos are most commonly found in lowland coastal localities where they have become established, either through the actions of man or by some other means, such as rafting.

The population recorded here is located near Ossohuna, 22 km from the north coast and 10 km from the south coast of Timor-Leste, at an elevation of 938 m. Although the distances to either coast are not great, the road from the north coast to Ossohuna is rough, long, and winding and the road from the south coast is only accessible seasonally by vehicles with off-road capability and by no means a reliable transport connector. This leads us to query whether the specimens represent the parthenogenetic *H. typus* or an undescribed sexual species, such as occur at inland locations in India, China, Southeast Asia, Sumatra, and Borneo. In most characters examined, the Timor specimens appear to fall within the characteristics of *H. typus* as detailed by Zug (2010b), and given that the only specimens collected to date are a juvenile and an adult female we are unable to disprove the parthenogenetic species argument. However, in light of the cryptic diversity seen in mainland Southeast Asian *Hemiphyllodactylus* populations (Grismer *et al.*, 2013, 2014), a molecular analysis of the Timor specimens is now being conducted (P. Wood, in prep.).

Family Scincidae—Skinks

Genus *Carlia* [IV–VII]

Common names. (E) Four-fingered Skinks, Rainbow Skinks. (G) Regenbogen-Skinke. (T) Mamór liman-fuan haat (mamór = skink, haat = four, liman fuan = finger).

Known distribution. During Phases I–III we collected *Carlia* in six of Timor's mainland districts (Ainaro, Baucau, Ermera, Lautém, Oecusse, and Viqueque), but did not locate the genus on Ataúro Island (Table 3), despite reports of the genus from Alor to the northwest and Wetar to the northeast (Zug, 2010a). Our vouchers comprised two apparently montane forms: *Carlia* sp. 'Maubisse' (Figure 19A) from Ainaro District (Maubisse; Locality 16), and *Carlia* sp. 'Meleotegi River' (Figure 19B) from Ermera District (Sta. Bakhita Mission and Meleotegi River; Locality 8), and three seemingly lowland forms: *Carlia* sp. 'South Coast' (Figure 19C) from Loré village, southeast Lautém District and Beaçu on the coast of Viqueque District, *Carlia* sp. 'Baucau' (Figure 19D) from Afacaimau, Baucau District (Locality 23), and *Carlia* sp. 'Abanat River' from the Oecusse District. For reports from these localities, see Kaiser *et al.* (2011), O'Shea *et al.* (2012), and Sanchez *et al.* (2012).

New localities. During 2011 and 2012 (Phases IV–VII) we collected additional vouchers of all the above species, except *Carlia* sp. 'Abanat River.' *Carlia* spp. 'Maubisse' and 'Meleotegi River,' which were only found at their original locations. However, vouchers of *Carlia* sp. 'South Coast' were collected as a series from Nancuro (Natarbora, 8 km S Umaboco, Manatuto District; Locality 20; USNM 579319–27), and as single specimens from the southern shore of Lake Lenas (near Fatucahi, Manufahi District; Locality 19; USNM 579328) and a roadside ditch on the road between Fatucahi and Betano (Manufahi District; Locality 18; USNM 579329), greatly extending the westerly range of this taxon from Beaçu, Viqueque District, and providing the first *Carlia* records for Manatuto and Manufahi Districts. Another single specimen obtained by one of us (LLA) at the Betano "wet site" may also belong to this taxon and extends the range further west, although it is currently documented as *Carlia incertae sedis*. *Carlia* sp. 'South Coast' was also collected for the first time along the north coast, when two specimens were obtained from the ruins of the Pousada de Com (Lautém District; Locality 26; USNM 579448–49). A single additional specimen of *Carlia* sp. 'Baucau' was collected at Afacaimau (Baucau District; Locality 23; USNM 580506), a site known to the project as the "*Carlia* spot," and another single specimen, seemingly also of *Carlia* sp. 'Baucau,' was collected on the sandstone cliff above the Japanese caves at Venilale (Baucau District; Locality 22; USNM 580505), although this specimen was taken at an elevation of 675 m while the "*Carlia* spot" vouchers were collected at 290–370 m. *Carlia* populations have now been documented for eight mainland districts (Table 3).

Natural history. Members of the genus *Carlia* in Timor-Leste appear to be habitat generalists, found in both dry and moist habitats, as well as both pristine and disturbed areas. When out in the open, we have observed individuals foraging in and around leaf litter and decaying plant material, or basking on exposed "perches," such as small boulders, tree trunks, fallen banana plants, or retaining walls near human habitations. These lizards also interact with one another by signaling (e.g., tail waving: Langkilde *et al.*, 2004; O'Shea, 1993) and were occasionally observed chasing each other as part of aggressive or mating encounters. Where they occur, *Carlia* can be very abundant lizards: at the Sta. Bakhita Mission, *Carlia* sp. 'Meleotegi' occurs at numbers of perhaps as many as one or two individuals per m^2 on the

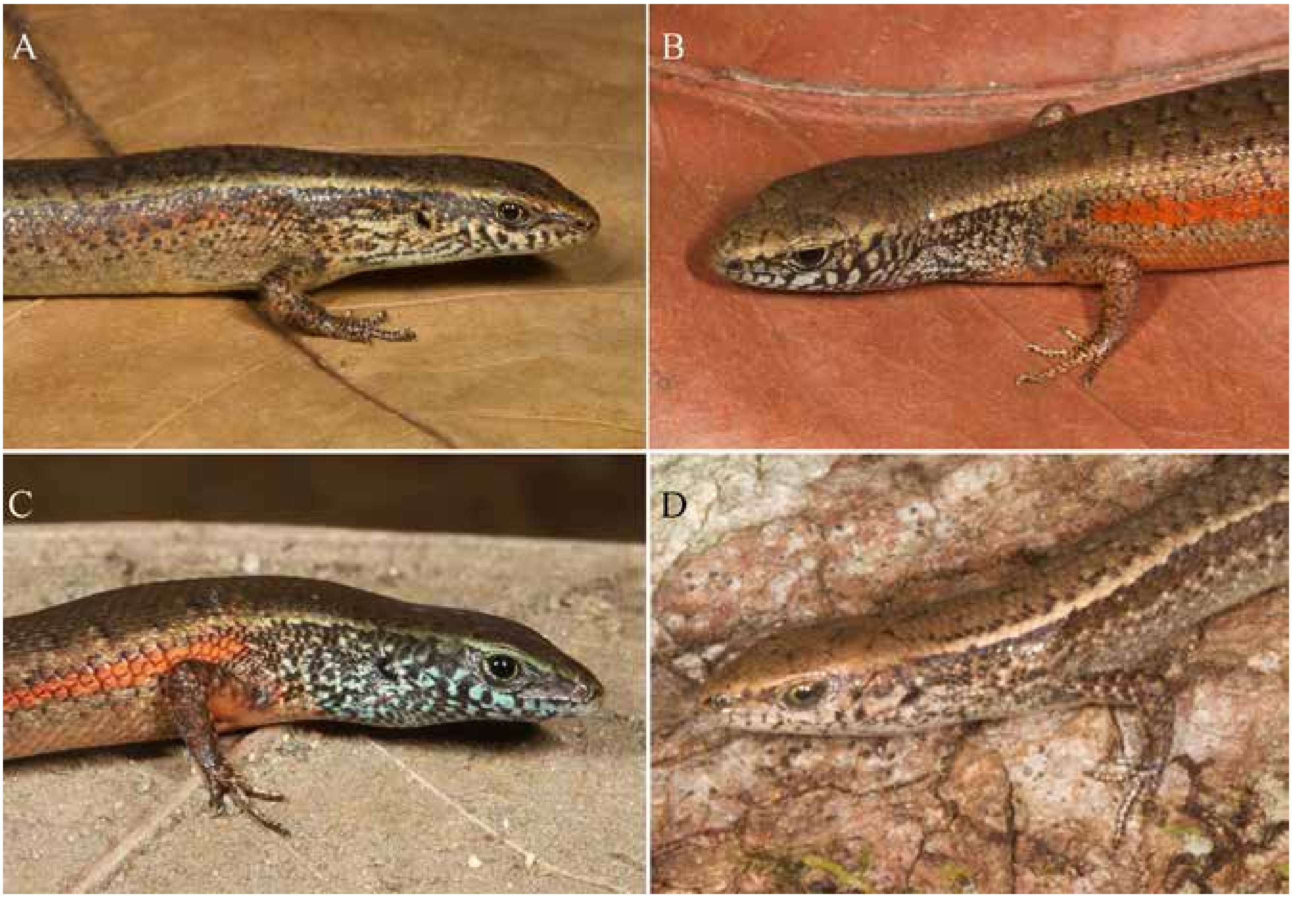

Figure 19 Representatives of four populations of four-fingered skinks (genus *Carlia*) we consider to be distinct at the species level. Important characteristics to differentiate these forms in the field include the coloration of the throat and venter of breading males as well as the presence, color, and extent of lateral stripes in both sexes. (A) Adult female (SVL = 44 mm) from the grounds of the Portuguese Pousada at Maubisse (USNM 579334, Locality 16). (B) Adult male (SVL = 46 mm) from man-made gardens at the Sta. Bakhita Mission (USNM 579450, Locality 8). (C) Adult male (SVL = 42 mm) from among the leaf litter in wet coastal forest at Nancuro (USNM 579324, Locality 20). (D) Adult male (SVL = 40 mm) from banana plant debris in an agricultural environment (USNM 580506, Locality 23). Photos by Mark O'Shea.

terraced hillside. In other localities, abundance clearly depends on the presence of a potential source of food (e.g., invertebrates in a pile of decaying leaves). Only rarely did we encounter single individuals.

We have been unable to observe particular adaptive specializations among the four or five putative taxa occurring in Timor-Leste (see Taxonomic comments below), which can be expected when dealing with a habitat generalist. One of us (SM) was able to observe that male *Carlia* from highland locations (Bakhita and Meleotegi) held in captivity become flushed with color during the breeding season. Females, from those locations, however, may also show a color change towards a more intense coloration (limited to a mid-lateral stripe), which is related to reproductive readiness. On the other hand, such drastic changes in coloration in specimens from the lowland rainforest of Nancuro were not observed (SM, pers. obs.). More detailed observations will be possible once the taxonomic status of these populations has been clarified.

Taxonomic comments. Prior to the initiation of this survey in 2009, two species of *Carlia* were documented for the island of Timor: *Carlia peronii* (Duméril and Bibron, 1839) and *C. spinauris* (Smith, 1927). Although Greer (1976) treated *C. spinauris* as a synonym of *C. peronii*, Zug (2010a) recognized them to be separate but related species within the *C. peronii* species group (sensu Greer, 1976), a group that also extends onto other islands in Indonesia's provinces of East Nusa Tenggara (e.g., Roti, Semau, Alor) and southern Maluku (e.g., Wetar, Kisar). This species group also includes the recently described *C. sukur* Zug and Kaiser, 2014 from Pulau Sukur, a small island north of Flores (Zug and Kaiser, 2014).

In addition to a suite of morphological and morphometric characters, Zug (2010a) separated *C.*

peronii and *C. spinauris* spatially, stating that the former was a lowland species, whereas the latter was a highland species. The type locality for *C. peronii* was erroneously given as "Île de France" (= Mauritius), having been reassigned to Kupang, West Timor by Greer (1976), the only location on Timor visited by the collector, François Auguste Péron. This species is also known from other low-lying locations to the east of Kupang (e.g., Kokabris, Noil Toko, Djamplong = Camplong). In contrast, the type locality for *C. spinauris* is Lelogama (elevation 750 m), where it was personally collected by M. A. Smith and his wife in 1924, and it was also recorded from Soë (elevation 800 m) by de Jong (1927). To date neither of these species has been recorded in Timor-Leste. The material available to us has already undergone preliminary molecular analysis and there is strong evidence to support the recognition of four or five different species, distinct from the aforementioned West Timorese taxa.

Cryptoblepharus leschenault (Cocteau, 1832) [IV, VI–VII]

Common names. (E) Leschenault's snake-eyed skink. (G) Leschault-Schlangenaugenskink. (T) Mamór matan samea leschenault (mamór = skink, matan = eye, samea = snake).

Known distribution. During Phase I (2009) *Cryptoblepharus leschenault* (Figure 20) was documented from lowland locations in Lautém and Baucau Districts, with three and one vouchers collected, respectively (Kaiser *et al.*, 2011), and a single voucher was collected from a coastal location on Ataúro Island, part of Dili District (Kaiser *et al.*, 2013b). *Cryptoblepharus leschenault* is therefore known from three districts to date.

New localities. Single vouchers of *C. leschenault* were collected on each of our visits to the coastal forest at Nancuro (Natarbora, 8 km S Umaboco, Manatuto District; Locality 20; USNM 579335, 580520), bringing to four the number of districts where the species has been collected (Table 3).

Natural history. *Cryptoblepharus leschenault* is an infrequently encountered species, but where it occurs it may be relatively abundant but difficult to capture. Specimens would run rapidly up the trunks of large hardwood trees, from where they could usually only be captured using blowpipes. Despite intensive searches in many locations these small skinks appeared to be much more patchily distributed than the other tree-bole inhabiting lizards, the larger *Draco timoriensis* and *Lamprolepis smaragdina* cf. *elberti.* The two Nancuro specimens collected during Phase IV (2011) and Phase VII (2012) were also found on the boles of trees, 5.0 m and 3.0 m from the ground, respectively.

Figure 20 Adult male of *Cryptoblepharus leschenault* from 3 m above ground on the trunk of a tree in wet coastal forest at Nancuro (USNM 580520, Locality 20). Photo by Mark O'Shea.

Taxonomic comments. Prior to the initiation of this survey two species of *Cryptoblepharus* had been recorded from Timor Island, *C. leschenault* and *C. schlegelianus*. Whereas the former was only recently documented for Timor-Leste (Kaiser *et al.*, 2011), the latter is known only from Semau, a small island off West Timor, where it apparently occurs in sympatry with *C. leschenault* (Brongersma, 1942). The dorsal pattern of *C. leschenault* consists of a dark background with a pair of narrow light dorsolateral stripes from snout to tail and a narrow light vertebral stripe from the snout to a point anterior to the forelimbs, where it then splits, in the shape of a tuning fork, to continue to the tail as a pair of even narrower paravertebral stripes. The pattern of *C. schlegelianus* comprises a pale background without a vertebral stripe, but with a pair of relatively broad, pale dorsolateral stripes above a narrower pair of dark narrow stripes that continue to the tail (Horner, 2007). Without the benefit of a detailed review of available material, we are unconvinced that *C. schlegelianus* is present in Timor-Leste; the species has only been verified for Semau Island, in the absence of actual specimens from the western end of Timor (Horner, 2007; Mertens, 1931), although a very similar, perhaps conspecific form is present in Timor-Leste (see account of *C.* cf. *schlegelianus* below).

Cryptoblepharus sp. 'Bakhita' [V]

Common names. (E) Bakhita snake-eyed skink. (G) Bakhita-Schlangenaugenskink. (T) Mamór matan samea bakhita (mamór = skink, matan = eye, samea = snake). The common name 'Bakhita' is used in reference to the Sta. Bakhita Mission, the location from which our exploration of the nearby Meleotegi River habitat originated.

Identification. This hitherto undescribed species of

Cryptoblepharus (Figure 21) has a dorsal stripe pattern similar to that of *C. leschenault*, but with a critical difference. The dorsal pattern of *C. leschenault* consists of a black background with a pair of narrow light yellow dorsolateral stripes from snout to tail and a yellow vertebral stripe, from the snout to a point anterior to the forelimbs, where it then splits into two narrower paravertebral stripes that continue to the tail, the overall impression being of a 'tuning-fork' pattern. In the two Meleotegi specimens, the vertebral stripe does not fork on the back and continues to the tail as a single stripe.

Known distribution. During Phase II (2010) a single specimen of *Cryptoblepharus,* collected from a tree on the Meleotegi River, near the Sta. Bakhita Mission (Eraulo, Ermera District; Locality 8), was considered sufficiently distinct from known species (*C. leschenault* and *C. schlegelianus*—see Taxonomic comments below) to warrant recognition as a third Timorese species, pending the collection of additional material.

New localities. During Phase V (2011) a second voucher (USNM 579472) was obtained from the same locality as in Phase II.

Natural history. With only two specimens known, our knowledge of this species' natural history is obviously very scant. Both specimens were discovered at a considerable height above ground on the trunks of large trees (as high as 7 m), and their somewhat jerky movements and body aspect remind us of other small tree-dwelling skinks in Southeast Asia, such as *Lipinia vittigera* (Boulenger, 1894). Both individuals appeared to be foraging on the bark surface when first seen, moving downwards along the tree trunk. When disturbed they reversed course and began moving back up the tree, though unhurriedly and once again appearing to forage. Specimens of both *C. leschenault* and *Cryptoblepharus* sp. 'Bakhita' are infrequently encountered, and when seen appear as individual lizards without conspecifics present, in contrast to *C.* cf. *schlegelianus*.

Taxonomic comments. The presence/absence and condition of various types of dorsal and lateral stripes is an important characteristic in the recognition of *Cryptoblepharus* species, with a number of species (Horner, 2007) exhibiting the 'tuning-fork' vertebral stripe pattern. These include *C. leschenault* from Timor and Flores and *C. balinensis* Barbour, 1911 from Bali. Other taxa exhibit a non-forking vertebral stripe, including *C. balinensis sumbawanus* Mertens, 1928 from Sumbawa, *C. renschi* Mertens, 1928 from Sumba and Komodo, and *C. keiensis* (Roux, 1910) from the Kei Islands. All of the aforementioned taxa occur at elevations up to 500 m, and in this assemblage highland forms (above 800 m) are uncommon. The presence of a population of *Cryptoblepharus* in the highlands of Timor exhibiting the non-forked vertebral pattern on a dark background is therefore indicative of a species undescribed so far (Kaiser *et al*., in prep.).

Cryptoblepharus cf. *schlegelianus* [V, VII–VIII]

Common names. (E) Timor north coast snake-eyed skink. (G) Schlegel-Schlangenaugenskink. (T) Mamór matan samea tasi ibun utara (mamór = skink, matan = eye, samea = snake, tasi ibun utara = north coast).

Identification. Differentiation of this coastal form (Figure 22) from both other species of *Cryptoblepharus* so far found in Timor-Leste (*C. leschenault, Cryptoblepharus* sp. 'Bakhita') is quite simple, considering the absence of prominent yellow or cream dorsal stripes. Coastal specimens tend to be brown or black with broad (1.5–2.0 scales wide), lighter brown longitudinal dorsolateral stripes over a broader (3.0–4.0 scales wide), darker irregular stripe that occupies much of the upper flanks of the body. The mid-dorsal region is brown with lighter flecking on some of the keeled margins of the scales and occasional scattered dark-brown spots. Specimens from the Tasi Tolu series (Dili District; Locality 1) had more extensive dark markings that obscured the ground color and exaggerated the light brown dorsolateral stripes; one specimen was virtually melanistic.

Known distribution. *Cryptoblepharus schlegelianus* Mertens, 1928 is known from specimens collected on Semau Island, off the southwestern part of Timor, near the port of Kupang in West Timor, but we have been unable to find any specimens from Timor associated with this species name in museum collections. We are therefore unable to confirm the occurrence of *C. schlegelianus* on mainland Timor. Although Mertens (1928) listed the species for Timor in his original description, that listing is based on material the Senckenberg Museum (Frankfurt, Germany) obtained in an exchange from the collections at Gießen, Germany, in 1854. Given that the port of Kupang was the main shipping center in this region in the early part of the 19th century, and given that at least one other species' origin was in error based on shipping and not collection locality – *Malayopython timorensis* (Peters, 1876), which does not occur on Timor Island (Barker and Barker, 1996; O'Shea *et al.*, 2012) – we consider the provenance of the Gießen material problematic and wonder whether the distribution of *C. schlegelianus* actually includes Timor (see Taxonomic Comment below).

New localities. *Cryptoblepharus* cf. *schlegelianus*, was

Figure 21 Adult male of *Cryptoblepharus* sp. 'Bakhita' from 5 m above ground on the trunk of a large tree in coffee forest at the Meleotegi River (USNM 579181, Locality 8). Note the absence of a forked line pattern, unlike that seen in *C. leschenault*. Photo by Mark O'Shea.

Figure 22 Adult individual of *Cryptoblepharus* cf. *schlegelianus* from the rocky shore at Tasi Tolu, Dili (USNM 580513, Locality 1). Photo by Mark O'Shea.

sampled as small series from each of three northern coastal locations. During Phase V (2011) a voucher series was collected on the wharf at Com (Lautém District; Locality 26; USNM 579455–71), in the final days of Phase VII (2012) a second voucher series was collected along the rocky beach at Tasi Tolu, near Dili (Dili District; Locality 1; USNM 580512–19), and during Phase VIII (2013) we discovered a population on the other side of Dili, below the Cristo Rei monument (Dili District; Locality 2; USNM 581114–27).

Natural history. These skinks were found in densely populated colonies, exclusively in locations right at sea level. At Com (Locality 26) they were found hiding in cracks on the sloping concrete of the wharf walls, or hunting in the flotsam, rocks, coral debris, and seaweed below the wharf walls. Much of this foraging activity was in the saltwater splash zone and while the animals seemed unperturbed by the spray, they actively avoided swells. Individuals were more commonly encountered on the landward, more protected inner side of the wharf but were also in evidence on the seaward, outer wall, where they were much more exposed to wave activity. At Tasi Tolu (Locality 1) skinks were found in almost an identical scenario as in Com, on a wharf and on the rocky shore right at sea level. Near Cristo Rei (Locality 2), individuals were encountered on large boulders, in rocky crevices, as well as in the pebbles of the splash zone.

Cryptoblepharus cf. *schlegelianus* occurs at much greater densities than either *C. leschenault* or *Cryptoblepharus* sp. 'Bakhita' and obviously has a much different ecological niche. It displays a propensity to forage in the saltwater splash zone, where it will have access to terrestrial arthropods feeding on exposed littoral vegetation as well as tidal invertebrates, and where the food supply would permit the observed population densities.

Taxonomic comments. In general appearance, specimens of *C.* cf. *schlegelianus* resemble dark specimens of *C. schlegelianus* from Semau. However, differences in pattern, scalation, and ecology (HK, pers. obs.), as well as the geographic separation between populations in Timor-Leste and the southwestern end of Timor Island where Semau is situated, lead us to question whether the form found in Timor-Leste is indeed conspecific with *C. schlegelianus*. We therefore conservatively assign the name *C.* cf. *schlegelianus* to this form.

Genus *Eremiascincus* [IV–VIII]

Common names. (E) Night Skinks. (G) Glatte Nachtskinke. (T) Mamór kalan (mamór = skink, kalan = night).

Known distribution. Night skinks (genus *Eremiascincus*; Figure 23) have been collected on most phases of the project, but their status and identity has been the source of some confusion (see Taxonomic comments below). During Phases I and II, species of *Eremiascincus* were documented from four mainland districts (Ainaro, Ermera, Lautém, and Manufahi; see Kaiser *et al.*, 2011; O'Shea *et al.*, 2012), followed during Phase VI by the first specimens collected on Ataúro Island (Dili District; see Kaiser *et al.*, 2013b). *Eremiascincus* is therefore known from five districts of Timor-Leste to date.

New localities. During Phases IV–VIII *Eremiascincus* was again encountered and collected and those records pertaining to mainland Timor-Leste and Jaco Island are included here. Additional vouchers were obtained from the Meleotegi River (Ermera District; Locality 8; USNM 579474, 579760, 580521–24, 581128–39), Maubisse

(Ainaro District; Locality 15; USNM 579339–45), and Mirbuti village, near Same (Manufahi District; 17; USNM 579336–38). New records for Lautém District were supported by voucher material from Raça (Locality 27; USNM 581762) and Jaco Island (Locality 30; USNM 579473), the former only as an autotomized tail as the skink escaped into a limestone hole.

Natural history. Individuals of *Eremiascincus* were invariably found by turning over rocks and logs, in both moist and dry substrate, and never out in the open, either during the day or by night. It appears that these animals require shelter by day and are fairly indiscriminate how they find it. We have found some individuals in man-made rock piles and underneath large flat rocks near human habitations, while elsewhere (such as in the dry coastal forest on Jaco Island; Locality 30) we encountered them under rotten logs. The daytime refuges also appear to require a certain level of moisture.

Taxonomic comments. The genus *Eremiascincus* was initially formed for a group of closely related Australian sand-swimming skinks nested within the genus *Sphenomorphus* (Greer, 1979). It was then expanded to include a number of taxa from the genus *Glaphyromorphus* (Mecke *et al.*, 2009), including the Lesser Sunda taxa *E. antoniorum* (Smith, 1927), *E. butlerorum* (Aplin *et al*., 1993), *E. e. emigrans* (van Lidth de Jeude, 1895), *E. e. wetariensis* (Mertens, 1928), and *E. timorensis* (Greer, 1990). Three *Eremiascincus* species have been documented for Timor so far (*E. antoniorum, E.* cf. *emigrans,* and *E. timorensis*), but the taxonomy of *Eremiascincus* populations in the Lesser Sunda Islands, let alone Timor Island, is far from resolved. All previous reports of *E. antoniorum* and *E. timorensis* are from the central mountains of West Timor (Aplin *et al.*, 1993; Greer, 1990; Smith, 1927), whereas reports of *E.* cf. *emigrans* are from the south coast at Loré, Lautém

Figure 23 Representatives of populations of *Eremiascincus*. Images (A)–(B) show the *timorensis* morphotype, (C) depicts *Eremiascincus* 'Ermera', and (D) and (E) show specimens of the *emigrans* morphotype. (A) Adult male *E.* cf. *timorensis* (SVL = 96 mm) from under a man-made rock pile at the edge of the Meleotegi River (USNM 579760, Locality 8). (B) Adult male *Eremiascincus* sp. 'Montane' (SVL = 72 mm) from the grounds of the Portuguese Pousada at Maubisse (USNM 579339, Locality 16). This population has undetermined species affinities and may represent an undescribed species. (C) Adult male *E.* 'Ermera' (SVL = 53 mm) from a dry bamboo root mass alongside the Meleotegi River (USNM 580522, Locality 8). (D) Adult individual of *Eremiascincus* sp. 'Lautém' (SVL = 51 mm) from underneath palm leaf litter in a near-coastal habitat (USNM 579194, Loré, Lautém District; see Kaiser *et al*., 2011). (E) Adult individual of *Eremiascincus* sp. 'Jaco' (SVL = 39 mm) from underneath a coralline rock in dry coastal forest (USNM 579473, Locality 30). Photos by Mark O'Shea.

District (Kaiser *et al.*, 2011).

After collecting over sixty voucher specimens from five districts at elevations ranging from 10–2046 m we believe that as many as five species of *Eremiascincus* are present in Timor-Leste. Overall morphology ranges from large species with stout limbs and a relatively short trunk (a *timorensis* morphotype), to small-sized species, with reduced limbs and an elongated body that are superficially similar to *E. emigrans*.

Among the forms with the *timorensis* morphotype are those exhibiting an orange venter, but with the ventral coloration not extending onto the chin region (Figure 23A). These are the largest, most strongly built forms in Timor-Leste, and they have been collected on the Meleotegi River at an elevation around 1180 m (Ermera District; Locality 8); they are herein listed as *Eremiascincus* cf. *timorensis*. A second member with this stout morphology is a slightly smaller, more slender, yellow-bellied form, whose ventral coloration extends across the gular region to the snout. This form is found at other highland locations (e.g., Maubisse, Ainaro District; Locality 16), the slopes of nearby Mt. Ramelau, and at various locations around Same (Manufahi District; Locality 17); it might be conspecific with *Eremiascincus* cf. *timorensis* or represent an undescribed taxon, and it is listed here as *Eremiascincus* 'Montane' (Figure 23B). A third highland taxon, similar to *E. antoniorum* in some respects (Figure 23D), has a yellow venter that does not extend into the gular region, and displays a more slender and elongated body than forms with the *timorensis* morphotype. This form is known from the Meleotegi River and surrounds (Ermera District; Locality 8), and we did not find it anywhere else in Timor-Leste. We refer to this species as *Eremiascincus* 'Ermera.' In each case, both male and female specimens show the respective ventral coloration, but intraspecific variation or color change related to reproductive readiness cannot be excluded at this point.

The *emigrans* morphotype appears to inhabit only lowland habitats in Timor-Leste (below 500 m elevation, and most frequently near the coast), which is consistent with the distribution of *E. emigrans* complex forms on other islands in the region. The Lautém taxon listed by Kaiser *et al.* (2011) is referred to as *Eremiascincus* sp. 'Lautém' here (Figure 23C), and this population may inhabit the limestone habitats that make up the eastern end of Timor Island, at elevations from sea level up to 462 m. The mainland Lautém form is similar to, and may be conspecific with, a population found on Jaco Island, which we call *Eremiascincus* 'Jaco' (Figure 23E). Finally, the population found at coastal localities on northeastern Ataúro Island (Dili District) is referred to as *Eremiascincus* 'Ataúro' (Kaiser *et al.*, 2013b), a taxon certainly different from *E. emigrans wetariensis* from nearby Wetar Island. A comprehensive study of these forms is currently underway (Mecke *et al.*, in prep.).

Eutropis cf. *multifasciata* [IV, VI–VII]

Common names. (E) Common Sun Skink, Many-lined Sun Skink. (G) Vielstreifen-Skink. (T) Mamór loro (mamór = skink, loro = sun).

Known distribution. *Eutropis* cf. *multifasciata* (Figure 24) has so far been documented from Ermera, Lautém, and Oecusse Districts, on the mainland (Kaiser *et al.*, 2011; O'Shea *et al.*, 2012; Sanchez *et al.*, 2012), and also from Ataúro Island (Kaiser *et al.*, 2013b).

New localities. During Phases IV–VII additional vouchers of *Eutropis* cf. *multifasciata* were collected from the Meleotegi River and Sta. Bakhita Mission (Ermera District; Locality 8; USNM 579787–88), while first district records were obtained for Manufahi District, at Betano "wet site" (Locality 18; USNM 579347–49), and for Manatuto District, in the Nancuro coastal forest at Natarbora, 8 km south of Umaboco (Locality 20; USNM 580525–26), bringing to six the districts of Timor-Leste where this taxon has been documented.

Natural history. Skinks of this species were most frequently seen moving around in the open during daytime and were found in a variety of habitats, including rain and dry forests, grasslands, as well as coastal environments. We also encountered them on paths, roadways, and patios near human habitations. A single juvenile specimen was found underneath a flat rock along the Meleotegi River (Locality 8).

Taxonomic comments. We refer to the population of *Eutropis* in Timor-Leste as *E.* cf. *multifasicata* because other than a resemblance to other Southeast Asian populations of the *E. multifasciata* species complex, there is insufficient evidence to align it more closely with any other island or mainland population. The taxon currently referred to as *E. multifasciata* (Kuhl, 1820) has a very wide distribution, from the Southeast Asian mainland down to Timor and east to the Philippines. It is in dire need of taxonomic revision and once this has been carried out it may be possible to be more precise about the status of the Timorese populations. In the Lesser Sunda region, the population on Bali currently has subspecific status as *E. m. balinensis* (Mertens, 1927).

Lamprolepis smaragdina cf. *elberti* [IV–VII]

Common names. (E) Emerald or Green Tree Skink.

Figure 24 Adult male *Eutropis* cf. *multifasciata* from a sun spot in leaf litter in wet coastal forest at Nancuro (USNM 579346, Locality 20). Photo by Mark O'Shea.

(G) Elbert-Smaragdskink. (T) Mamór modok (mamór = skink, modok = green).

Known distribution. *Lamprolepis smaragdina* cf. *elberti* (Figure 25) has been documented from Baucau, Lautém, Oecusse, and Viqueque Districts on the mainland (Kaiser *et al.*, 2011; O'Shea *et al.*, 2012; Sanchez *et al.*, 2012), and also from Ataúro Island (Kaiser *et al.*, 2013b).

New localities. During Phases IV–VII we added further records for Lautém District, from Raça (Locality 27; USNM 579357–58) and the Pousada de Tutuala (Locality 28; USNM 579475–76), as well as the first district records for Manatuto District, from the Nancuro coastal forest at Natarbora (8 km south of Umaboco, Locality 20; USNM 579350); for Manufahi District, from Betano ("wet site," Locality 18; USNM 579356); for Covalima District, in western Suai (Locality 13; USNM 579351–52); and for Bobonaro District, from a heavily grazed forest at Fiuren (near Balibo, Locality 9; USNM 580527–28), bringing the total number of districts where *L. s.* cf. *elberti* has been documented to nine.

Natural history. Specimens of *L. s.* cf. *elberti* were primarily collected by blow-piping or hand-slapping from the trunks of trees. The majority of individuals was encountered fairly high above ground level (3–7 m) on tree trunks with varying diameters (> 20 cm). This position is used as a perch for basking, as a base for foraging, and as an eyrie from which to observe the surroundings. Our earlier observation (Kaiser *et al.*, 2011) of site fidelity for this skink appears to be confirmed by additional observations: specific individuals seem to remain on the same tree during a days-long period of incidental observations.

Taxonomic comments. Preliminary examinations of the subspecies of *Lamprolepis smaragdina* undertaken by HK and AK revealed that the form encountered on Timor would most likely be *L. s. elberti* (Sternfeld, 1918), a subspecies described from Wetar Island in the Inner Banda Arc, across the Wetar Strait from Timor. However, our examination of the holotype and topotypic specimens of that subspecies has revealed differences in color pattern and pholidosis, and we therefore find the use of *L. smaragdina* cf. *elberti* the most appropriate approach. It is interesting to note that coloration of this skink is quite variable and may deviate considerably from the emerald-green suggested by the name. While there are no individuals with entirely green body coloration in Timor-Leste, we have seen individuals possessing a bright green anterior half of the body that transforms in the medial section of the body into a "pepper-and-salt pattern" on a bronze-brown background (Figure 25A). This dorsal "pepper-and-salt pattern" still has the remnants of green coloration ventrally and on to the lower lateral parts of the body, but turns entirely bronze-brown on the tail. The alternative form is one devoid of any green coloration,

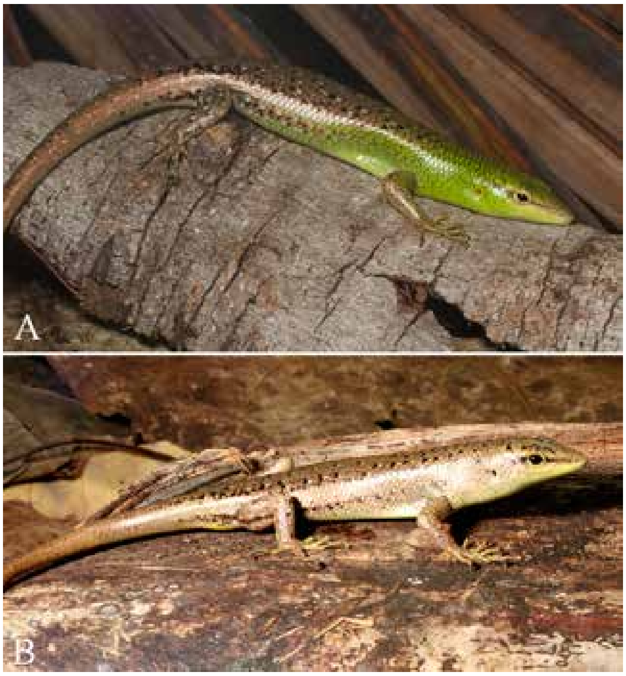

Figure 25 Individuals of *Lamprolepis smaragdina* cf. *elberti* showing variation in dorsal coloration. This is not an example of sexual dimorphism, as both male and female individuals may possess either color pattern. Both specimens shown here were seen on tree limbs in their respective habitats. (A) Adult male presenting the two-part color pattern with a green anterior half of the body and a pepper-and-salt pattern on bronze background covering the posterior half and the tail (USNM 579213, Viqueque town, Viqueque District; see Kaiser *et al.*, 2011). (B) Adult male from coastal wet forest at Nancuro presenting the unicolor dorsal pattern that includes light green portions of the venter and the bronze dorsal coloration with pepper-and-salt patterning along the entire body (USNM 579350, Locality 20). Photos by Mark O'Shea.

with perhaps only a greenish sheen on the venter (Figure 25B).

Genus *Sphenomorphus* [IV–VIII]

Common names. (E) Forest or Wedge skinks. (G) Waldskinke. (T) Mamór ai laran (mamór = skink, ai laran = forest).

Known distribution. The genus *Sphenomorphus* (Figure 26) has so far been recorded from four districts (Ainaro, Ermera, Lautém, and Manufahi; see Kaiser *et al.*, 2011; O'Shea *et al.*, 2012).

New localities. During Phases IV–VIII additional records for the genus *Sphenomorphus* were obtained for Lautém District at Raça (Locality 27; USNM 579371–72, 579477–81), the Mainina sink-hole (Locality 29; USNM 579482–83), and Jaco Island (Locality 30; USNM 579484–86); for Ermera District (Meleotegi River, Locality 8; USNM 579487–89, 579765–66, 580539); and for Manufahi District (Betano "wet site," Locality 18; USNM 579369–70). First district records for Manatuto District are supported by voucher specimens from Nancuro (Natarbora, 8 km S of Umaboco, Locality 20; USNM 579359–67, 580529–33, 580534–38), and for Baucau District from the Japanese caves at Venilale (Locality 22; USNM 580540–41), increasing the number of districts from which *Sphenomorphus* skinks have been documented to six. The genus has yet to be documented for Ataúro Island.

Natural history. Among the forms of *Sphenomorphus* found in Timor-Leste, it may be possible to declare a distinction between lowland and highland forms. Some lowland forms (including those in the wet coastal forest of Nancuro and Betano as well as the dry forest on Jaco Island) are likely closely related to or identical with *S. melanopogon* (Duméril and Bibron, 1839). We have encountered these fairly robust and long-limbed animals

Figure 26 Representative individuals of several different phenotypes of forest skinks, genus *Sphenomorphus*. (A) Male individual of *S. melanopogon* (SVL = 69 mm) from a root buttress in coastal wet forest at Nancuro (USNM 579364, Locality 20, near sea level). (B) High-altitude color variation is seen in this adult *S.* cf. *melanopogon* (SVL = 64 mm) found on the trunk of a tree in coffee forest (USNM 579368, Locality 17 at 1200 m elevation). (C) Male individual of *Sphenomorphus* sp. 'Highland large' (SVL = 55 mm) from the wall of a limestone cave near Raça (USNM 579479, Locality 27 at 550 m elevation). (D) Male specimen of the Jaco Island population of *Sphenomorphus* (SVL = 75 mm, USNM 579486, Locality 30). Individuals of this population are seen quite commonly running across the leaf litter covering the limestone karst on their way into refugia that run deep into the rock. (E) Male individual of *Sphenomorphus* sp. 'Highland small' (SVL = 42 mm) from the leaf litter outside the man-made caves at Venilale (USNM 580540, Locality 22). Photos by Mark O'Shea.

most frequently in a head-down posture on the trunks of trees or root buttresses, from where they can launch themselves quickly and escape into the underbrush. We also found juvenile *Sphenomorphus* skinks in all areas where we recorded this genus, attesting to a fairly high reproductive rate and a high population density. In contrast, there are fewer individuals of the highland form found, for example, in the coffee forest along the Meleotegi River (Locality 8) or in the drier forest of the karst plateau of Lautém District (e.g., in Raça and Mainina, Localities 27 and 29, respectively). In addition, we have seldom encountered juveniles of this latter form (or these forms), and their bodies have a more vivid coloration in general, and on the belly in particular. Until a thorough taxonomic treatment is concluded, it is not feasible to provide detailed, taxon-specific data regarding the natural history.

Taxonomic comments. The taxonomy of *Sphenomorphus* in Timor-Leste appears to be even more complex than that of *Eremiascincus*. We may have collected specimens belonging to different taxa but are unable to attribute them to any known species at this time. Shea (2012) investigated the Lesser Sunda and New Guinea populations of *Sphenomorphus melanopogon*, and selected as the lectotype for this species a syntype collected by Péron on Timor, presumably in West Timor. This confirms that *S. melanopogon sensu stricto* is a Lesser Sunda-Moluccan endemic, and New Guinean populations formerly considered conspecific with *S. melanopogon* are now treated as *S. meyeri* (Doria, 1874). Some of our lowland specimens from Lautém and Manatuto Districts may be referable to *S. melanopogon* (Figure 26A), but there remain some differences in coloration and *gestalt* (Figure 26B). Those with a similar overall morphotype but different coloration collected on the Meleotegi River and on the Lautém karst plateau appear distinct and are referred to as *Sphenomorphus* sp. 'Highland large' (Figure 26C), but once again, there is merely similarity but not identity with forms from Jaco Island (Figure 26D). One other, small and slender form from the Venilale caves, with a very distinct pattern of stripes and blotches, may be referred to as *Sphenomorphus* sp. 'Highland small' (Fig, 26E). All other specimens, including those from the Meleotegi River collected during Phases I and III, are currently retained as *incertae sedis* within *Sphenomorphus*.

Family Varanidae—Monitor Lizards

Varanus timorensis Gray, 1831 [IV, VI–VIII]

Common names. (E) Timor Tree Monitor, Spotted Tree Monitor. (G) Timor-Waran. (T) Lafaek rai-maran (lafaek = crocodile or large lizard, rai = dirt, maran = dry).

Known distribution. *Varanus timorensis* (Figure 27A) is the only varanid currently known to occur on Timor and it was recorded from Lautém during Phase I and the north coast of Manatuto District during Phase III (Kaiser *et al.*, 2011; O'Shea *et al.*, 2012). Bethencourt Ferreira (1898) also reported specimens collected by Rafael das Dôres in Liquiça District, at Lahane, Fatunaba, and Maubara, which were subsequently lost to a fire at the Museu Bocage in Lisbon.

New localities. Phases IV, VI, and VII produced additional records from northern Lautém and Manatuto Districts, and new records from Baucau District (along the coastal road; USNM-HI 2831–33), Dili District (Timor Lodge Hotel; Locality 1; USNM-HI 2834), and Covalima District (northwest of Maubesi, near Tilomar; Locality 15; USNM 579389). Since this is a CITES protected species we have voluntarily limited our collecting to either tissue samples or road-killed specimens, where these were fresh enough to be sampled. Live specimens were collected, photographed *in situ* and released. The exception to this

Figure 27 (A) Adult *Varanus timorensis* (not vouchered) displaying the characteristic morphology and coloration seen in individuals encountered all along the northern low-lying coastal habitats in Timor-Leste. (B) An unusual specimen we refer to as *V.* cf. *timorensis* due to its aberrant color pattern, habitat, and behavior. We found this specimen ca. 5 m high on a roadside tree at an elevation of 520 m (USNM 579389, Locality 15). Photo by Mark O'Shea.

was the specimen from Tilomar (Figure 27B), given that its morphology, color pattern, and occurrence at higher altitude (520 m) gave the appearance that it might be a specimen of *V. auffenbergi* Sprackland, 1999, a species described from neighboring Roti Island. However, according to Böhme (2003) and Moldovan (2007), the status of *V. timorensis* populations on Timor and neighboring Roti and Kisar is still unresolved. *Varanus timorensis*, inclusive of the unusually colored Tilomar specimen, is now known to occur in five mainland districts at an elevational range from 6 m to as high as 520 m.

Natural history. Most of our observations of this species have been fleeting glimpses of lizards dashing across roads, or through the examination of road-killed specimens. Lizards appear to be particularly abundant in the vegetation associated with active and unplanted rice paddies, but we believe them to be present in essentially any lowland habitat. Even in residential areas, such as the compound of the Timor Lodge Hotel in Dili (Locality 1), these lizards are able to make a living, perhaps attracted by the presence of small vertebrates and invertebrates associated with human habitations.

Taxonomic comments. Various varanids have been listed as present on Timor by previous authors, including *Varanus timorensis, V. indicus,* and *V. salvator. Varanus timorensis* is a tree monitor species present on both the northern and southern coasts but the species is also found further inland, although it has yet to be recorded at or above 600 m. The specimen from Covalima is the only specimen found an appreciable distance (approx. 12 km) inland and since this specimen differed slightly in appearance from the usual *V. timorensis* and is perhaps conspecific with *V. auffenbergi*, it was tentatively listed as *V.* cf. *timorensis*. *Varanus indicus* is probably recorded from Timor in error, as it is known to be a mangrove- and estuarine-dwelling species from New Guinea and the Moluccan islands of Aru, Kei, Seram, and Buru (Böhme, 2003). *Varanus salvator* is not known from the main island of Timor but a population of *V. salvator*-like lizards has been documented from Ataúro Island (Kaiser *et al.*, 2013b).

SNAKES (ORDER SERPENTES)

Family Acrochordidae—Filesnakes

Acrochordus granulatus (Schneider, 1799) [VI]

Common names. (E) Little filesnake. (G) Indische Warzenschlange, Zwerg-Warzenschlange. (T) Samea kulit krukut (samea = snake, kulit = skin, krukut = rough).

Identification. Due to their excessively baggy, highly tuberculate skin, the three extant members of the genus *Acrochordus* are instantly recognizable, and afforded common names such as "wartsnake," "filesnake," or "elephant's trunk snake" (this latter the case for the larger freshwater species). *Acrochordus granulatus* (Figure 28A) is the smallest member of the genus, with a maximum length of 1.6 m (McDowell, 1979), although most specimens are less than 1.0 m long.

Known distribution. One historic locality record for the occurrence of *A. granulatus* exists for Timor-Leste (Table 4), documented from a single specimen collected by Francisco Newton, at "Dilly" (= Dili, Dili District, Locality 1), and reported by Bethencourt Ferreira (1898) as present in the Museu de Lisboa; this specimen was lost in the museum fire of 1978. *Acrochordus granulatus* is also known from West Timor (from Kupang and Tuakdale Lagoon; de Lang, 2011).

New localities. One individual (Figure 28B) was collected by AVR in the mangrove swamp at Metinaro (Dili District; Locality 3; USNM-FS 255498; field tag only, specimen to remain on exhibit in Timor-Leste; USNM-HI 2825).

Natural history. The unusual tuberculate skin is an essential aid for the identification of these snakes in Timor-Leste. *Acrochordus* are ambush predators or active foragers, that grasp and coil around their slippery fish prey, with the tubercles maintaining a strong and inescapable, constriction-like grip as the fish is maneuvered into a head-first ingestible position. It has also been suggested that the tuberculate skin may prevent the snakes from drying out if exposed to the air (Greer, 1997), and tubercles may also serve a sensory purpose in prey location (McDowell, 1979; Shine and Houston, 1993).

Filesnakes are completely aquatic, found in coastal, brackish and occasionally fresh water, being ill-adapted to movement on land due to their extremely small ventral scales and flabby bodies. What makes locomotion laborious and impossible in a terrestrial environment enables filesnakes to become efficient inhabitants of aquatic environments as the body can be flattened laterally as a broad ribbon for effortless swimming. Other notable external aquatic features include dorsally positioned valvular nostrils, small eyes, and a row of small, tight-fitting supralabial scales along the lips, perhaps to reduce water ingress into the oral cavity. More subtle physiological aquatic adaptations include a low metabolic rate and almost twice the blood content of terrestrial snakes of similar size, which, coupled with high levels of oxygen-carrying red blood cells, have enabled captive specimens of *A. granulatus* to remain submerged for up

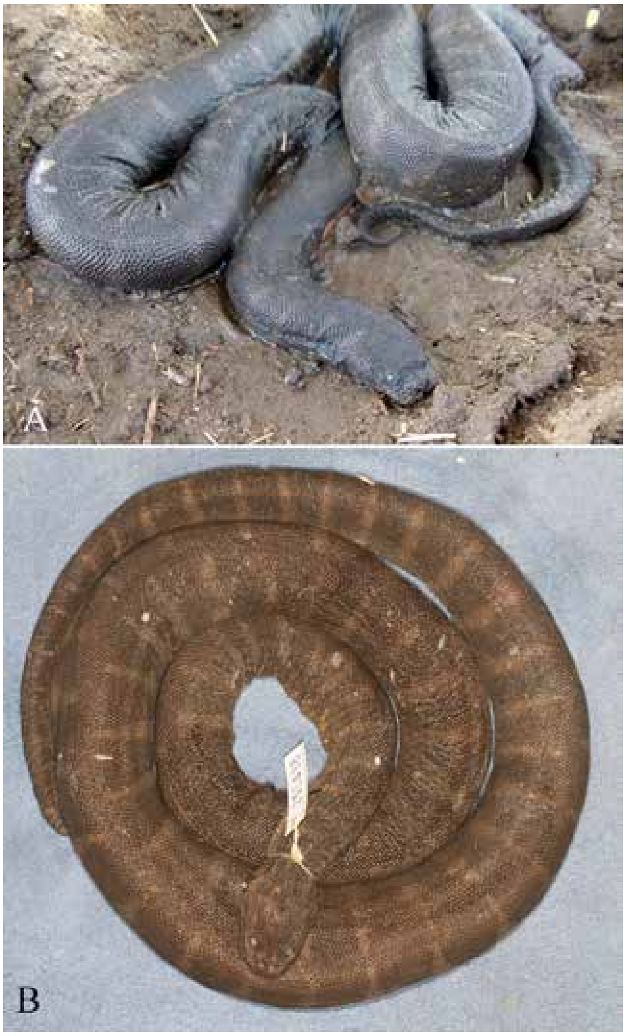

Figure 28 Individual of *Acrochordus granulatus* from Metinaro Swamp (USNM-FS 255438, Locality 3). (A) Photo taken by Agivedo Varela Ribeiro right after capture. (B) Specimen after preservation shows a color shift to brown, indicating the characteristic banding pattern of the species. Photo by Mark O'Shea.

to 139 minutes (Whitaker and Captain, 2004). Filesnakes may remain motionless for prolonged periods of time, whether resting or in ambush, using their prehensile tails to maintain an anchorage against prevailing currents.

Acrochordus granulatus is probably the most adaptable of *Acrochordus* species, occurring in marine, brackish, and freshwater habitats, and although there is one record of a specimen from an elevation of 90 m (McDowell, 1979), this is a low elevation species. Although it is most often associated with mangrove swamps and turbid river estuaries, this species is also encountered in shallow, crystal-clear coral reef environments (MOS, pers. obs). *Acrochordus granulatus* is also the most widely distributed member of the genus, occurring from the western coastline of India, east to Indochina, southeast to northern Australia, and eastwards to the Solomon Islands. It has been collected 10–15 km from shore and at a depth of 20 m (Stuebing and Voris, 1990; Voris and Glodek, 1980), but it is considered an inshore rather than an open water species.

Prey of *A. granulatus* is composed entirely of inshore or estuarine fish (McDowell, 1979); the presence of crabs or snails in gut contents is likely attributable to secondary ingestion (Greer, 1997). *Acrochordus granulatus* has been observed foraging actively, swimming and probing the substrate for hidden prey (Gorman *et al.*, 1981). Both the chemosensory forked tongue and tactile sensory bristles on the tubercles may be utilized in prey location and capture (Greer, 1997), resulting in the opportunistic capture of fish coming into contact with a resting filesnake as much as the active foraging for prey.

In contrast to its two larger, primarily nocturnal, relatives, *A. granulatus* is equally active both by day or night (Greer, 1997), although in our experience (MOS, pers. obs.) they are more frequently encountered surfacing for air in estuarine habitats after dark. *Acrochordus* is a viviparous genus, with female *A. granulatus* producing 1–12 neonates (McKay, 2006).

Taxonomic comments. In the historic literature, *A. granulatus* is frequently referred to as *Chersydrus granulatus* (e.g., Schneider, 1801; Merrem, 1820; Boulenger, 1893; de Rooij, 1917), distinct from the only other known species at the time, the much larger *A. javanicus* Hornstedt, 1787, which was itself split into two species by McDowell (1979): the freshwater-brackish Southeast Asian *A. javanicus* and the entirely freshwater Australo-Papuan *A. arafurae* McDowell, 1979.

Despite its huge geographical range, and the antiquity of the family, with species divergence times of 20–16 Mya, a recent study (Sanders *et al.*, 2010) found no evidence that *A. granulatus* might be a composite of several different species. The family and genus are remarkably species-poor with one extinct species, *A. dehmi* Hofstetter, 1964 described from Pakistan (Head, 2005; Hoffstetter, 1964).

Family Colubridae—Typical Snakes

Coelognathus subradiatus (Schegel, 1837) [VI–VIII]

Common names. (E) Lesser Sunda Racer, Lesser Sunda Trinket Snake, Timor Racer. (G) Indonesische Kletternatter. (T) Samea laho (samea = snake, laho = rat).

Known distribution. During Phases I and III we collected two specimens of *Coelognathus subradiatus* (Figure 29) in Baucau and Viqueque Districts, both on the outskirts of the towns bearing the districts' names (Kaiser *et al.*, 2011; O'Shea *et al.*, 2012), and recorded a third specimen as a roadkill on the Atambua-Kefamenanu road in West Timor

Table 4 Records of snake species for the districts of Timor-Leste. Black circles indicate previously known records, red circles denote new records. Black open circles are literature records. Records listed in grey denote literature records from West Timor, with closed circles representing road-killed specimens we found and open circles representing known museum specimens. Check marks denote encounters with positive identifications, but without voucher specimens.

Taxon	District															References*
	Aileu	Ainaro	Baucau	Bobonaro	Covalima	Dili (Timor)	Dili (Ataúro)	Ermera	Lautém	Liquiça	Manatuto	Manufahi	Oecusse	Viqueque	W.Timor	
ACROCHORDIDAE																
Acrochordus granulatus						🔴									○	4,6,10
COLUBRIDAE																
Coelognathus subradiatus subradiatus			●			🔴	●		○	🔴	🔴			●	●	1,2,4–6,10
Dendrelaphis inornatus timorensis						○	√		●		√	🔴		●	○	1,5,6
Lycodon capucinus	🔴		🔴	🔴	🔴	🔴	●		🔴			●			●	1,2,4–6
Lycodon subcinctus									🔴			●				1,4,6
Stegonotus sp.											🔴	🔴				4
CYLINDROPHIDAE																
Cylindrophis cf. *boulengeri*			○						🔴						○	4,6,8
ELAPIDAE																
Laticauda colubrina						🔴	√						●			3,4
HOMALOPSIDAE																
Cantoria violacea						○										6,7,10
Cerberus rynchops			●	○		○						🔴			○	1,2,4,6
Fordonia leucobalia						🔴									○	4,6
PYTHONIDAE																
Liasis mackloti mackloti			●		🔴	●									●	2,4
Malayopython reticulatus						●			○		🔴	🔴	●	●	○	2–4,6
TYPHLOPIDAE																
Indotyphlops braminus			🔴			🔴			🔴			●		●	○	1,4,6
Indotyphlops incertae sedis					🔴		●							🔴		1,4
Sundatyphlops polygrammicus			🔴						○			🔴				4,6,9
VIPERIDAE																
Trimeresurus insularis			●	🔴		○	●		●	○	🔴	🔴		●	●	1,2,4,6

[1] References are identified numerically as follows: 1 = Kaiser *et al*., 2011; 2 = O'Shea *et al*., 2012; 3 = Sanchez *et al*., 2012; 4 = this paper; 5 = Kaiser *et al*., 2013b; 6 = de Lang, 2011; 7 = de Rooij, 1917; 8 = Forcart, 1953; 9 = Barbour, 1912; 10 = Bethencourt Ferreira, 1898.

(O'Shea *et al*., 2012). A fourth specimen, from Ataúro Island, was documented elsewhere (Kaiser *et al*., 2013b). *Coelognathus subradiatus* was also reported from two Lautém locations, the towns of Lospalos and Muapitine, 7 km E of Lospalos (de Lang, 2011).

New localities. During Phase VII two further specimens were recorded, both as roadkills, one on the road from Baucau to Venilale, just south of Baucau (USNM-HI 2827), and on the road from Manatuto to Natarbora (USNM 580544), on the south side of the central mountain range. In March of 2011, HK visited Timor-Leste and photographed a road-killed individual on the road between Dili and Railaco, in Liquiça District (USNM-HI 2826a–c). During Phase VIII, one specimen was collected near the Dili port (USNM 581171). This specimen, together with the Liquiça and Manatuto records, constitute first district records, bringing to seven the districts for which *C. subradiatus* has been confirmed (Table 4).

Natural history. *Coelognathus subradiatus* is a

Figure 29 Adult male *Coelognathus subradiatus* collected at Palapasu, Dili (USNM 581171, Locality 1). Photo by Mark O'Shea.

crepuscular to nocturnal species that exhibits a considerable degree of habitat plasticity, occurring in a wide variety of environments across its Lesser Sunda range, which includes virtually every island from Lombok to Wetar and Timor, with the notable exception of Savu. Habitats range from coastal coconut plantations and low-lying steppe-grasslands to monsoon and montane rainforests, to elevations up to 1200 m (Schultz, 1996). Mertens (1930) also commented that this snake is often encountered in close proximity to human habitations, and this observation has been borne out by our own experiences on Timor (Kaiser *et al.*, 2011; O'Shea *et al.*, 2012). Although Schultz (1996) considered *C. subradiatus* to be primarily terrestrial, we obtained one particularly dark specimen (USNM 579779) on Ataúro Island (Kaiser *et al.*, 2013b) after it had escaped into a tree to a height of approximately 6 m, then leapt to the ground when pursued aloft.

The prey of *C. subradiatus* comprises primarily small mammals, such as rodents, which are killed by constriction by this relatively powerful, muscular species; birds may also be taken (Schultz, 1996). Auffenberg (1980) reported that juvenile Lesser Sunda racers on Komodo prey on geckos. A more catholic diet was reported by de Lang (2011), who listed "small mammals, birds, reptiles, amphibians, fish, and even insects." *Coelognathus subradiatus* is oviparous, but clutch size is largely unknown; Schultz (1996) discussed six hatchlings that emerged from a clutch of unknown size after having been laid in captivity by a wild-caught female.

When this species feels threatened it may elevate the anterior portion of its body into a vertical S-shape, inflate its neck, and make lunging strikes, biting freely if contact is made; being completely nonvenomous, this display is largely bluff.

Taxonomic comments. Bethencourt Ferreira (1897) described *Coluber melanurus* var. *timoriensis* (a synonym of *C. subradiatus*) from Timor, presumably from the Portuguese eastern end of the island, now Timor-Leste. This specimen was collected by Francisco Newton, who failed to provide a precise locality; it was lost in the Museu Bocage fire of 1978.

In the Lesser Sunda Islands there appear to be two different forms, which are referred to as "Groups" by Schultz (1996). Group 1 comprises slender-bodied snakes that achieve total lengths of 1200–1600 mm whereas Group 2 includes the more heavily-built snakes that achieve total lengths of 1500–2200 mm. Differences in patterning were noted by both Schultz (1996) and de Lang (2011). Racers found on Timor and the neighboring islands of Roti and Semau would fall within Group 1, whilst all other Lesser Sunda specimens would be part of Group 2. However, these groups have no taxonomic status and are purely subjective. A population of racers from Enggano Island (402.6 km^2), almost 1600 km west of the westernmost population of Lesser Sunda *C. subradiatus* on Lombok and separated by the island of Java, was for a time treated as a subspecies of *subradiatus*, *C. s. enganensis* (Vinciguerra, 1892), but it has lately been treated as a full species (Das, 2012; Wallach *et al.*, 2014).

***Dendrelaphis inornatus timorensis* Smith, 1927** [VI]

Common names. (E) Timor Bronzeback, Lesser Sunda Treesnake. (G) Timor-Bronzenatter. (T) Samea kotuk kór kafé (samea = snake, kotuk = back, kór kafé = brown).

Known distribution. During the early phases of the project (2009 and 2010) *Dendrelaphis inornatus timorensis* (Figure 30) was documented for Lautém and Viqueque Districts (Kaiser *et al.*, 2011; O'Shea *et al.*, 2012), whereas de Lang (2011) included Dili (Dili District) in its distribution. It is a species commonly documented in West Timor (Table 4).

New localities. The only voucher specimen of this species obtained during the later phases of the project was from the Betano "wet site" (Manufahi District; Locality 18; USNM 579378) on the southern coast. There were unconfirmed sightings of "treesnakes" tentatively identified as *D. i. timorensis* in the Nancuro coastal forest (Manatuto District; Locality 20) and on Ataúro Island (Dili District) during Phases IV and VI respectively, but no vouchers were obtained.

Natural history. This is a fast-moving and highly elusive diurnal species that often evades capture, either through speed or its ability to blend in with the vegetation when motionless. It is the only member of the genus

Figure 30 Individual of *Dendrelaphis inornatus timorensis* (sex not determined) collected from low shrubs by night (USNM 573686, Wailakurini, Viqueque District; see Kaiser *et al*., 2011). Photo by Mark O'Shea.

Dendrelaphis to occur on Timor and one of only two found in the Lesser Sunda Islands. Elsewhere in the Indo-Malayan region this is a commonly encountered and fairly well represented genus with numerous species in Southeast Asia and the Philippines, where they are known as "bronzebacks," and nine species occurring in New Guinea, the Kei Islands, Palau, the Solomon Islands, and Australia (van Rooijen *et al*., 2015), where they are known as "treesnakes."

Timorese *D. i. timorensis* inhabit wooded hill country with an understory of grass and often a geology of black limestone outcrops (de Lang, 2011), which is precisely the habitat in which one of us (AVR) observed a specimen that evaded capture on Ataúro Island (Kaiser *et al*., 2013b). Smith (1927) stated that *D. i. timorensis* occured at elevations from 100–800 m, but we have found this species to be most abundant right at sea level in Loré, Lautém District (USNM 573687–88), where two additional specimens evaded capture (Kaiser *et al*., 2011); another evaded capture at sea level in the coastal forest at Nancuro (Manatuto District; Locality 20).

Virtually no information exists regarding the natural history and biology of the Timorese subspecies. The Komodo population of the nominate form (Auffenberg, 1980) preys on geckos (*Hemidactylus*) and skinks (*Sphenomorphus*), whilst frogs (*Fejervarya*) are known from the diet of Sumbawa and Flores specimens (Mertens, 1930). All these potential prey genera occur on Timor. *Dendrelaphis inornatus* is an oviparous species with clutch sizes reported from 2–18 (de Lang, 2011), but no data exist specifically for *D. i. timorensis*.

Taxonomic comments. The subspecies *D. i. timorensis* occurs on Timor and the neighboring eastern Nusa Tenggara and southern Maluku islands of Roti, Semau, Pantar, Alor, and Wetar. The nominate subspecies is found on the western islands of Nusa Tenggara, west of and including Lomblen and Savu.

***Lycodon capucinus* (Boie, 1827)** [IV–VIII]

Common names. (E) Common (island) Wolfsnake. (G) Kapuzen-Wolfszahnnatter. (T) Samea lobo (samea = snake, lobo = wolf).

Known distribution. During Phase I *Lycodon capucinus* (Figure 31) was recorded from Same (Manufahi District; Locality 17; Kaiser *et al*., 2011), and as a roadkill on the Sakato-Atambua road in West Timor in Phase III (O'Shea *et al*., 2012). During Phase VI it was also recorded as common on Ataúro Island (Kaiser *et al*., 2013b).

New localities. During Phases IV–VIII this species was encountered with increasing frequency, primarily as roadkills. We collected live specimens in Dili District (grounds of the Timor Lodge Hotel, Locality 1; USNM 579781); Lautém District (Com and Raça, Localities 26 and 27; USNM 579381–82, 579494–95); Manufahi District (Ladiki coffee forest near Same, Locality 17; USNM 579380); and Bobonaro District (degraded forest at Fiuren, near Balibo, Locality 9; USNM 580547). It was also reported to occur at Malahara (Lautém District; Locality 29; de Lang, 2011). Roadkills were documented, and sampled when possible, from Covalima District (north of Suai, Locality 13; USNM 579379); Baucau District (near Baucau; USNM 580546); Aileu District (near Lahae town); and Bobonaro District (on the Maliana-Balibo road; USNM 580548). *Lycodon capucinus* has now been recorded from seven mainland districts, and Ataúro Island (Table 4).

Natural history. *Lycodon capucinus* is a very common and widespread, but nocturnal and secretive snake that is easily overlooked in cursory searches, although it may be encountered abroad at night, especially after heavy rain.

Figure 31 Adult male *Lycodon capucinus* from the leaf litter at the ruins of the Portuguese *pousada* at Com (USNM 579494, Locality 26). Photo by Mark O'Shea.

We have found it in almost every habitat investigated, from townships to coffee forest, and from the ruins of a coastal *pousada* close to sea level, to elevations of over 1150 m (Ainaro District; Locality 16), greatly exceeding the 600 m documented for Komodo Island specimens (Auffenberg, 1980; Darevsky, 1964; Dunn, 1927). It appears to have adapted well to living alongside humans and is even found in major cities, such as the Indonesian capital at Jakarta (van Hoesel, 1959). This was easily the most frequently encountered snake species during our surveys to date, with 21 specimens documented, from juveniles to adults; two of these records were based on sloughed skins, which could be unequivocally identified to belong to individuals of this species based on scale counts and head scale morphology.

Lycodon capucinus is a small species that rarely achieves a length in excess of 600 mm, although our highest elevation specimen (see above), a roadkill that was sampled for tissue only, had an SVL of 580 mm and a TTL of 720 mm. Although primarily a terrestrial species, *L. capucinus* is agile and may be encountered climbing in vegetation or on buildings. *Lycodon capucinus* will bite readily when handled.

Prey of *L. capucinus* comprises primarily geckos, especially perianthropic species of the genera *Hemidactylus* and *Gehyra*, but across its extensive range *L. capucinus* is reported to have taken the skink *Eutropis multifasciatus* (Kopstein, 1936) and even mice (Mertens, 1930). According to McKay (2006) it also eats frogs and reptile eggs. It is an oviparous species, and clutches of up to eleven eggs have been reported (David and Vogel, 1996). On Timor, it has been reported as being parasitized by tapeworms (Goldberg *et al.*, 2010).

Taxonomic comments. *Lycodon capucinus* was long treated as either a synonym or a subspecies of the widespread South and Southeast Asian *L. aulicus* (Linnaeus, 1758), to which it bears a striking resemblance, and only relatively recently has it been consistently treated as a distinct and separate species based on the work of Taylor (1965) and David and Vogel (1996). This nomenclatural history has caused considerable confusion when the geographical range of this species needed to be determined (Kaiser *et al.*, 2011).

Lycodon subcinctus Boie, 1827 [IV]

Common names. (E) Malayan banded Wolfsnake. (G) (Weiß-) Gebänderte Wolfsnatter. (T) Samea kadali (samea = snake, kadali = ring).

Known distribution. In the early phases of the project a single specimen of *Lycodon subcinctus* (Figure 32) was obtained, from Mirbuti village near Same (Manufahi District; Locality 17), and close to the project's first collection locality for *L. capucinus* (Kaiser *et al.*, 2011).

New localities. A second specimen was obtained in Raça village (Lautém District, Locality 27; USNM 579382).

Natural history. Much less frequently encountered by us on Timor than its congener, *L. capucinus*, *L. subcinctus* is a secretive, nocturnal inhabitant of humid forests and dry woodlands, both in low-lying and montane locations up to elevations of 1660 m in Peninsular Malaysia (Smith, 1930) and 1800 m in Bali (McKay, 2006). It is also reported to occur in plantations, rice paddies and other agricultural habitats, and around human habitations (de Lang, 2011). The latter location agrees with the first of our two specimens, which we obtained when we were handed a badly damaged specimen that had been killed in a schoolyard near Same, Manufahi District (Locality 17; see Kaiser *et al.*, 2011).

Lycodon subcinctus is a larger species than *L. capucinus*, achieving total lengths of 800–1200 mm (de Lang, 2011). The larger size and semi-fossorial nature of this infrequently (on Timor) encountered species may be the basis for the "Timor krait" stories circulated by individuals who observed this species but who were perhaps familiar with banded kraits from other parts of Indonesia (including Bali in the Lesser Sundas). Indeed, its pattern of white bands on a black background, combined with the lack of a loreal scale, afford *L. subcinctus* a startling similarity to the highly venomous species *Bungarus candidus* (Linnaeus, 1758) and *B. fasciatus* (Schneider, 1801), with which *L. subcinctus* occurs in sympatry in other parts of its range.

Although species in the genus *Lycodon* are primarily terrestrial, *L. subcinctus* is also arboreal (McKay, 2006), with prey consisting of geckos and skinks (de Lang, 2011). Females are oviparous, laying from 5–11 eggs (de Lang, 2011).

Taxonomic comments. Three subspecies of the widely distributed *L. subcinctus* have been described. The nominate race is found through most of Southeast Asia and it is to this taxon that Lesser Sunda populations belong.

Stegonotus sp. [IV, VII]

Common names. (E) Timor Groundsnake. (G) Timor-Schiefernatter. (T) Samea rai kór-kafé (samea = snake, rai = ground, kór-kafé = brown).

Known distribution. There were no previous records for the genus *Stegonotus* (Figure 33) from Timor, the nearest known populations being those of *S. florensis* on Flores and Sumba (Daan and Hillenius, 1966; de Rooij, 1917; Forcart, 1954).

New localities. The first specimen of the genus *Stegonotus* from Timor was obtained during Phase IV, from the coastal forest at Nancuro, near Natarbora, 8 km south of Umaboco (Manatuto District; Locality 20; USNM 579383). A second specimen was collected by one of us (LLA) during a personal survey, part of a research project from Timor-Leste's national university, at Betano "wet site" (Manufahi District; Locality 18; USNM 579384). Two further specimens, one adult and one juvenile, were collected, in close proximity to each other and close to the original collection point in the Nancuro coastal forest, during Phase VII (USNM 580549–50). *Stegonotus* sp. is now known to occur in southern low-lying coastal forests in two districts (Table 4).

Natural history. Individuals of this species were found exclusively in moist coastal forests within a short distance of the southern coast of Timor-Leste (> 2 km). At Nancuro, one adult specimen was spotted moving through the leaf litter, while another was found in the hollow portion of a decaying log. The juvenile was found unexpectedly, in a vertical position, under loose bark of a standing tree. Whereas the adult in the log attempted to escape by retreating further into the rotting wood, the juvenile remained motionless when the bark was removed and was easily captured.

Stegonotus is a common and well-represented genus in Papua New Guinea (PNG) and one well familiar to MOS, who identified it immediately upon capture of the first (Nancuro) specimen. In PNG members of this non-venomous genus are rarely encountered abroad during the day, most being found on roads or on the ground in the bush during the evenings and at night, or discovered hiding under logs or other debris during daylight hours (MOS, pers. obs.). Small specimens have also been encountered inside ant plants (Myrmecophyta), presumably hunting the skinks that also inhabit ant plant chambers. Such microhabitats should be investigated, should these tropical Southeast Asian-Melanesian trees occur in Timor-Leste. Papuan *Stegonotus*, particularly the large *S. cucullatus* (Duméril *et al.*, 1854), will bite with vigor and little provocation (O'Shea, 1996), and some Timorese specimens exhibit similar behavior. Members of the genus *Stegonotus* are oviparous.

Taxonomic comments. The genus *Stegonotus* currently comprises ten species (Uetz and Hošek, 2014), distributed throughout New Guinea (four species, at least one also occurring in northern Australia), the Bismarck Archipelago (one species), the d'Entrecasteaux Archipelago (one species), the Maluku Islands (one species), Borneo (one species), the Philippines (one species), and the Lesser Sundas (one species reported from Flores and Sumba). This latter taxon, *S. florensis* (de Rooij, 1917), is the only member of the genus occurring close to Timor.

Figure 32 Adult male *Lycodon subcinctus* from the leaf litter at the limestone caves near Raça (USNM 579382, Locality 27). Photo by Mark O'Shea.

Figure 33 Adult female *Stegonotus* sp., collected from the inside of a rotting log in coastal wet forest at Nancuro (USNM 579383, Locality 20). Photo by Mark O'Shea.

Comparison of Timor specimens with the type material of *S. florensis* and a variety of museum specimens representing the other known species of *Stegonotus*, has allowed us to determine that the Timor specimens belong to an undescribed species based on scale counts and head scale morphology. We have also been able to recognize that the *S. florensis* material represents more than one species, with those from Sumba most likely warranting the resurrection of *S. sutteri* from synonymy (see Forcart, 1954). Beyond these comparisons, we have uncovered many inconsistencies in how names have been applied to *Stegonotus* populations throughout the range of the genus, and this topic is currently the subject of a comprehensive investigation (Christine Kaiser, unpubl. data.).

Family Cylindrophiidae—Asian Pipesnakes

Cylindrophis cf. *boulengeri* [VII]

Common names. (E) Boulenger's Pipesnake, Timor Pipesnake. (G) Boulenger-Walzenschlange. (T) Samea ulun rua (samea = snake, ulun = head, rua = two). This snake is locally known as the "two-headed snake," given that the body morphology and defensive behavior of pipesnakes do not allow for a ready identification of the head and make it appear as if both ends of the snake might pose a threat.

Known distribution. *Cylindrophis* cf. *boulengeri* (Figure 34) is recorded from Timor-Leste based on eight specimens collected by Prof. A. Bühler in 1935 at Baguia (Baucau District, no further data) and now deposited in the Naturhistorisches Museum Basel, Switzerland (NHMB 12908–15). Our visit to Baguia during Phase VII (2012) failed to produce any specimens or any recognition from the local population and villagers; when questioned and shown photographs, locals were unfamiliar with the snake (O'Shea and Kaiser, 2013).

New localities. In late 2012 one of us (AVR) obtained a specimen of *C.* cf. *boulengeri* in Lospalos, Lautém District (USNM-FS 255499; field tag only, specimen remaining on exhibit in Timor-Leste; photo vouchers USNM-HI 2835a–c), the first specimen of the taxon discovered in 77 years. We subsequently captured another specimens in a banana plantation at the confluence of the Comoro and Bemos Rivers on the Aileu District side (Locality 6; USNM 581170). This secretive snake is now known from three districts in Timor-Leste (Table 4).

Natural history. Pipesnakes of the genus *Cylindrophis* are nocturnal, semi-fossorial, and secretive. This lifestyle is the reason for our poor knowledge about the biology of the species currently recognized within the genus. One of the specimens we collected, at the confluence of the Comoro and Bemos Rivers (Aileu District: Locality 6) was found on the ground under a banana leaf. We had previously considered this type of habitat unproductive, with only a few striped treefrogs (*Polypedates* cf. *leucomystax*) being collected, and therefore had ignored such habitats during surveys. This is an excellent example for how collector's bias can influence collecting results.

Almost nothing is known of the natural history of Timorese *Cylindrophis*, although it may be presumed that they prey on blindsnakes (*Indotyphlops* and *Sundatyphlops*), and possibly cylindrical skinks (*Eremiascincus*) or invertebrates such as earthworms. All species for which reproductive biology is known are described as being ovoviviparous (Greene, 1997), a condition we consider to be a form of livebearing (Blackburn, 1994). However, examination of museum specimens by one of us (SM) revealed that some populations of *Cylindrophis*, which likely represent distinct species based on morphology, may be egglaying.

Cylindrophis exhibit an unusual defensive behavior, during which they hide the head in the coils of their body and elevate their tails, flashing the bright or contrasting ventral pattern in the process, a behavior reminiscent of Asian coral snakes (e.g., *Calliophis intestinalis* [Laurenti, 1768]).

Taxonomic comments. The populations historically associated with *C. boulengeri* Roux, 1911 are known from 12 specimens collected in the early 20th Century, eight from Baguia, Baucau District (Forcart, 1953; see above), one from an unspecified location in West Timor (de Lang, 2011), and three from Wetar (Brongersma, 1933b; Roux, 1911), an island in the Indonesian province of Maluku to the northeast of Timor and the type locality of the species. We have been unable to locate additional museum specimens that may belong to this species. A specimen collected on Babar Island to the east and originally referred to *C. boulengeri* (Brongersma, 1933a) may represent a distinct and undescribed species of *Cylindrophis*. Two other species occur in the vicinity of Timor: *C. opisthorhodus* Boulenger, 1879 on Sumbawa, Flores, and Lombok to the west, and *C. yamdena* Smith and Sidik, 1998 on Yamdena Island in the Tanimbar Island group, to the east (Smith and Sidik, 1998). Until we have completed a study now underway (Kieckbusch *et al.*, in prep.), we conservatively consider Timor material as *C.* cf. *boulengeri*.

Family Elapidae—Cobras and their allies

Laticauda colubrina (Schneider, 1799) [VII]

Common names. (E) Yellow-lipped sea krait, Colubrine sea krait. (G) Nattern-Plattschwanz, Gelblippen-Seeschlange. (T) Samea-tasi kor kadeli (samea-tasi = sea snake, kor = color, kadeli = ring).

Known distribution. The sea krait *Laticauda colubrina* (Figure 35) was recorded from only one location and one specimen during the survey (Table 4), the old military wharf at Pante Macassar, Oecusse District (Sanchez *et al.*, 2012). One of us (SM) observed an individual in the water near the shore on Ataúro Island (Dili District), but was unable to capture it.

New localities. Our second specimen was obtained by AVR on the rocky headland at Cristo Rei, near Dili (Dili District; Locality 1; USNM-HI 2837) and subsequently released.

Natural history. *Laticauda colubrina* is an amphibious snake, equally at home on land as in the ocean. Being oviparous, unlike true seasnakes, it is essential that *L. colubrina* be able to move onto land in order to lay its clutch of 6–20 eggs (Greene, 1997). This species is so capable on land that it may be encountered at the top of cliffs, aloft in low bushes, or in the center of small islands (O'Shea, 2005). At first glance, a sea krait even resembles a terrestrial elapid with its regular, imbricate, smooth scales arranged in transverse rows, and its large ventral plates for locomotion on land, but it is also highly adapted for life in the ocean with the laterally flattened, paddle-shaped tail typical of marine snakes, laterally positioned valvular nostrils (Wilson, 2005), and tight-fitting supralabial scales around the mouth.

Prey of *L. colubrina* comprises entirely fish, including those species that seek protection by mimicking *Laticauda*, such as the colubrine snake eel (*Myrichthys colubrinus*), which is taken frequently (O'Shea, 1996; Wilson, 2005). Although a front-fanged venomous elapid, *L. colubrina* is placid and does not attempt to bite even when handled.

Taxonomic comments. Two species of the genus *Laticauda* are reported from the seas around Timor, but only *L. colubrina* has been positively recorded. The other species, *L. laticaudata* (Linnaeus, 1758), could be mistaken for *L. colubrina* by a person unfamiliar with the characteristics that define the two species, and it is also possible this species does not occur this far west.

Family Homalopsidae—Oriental and Australasian Mudsnakes

Cerberus schneiderii (Schlegel, 1837) [IV, VII–VIII]

Common names. (E) Schneider's dog-faced watersnake, Schneider's bockadam, (G) Hundskopf-Wassertrugnatter, (T) Samea natar (samea = snake, natar = rice paddy).

Known distribution. During the early phases of the survey *Cerberus schneiderii* (Figure 36) was found to be relatively common in the low-lying paddy field east of Baucau town (Baucau District). This species was reported by de Lang (2011), from Bidau, Dili (Dili District), and Lake Be Malae, Batugade (Bobonaro District), also on the north coast. We were also informed of a large specimen reportedly killed in the grounds of the Chinese Embassy in Dili, which is located on the seafront, but were unable to confirm this report.

New localities. During the phases covered by this report we collected an extra voucher specimen, as a relatively fresh roadkill, from close to the original Baucau paddy-field location, and one of us (LLA) obtained a specimen from the Betano "wet site" (Manufahi District; Locality 18; USNM 579392), the first southern coastal record of the species from Timor-Leste, although de Lang (2011) listed records from the south coast of West Timor. In addition we collected four specimens in the mangrove swamp at Metinaro (Dili District; Locality 3) where they were found to occur in sympatry with *Fordonia leucobalia* (see below). Including the records of de Lang (2011), this species is now reported from four districts of

Figure 34 Adult *Cylindrophis* cf. *boulengeri* (sex not determined) from a banana plantation near the confluence of the Comoro and Bemos Rivers (USNM 581170, Locality 6). Photo by Mark O'Shea.

Figure 35 Adult sea krait (*Laticauda colubrina*) from a ruined wharf (USNM 579241, near Pante Makassar, Oecusse District; Sanchez *et al*., 2012). Photo by Mark O'Shea.

Figure 36 Adult *Cerberus schneiderii* from the mangrove swamp at Metinaro (USNM 581173, Locality 3). Photo by Mark O'Shea.

Timor-Leste, and confirmed with voucher specimens from three (Table 4).

Natural history. Populations of snakes in the genus *Cerberus* are usually associated with inshore marine or brackish habitats, such as mangrove swamps and estuarine mud-flats, but all species are able to survive in freshwater and may be found in freshwater creeks or rivers flowing into these brackish environments (Murphy, 2007; Murphy *et al.*, 2012); the Philippine *C. microlepis* Boulenger, 1896 is the only land-locked freshwater lake dweller (Murphy, 2007). *Cerberus schneiderii* is also able to move from saltwater to freshwater habitats, but while we have collected it in brackish mangrove swamps on the north coast at Metinaro (Dili District; Locality 3) and on the south coast at Betano (Manufahi District; Locality 18) we have found it in larger numbers in freshwater rice-paddy habitats, on the north coast at Baucau (Kaiser *et al.*, 2011; O'Shea *et al.*, 2012). Several specimens were found at Metinaro (USNM 580525–26, 581173–76), of which one was found during the late afternoon sheltering in a mud lobster (*Thalassina anomala*) burrow, while others were found in shallow muddy rivulets.

It has been suggested that *Cerberus* feed almost entirely on small fish (McKay, 2006; Murphy, 2007), including lizardfish (Synodontidae: *Synodus*) and gobies (Gobiidae: *Amblygobius*), although other authors (e.g., Auffenberg, 1980; Voris and Murphy, 2002) reported crustacean remains from the guts of some specimens. Whether these were the intended prey or secondarily ingested prey-of-prey is impossible to determine. *Cerberus* is a rear-fanged venomous genus possessing Duvernoy's glands, which contain toxic secretions to dispatch struggling prey. Since *Fordonia* is carcinophagous this would enable the two species to partition resources and survive in sympatry. However, we suspect that the *C. schneiderii* living in the rice-paddy habitat at Baucau may also be feeding on tadpoles and juveniles of the abundant population of rice-paddy frogs (*Fejervarya*).

No reproductive data currently exist for *C. schneiderii*, but the genus is known to be livebearing, as are most obligatorily aquatic snakes, and litter sizes for Australian *C. australis* have been quoted as 6–8 (Shine, 1991a) or even as high as 26 (Gow, 1989), while de Lang (2011) provides a maximum litter size for *Cerberus* of 47 neonates.

Taxonomic comments. The taxonomy of homalopsid snakes formerly known as *Cerberus rynchops* (Schneider, 1837) was recently revised (Murphy *et al.*, 2012). The taxon had previously been divided into an Australo-Papuan population, recognized as *C. australis* (Gray, 1842), and a localized Philippine population, now known as *C. microlepis* (Murphy, 2007). The taxon *C. rynchops* was then used for all other populations until the latest revision restricted *C. rynchops* to populations on mainland Asia and the Andaman Islands. A new name was proposed for Palau populations (*C. dunsoni* Murphy *et al.*, 2012) and the name *C. schneiderii* was resurrected for all other island and Southeast Asian populations.

In most respects, Timor specimens fall within the characters given by Murphy *et al.* (2012) for *C. schneiderii*, although there are some differences, notably in the dorsal head scalation. Since few specimens have been collected from this southeastern corner of the *C. schneiderii* range, the precise taxonomic status of the intervening Wallacean populations may require additional research, especially as *C. schneiderii* is believed to be a species complex (John Murphy, *pers. comm.*).

***Fordonia leucobalia* (Schlegel, 1837) [VI, VIII]**

Common names. (E) White-bellied mangrove snake, Crab-eating mangrove snake. (G) Krebs-Wassertrugnatter. (T) Samea parapa kabun-mutin (samea = snake, parapa = mangrove, kabun-mutin = white belly).

Known distribution. *Fordonia leucobalia* (Figure 37) was not previously recorded for Timor-Leste and only a single record exists for its presence in West Timor (Peters, 1876), where it was collected in the mangrove swamp at Atapupu, located on the northern coast between Timor-Leste and the Oecusse exclave (Table 4).

New localities. During Phase VI a single specimen was collected from the mangrove swamp at Metinaro (Dili District; Locality 3; USNM 579780), the first specimen of the taxon from Timor-Leste, only the second from Timor, and the first from Timor in 135 years. We were able to obtain another specimen in the same locality during Phase VIII (USNM 581177).

Natural history. *Fordonia leucobalia* is an inhabitant of mangrove and estuarine mud flats but it may be found considerable distances upstream in tidal rivers and up to 850 km upstream in freshwater watercourses. Nocturnal in habit, it shelters by day in the burrows of fiddler crabs (*Uca* spp.) or mud lobsters (*Thalassina anomala*), only venturing onto the surface of the mud at night when the tide is returning. *Fordonia* is a carcinophagous species, preying primarily on crabs. Crustaceans recorded in the diet of *Fordonia* (Gow, 1989; Murphy, 2007; Shine, 1991b; Voris and Murphy, 2002) include the crabs *Uca* sp. (Ocypodidae), *Macrophthalmus* sp. (Macrophthalmidae), *Dotillopsis brevitarsis* (Dotillidae), *Sarmatium germaini*, and an unidentified crab genus (Sesarmidae), and the mud lobster *Thalassina anomala* (Thalassinidae). Prey is grasped and dismembered with the legs broken off before the body is swallowed, although Voris and Murphy (2002) suggest that struggling crabs may autotomize their own legs. *Fordonia* is technically a rear-fanged venomous snake possessing Duvernoy's glands and enlarged, grooved rear-teeth, and its fangs are long enough to penetrate the carapace of decapods, and the venom is toxic to crabs (Kopstein, 1931; Savitzky, 1983; van Hoesel, 1959). *Fordonia* is a livebearing species, females producing litters of 2–17 neonates (Murphy, 2007).

Taxonomic comments. Currently *Fordonia* is a monotypic genus occurring from mainland Asia (Bangladesh) to the northern Philippines (Luzon) and south into the Australo-Papuan realm (Murphy, 2007).

Family Pythonidae—Pythons

Liasis mackloti Duméril and Bibron, 1844 [IV]

Common names. (E) Macklot's water Python, White-lipped Python. (G) Timor-Wasserpython, (T) Fohorai-atan (fohorai = python, atan = slave). We have been unable to learn the origin of the peculiar Tetun common name.

Known distribution. During Phase III *Liasis mackloti* (Figure 38) was documented from a single live specimen in Dili (Dili District) and roadkills in Baucau and northern Manatuto Districts (O'Shea *et al.*, 2012). De Lang (2011) also reported a specimen from Dili. This species was also encountered as roadkills in West Timor, enroute and returning from the Oecusse exclave (O'Shea *et al.*, 2012). Given our records and those shown on the distribution map in de Lang (2011), we consider the distribution of this species to be near-coastal and ranging throughout Timor in low-lying wetland habitats.

New localities. During Phase IV *Liasis mackloti* was encountered with some frequency, unfortunately only as roadkills, on the roads east and west of Suai (Covalima District; Locality 13; USNM 579390; USNM-HI 2782–83; two of these specimens, Christine M. Dwyer field numbers 802–03, deposited in the USNM Biorepository, are tissue vouchers only). Five roadkills were documented, photographed, and locality data were recorded; specimens that were not in a too advanced state of decomposition were sampled for tissue. *Liasis m. mackloti* has now been confirmed from four mainland districts (Table 4).

Natural history. *Liasis mackloti* is a water python that inhabits inundated lowland habitats such as rice paddies or overgrown coastal creeks. Snakes are most frequently encountered in the wet season, when many become road-killed casualties when traveling across their fragmented habitat.

Figure 37 Adult *Fordonia leucobalia* from a mud lobster burrow in the mangrove swamp at Metinaro (USNM 579780, Locality 3). Photo by Mark O'Shea.

Figure 38 Unvouchered adult *Liasis mackloti* collected from beneath a container adjacent to the seafront in Dili (Locality 1). Photo by Mark O'Shea.

The nominate subspecies *L. m. mackloti*, found on Timor, is a relatively large snake that can achieve a maximum length of approximately 1.6 m, intermediate between the smaller *L. m. savuensis* and the larger but otherwise rather similar *L. m. dunni* Stull, 1932. It is a relatively powerful constrictor capable of subduing small- to medium-sized mammals and water birds. Various authors (e.g., de Lang, 2011) have included bird eggs, reptiles, and even frogs and fish in the diet of *L. mackloti* but there have been no studies of this species' diet in nature. The possibility that it may represent a climax predator in shallow freshwater habitats is supported by the feeding ecology of its close relative, *L. fuscus*, which is documented to take small crocodiles in southern New Guinea and northern Australia (Parker, 1982; Wilson and Swan, 2003). All pythons are oviparous, and females of *L. mackloti* have been reported to produce clutches of 8–14 eggs in captivity (Ross and Marzec, 1990).

Taxonomic comments. *Liasis mackloti* has three described subspecies, with only the nominate form, *L. m. mackloti*, occurring on Timor. The other subspecies are *L. m. dunni* from Wetar, northeast of Timor, and *L. m. savuensis*, from Savu, southwest of Timor. *Liasis mackloti* is very closely related to *L. fuscus* of northern Australia and southern New Guinea (Rawlings *et al.*, 2004), so much so that southern Papuan water pythons were originally treated as *L. mackloti* (Parker, 1982). Water pythons in the Northern Territory, Australia, were found to be more closely related to Indonesian water pythons than eastern Australian/New Guinea *L. fuscus* (Rawlings *et al.*, 2004) but the authors of this finding did not commit to referring to this population as *L. mackloti.*

***Malayopython reticulatus* (Schneider, 1801)** [IV, VII]

Common names. (E) Reticulated Python. (G) Netzpython. (T) Fohorai-boot (fohorai = python, boot = big).

Known distribution. During Phase III we encountered a number of captive adult reticulated pythons around Dili (Dili District) and juveniles in Viqueque District (O'Shea *et al.*, 2012) (Figure 39). A captive specimen in Oecusse District was reported elsewhere (Sanchez *et al.*, 2012). De Lang (2011) also reported specimens from Laleia (northern Manatuto District) and Malahara (Lautém District).

New localities. During Phase IV a locally caught specimen was photographed and its tissue sampled at the Convent of St. Antony d'Lisboa (Manufahi District; Locality 19), and during Phase VII a dead specimen was encountered on the road between Natarbora and Fatucahi, approximately 6 km NE of the convent. This specimen was not a roadkill, there was evidence it had been killed elsewhere and dragged onto the road. The condition of the cadaver made tissue sampling impossible but a voucher photograph was taken (USNM-HI 2788). *Malayopython reticulatus* has now been confirmed for six mainland districts (Table 4).

Natural history. *Malayopython reticulatus* is the longest snake species in the world, the largest potentially reliable account being that of a 9.98 m specimen killed and measured with a surveyor's tape in Sulawesi in 1912 (Murphy and Henderson, 1997). Other large specimens have been reported from the Philippines, Malay Peninsula, Borneo, and Sumatra, but individuals on small islands are often considerably smaller, perhaps due to island miniaturization or due to the hunting pressure on larger individuals (McKay, 2006). The largest Timorese specimen encountered during the survey was a captive from Becora (Dili District; Locality 2), with a total length just over 3.5 m.

Malayopython reticulatus is an inhabitant of rainforests and monsoon forests, particularly in close proximity to watercourses, where young specimens sleep on overhanging branches and plunge into the water below if they detect the approach of a potential threat (O'Shea *et al.*, 2004). This vegetated habitat also affords pythons the cover required to function as ambush predators of vertebrates, such as mammals. The species is also often found in bat caves, with these mammals providing a constant food source (McKay, 2006). However, reticulated pythons may also be found in cultivated or agricultural habitats, such as plantations (O'Shea, 2007), and individuals have been known to enter towns and even large cities (Cox, 1991). Several Timorese specimens were reportedly captured by locals on the outskirts of the capital, Dili. The species may occur at elevations from sea level to at least 1500 m (Malkmus *et al.*, 2002; Manthey and Grossmann, 1997).

The prey of *M. reticulatus* is composed primarily of mammals, with birds and large lizards occasional prey items (Malkmus *et al.*, 2002). The size range of mammals consumed by reticulated pythons is astounding: small or young pythons prey on rodents, but at 3–4 m body length their preference changes and they are documented to prey upon much larger and potentially more difficult or dangerous mammals, such as pangolins, porcupines, monkeys, wild pigs, mouse deer (Shine *et al.*, 1998), goats and adult deer (Taylor, 1922), sun bear (Fredriksson, 2005), and, on rare occasions, even humans (McKay, 2006). There exist anecdotal reports of leopards being killed, and one of us (MOS) encountered an injured *M. reticulatus* of approximately 3.0 m total length in Thailand that had obviously come off badly in an encounter with

Figure 39 Unvouchered captive individual of *Malayopython reticulatus* from the Convent of St. Antony d'Lisboa (Locality 19). Photo by Mark O'Shea.

a large feline. Shine *et al.* (1998) reported that females shift their attention to large prey species at a smaller size than males. *Malayopython reticulatus* is oviparous, with females of 5.5–6.0 m body length producing clutches of up to 100 eggs (McKay, 2006).

Taxonomic comments. For most of the two centuries following its description by Johann Gottlob Schneider (1801), the reticulated python remained in the Afro-Asian genus *Python*. However, the species is morphologically and biochemically quite distinct from all other members of this genus, with the exception of *M. timoriensis*. Rawlings *et al.* (2008) determined that the taxa *reticulatus* and *timoriensis* were sufficiently distinct phylogenetically from other species in the genus *Python* to warrant separate generic recognition. In a recent paper, Reynolds *et al.* (2014), provided the genus name *Malayopython* in recognition of the type locality for the species *M. reticulatus* as the Malay Archipelago (*fide* Alfred Russel Wallace). By using the genus name *Malayopython*, we follow the recommendations of Kaiser *et al.* (2013a).

Malayopython reticulatus is the most widely distributed python in Asia. The island of Timor lies at its extreme southern limit but the species has been recorded from virtually the entire Indo-Malayan and Philippine Archipelagos, east of Lydekker's Line and as far north on mainland Southeast Asia as Myanmar. The northernmost limit of its range is currently Itbayat Island (N 20.75°, E 121.83°), in the northern Philippine Batanes Group, only 200 km south of Taiwan, China (O'Shea and Lazell, 2008). Despite this extensive geographical range only two subspecies are currently recognized as distinct from the nominate form, *M. r. jampeanus* (Auliya *et al.*, 2002) and *M. r. saputrai* (Auliya *et al.* 2002), both from isolated islands south of Sulawesi (Auliya *et al.*, 2002); all other proposed subspecies have no scientific validity (Kaiser *et al.*, 2013a). Even so, it would be presumptuous to assume that all other populations belong to the nominate subspecies *M. r. reticulatus*, and for that reason no subspecific designation is used to distinguish the Timorese population below the species level.

Conservation. *Malayopython reticulatus* is a species listed on CITES Appendix II and therefore protected from international trade. However, unlike the smaller *Liasis mackloti*, it is being harvested for skins, meat, and gall bladders (e.g., Iskandar and Erdelen, 2006), and this highly destructive activity may exert a much greater pressure on wild populations than the exportation of live specimens to the trade. Despite its abundance in other parts of its range *M. reticulatus* does not appear to be a commonly encountered species on Timor.

Family Typhlopidae—Blindsnakes

Indotyphlops braminus (Daudin, 1803) [IV–VII]

Common names. (E) Brahminy blindsnake. (G) Blumentopfschlange, (T) Samea matan delek isin lotuk (samea = snake, matan delek = blind, isin lotuk = small body).

Known distribution. During Phase I we collected vouchers of this widespread, parthenogenetic species (Figure 40), two from Ladiki, near Same Manufahi District, and one from Loihuna, Viqueque Districts (Kaiser *et al.*, 2011).

New localities. During the later phases of the survey, six specimens of *I. braminus* were collected and vouchered. Three were taken in the gardens of the Pousada de Maubisse (elevation 1495 m; Ainaro District; Locality 16; USNM 579373–75), our highest record for a snake in Timor-Leste. Given the means by which the ancestral stock of this population probably arrived at this location, in plant pots, we do not consider this a naturally occurring elevation record. At much lower altitudes individual specimens were collected at the Timor Lodge Hotel, Dili (Dili District; Locality 1; USNM 579778) and in the ruins of the Pousada de Com (Lautém District, Locality 26; USNM 579496), both north coast localities. A specimen was also vouchered at the Convent of St. Antony d'Lisboa, Fatucahi (Manufahi District; Locality 19; USNM 565896) after it was found protruding from the cloaca of a Black-spined toad (*Duttaphrynus melanostictus*; see O'Shea *et al.*, 2013). *Indotyphlops braminus* has now been documented from six mainland districts.

Natural history. One commonly used vernacular name for *Indotyphlops braminus* is "Flowerpot Snake," (German: *Blumentopfschlange*) a name that these pencil-thin, small snakes (total length up to 180 mm) earned because they are often found either in the root balls of plants in plant pots, or in the humid darkness underneath plant pots. A close association with tropical plants exported during trade is likely the secret to how *I. braminus* became the most widely distributed snake in the world. It is the only known obligatorily parthenogenetic snake species (no male has ever been documented; see Booth *et al.* 2014 for a review of facultative parthenogenesis in pythons), and as such only a single adult specimen is required to colonize a new habitat. Since these snakes often inhabit the soil of tropical plant root balls, they can easily be transported internationally within plants and establish colonies wherever they arrive. Snakes tend to be more resistant to the effects of plant quarantine than insect larvae or other invertebrates, and thus a bridgehead can easily be established. This is

Figure 40 Specimen of *Indotyphlops braminus* from the leaf litter at the Portuguese pousada at Com (USNM 579496, Locality 26). Photo by Mark O'Shea.

undoubtedly how the population of *I. braminus* became established at an uncharacteristically high elevation in the gardens of the former Portuguese Governor's *pousada* at Maubisse. *Indotyphlops braminus* is an oviparous species, producing clutches of 1–8 eggs (de Lang, 2011; McKay, 2006).

Like all blindsnakes, *I. braminus* is a fossorial species that is more commonly found on the surface when flooded out of burrows by heavy rain. Its rudimentary eyes are simple pigmented areas under translucent scales that warn the snake when it has been uncovered, and this triggers the response to burrow rapidly. Prey comprises soft-bodied invertebrates, primarily termite and ant larvae and eggs (de Lang, 2011). This small snake may itself become the prey of many larger vertebrates, including the pipesnake *Cylindrophis* cf. *boulengeri* and the introduced bufonid *Duttaphrynus melanostictus* (O'Shea *et al.*, 2013).

Taxonomic comments. The genus *Indotyphlops* was recently erected by Hedges *et al.* (2014) to accommodate the South Asian blindsnake clade. Prior to this revision, the species *braminus* was placed in the genus *Ramphotyphlops*, which is now restricted to Western Pacific taxa.

Indotyphlops spp. [IV, VI–VII]

Common names. (E) Blindsnakes. (G) Wurmschlangen, Blindschlangen. (T) Samea matan delek (samea = snake, matan delek = blind).

Known distribution. A series of seemingly aberrant *Indotyphlops* were collected on Ataúro Island and were documented elsewhere (Kaiser *et al.*, 2013b) as *Ramphotyphlops* sp. 'Ataúro'.

New localities. A striped *Indotyphlops* (Figure 41A) collected at an altitude of over 905 m in a rock pile on the Tilomar road in Covalima District (Locality 15; USNM 579376) during Phase IV, could not be attributed to either *I. braminus* or *Sundatyphlops polygrammicus* (see below) and is recorded here as *Indotyphlops* sp. 'Tilomar'. Similarly, an unusual *Indotyphlops* with a bluish body coloration (Figure 41B) was collected on the trail to Mt. Mundo Perdido, Viqueque District (Locality 21; USNM 580542) at an elevation of 1162 m; we recognize it here as *Indotyphlops* sp. 'Mundo Perdido.' We considered that the coloration of this individual might be due to incipient ecdysis, but examination of the two injured areas and the head, as well as of the specimen after several months in preservative, do not support this idea. Both of these mainland specimens, as well as the series from Ataúro Island, await closer examination. Currently all three are *incertae sedis* within *Indotyphlops*.

Natural history. No natural history notes are available for the two aberrant *Indotyphlops* specimens from Tilomar (USNM 579376) and Mt. Mundo Perdido (USNM 580542), although they were both found sheltering under rocks at relatively high elevations, 905 and 1162 m respectively, the highest recorded for any

Figure 41 (A) Aberrant specimen of *Indotyphlops* from under a rock pile at Tilomar (USNM 579376, Locality 15, elevation 905 m). The fine lined pattern along the body indicates that this individual is not conspecific with *I. braminus*, and we refer to it as *Indotyphlops* sp. 'Tilomar.' (B) Aberrant specimen of Indotyphlops from the path to Mt. Mundo Perdido (USNM 580542, Locality 21, elevation 1162 m), showing injuries and a bluish, presumably pre-ecdysis, coloration. Photos by Mark O'Shea.

Timorese typhlopid, excluding the artificially introduced *I. braminus* at Maubisse (see above). Both locations where these two snakes were found are remote, at the end of a road into a highland area and along a mountain trail, respectively, and it seems unlikely that either of these snakes were transported to their respective locations by the agencies of man.

Sundatyphlops polygrammicus (Schlegel, 1839) [IV, VII]

Common names. (E) Timor blindsnake. (G) Timor-Wurmschlange, Timor-Blindschlange. (T) Samea matan delek isin baibain (samea = snake, matan delek = blind, isin baibain = normal body size).

Known distribution. No specimens of *Sundatyphlops polygrammicus* (Figure 42) were collected during Phases I–III, although Forcart (1953) reported eight specimens, now in the Basel collection (NHMB 12888–95), collected by Prof. A. Bühler near Baguia (Baucau District).

New localities. During Phase IV, a large specimen of *Sundatyphlops polygrammicus* (Figure 42) was collected, in heavy rain as it climbed a sandstone cliff-face near a path, on the Trilolo River, close to Same (Manufahi District; Locality 17). A second specimen was collected during Phase VII at the "*Carlia* site" at Afacaimau (Baucau District; Locality 23; USNM 580543).

Natural history. *Sundatyphlops polygrammicus* is an infrequently encountered species, with only two specimens collected in eight survey phases. As with most blindsnakes, *S. polygrammicus* is rarely seen on the surface except during or following heavy rain. Our Trilolo River specimen (USNM 579377) was collected as it climbed a sandstone cliff-face besides the path down to the river, the only reptile or amphibian encountered by the entire team during an evening search in heavy rain.

Like other typhlopid snakes, *S. polygrammicus* is a predator of soft-bodied invertebrates, primarily the larvae and eggs of termites and ants, but its larger size (larger than species such as *I. braminus*) should place adult ants and termites, and possibly also beetle larvae, within its dietary range. Large numbers of prey items may be consumed in rapid succession, from 50 to over 500 termites (de Lang, 2011). However, the majority of natural history notes available for this species relate to the former populations from Queensland, Australia, and Western Province, Papua New Guinea, which are now treated as a separate species in a different genus, *Anilios torresianus* (see Taxonomic comments below).

Taxonomic comments. The genus *Sundatyphlops* was recently erected by Hedges *et al.* (2014) to accommodate a clade of exclusively Lesser Sunda blindsnakes. Prior to this revision, the species *polygrammicus* was placed in the genus *Ramphotyphlops*. While this most recent taxonomic arrangement will still need to stand the test of time, *Sundatyphlops* is the most current available name for *polygrammicus*, and our use of this name here should not be misconstrued as a taxonomic endorsement but merely an acknowledgment of acceptable research. *Sundatyphlops polygrammicus* is currently believed to contain five subspecies distributed throughout the Lesser Sunda Islands, with the nominate form present on Timor (de Lang, 2011; Hedges *et al.*, 2014). With three of the other subspecies endemic to Sumba, Lombok, and Flores, and a fourth reported from Sumbawa and neighbouring Komodo and Moyo, it is unlikely that the rest of this considerable range is inhabited by just the nominate subspecies. This is a taxon clearly in need of revision. As formerly recognized, *S. polygrammicus* was a polyphyletic species and caused Hedges *et al.* (2014) to resurrect *torresianus* (now in the genus *Anilios*) for Queensland and southern Papuan populations, and to confine *S. polygrammicus* to Lesser Sunda populations.

Family Viperidae—True Vipers and Pitvipers

Trimeresurus (*Trimeresurus*) *insularis* (Kramer, 1977) [IV–VIII]

Common names. (E) Lesser Sunda Island Pitviper, Island Pitviper, Lesser Sunda White-lipped Pitviper. (G) Insel-Bambusotter, Wetar-Bambusotter. (T) Samodok (a proper noun).

Known distribution. During the first three research phases, *Trimeresurus insularis* was documented from three mainland districts (Baucau, Lautém, Viqueque; see Kaiser *et al.*, 2011; O'Shea *et al.*, 2012). It was also reported from Ataúro Island (Kaiser *et al.*, 2013b). Bethencourt Ferreira (1898) reported a juvenile specimen from Aipello (Liquiça District), and de Lang (2011) included Dili (Dili District) and additional localities in Baucau and Lautém Districts, bringing to five the number of districts where this pitviper has been recorded. *Trimeresurus insularis* is also common and widely distributed in West Timor, with specimens being documented enroute and returning from the Oecusse exclave (Sanchez *et al.*, 2012).

New localities. The later phases produced additional live specimens from Lautém District at Raça village (Locality 27; USNM 579386–87) and Com (Locality 26; USNM 579493); from Manufahi District at Betano ("wet site," Locality 19; USNM 579385); from Manatuto District (Nancuro coastal forest, Natarbora, S of Umaboco, Locality 20; USNM 580551; Figure 43); and a road-killed specimen from Bobonaro District on road between Bobonaro and Maliana road (near Locality 12). The Bobonaro specimen was in too poor a condition to voucher, and we instead documented it photographically (USNM-HI 2791). *Trimeresurus insularis* is now known to occur in eight mainland districts and on Ataúro Island, but thus far not at elevations over 900 m.

Natural history. With its lithe body shape and prehensile tail, the island pitviper *T. insularis*, is usually considered an arboreal species, but most specimens encountered during our surveys have been found on the ground, at night in relatively wet habitats, waiting in ambush for prey. Prey appears to consist largely of frogs, particularly rice-paddy frogs (genus *Fejervarya*; HK, pers. obs.) but it is possible that small mammals or lizards may also be taken on occasion, as reported by de Lang (2011) from other islands in the archipelago. The most common color phase is green but cyan coloration is known from Komodo (de Lang, 2011; MOS, pers. obs.), and bright yellow occurs on Wetar and Timor-Leste (USNM 581178). As with most pitvipers, *T. insularis* is a livebearing species. This species (under the generic name *Cryptelytrops*) was recorded as a paratenic host of spargana tapeworms (Cestoda) by Goldberg *et al.* (2010).

At this point in time this is the only terrestrial snake known to occur on Timor or in Timor-Leste, which includes Ataúro Island to the north, capable of delivering a lethal bite to a human. Deaths following the bites of *T. insularis* are on record in Timor-Leste and at the very least a bite and ensuing envenomation can be an unpleasant experience (MOS, pers. obs.).

Taxonomic comment. Until recently, we referred to this species as *Cryptelytrops insularis* (e.g., Goldberg *et al.*, 2010; Kaiser *et al.*, 2011). We here follow the nomenclature proposed by David *et al.* (2011), which we believe to be correct after a careful reading of their assessment. According to these authors, *Trimeresurus viridis* Lacépède, 1804 (= *T. albolabris insularis* Kramer, 1977) is the true type species of the genus *Trimeresurus*, and not *Coluber gramineus* Shaw, 1802, as previously believed. Rearrangement of the nomenclature requires that the species *insularis* bear the generic name *Trimeresurus*, with the optional use of the subgeneric name *Trimeresurus* to preserve added taxonomic information. The genus *Cryptelytrops* Malhotra and Thorpe, 2004 is now considered a junior synonym of *Trimeresurus*.

Family Crocodylidae—Crocodiles

Crocodylus porosus Schneider, 1801 [IV–V, VIII]

Common names. (E) Saltwater crocodile, Estuarine crocodile, Naked-neck crocodile, Indo-Pacific crocodile. (G) Leistenkrokodil, Salzwasserkrokodil. (T) Lafa'ek tasi (Lafa'ek = crocodile, tasi = sea).

Figure 42 Individual of *Sundatyphlops polygrammicus* from under a flat rock in a disturbed area south of Baucau (USNM 580543, Locality 23). Photo by Mark O'Shea.

Figure 43 Adult female *Trimeresurus insularis* (green phase) found in ground vegetation in coastal wet forest at Nancuro (USNM 580551, Locality 20). Photo by Mark O'Shea.

Known distribution. During earlier phases we documented free-living crocodiles in the Malailala River (Lautém District), and captives caught locally at Uma Boot (Viqueque District). One captive (Figure 44) from the south coast near Betano (Manufahi District; near Locality 18) has been kept in an enclosure in the town of Aileu (Aileu District) for nearly a decade, while a juvenile was kept in an old oil drum nearby (Kaiser *et al.*, 2009, 2013c).

New localities. During Phase IV we documented another captive crocodile on the Fatucahi to Betano road (Manufahi District; Table 5), which local residents had confined to an old oil drum. During Phase V a large adult crocodile was seen stalking water buffalo calves on the southern shore of Lake Ira Lalaro at Malahara (Lautém District; Locality 29; USNM-HI 2798). In 2012, a specimen was photographed at Tibar, a popular beach area west of Dili (Liquiça District; USNM-HI 2836). In

2013 (Phase VIII), we documented crocodiles on riverine sand banks along the north coast road in Lautém District (USNM-HI 2828).

Natural history. The saltwater crocodile is the most widely distributed crocodile in the Australasian region and the largest crocodilian in the world, achieving lengths of over 6.0 m (Wilson, 2005) and weights in excess of 1300 kg (Alderton, 1991; Steel, 1989). It is the climax predator wherever it occurs. This species is the only crocodilian found in Timorese waters where it has achieved mythological status as part of the island's creation story (Kaiser *et al.*, 2009; Morris, 2011). Many local people respect the crocodile, but this respect is not reciprocated, as crocodiles are responsible for an increasing number of human fatalities, usually fishermen or children near the water's edge, every year (B. Sidelau, *pers. comm.*). Reporting of such incidences is not universal, and the real impact on the human population is as yet unknown (HK and MOS, pers. obs.). Crocodiles are most common in estuarine river mouths or mangrove swamps, where the turbid water obscures their presence. We have observed them lingering under bridges along the coast roads, basking on riverine sandbanks, and resting nearly submerged in water among mangrove roots, but they may also arrive on sandy beaches close to major towns or tourist locations (J. Ramos-Horta, *pers. comm.*). There exists a land-locked population, estimated to number in excess of 300 individuals, in Timor-Leste's largest lake, Lake Ira Lalaro (Lautém District: Locality 29; Middleton *et al.*, 2006; M. Mendes and C. Trainor, *pers. comm.*).

Taxonomic comments. It is interesting to note that the population in Lake Ira Lalaro, a freshwater catchment in a limestone polje, is isolated by distance (9 km by air to the nearest coastline, with the 934 m high Paitxau Mountain range in the way) and altitude (at an elevation of nearly 500 m) from other saltwater crocodile populations. Therefore, this isolate may be considered a population of interest for studies of isolated crocodile populations.

Crocodile attacks. As human activity along the coastline and the shores of Lake Ira Lalaro has increased, reports of crocodile attacks including numerous human fatalities have risen dramatically. While there are currently no formal statistics on these attacks, we have heard reports with greater frequency during every research phase, and there is increased awareness on the part of the government that this might need to be considered an important public health issue (HK, pers. obs.). It appears to us that in the mindset of the Timorese populace, a people that has experienced great violence in the recent past and which is fighting to emerge from extreme poverty, such attacks may simply be considered a fact of normal life, akin to motorcycle accidents or falls

Table 5 Records of crocodilians and turtles for the districts of Timor-Leste. Black circles indicate previously known records, red circles denote new records.

Taxon	District														References*
	Aileu	Ainaro	Baucau	Bobonaro	Covalima	Dili (Timor)	Dili (Ataúro)	Ermera	Lautém	Liquiça	Manatuto	Manufahi	Oecusse	Viqueque	
CROCODYLIDAE															
Crocodylus porosus									●			🔴		🔴	1–4
CHELIDAE															
Chelodina mccordi timorensis									●						1
CHELONIDAE															
Chelonia mydas									●		🔴				1,2
Eretmochelys imbricata									🔴						2
GEOEMYDIDAE															
Mauremys reevesii			●			🔴									1,6
TRIONYCHIDAE															
Pelodiscus sinensis															5

[1] References are identified numerically as follows: 1 = Kaiser *et al.*, 2011; 2 = this paper; 3 = Kaiser *et al.*, 2009; 4 = de Rooij, 1917; 5 = Bethencourt Ferreira, 1898; 6 = Kaiser *et al.*, 2010.

Figure 44 Captive *Crocodylus porosus* in an enclosure at Aileu (see Kaiser *et al*., 2009, 2013c). Photo by Mark O'Shea.

from coconut palms. However, crocodile attacks do not have to be part of a valiant, post-conflict socioeconomic struggle. In an earlier report (Kaiser *et al.*, 2009), we outlined some of the challenges resulting from the interactions between humans and crocodiles, as well as some of the misconceptions about living with crocodiles as neighbors. While there are no simple solutions, it does not appear that any systematic evaluation of the issue has taken place. We therefore propose that the Government of Timor-Leste make reports of crocodile attacks compulsory (including name and age of the victim as well as the locality, and the activity during which the attack occurred) and form an inter-ministerial task force, to include members from departments handling public health, internal security, environment, and tourism, to create and implement an educational plan so that the risk of death from crocodile attacks can be minimized.

Family Cheloniidae—Sea Turtles

Chelonia mydas (Linneaus, 1758) [IV]

Common names. (E) Pacific Green Sea Turtle. (G) Suppenschildkröte, Grüne Meeresschildkröte. (T) Lenuk tasi kór-matak (lenuk tasi = sea turtle, kór-matak = green).

Known distribution. There have not been any confirmed records of *Chelonia mydas* for Timor-Leste. However, it is listed in the IUCN Red List of Threatened Species (Seminoff, 2004) as native in that country.

New localities. During Phase IV we found a dismembered carapace of *C. mydas* above the shoreline in the Nancuro coastal forest, Natarbora, S of Umaboco (Manatuto District; Locality 20; Table 5). The carapace was reconstructed using beach sand for support and a voucher photograph was obtained (Figure 45, USNM-HI 2792).

Natural history. This turtle may achieve a carapace length of 1.5 m (Wilson, 2005) and weights up to 200 kg (Spotila, 2004). *Chelonia mydas* migrates long distances between breeding beaches, the open ocean, and shallow, inshore, clear water bays with sea grass where they graze on algae and other marine vegetation. Adults are primarily, if not totally, herbivorous, but juveniles do include marine animals in their diets (Wilson, 2005). The lifespan of this turtle may exceed 50 years (Zug and Balazs, 1985).

Taxonomic comments. Some authors recognize two, others three, subspecies of *C. mydas*. The population on the coast of Timor could be attributed to either *C. m. agassizi* (Bocourt, 1868) or *C. m. japonica* (Thunberg, 1787).

Conservation. *Chelonia mydas* is an endangered species that was harvested well into the 20th century as part of the natural products trade, for its eggs, and for its meat for turtle soup (the German name *Suppenschildkröte* = "turtle used for soup" refers to the usage of the species as part of human diet). Although such trade is now banned, it is very difficult to prevent further exploitation of this turtle or its nests in economically challenged countries where a specimen may represent a financial windfall. We have on at least three occasions observed individuals offering sea turtle eggs, of uncertain species affinity, for sale along the main coastal road in Dili, with neat displays of four eggs per order sold alongside of the day's catch of fish or octopus. Whereas this type of trade is illegal in Timor-Leste, timing hinders enforcement, given that one motivated buyer may take the proof and leave no grounds for legal action. This same comment regarding local exploitation equally applies to other sea turtle species, including *Eretmochelys imbricata*, the only other species so far identified during our surveys.

Figure 45 Carapace of a hunted and killed specimen of *Chelonia mydas*, of which we found and reassembled all elements, just inland from the shore at the Nancuro Protected Area (Locality 20). Even though the remaining portions of the skeleton were missing, we were able to determine that there was human involvement by the presence of recent (i.e., not healed) harpoon damage. The flashlight (length = 146 mm) is provided as a scale. Photo by Mark O'Shea.

Eretmochelys imbricata (Linneaus, 1766) [V]

Common names. (E) (Pacific) Hawksbill (Sea) Turtle. (G) Echte Karettschildkröte. (T) Lenuk tasi eretmochelys (lenuk tasi = sea turtle, ibun = beak, makitik = hawk).

Known distribution. No confirmed records existed for *Eretmochelys imbricata* for Timor-Leste.

New localities. During Phase V the carapace of a juvenile specimen of *E. imbricate* was found on Jaco Island (Lautém District; Locality 30; Table 5). A voucher photograph was obtained (Figure 46, USNM-HI 2793).

Natural history. Adults of *E. imbricata* may achieve a carapace length of up to 1.0 m (Wilson, 2005) and a weight approaching 80 kg (Spotila, 2004). Although this highly migratory species may be encountered in a wide variety of marine habitats, from open ocean to mangrove swamps and estuarine river mouths, it is most often associated with the clear, shallow waters of coral reefs, where it feeds primarily on sponges (Porifera). Hawksbill turtles also prey upon molluscs (Mollusca), jellyfish (Scyphozoa), including highly venomous species, sea combs (Ctenophora), sea anemones and soft corals (Anthozoa), and marine algae (Ernst *et al.*, 1994). Juveniles are solely carnivorous (Wilson, 2005). Hawksbill turtles may live for 30–50 years (Ernst *et al.*, 1994).

Taxonomic comments. Two subspecies are recognized, with the Indo-Pacific populations belonging to *E. i. bissa* (Rüppell, 1835).

Conservation. *Eretmochelys imbricata* is a critically endangered species that has suffered historically from harvesting for the turtle shell industry, a practice now outlawed but continuing. Given their size, they are also harvested for food, and their eggs are collected from nesting sites or from slaughtered females.

Family Geoemydidae—Asian Hard-shelled Turtles

Mauremys reevesii (Gray, 1831) [IV, VI]

Common names. (E) Chinese pond turtle. (G) Chinesische Dreikielschildkröte. (T) Lenuk kakorok riskadu (lenuk = turtle, riskadu = striped, kakorok = neck).

Known distribution. During Phase I we vouchered a specimen of *Mauremys reevesii* from Baucau (Baucau District; Kaiser *et al.*, 2010) and reported the presence of a population in Dili (Dili District; Kaiser *et al.*, 2011).

New localities. During Phase IV we were able to confirm the presence of a population of *Mauremys reevesii* in a kangkong (*Ipomoea aquatica*) patch in Becora, eastern Dili (Dili District; Locality 1; USNM 579393; see Kaiser *et al.*, 2013c). We also encountered a number of specimens kept as garden pets in Comoro, western Dili (Table 5).

Natural history. *Mauremys reevesii* is an introduced turtle that probably arrived as a deliberate introduction from the Asian mainland, for food or to be used in traditional Chinese medicine, or as a totem associated with Chinese culture and long life. It appears to have been present in the Dili area for several decades (Kaiser *et al.*, 2010). As shown by the presence of a male individual in black breeding colors (Figure 47), the population is reproductively active and perhaps even self-sustaining in their human-maintained habitat.

Conservation. Even though the population found in Timor-Leste was introduced, it may be of significance in terms of the long-term conservation management of the species. In its native habitat in temperate and subtropical regions of mainland East Asia (China, North Korea, South Korea) *M. reevesii* has been severely exploited and has become very rare in the wild, having earned the IUCN status of Endangered A2bcd+4bcd (van Dijk, 2013). While populations also occur in Taiwan and Hong Kong of China, and Japan, these appear to have been exposed to hybridization with escapees from the trade (Taiwan, China; Fong and Chen 2010) or with *M. japonica* (Temminck and Schlegel, 1835), a close relative (Japan; Suzuki *et al*. 2011). Thus, the population in Timor-Leste, which by our findings appears to be a robust, self-sustaining population, may represent an important genetic reservoir of pure *M. reevesii*.

Family Chelidae—South American and Australasian Side-necked Turtles

Chelodina mccordi Rhodin, 1994 [I]

Common names. (E) Timor Snake-necked Turtle. (G) McCord-Schlangenhalsschildkröte. (T) Lenuk kakorok ular (lenuk = turtle, kakorok = neck, ular = snake).

Known distribution. Snake-necked turtles on Timor are limited in distribution to Lake Ira Lalaro in Lautém District and the surrounding swampy grasslands (Table 5).

New localities. Although we have not personally encountered or even pursued *C. mccordi* after our initial survey in 2009, we received several reports regarding their presence. These primarily came from local residents of Malahara village, at Lake Ira Lalaro's southern shore, from forest guards working in the vicinity of the lake, and from expatriates working in Timor-Leste. They lead us to conclude that *C. mccordi* exists in all near-shore habitats around the lake (Kuchling *et al.*, 2007).

Natural history. *Chelodina mccordi* (Figure 48) is regarded as one of the world's 25 most endangered turtle species (Rhodin *et al.*, 2011). Amongst the reasons for this designation are its highly localized populations

Figure 46 Carapace of a juvenile *Eretmochelys imbricata* from Jaco Island (Locality 30). The dollar bill (length = 156 mm) is provided as a scale. Photo by Mark O'Shea.

Figure 47 Adult male *Mauremys reevesii* from the kangkong paddies at Balide, a part of the city of Dili (USNM 579393, Locality 1; see Kaiser *et al.*, 2013c). Photo by Mark O'Shea.

Figure 48 Unvouchered adult individual of *Chelodina mccordi* from Lake Ira Lalaro, Lautém District (see Kaiser et al., 2011). Photo by Mark O'Shea.

(one in a single lake in Timor-Leste, one in two lakes on Roti Island), the uncertain population dynamics (e.g., population size, recruitment, density), and the high potential for extirpation due to local dietary and cultural customs or incipient exposure to international trade. Very little is known about the ecological parameters of *C. mccordi* in Timor-Leste, although a study has just commenced (C. Eisemberg, *pers. comm.*). Individuals of *C. mccordi* are most frequently encountered by local residents during the drier months of the year, when the waters of Lake Ira Lalaro recede and smaller patches of densely vegetated freshwater become isolated. Malahara villagers may have captured up to 30 specimens of *C. mccordi* from the environs of Lake Ira Lalaro during a single day (Kuchling *et al.*, 2007), likely in support of an annual cultural event. An educational booklet was recently produced and is now used in schools to encourage conservation of the species (Eisemberg and Perini, 2014).

Taxonomic comments. Even though McCord *et al.* (2007) described this population as a distinct species, their taxon was implicitly synonymized later that year by Kuchling *et al.* (2007), who considered the Lake Ira Lalaro population in Timor-Leste to be a subspecies of *C. mccordi* and gave it the name *C. m. timorlestensis*. The taxon name *timorensis* takes nomenclatural priority over *timorlestensis*, and thus this population should be referred to as *C. m. timorensis* (McCord *et al.*, 2007) if a subspecific name were to be used. Two other subspecies of *C. mccordi* are recognized, the nominate form from western Roti Island and *C. m. roteensis* McCord *et al.*, 2007 from eastern Roti Island (van Dijk *et al.*, 2014)

4. Discussion

Species Distribution

The mosaic geological structure of Timor Island and the exploitation of organic natural resources during colonial times and throughout the Indonesian occupation (i.e., cutting of sandalwood and tropical hardwoods, development of coffee monoculture, rice farming and other large-scale agricultural practices, human settlement) inescapably lead to certain assumptions about the distribution of the local herpetofauna. Habitat disturbances and destruction are known to effect significant changes in species distributions (e.g., Gardner *et al.*, 2007; McKinney, 2002; Wolf *et al.*, 2013), and this is perhaps most pronounced in tropical environments. We are therefore pleased that the reports of our herpetofaunal surveys to date (Kaiser *et al.*, 2011, 2013b; O'Shea *et al.*, 2012; Sanchez *et al.*, 2012; this paper) appear to document much higher herpetofaunal diversity than we had expected, which includes a series of putatively single-island endemics (e.g., *Cyrtodactylus*, *Eremiascincus*, *Kaloula*, *Stegonotus*).

When considering species distributions, two of the most common ways to showcase diversity are to use political boundaries or habitat types. In Timor-Leste, the most convenient method is to use established political boundaries (Districts), especially since habitats are fragmented, disturbed, or otherwise not cohesive. It would be difficult to predict detailed countrywide species distributions for Timor-Leste based on the coverage of specific habitats due to the high degree of habitat degradation, the presence of habitat fragments of diverse types, sizes, and ecological qualities, and the existence of uncertain corridors between such habitats. Furthermore, it is clear that our sampling effort plays a significant role in how we can account for species distributions: while we have been able to sample in all 13 districts of Timor-Leste, some districts received a disproportionate amount of attention when sampling, entirely for logistical reasons. Whereas the political boundary method admittedly falls short of the most productive approach to make statements about species biology, it allows us to provide a geographic overview even while comprehensive studies of habitats are still very limited. The best available information regarding habitat distributions is still that provided by Trainor *et al.* (2007).

As expected, there does not appear to be any general signal in the species diversity when looking at political boundaries, with the exception of Lautém District (Table 6), which comprises the entire eastern end of Timor Island and includes Lake Ira Lalaro, the country's largest body of freshwater. Even though we visited Lautém only three times during Phases IV–VIII, we found 31 species, among them 16 lizard and nine snake species. In contrast, all of our surveys begin and end in Dili District, and our species count there is 21 species, with seven lizards and ten snakes. Aileu and Ainaro are the only districts with a species count below ten, and this is due to a lack of sampling effort. With a number of diverse mountain habitats, it is all but certain that the diversity in these districts should match that reported for other mountainous districts (e.g., Manufahi; Table 6).

One other way to provide a general approach to species distribution patterns in Timor-Leste is to consider the north-south distribution, which largely reflects a dry-moist divide, respectively. The high mountains that form the spine of Timor act as a barrier to clouds from the south, effectively placing most of the habitats along the northern shore of Timor-Leste into a rain shadow. Portions of northern coastal Manatuto and Baucau Districts rank amongst the driest parts of Southeast Asia (Monk *et al.*, 1997). While some may consider lush tropical habitats to be those with the greater species diversity, perhaps due to the greater stratification of vegetation and the concomitant availability of niches, our data to date do not agree: species richness in the north is 34, in the south it is 35 species. As discussed above, we believe this to be a function of sampling effort, given that the south coast of Timor-Leste has limited infrastructure to support scientific surveys, rivers in places are unfordable even for 4 × 4 vehicles, and some areas are effectively isolated from study. This situation may improve as bridges are built or rebuilt, and other aspects of the infrastructure are improved. With increased access to the more remote areas we expect the list of Timorese reptiles and amphibians

Table 6 Known species diversity of amphibians and reptiles in the districts of Timor-Leste.

Taxon	District													
	Aileu	Ainaro	Baucau	Bobonaro	Covalima	Dili (Timor)	Dili (Ataúro)	Ermera	Lautém	Liquiça	Manatuto	Manufahi	Oecusse	Viqueque
Frogs	2	1	4	3	3	3	-	5	2	3	4	4	3	3
Lizards	-	3	11	5	5	7	10	7	16	7	12	10	9	6
Snakes	1	-	8	3	3	10	4	-	9	1	4	9	2	6
Turtles	-	-	1	-	-	1	-	-	3	-	-	-	-	-
Crocodilians	-	-	-	-	-	-	-	-	1	-	1	-	-	1
TOTAL	**3**	**4**	**24**	**11**	**11**	**21**	**14**	**11**	**31**	**11**	**21**	**23**	**14**	**16**

to continue to grow. The same can be expected for some of the more inaccessible mountainous areas. We also expect that the Department of National Parks of Timor-Leste will begin to conduct surveys for amphibians and reptiles independently of our own effort in the coming years, particularly in the Protected Areas and Nino Konis Santana National Park, and that this work will result in a more equitable sampling effort throughout the 13 districts of the country, as well as across the north-south divide.

Endemism

Our surveys uncovered a significant amount of single-island endemism. Before we began our surveys, the number of single-island endemics stood at eight (*Limnonectes timorensis*, *Litoria everetti*, *Draco timoriensis*, *Carlia peronii*, *C. spinauris*, *Eremiascincus antoniorum*, *E. timorensis*, *Chelodina mccordi timorensis*). For frogs, we have ascertained that at least two species of *Fejervarya* coexist in Timor-Leste, neither one of which is conspecific with *F. verruculosa* (Roux, 1911), their geographically closest congener found on neighboring Wetar Island. Furthermore, the population of *Kaloula* from the southern coast of Manatuto and Manufahi is a species distinct from *K. baleata sensu stricto* as well as from the recently described *K. indochinensis* and *K. latidisca*. This more than doubles the number of endemic frog species, with all of the new discoveries linked by a Southeast Asian biogeographic ancestry. Endemism is even more pronounced in lizards, and in their case the ancestry is a mixture of cis- and trans-Wallacean elements. Whereas *Cyrtodactylus* (as many as six putative new species), *Hemiphyllodactylus* and *Draco* are certainly taxa of Southeast Asian origin, *Carlia* (up to five putatively new species) and *Sphenomorphus* (up to four putatively new species) are Indo-Papuan, and *Eremiascincus* (up to four new species) is Australian. The snake fauna also includes endemics, and some are still being recognized. In addition to the known endemics, *Sundatyphlops polygrammicus* and *Dendrelaphis inornatus timorensis* (the latter of which may deserve recognition at the species level; Gernot Vogel, *pers. comm.*), we have discovered at least one new species from the Australo-Papuan realm (genus *Stegonotus*), and perhaps two new species of *Indotyphlops*. Given our relatively patchy sampling effort in both geographic and temporal terms, we are certain that our estimate of endemism for Timor, the largest Lesser Sunda Island, is still conservative. Our findings therefore contradict those of Malcolm Smith, who stated, "from a herpetological point of view, Timor is one of the most disappointing places that one can visit" (Smith 1927:199).

Timor-Leste's Herpetofaunal Diversity in the Literature

Only four historical publications exist that are entirely devoted to the herpetofaunal diversity of the land area now called Timor-Leste (Bethencourt Ferreira, 1898; Manaças, 1956, 1972; Themido, 1941), and each of these is very limited in scope. Several other publications focus on the western part of Timor Island (e.g., Smith, 1927; van Lidth de Jeude, 1895) or on the entire island as part of more general surveys (e.g., Barbour, 1912; de Rooij, 1915, 1917; van Kampen, 1923). Where erroneous records were presented, either because of misidentification or due to errors perpetuated via faulty taxonomy, we corrected these in our earlier papers (Kaiser *et al.*, 2011; O'Shea *et al.*, 2012).

Conservation

The newly identified high degree of endemism provides both a challenge and an opportunity for species management and conservation. The challenge lies with the landmass itself and the economic development of a population whose free market economic drive has been regulated for centuries by external forces. The landscapes in Timor-Leste are made of extremes, both in terms of terrain (much of the habitat is steeply sloped) and climate (dry spells may be long and devastating, rains may be torrential and destructive). As a consequence, any reporting on species diversity and distribution will retain a certain geographic and temporal patchiness. While the Government of Timor-Leste has set aside a significant portion of Lautém District as Nino Konis Santana National Park and has formally protected nearly 30 key areas (as *Areas Protegidas*), the establishment and implementation of management plans for these locales is only being realized very slowly due to issues with both capacity-building and governmental priorities. It is easy to enforce environmental policies in the absence of poverty, but it is nearly impossible or desirable when a family's next meal must come from the land of a protected area. As a consequence, the quickly developing market economy of Timor-Leste cannot and should not be curbed by copying environmental legislation from elsewhere; we feel that education about diversity and conservation, as well as the scientific use of the protected areas, is the best initial step to promoting broad-scale conservation in the country. It is fortunate that, based on our own experience with government leaders, the country is beginning to take these steps.

The opportunity for species management and conservation arises through the potential scientific utility of the national park and the protected areas. Currently, these areas are staffed by a cadre of forest guards (*Guarda Florestal*), and several individuals may be assigned to serving a single protected area. The national park also has a special office in Lospalos, Lautém District, which houses the administrative base for the area. At this point, forest guards are under-utilized in their activities and represent hidden scientific potential. Once educated and equipped, these individuals could readily be assigned repeatable tasks, including: (1) twice daily recording of basic environmental data (e.g., temperature, precipitation, humidity, cloud cover, etc.); (2) conducting digital camera-assisted visual encounter transects (Heyer *et al.*, 1994) in their area; and (3) filing monthly reports of photo-vouchered species encounters. In a few years, Timor-Leste, with its existing protected area network and personnel infrastructure, could perhaps become one of the best-researched tropical countries in Southeast Asia.

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4.3 Paper 2

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First Report on the Herpetofauna of Ataúro Island, Timor-Leste

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Abstract: We describe for the first time the terrestrial herpetofauna of Ataúro Island, Timor-Leste, a small mountainous island in the Inner Banda Arc of the Lesser Sunda Archipelago. The island supports a fauna of ten lizard species in three families (Gekkonidae, n = 5; Scincidae, n = 4; Varanidae, n = 1) and four snake species in three families (Colubridae, n = 3; Typhlopidae, n = 1; Viperidae, n = 1). In addition to a set of lizards (e.g., *Cryptoblepharus*, *Eutropis*, *Gehyra*, *Gekko*, *Hemidactylus*, *Lamprolepis*) and snakes (e.g., *Lycodon*, *Ramphotyphlops*, *Trimeresurus*) typical for the Lesser Sunda Islands, there appear to be undescribed endemic species of *Cyrtodactylus*, *Eremiascincus*, and *Varanus* on Ataúro. Our surveys to date have not revealed the presence of any amphibians, turtles, or crocodiles.

Introduction

Ataúro Island is a small (area = 105 km^2) volcanogenic landmass with geological and geographic affinity to the Inner Banda Arc of the Lesser Sunda Archipelago. Although all neighboring islands, such as Alor to the northwest or Wetar to the northeast, are part of Indonesia, Ataúro itself is politically part of Timor-Leste, which comprises the eastern half of Timor island and is Asia's newest country. The island is inhabited by about 8000 people comprising at least three language groups, who are engaged primarily in subsistence farming and fishing.

Historically, Ataúro appears to have been quite isolated, both culturally and economically, even though it lies merely 25 km off Timor-Leste's biggest port at Dili, the country's capital. During Portuguese colonial times (ca. 1525–1975), Dili itself was described as an undesirable way station for the early ocean-faring voyages (*e.g.*, de Freycinet 1828), and we have been unable to locate any historical accounts of life on Ataúro during that period. During the Indonesian occupation (1975–99) Ataúro was essentially left alone due to its lack of resources and amenities, and because by its remoteness it could not play a significant part in the Timorese resistance. In fact, during both Portuguese and Indonesian times, Ataúro was used as a natural prison, a place to exile those undesirable to the ruling class. Even today, Ataúro remains quite disconnected from the rest of Timor-Leste, with transportation limited to a once-weekly ferry service and many smaller boats across a very treacherous ocean passage. Largely as a consequence of this historical isolation, Ataúro has very little in the way of modern infrastructure and, recent improvements and efforts to introduce eco-friendly solutions notwithstanding, even basic needs of the population (*e.g.*, electricity, water supply, roads) are not always addressed.

Even given the logistics-based isolation, Ataúro is in the process of becoming known as a nature tourism destination, remote yet accessible from mainland Timor-Leste, and it is becoming particularly renowned for its excellent diving sites. However, the impact of ecotourism on the island cannot be accurately assessed at this point in time since baseline surveys of neither terrestrial nor aquatic biodiversity have been conducted. The notable exception is surveys of birds (Trainor and Soares 2004; Trainor and Leitão 2007). As part of a larger survey of Timor-Leste's herpetofauna (Kaiser *et al*. 2011; O'Shea *et al*. 2012; Sanchez *et al*. 2012), we visited Ataúro on several occasions to determine the species composition of amphibians and reptiles and to investigate whether any differences existed compared to Timor, in the Outer Banda Arc. We here present the initial report of our findings.

Materials and Methods

Localities

We surveyed for amphibians and reptiles at 11 principal localities on Ataúro (Figure 1; Table 1), focusing primarily on the island's east coast and its interior highlands for reasons of accessibility. In the species accounts (see below), the locality numbers provided correspond to those listed in Table 1.

Ataúro's main population centers (*e.g.*, Vila, Beloi) are situated in a strip of coastal lowlands, connected by the only compacted-surface road (Figure 2A). This coastal road crosses several seasonally dry streambeds (Figure 2B) and separates the beachfront from swampy habitat (Figure 2C) and agricultural plots (Figure 2D), all of which may reach into the foothills. From Beloi a road accessible only by four-wheel drive leads steeply upwards through primarily grassy vegetation across limestone substrate (Figure 2E)

Figure 1. Map of Ataúro Island, Timor-Leste. Collecting localities are identified by numbers corresponding to the descriptions in Table 1. Map by Mark O'Shea.

Figure 2. Representative habitat types on Ataúro Island, Timor-Leste. (A) Shown is the main road, which connects the ferry dock at Beloi with Ataúro's main town, Vila. In these towns, many types of human-made habitats exist, ranging from houses and fences to gardens and plantations (Locality 7). (B) Several rocky streambeds, such as shown in this photo of the Ankarana River (Locality 4), extend in an eastward direction from the foothills towards the beach. (C) There are several swampy habitats (Locality 5) that temporarily hold rainwater runoff. These are fast-changing habitats, since in the absence of replenishment the water will drain through the porous substrate. (D) Highland areas unable to support lush forest growth due to shallow soils and a lack of nutrients are richly covered with grasses and support small, widely spaced trees (area of Locality 2). (E) A small patch of rainforest along the interior road. (F) Habitat in the transition zone between the flat lowlands and the interior slopes, characterized by many loose limestone rocks. This is the type of habitat where we located *Eremiascincus* sp. 1 (Locality 4). (G) A roadside ravine near the coast, habitat for *Cyrtodactylus* sp. 2 and *Ramphotyphlops* sp. (Locality 1). (H) Vegetation on the slopes of Mt. Manucoco (area of Locality 9). Photos by Hinrich Kaiser (D, H), Mark O'Shea (B, C, E, F), and David Taylor (A, G).

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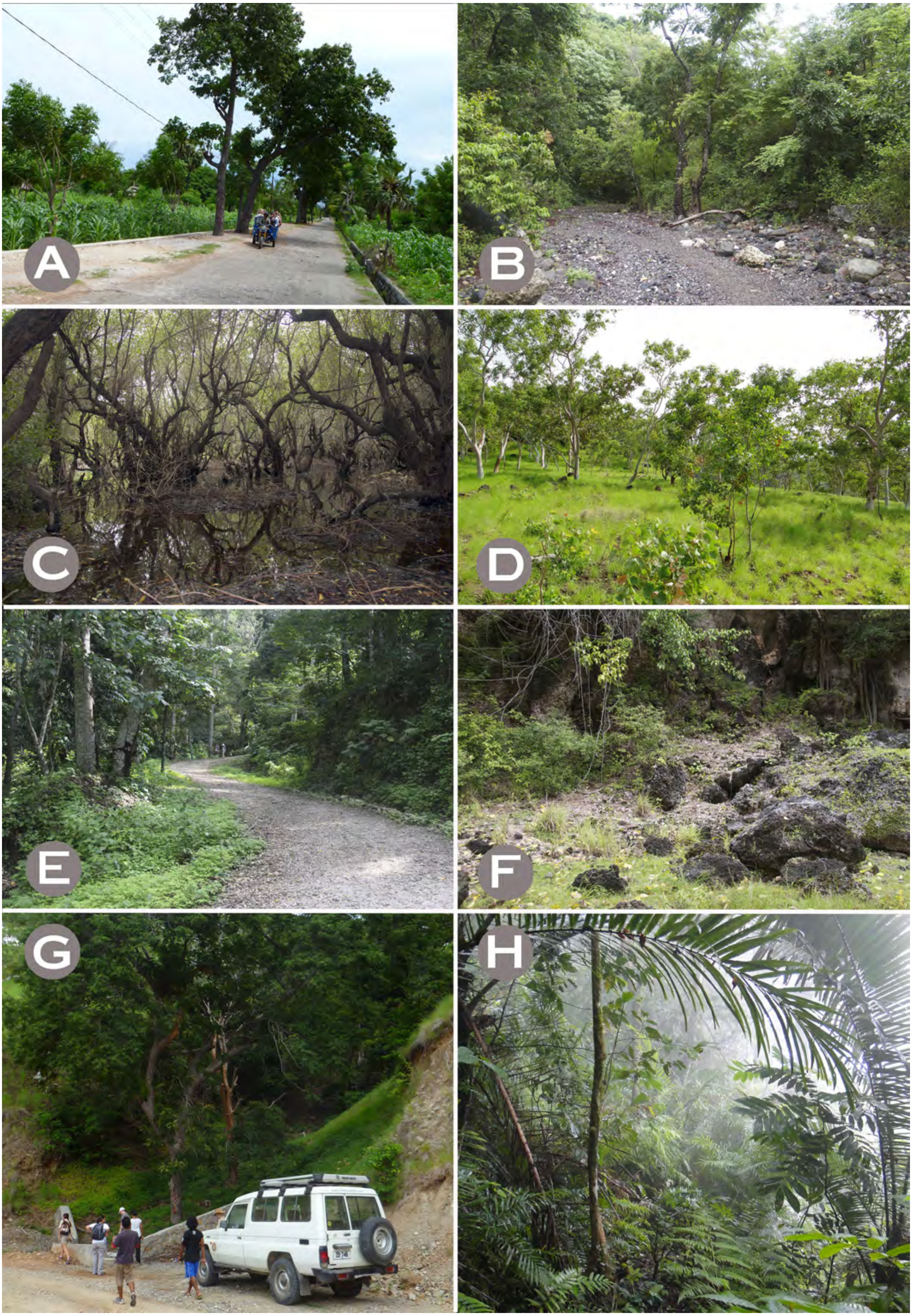
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into the more verdant higher elevations of Ataúro. Along the road into the interior there are several patchily distributed forested habitats with seasonal surface water sources (*e.g.*, Figure 2F). The road ends in the village of Anartutu (elevation ca. 500 m; Figure 1) from which paths allow access to the Mount Manucoco Protected Area (maximum elevation 996 m; Figure 2G). The steep slopes of Ataúro have resulted in considerable habitat diversity based on temperature and precipitation gradients; whereas the coastal plains of the island can remain dry for months at a time with constant temperatures above 30°C, there is nearly daily precipitation or fog-induced high humidity with temperatures in the 10–20°C range at altitude. Near the twin summits of Mt. Manucoco the vegetation is lush and moist (Figure 2H), reminiscent of cloud forest habitat normally seen at much higher elevations in Southeast Asia.

Specimen Collection

We conducted three formal surveys of Ataúro (29 Jan–1 Feb 2010, 31 Jan–2 Feb 2011, 28 Jan–3 Feb 2012). In addition, four of us (HK, LLA, AVR, ZAS) visited Ataúro on 3 Sep 2010 to ascertain the presence of monitor lizards on the island (see below). Surveys were generally restricted to areas accessible by road, with the exception of dry riverbeds in the lowlands and the Mt. Manucoco paths. We followed the methodology detailed by Kaiser *et al.* (2011). GPS coordinates (conforming to WGS-84) were recorded using a Garmin Oregon 400t handheld global positioning system (Garmin International Inc., garmin.com), and were later verified using Google Earth. We have carefully considered the utility of our own GPS coordinates vs. those based on the Landsat measurements and imagery used by Google Earth. Both systems deliver data with inherent, unavoidable inaccuracies. Whereas potential errors derived from our handheld GPS include a potentially low number of captured satellites due to local topography and ground cover, those in Google Earth are related to resolution. In order to standardize a protocol, we approach an area in Google Earth using our own GPS coordinates and then determine whether there is concordance between our datum and the 'ground truth' displayed by Google Earth, based on our familiarity with the sites. Whenever possible, we pinpoint a locality using Google Earth, and we augment these data with our own measures of elevation when necessary.

Processing

The basic methodology employed for specimen processing was described by Kaiser *et al*. (2011). Briefly, specimens were euthanized using intracardial injection with a 5% procaine solution according to standard methods. Tissue samples were taken from all specimens. Snout-vent length (SVL) was measured to the nearest 0.1 mm using Mitutoyo IP67 calipers. Species accounts use the accepted scientific name of each species as of 15 September 2012 (Uetz 2012). The use of the abbreviation 'cf.' between genus and species name flags instances where the sampled population is very similar to an existing species but where additional research is needed to confirm the identification. Scientific names are supplemented with common names in English (E) and Timor-Leste's official language Tetun (T). English common names are those of preferred usage by professional herpetologists, whereas Tetun names with asterisks (*T) are newly coined and formed to reflect the meaning of English names. Voucher specimens (Appendix 1) have been deposited in the Division of Amphibians and Reptiles, National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM) and the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany (ZFMK).

RESULTS

The paragraphs below contain accounts to detail the identity and natural history of the species encountered. Populations we consider to represent new species are listed with the correct genus name and an integer (*e.g.*, *Cyrtodactylus* sp. 1) so that they can be differentiated in this and future discussions. We have not yet found two commonly reported components of the mainland Timor-Leste herpetofauna on Ataúro, namely amphibians and flying lizards (genus *Draco*). Their presence at this point appears to be unlikely, based on formal interviews with local residents using Species Identification Cards (O'Shea and Kaiser 2013) and many anecdotal reports regarding herpetofaunal records for Ataúro.

Family Gekkonidae—True Geckos

Cyrtodactylus sp. 1 (Figure 3A). (E) Manucoco Bent-toed Gecko. (*T) Teki ain-fuan kleuk Manucoco. We found a single adult male specimen of this small (SVL = 39.3 mm) species of *Cyrtodactylus* during the day, under the bark of

TABLE 1. List of localities we surveyed on Ataúro Island, Timor-Leste, during visits in 2010, 2011, and 2012. Localities listed here are numbered and correspond to the locality indicators on the map (Figure 1).

LOCALITY	DESCRIPTION	ELEVATION (m)	GPS COORDINATES[a]
1	promontory in grassy habitat	295	08°12'10" S, 125°36'00" E
2	ravine N Beloi	70	08°12'10" S, 125°37'20" E
3	cliff face N Beloi	10	08°12'42" S, 125°36'40" E
4	Barry's Place and surrounds, Beloi	0–20	08°13'10" S, 125°36'40" E
5	Ankarana and Atipasa Rivers	20–60	08°13'30" S, 125°36'10" E
6	coastal swamp and surrounds	7–50	08°14'10" S, 125°36'20" E
7	Tua Ko'in Ecolodge and surrounds	0–8	08°15'11" S, 125°36'26" E
8	Vila town and surrounds	0–15	08°15'50" S, 125°36'20" E
9	Anartutu village and surrounds	550–600	08°15'40" S, 125°33'10" E
10	western slopes of Mt. Canilatuto	600–725	08°15'39" S, 125°33'32" E
11	western slopes of Mt. Manucoco	675–750	08°16'12" S, 125°33'30" E

[a] GPS coordinates are approximate to define the surveyed area. Precise localities are not provided to protect some of the unique and fragile habitats on Ataúro Island.

a decaying log, in a limestone hollow on the western slope of Mt. Manucoco (Locality 11). The individual attempted to escape by seeking refuge under pieces of loose bark, from which we were able to retrieve it. Based on a suite of morphological characters, we have no doubts that this Mt. Manucoco population of *Cyrtodactylus* is a new species to science (Kathriner *et al*. in prep).

Cyrtodactylus sp. 2 (Figure 3B). (E) Ataúro Bent-toed Gecko. (*T) Teki ain-fuan kleuk Ataúro. Individuals of this species were encountered in several diverse habitats, including a limestone cliff face and a nearby ravine (Localities 2, 3), a coconut grove with agricultural impact (Locality 6), and in tropical dry forest and in a rock pile near Barry's Place (Locality 4). The position of individuals in their respective habitats when observed ranged from underneath solid cover (*e.g*., rocks, logs) by day, to probable foraging on level ground, to resting on the vertical cliff face at eye height (ca. 1.75 m) above level ground. Even though this population appears to be superficially similar to *C. darmandvillei* (Weber, 1890) from Flores, a more careful morphological and genetic analysis to ascertain the taxonomic status of this population is currently underway (Kathriner *et al*. in prep.).

Gehyra mutilata (Wiegmann, 1834) (Figure 4A). (E) Mutilated Gecko, Four-clawed Gecko. (T) Teki kulit kanek. Specimens of this perianthropic species were all captured during the day, in the high elevation habitats near Anartutu village (Locality 9) and on the slopes of Mt. Canilatuto (Locality 10), and in the lowland habitats at Vila (Locality 8) and Beloi (Locality 4). The specimen from the highest elevation (719 m) was found inside an ant colony in a rotten log. Additional specimens were observed on a rock wall along a village path and underneath rocks and logs.

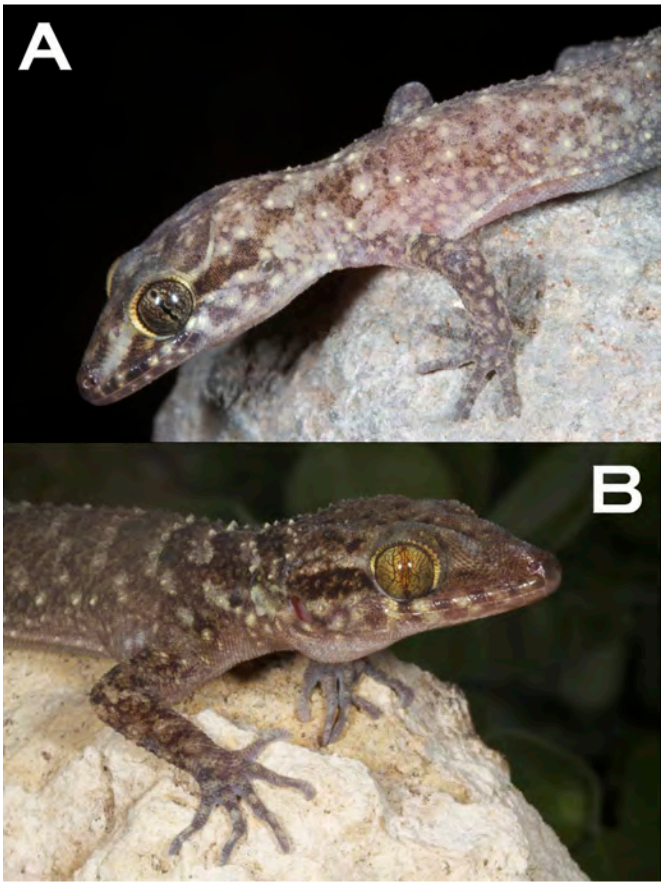

Figure 3. Bent-toed geckos found on Ataúro Island, Timor-Leste. (A) Male individual of *Cyrtodactylus* sp. 1 (SVL = 39.3 mm) from the slopes of Mt. Manucoco. (B) Male individual of *Cyrtodactylus* sp. 2 (SVL = 76.0 mm) from a lowland habitat north of Beloi. Photos by Mark O'Shea.

Gekko gecko (Linnaeus, 1758) (Figure 4B). (E) Tokay Gecko. (T) Toke. The characteristic vocalizations of this species are widely heard in all lowland habitats of coastal eastern Ataúro. It is quite common, and we deliberately limited our sampling effort to the three voucher specimens we captured during our first Ataúro survey, with photographic vouchers collected thereafter. These large geckos are commonly seen in the rafters of human residences after nightfall, including in a restaurant in Vila, the Tua Ko'in Resort, and Barry's Place (Localities 4, 7, 8).

Tokay geckos were frequently encountered in the accommodation at both Tua Ko'in Lodge and Barry's Place, where these animals appeared to reside in the wooden

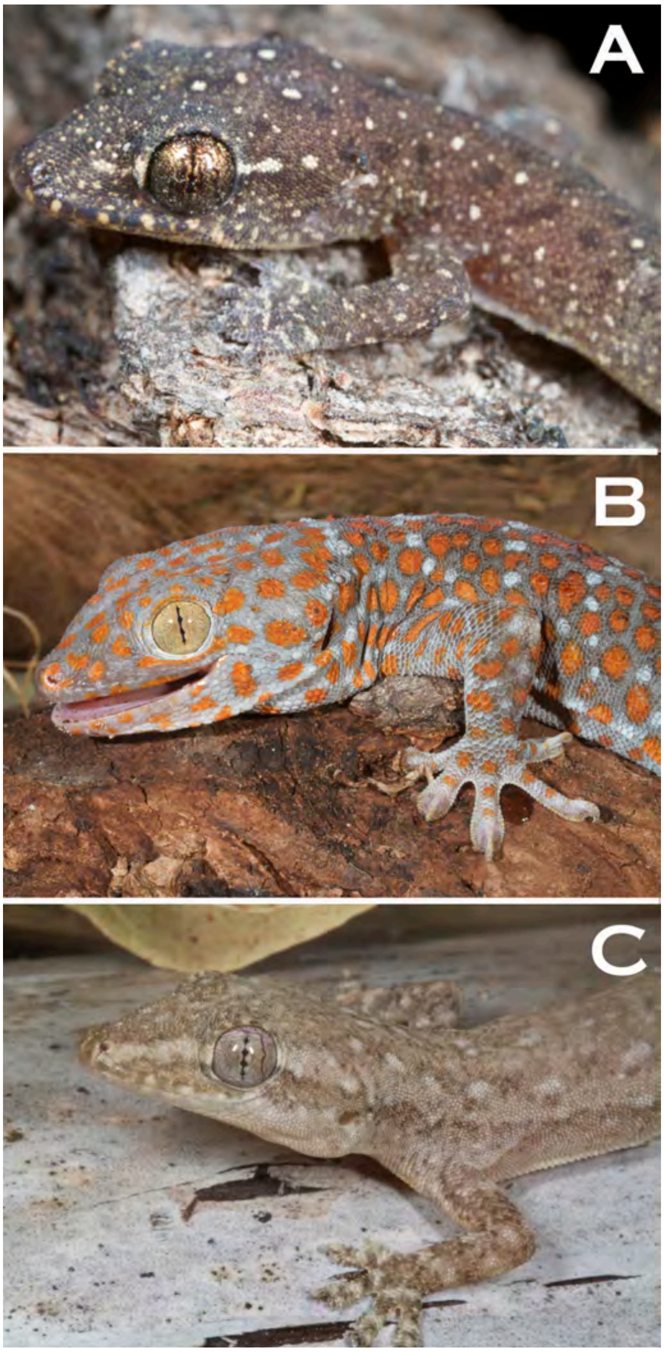

Figure 4. Common geckos found on Ataúro Island, Timor-Leste. (A) *Gehyra mutilata*. (B) *Gekko gecko*. (C) *Hemidactylus frenatus*. Photos by Mark O'Shea.

cabanas. They invariably display aggressively when disturbed, which includes opening the mouth widely and vocalizing threateningly. In one instance, a house gecko (*Hemidactylus*) we had captured and set on a bed in a plastic bag pending processing was dragged into the wall of the cabana by a tokay, together with the bag that held it captive. We discovered this by the rustling sounds the tokay made to break into the bag. During our attempts to retrieve the smaller gecko, the tokay held on tightly and tore the plastic bag.

Hemidactylus frenatus Schlegel, 1836 (Figure 4C). (E) Common House Gecko. (T) Teki uma baibain frenatus. Based on the frequency with which we have seen these perianthropic geckos on Ataúro, they appear to be the most common reptiles on the island. Along with *Gehyra mutilata,* they also appear to be able to tolerate the greatest breadth of habitats, ranging from the cooler, montane environments of Anartutu (Locality 9) and Mt. Canilatuto (Locality 10) to the warmer and drier habitats on the east coast of Ataúro (*e.g.*, Barry's Place; Locality 4).

Family Scincidae—Skinks

Cryptoblepharus leschenault (Cocteau, 1832) (Figure 5A). (E) Leschenault's Snake-eyed Skink. (*T) Mamór matan samea leschenault. A single individual of this normally coastal snake-eyed skink was observed high above the ground on a tree, in the transition zone from lowland swamp to hillside forest (near Locality 6). It was captured by shooting it with a blowgun.

Eremiascincus sp. 1 (Figure 5B). (E) Ataúro Glossy Night Skink. (*T) Mamór kalan Ataúro. Specimens of this population of night skinks were found during two afternoon surveys along the Akarana River and the adjacent Atipasa River (Locality 5). Glossy night skinks were encountered hiding under rocks, logs, and in leaf litter, where they exhibited an uncanny ability to merge into the loose substrate and root matter underneath. This resulted in a relatively low seen-to-capture ratio. In one instance, a juvenile skink was found alongside a wolfsnake (*Lycodon capucinus*), a possible predator of these lizards. *Eremiascincus* sp. 1 was also found in sympatry with *Eutropis* cf. *multifasciata.* We were able to collect adult as well as subadult and juvenile specimens.

Eutropis cf. *multifasciata* (Figure 5C). (E) Common Sun Skink. (T) Mamór loro. Individuals of this large skink (SVL up to 120 mm, total length up to 296 mm) were observed in both the highland and lowland localities (Mt. Manucoco: Locality 11; Beloi: Locality 4). Whereas we were unable to voucher an individual seen in a forested area on the eastern versant of Mt. Manucoco, we obtained one specimen in Anartutu village and a second one in a betel nut plantation near Beloi. We also observed individuals in a palm grove along the coastal road by night, sleeping under a palm leaf, and in the dry beach vegetation near Barry's Place and along the Akarana River during the day.

Lamprolepis cf. *smaragdina* (Figure 5D). (E) Emerald Tree Skink. (T) Mamór modok. We observed several individuals of this colorful skink, both in the montane locality (Anartutu village; Locality 9) as well as in lowland areas near Beloi (Localities 4, 6). To date, our collection consists exclusively of adult specimens displaying the green-brown coloration, punctuated with a middorsal

Figure 5. Skinks from Ataúro Island, Timor-Leste. (A) *Cryptoblepharus leschenault.* (B) *Eremiascincus* sp. 1. (C) *Eutropis* cf. *multifasciata.* (D) *Lamprolepis* cf. *smaragdina.* Photos by Mark O'Shea.

pepper-and-salt scale pattern; on Ataúro we have not yet seen an entirely brown adult individual, as we have encountered in mainland Timor-Leste and in the Oecusse exclave (Kaiser *et al.* 2011; O'Shea *et al*. 2012; Sanchez *et al*. 2012). One juvenile individual we collected displayed uniform green coloration, in a lighter green than some of the adults.

Family Varanidae—Monitor Lizards

Varanus sp. (Figure 6). (E) Ataúro Monitor. (*T) Lafaek raimaran Ataúro. We initially observed two individuals of this medium-sized (total length in excess of 150 cm) monitor during our 2011 survey of Ataúro, but both escaped by running into burrows in dense undergrowth. Four of us (HK, LLA, AVR, ZSA) subsequently traveled to Ataúro in August 2011 in order to let local residents know that we were seeking information regarding the distribution of these lizards on Ataúro. During this visit we found two specimens. The first was a carcass, entangled in washed up beach debris (Figure 6A). The second individual had been held captive in a plastic drum, but had died and had begun to decay (Figure 6B). We were able to secure tail clips from both specimens for initial molecular analysis.

In September 2011, we were notified that a resident of Vila had serendipitously captured a monitor lizard (Figure 6D) and was holding it for pick-up. LLA, ZSA, and AVR, along with our colleague Venancio Lopes Carvalho, returned to Ataúro to negotiate for the release of the lizard for scientific purposes. Whereas the resident was clearly hoping to receive cash for the lizards, it was explained to him that under our collecting guidelines we could not pay for the specimen, although we would be able to recognize the effort made by providing a 25-kg bag of rice and a $20 reimbursement for labor and expenses incurred while holding the lizard. The lizard was initially seen when it displaced a chicken from its nest using its snout. With the chicken gone, it smashed an egg with a sideways swipe of its snout and consumed the egg before the chicken's owner was able to react. He threw a piece of wood at the lizard, which moved away, and which he then pursued. The monitor attempted to escape into a burrow but could be captured because the burrow was too shallow to hold the entire lizard, and its tail remained within reach.

During our 2012 visit to Ataúro, we encountered several monitor lizards and were able to apprehend two individuals in a forested swampy area south of Beloi (Locality 6). The first of these was initially seen resting in a vertical position on a tree trunk (Figure 6C). It was captured by hand after we had surrounded the tree and it jumped from its perch. The second individual was caught in a specially modified baited funnel trap (O'Shea *et al*. in prep.) that had been positioned on a branch overhanging the swamp.

Family Colubridae—Typical Snakes

Coelognathus subradiatus (Schlegel, 1837) (Figure 7A). (E) Lesser Sunda Racer. (T) Samea laho. This snake was observed in the branches of a tree at the edge of agricultural land in the Mt. Canilatuto highlands above Anartutu village (Locality 10). When its human pursuer began climbing the tree, the snake initially moved to higher branches in the tree (up to a height of ca. 6 m), then to the outer branches from where it launched itself into the air, landing on the ground several meters away from the tree. It moved very rapidly in the grassy ground cover to escape, but it was captured despite its rapid movement and aggressive defensive strikes. The very dark brown coloration of this individual is rather atypical for the species and did not permit easy identification during the hurried pursuit. Care should be taken that the potentially occurring, similarly colored, spitting cobra (*Naja* cf. *sputatrix*; see below) is not mistaken for the harmless racer.

Lycodon capucinus (Boie, 1827) (Figure 7B). (E) Common Wolfsnake. (T) Samea lobo. Just as on mainland Timor, these wolfsnakes appear to be a relatively common component of the snake fauna, and we were able to capture three individuals. Whereas two individuals were collected at the Akarana River (Locality 5), the third was observed behind equipment in the workshop at Barry's Place (Locality 4).

Family Typhlopidae—Blindsnakes

Ramphotyphlops sp. (Figure 7C). (E) Blindsnake. (T) Samea matan delek. Several specimens of blindsnake that could not readily be associated with *R. braminus* (Daudin, 1803) or *R. polygrammicus* (Schlegel, 1839), species found on neighboring islands, were found primarily in lowland habitats (Localities 2–4).

Family Viperidae—True Vipers and Pitvipers

Trimeresurus insularis Kramer, 1977 (Figure 7D). (E) Lesser Sunda Island Pitviper. (T) Samodok. We collected a single specimen from a residence in the hills below Mt. Canilatuto (Locality 10). The individual had been observed and killed earlier in the day by local residents. Its body was retrieved from the branch over which it has been draped; placing the carcass over the branch inadvertently prevented further damage to the specimen, such as from scavenging invertebrates such as ants or beetles, or its loss from being carried off by feral mammals.

Unverified Species

Naja cf. *sputatrix*. (E) Spitting Cobra. (*T) Samea kaben veneno (Local residents know this snake as *samea hu-mau*, meaning "snake that blows spit." In the interest of public safety, we here promote the name *samea kaben veneno*, the "snake that spits venom," so that the potential danger from this animal is readily apparent). Even though we have not seen or captured a spitting cobra on Ataúro, we have had numerous anecdotal reports that the species is present in some lowland habitats, including near human habitations (*e.g.,* Vila; Locality 8). These reports include anecdotes that we assessed for their veracity with the help of Species Identification Cards (O'Shea and Kaiser 2013) picturing the cobra. All reports agree that the snake is considered to be relatively small (fingertip-to-elbow is shown as its length in all accounts) and invariably included a description of hooding behavior and venom spitting. The reaction to a bite is described as very painful and lasting from three days to a week. Venom sprayed into the eyes caused considerable discomfort but subsides within several hours when rinsed out with water. If these descriptions are accurate, the population of spitting

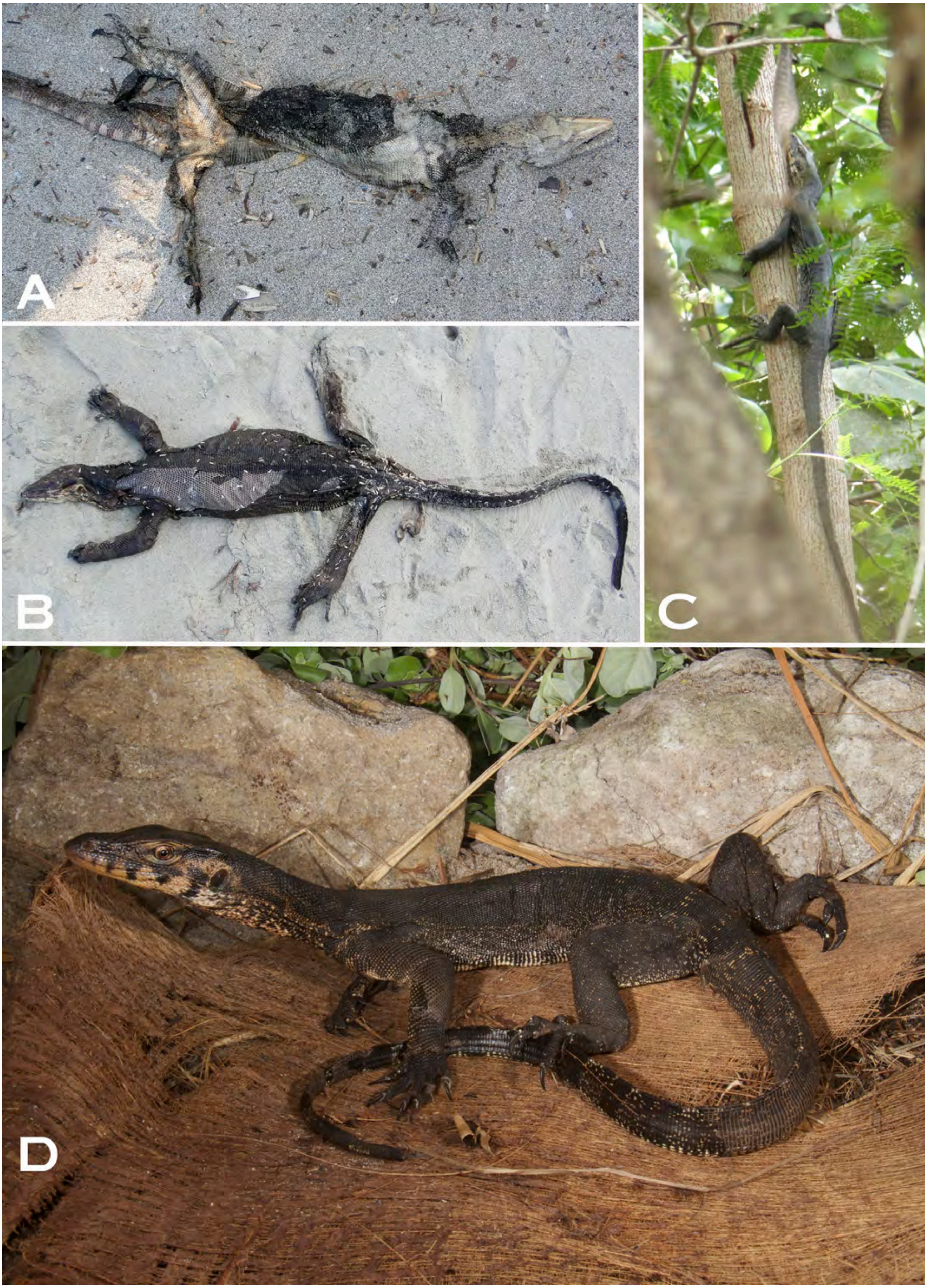

Figure 6. Monitor lizard (*Varanus* sp.) from Ataúro Island, Timor-Leste. (A) Carcass found on the beach. (B) Decaying specimen with insect larvae (small white patches). (C) Individual resting on a tree trunk in a swampy area. Photos by Hinrich Kaiser. (D) Individual in (C) photographed after capture. Photo by Mark O'Shea.

cobra on Ataúro appears to be a miniaturized form with somewhat lessened venom toxicity, compared with specimens known from neighboring Alor. No fatalities are known from its bite on Ataúro.

Four additional snake species may occur based on our own observations and those made by local residents: *Dendrelaphis inornatus* Boulenger, 1897; *Laticauda colubrina* (Schneider, 1799); *Liasis mackloti* Duméril and Bibron, 1844; and *Boiga hoeseli* Ramadhan *et al*., 2010. All four of these species are known from neighboring islands. The first three are known from Timor, with *L. mackloti* also known from Wetar. *Boiga hoeseli* is found on Alor. A fleeting glance by CS of a slender snake with a bulbous head in a tree near Barry's Place (Locality 4) may be attributable to *B. hoeseli*, whereas a chase of what was almost certainly a *D. inornatus* in grassy habitat (Locality 1) by AVR was unsuccessful.

DISCUSSION

Our findings to date indicate that the herpetofaunal diversity on Ataúro is considerably less than that of Timor, and that there are no genera recorded so far that might be considered distinctively Inner Banda Arc elements. At this time it is not possible to make a similarly comprehensive statement about comparisons with the two close larger Inner Banda Arc islands Wetar and Alor since neither of these islands has been comprehensively surveyed.

The most striking feature of Ataúro's herpetofauna is perhaps the absence of amphibians. Given the proximity of islands such as Alor, Timor, or Wetar, where populations of foam-nesting treefrogs (genus *Polypedates*), rice-paddy frogs (genus *Fejervarya*), or introduced toads (*Duttaphrynus melanostictus* [Schneider, 1799]) are known to occur, one might assume that historical or recent human economic activity, let alone natural dispersal, would have allowed a population of these taxa to become established. However, these activities may not be frequent enough and may not involve the habitat components by which human-mitigated introductions are usually made. For reasons primarily related to topography and water availability, there are no rice paddies on Ataúro, and this essentially eliminates one possible means of colonization for rice-paddy frogs. There may also not have been sufficiently frequent imports from the mainland to facilitate the arrival of treefrogs in building materials or decorative plants, and there are few locations on Ataúro where natural moisture or irrigation can provide reliable breeding opportunities for these frogs. Lastly, even though Asian toads have become well established on Timor in recent decades, transport to Ataúro is so infrequent and involves loads of such limited size that it is likely very difficult for toads to stow away and make the crossing from Dili. We expect that the expansion of tourism facilities on Ataúro will increase the opportunity for amphibian introduction, and that at least toads will colonize the island in the next decade.

Among the most interesting records identified on Ataúro are the two species of bent-toed gecko (genus *Cyrtodactylus*), the monitor lizard (genus *Varanus*), and the glossy night skink (genus *Eremiascincus*), all of which may represent new and endemic species. Whereas the overall biodiversity and distribution of *Cyrtodactylus* in Southeast Asia and into Australia is as yet unknown and appears to

FIGURE 7. Snakes of Ataúro Island, Timor-Leste. (A) Lesser Sunda racer, *Coelognathus subradiatus*. (B) Common wolfsnake, *Lycodon capucinus*. (C) Blindsnake, genus *Ramphotyphlops*. (D) Lesser Sunda Island pitviper, *Trimeresurus insularis*. The individual shown in this image is from the mainland of Timor-Leste, given that the only known specimen from Ataúro had been killed before we were able to secure it. Photos by Mark O'Shea.

include much tightly focused regional and island endemism (e.g., Bauer and Doughty 2012; Grismer *et al*. 2012), this observation has not yet been borne out in the Lesser Sunda Archipelago. To the contrary, *C. darmandvillei* appears to have a relatively wide distribution, ranging from Lombok to Flores, and no species of the genus *Cyrtodactylus* has been described to date from Outer Banda Arc islands. We suggest that the current distribution of these geckos in the Lesser Sunda Islands is not a reflection of their true diversity but of a lack of fieldwork on these islands that is only now in the process of being rectified (Jim McGuire, pers. comm.).

In the Inner Banda Arc, monitor lizards have been identified as belonging to the *V. salvator* complex, to which the name *V. s. bivittatus* (Kuhl, 1820) has been applied (Koch 2010; Koch *et al*. 2007). An initial morphological and molecular analysis of the Ataúro monitor (Koch *et al.* in prep.) confirms that this population is probably neither conspecific with *V. salvator* nor shows any affinity with other regionally distributed monitor species, such as members of the the *V. indicus* complex sensu Ziegler *et al*. (2007) and the much smaller *V. timorensis* Gray, 1831 from the Outer Banda Arc. As a consequence of this uncertainty, we are not able to assign the Ataúro monitor population to an existing species or subspecies with confidence, beyond an assignment to the subgenus *Varanus*. As a member of the genus *Varanus*, the population is protected under CITES Appendix II. With one voucher specimen secured and accessioned and the population of indeterminate size, we will collect no further whole specimens.

Glossy night skinks (genus *Eremiascincus*) are a group of lygosomine skinks known for its underestimated diversity in Australia (*e.g*., Mecke *et al*. 2009 and in prep.), where some species have also invaded arid desert habitats. Our recent work on Timor (Kaiser *et al*. 2011; O'Shea *et al.* 2012) and the examination of material in the collections of several museums indicates that a higher level of diversity than originally proposed (Greer 1990) also exists in the Outer Banda Arc, where we have discovered several endemic *Eremiascincus*. The known diversity of glossy night skinks in the Inner Banda Arc has so far been limited to the widespread taxon *E. emigrans* (van Lidth de Jeude, 1895), although preliminary analyses have shown that the populations currently referred to as *E. emigrans* constitute a species complex (Mecke *et al.* in prep.). Thus, the presence of an undescribed member of this secretive and taxonomically complex genus on Ataúro is not surprising.

Whereas we have been able to establish many interesting species records during our visits to Ataúro, we are convinced that additional species are present. In addition to the spitting cobra, there are several snakes we think may be present on the island. Based on tentative visual identification of escaping animals, we anticipate the presence of a species of bronzeback (genus *Dendrelaphis*), which is known to be present on Timor, as well as the presence of a species of treesnake (*Boiga*), present on Alor. On the other hand, we do not believe that, based on the near absence of mangrove habitat, the coast of Ataúro is suitable for filesnakes (genus *Acrochordus*), homalopsid snakes (e.g., genera *Cantoria, Cerberus, Fordonia*), or for the saltwater crocodile (*Crocodylus porosus* Schneider, 1801), which exist on Timor (Kaiser *et al*. 2009) Furthermore, we do not expect to record flying lizards (genus *Draco*) or Timor spotted monitors (*Varanus timorensis*) on Ataúro, since these are generally highly visible, well known faunal elements and easily identified by local residents when present; we have had not a single anecdotal report from Ataúro's residents.

The overall herpetofaunal diversity of Ataúro represents a subset of the herpetofauna found on larger islands, with Timor providing the best comparison because its fauna is now better known than those of Alor or Wetar, two geographically closer and geologically more similar islands. It is nevertheless intriguing that this small island appears to support endemics of relatively secretive organisms (*e.g*., *Cyrtodactylus, Eremiascincus*) as well as a hitherto unrecognized monitor lizard. These endemic forms add to the luster Ataúro is garnering as a tranquil nature isle that is off the beaten path.

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Appendix 1. This list includes one voucher specimen for each verified species. In many cases, multiple specimens were captured and deposited in the USNM collection.

Lizards.—Gekkonidae: *Cyrtodactylus* sp. 1 (USNM 579046); *Cyrtodactylus* cf. *darmandvillei* (USNM 579718); *Gehyra mutilata* (USNM 579063); *Gekko gecko* (USNM 579056); *Hemidactylus frenatus* (USNM 579085). Scincidae: *Cryptoblepharus leschenault* (USNM 579748); *Eremiascincus* sp. 1 (USNM 579750); *Eutropis* cf. *multifasciata* (USNM 579785); *Lamprolepis* cf. *smaragdina* (USNM 579761). Varanidae: *Varanus* sp. (ZFMK 91937).

Snakes.—Colubridae: *Coelognathus subradiatus* (USNM 579779); *Lycodon capucinus* (USNM 579782). Typhlopidae: *Ramphotyphlops* sp. (USNM 579767). Viperidae: *Trimeresurus insularis* (USNM 579784).

4.4. Conclusions

With the inventories presented in this chapter, the number of herpetofaunal taxa reported from Timor-Leste increased from 22 species before the survey work by Kaiser *et al*. began to > 60, including > 20 candidate species. With this richness, Timor-Leste stands out as a biodiversity hotspot in the Lesser Sunda Archipelago, reinforcing the need for the protection of the country's herpetofauna. Unfortunately, most of the surveys conducted for the presented inventories took part during the dry season in Timor-Leste (May–November), when reptile and especially amphibian activity and abundance are relatively low, with some taxa likely to enter a period of dormancy. As shown in Fig. 1 in paper 1, some areas in mainland Timor-Leste, especially within the central districts of Manatuto and Viqueque, were not surveyed for the studies presented (although major collection gaps were filled during another survey that took place in July and August 2014). On Ataúro, only the east coast and the islands' highest mountain, Mount Manucoco (996 m), were surveyed. Hence, the inventories presented here are preliminary assessments of Timor-Leste's amphibian and reptile diversity, and future surveys can be expected to considerably increase the list of the regional herpetofauna. In particular, further surveys during the wet season need to be conducted to give a more accurate idea of amphibian richness.

Based on the inclusion of > 20 candidate species in these inventories, it is clear that resolving the taxonomy of several groups (e.g., *Cyrtodactylus* and *Cylindrophis*), including the descriptions of new species, will be a future goal (see Outlook). Some discoveries in Timor-Leste gave rise to revisions of entire generic groups (see chapter 5) that need to be conducted before any species from Timor-Leste can reliably be described. Only after the alpha taxonomy of the forms in question is resolved can their conservation status be unequivocally assessed and, if necessary, final management recommendations be made.

Even without final taxonomic resolution, general protective measures of the Timorese herpetofauna are nevertheless essential. Coffee is Timor-Leste's major agricultural export commodity, with an estimated 320 km^2 of coffee plantations (Amaral 2003). Since large areas are planted with coffee, plantation management plans incorporating sustainable agricultural methods are urgently needed so that enough suitable refugia remain to harbor secretive herpetofaunal species (e.g., *Cylindrophis*, *Cyrtodactylus*, *Eremiascincus*). Long-term monitoring of some low range endemic species (e.g., *Kaloula* sp. nov.) is necessary to establish baseline data. The undescribed species of

Kaloula occurs together with the recently introduced Asian toad (paper 1), and some level of competition is likely among these perianthropic anurans.

One goal of the survey work not discussed in the publications herein but elsewhere (see Kaiser *et al*. 2013b) was to promote nature conservation education. One manner in which we accomplished this goal was by training Timorese students who participated in the project, several of whom are authors on the publications presented here. With these students we also had access to local communities, exchanging knowledge and information, including, but not limited to, the natural history, ecology, and conservation of amphibians and reptiles. We also conducted outreach events with live animals, seeking to combat the prejudices and misconceptions that exist about amphibians and reptiles in the population at large as well as among the country’s leadership, and trying to promote interest in herpetofaunal biology. These educational efforts contributed to the plan to ensure the continued survival of Timor-Leste’s amphibians and reptiles. Besides research, our surveys thus also served as a tool to advance biological knowledge and to cultivate this among the Timorese communities by acting as an educational vehicle.

5 Taxonomy and Distribution of Selected Southeast Asian Reptiles (Museum-based Studies)

Cover page of *Zootaxa*, **4903**(1) featuring *Cylindrophis subocularis* Kieckbusch, Mecke, Hartmann, Ehrmantraut, O'Shea & Kaiser, 2016 and illustrating the work published in Kieckbusch & Mecke *et al*. (2016): An inconspicuous, conspicuous new species of Asian pipesnake, genus *Cylindrophis* (Reptilia: Squamata: Cylindrophiidae), from the south coast of Jawa Tengah, Java, Indonesia, and an overview of the tangled taxonomic history of *C*. *ruffus* (Laurenti, 1768) (paper 6, this chapter)

5.1 Introduction

Even though a considerable amount of research has been conducted on Southeast Asian reptiles, significant gaps in our knowledge of the taxonomy and distribution of many groups remain (Mecke 2017, see Appendix). Based on museum vouchers, I initiated and performed studies on selected, putatively widely distributed reptiles to clarify their exact identities and distributions. These studies are a necessary extension of the continuing herpetofaunal inventories in Timor-Leste presented in the previous chapter. As indicated in the Conclusions of chapter 4, it was scientifically untenable to limit research to Timor-Leste, and the complex taxonomy and distribution of many herpetofaunal groups from the region made it necessary to perform larger revisions before any candidate species documented from Timor-Leste could be reliably described as new.

The tamarind bent-toed gecko (*Cyrtodactylus fumosus*; for a suggested new vernacular name see paper 5, herein) and the marbled bent-toed gecko (*C. marmoratus*), as well as the red-tailed pipesnake (*Cylindrophis ruffus*), certainly rank among the Southeast Asian reptile taxa with the most complex taxonomy. Their exact identities were never adequately resolved, and their distributions were constantly shifted in the course of time. The name "*Cyrtodactylus fumosus*" – a species originally described from Sulawesi (Müller, 1895) – was used indiscriminately for gecko populations from Sumatra, Java, Bali, Sulawesi, and Halmahera, islands belonging to different biogeographic realms (e.g., De Rooij 1915; Mertens 1929, 1934; Manthey & Grossmann 1997; Endarwin 2006). Moreover, *Cyrtodactylus fumosus* is frequently confused with *C. marmoratus*, with the latter originally described from Java (see Brongersma 1934; Koch 2012) and subsequently reported from many islands in the Malay Archipelago, including Timor (Smith 1927). The distribution of "*Cylindrophis ruffus*" (type locality: Java) as traditionally defined, covers most parts of mainland Southeast Asia and the Greater Sunda Islands (e.g., O'Shea 2007; Koch 2012; Das 2016), with similar forms reported from islands of the Lesser Sunda Archipelago, including Timor (see paper 1, chapter 4). Evidence was gathered to decide if these three taxa were indeed widely distributed species or whether as yet unrecognized and geographically restricted diversity was masquerading under the known names.

In chapter 5, *Cyrtodactylus fumosus* is redefined and its originally proposed distribution significantly restricted. The type series of *C. marmoratus* is examined and described for the first time. Based on detailed morphological examinations and a review of all relevant literature sources, I am also able to demonstrate that subsequently unrecognized species are hiding under the names *Cyrtodactylus fumosus* and *Cylindrophis ruffus*. Two new species are described herein: *Cyrtodactylus klakahensis* Hartmann, Mecke, Kieckbusch, Mader & Kaiser, 2016 (Klakah bent-toed gecko) and *Cylindrophis subocularis* Kieckbusch, Mecke, Hartmann, Ehrmantraut, O'Shea & Kaiser, 2016 (Javan pipesnake). Every taxonomic treatment is complemented by a review of the taxonomic history of the respective species. A new island record is provided for the skink *Sphenomorphus oligolepis* (Boulenger, 1914). Morphological evidence allowed me to extend the distribution of this Papuan skink into Wallacea. For the studies presented, I examined material from 13 collections, including all relevant types and available topotypic specimens. The publications presented on the above mentioned taxa are part of my own continuing studies that aim to improve our knowledge of Southeast Asian reptiles by identifying the true extent of their diversity (see Outlook).

The terminology and definition of morphological characters used for the taxa under investigation may, for historical reasons, have become unduly complex, with authors measuring or enumerating differently and using idiosyncratic rather than standard protocols. Standards across most of the more diverse reptile groups, such as geckos, have yet to be established (but see Outlook). This may mean that a commonly used name for a character is not necessarily consistently applied among groups, so that "head length" may be measured differently in geckos, skinks, or snakes, and even within geckos. As a result of these flawed traditions, abbreviations used for a character state may also differ between groups. Conversely, several names might be applicable to a single character within the same taxonomic group. The key morphological characters used herein are described in each of the individual publications presented, with universal and objective definitions provided for previously poorly defined characters (see for example the discourse on precloacal depressions in paper 4, herein). Whenever characters were measured or counted differently from previously published studies, this is indicated and, if necessary, data are compared. For the readers' convenience, characters routinely measured or counted are depicted in Fig. 2 on the following pages.

Taxonomic treatments, including the redescriptions of species and the descriptions of new taxa, are largely in accordance with the lineage-based evolutionary species concept first formulated by Simpson (1951, 1961). The species redescribed and newly described in this chapter are isolated from similar lineages geographically (allopatry), and differ from these by a number of conspicuous diagnostic characters that had proven to be reliable in other studies. Some of these characters may be regarded as apomorphies (e.g., the subocular scale in *Cylindrophis subocularis*), since they appear to be unique to a species or species group. Taxonomic treatments are not solely based on phenetics and geography, as some species are also adapted to different habitat types. Some bent-toed geckos referred to as "*Cyrtodactylus fumosus*" are only found in the lowlands, whereas others only occur in mountain rainforests above 1,000 m. Hence, the species dealt with in this chapter are lineages evolving separately from others with their own unique evolutionary roles and tendencies (*sensu* Simpson 1961). As the specimens described and redescribed are almost a century old, it was impossible to obtain molecular data to support species delineation. For some of these species fresh tissue samples have become available after publication of the papers presented here. Molecular genetic studies to investigate their phylogenetic affinities are in preparation (see Outlook).

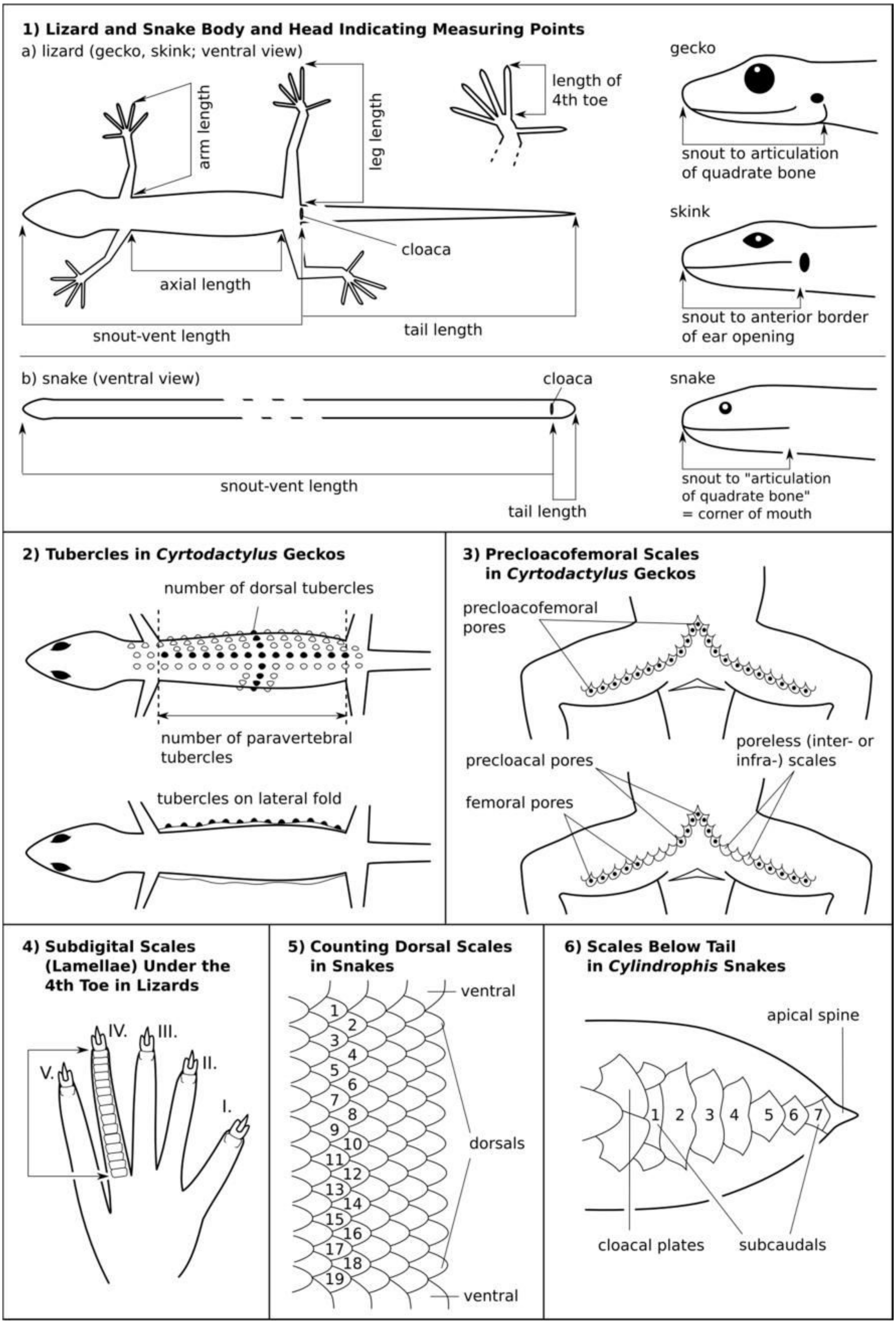

Fig. 2. External features and methods of measurement and scale count of lizards and snakes. Illustrations are simplified, schematically drawn and not to scale. The intention was not to depict a specific voucher, but similarities found in higher-level groups. Figure prepared by Heike Worth.

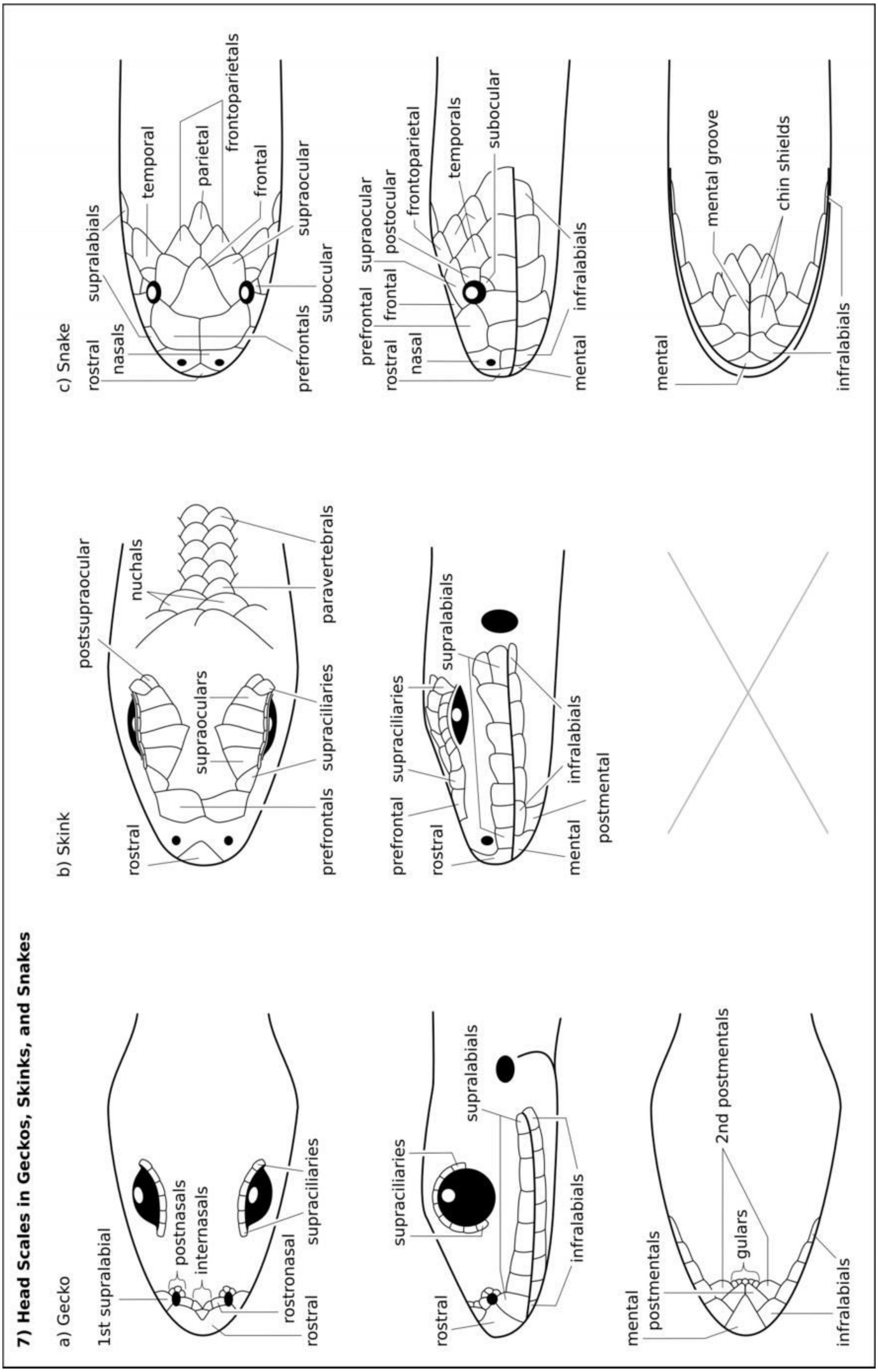

Fig. 2. (*continued*). Ventral head scalation of skinks was not used for descriptions in this thesis.

5.2 Paper 3

Hartmann, L., **Mecke, S.** (joint first authors), Kieckbusch, M., Mader, F. & Kaiser, H. (2016): A New Species of Bent-toed Gecko, Genus *Cyrtodactylus* Gray, 1827 (Reptilia: Squamata: Gekkonidae) from Jawa Timur Province, Java, Indonesia, with Taxonomic Remarks on *C. fumosus* (Müller, 1895). *Zootaxa*, **4067**(5): 552–568.

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A new species of bent-toed gecko, genus *Cyrtodactylus* Gray, 1827 (Reptilia: Squamata: Gekkonidae), from Jawa Timur Province, Java, Indonesia, with taxonomic remarks on *C. fumosus* (Müller, 1895)

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Abstract

A new species of the gekkonid lizard genus *Cyrtodactylus* Gray, 1827 is described from Klakah, Lumajang Regency, Jawa Timur Province, Java, Indonesia. *Cyrtodactylus klakahensis* **sp. nov.** can be distinguished from all other congeners by the presence of (1) a deep precloacal groove in males, (2) three rows of enlarged precloacofemoral scales, of which the third row bears 37–38 pores in males, (3) three or four rows of enlarged scales between the precloacofemoral scale rows and the cloaca, forming distinct chevrons, (4) raised and strongly keeled dorsal tubercles in 15–19 rows at midbody, (5) an indistinct lateral fold, (6) 17–20 subdigital lamellae under the 4th toe, and (7) subcaudal scales which are not transversely enlarged. *Cyrtodactylus klakahensis* **sp. nov.** is only the third bent-toed gecko species described from Java, indicating that the diversity of this genus on this island has been neglected in the past. Furthermore, we confirm that *C. fumosus* (Müller, 1895) is a species that possesses a precloacal groove in males and is most likely restricted to northern Sulawesi. That species is defined by a single female holotype (NMB-REPT 2662). Specimens in museum collections catalogued as *C. fumosus* from localities elsewhere are misidentified and likely represent undescribed species.

Key words: *Cyrtodactylus klakahensis* **sp. nov.**, *C. fumosus*, *C. marmoratus*, Lacertilia, Gekkonidae, bent-toed geckos, East Java, Indonesia, Greater Sunda Islands, morphology

Zusammenfassung

Eine neue Bogenfingergecko-Art der Gattung *Cyrtodactylus* Gray, 1827 wird aus Klakah, Lumajang, Jawa Timur, Java, Indonesien, beschrieben. *Cyrtodactylus klakahensis* **sp. nov.** unterscheidet sich von allen anderen Arten der Gattung durch (1) eine ausgeprägte Präkloakal-Grube bei Männchen, (2) drei Reihen vergrößerter Präkloakalfemoral-Schuppen, von welchen die dritte Reihe bei Männchen 37–38 Poren aufweist, (3) drei bis vier Reihen vergrößerter Schuppen zwischen den Präkloakalfemoral-Schuppenreihen und der Kloake, die ein distinktes Chevron formen, (4) erhabene und stark gekielte dorsale Tuberkel, die in der Körpermitte in 15–19 Reihen angeordnet sind, (5) eine schwach ausgeprägte laterale Falte, (6) 17–20 subdigitale Lamellen unter der vierten Zehe und (7) das Fehlen von verbreiterten Subcaudal-Schuppen. *Cyrtodactylus klakahensis* **sp. nov.** ist erst die dritte von Java beschriebene Bogenfingergecko-Art, was darauf hindeutet, dass die Artenvielfalt der Gattung auf dieser Insel bislang unterschätzt worden ist. Zudem bestätigen wir, dass es sich bei *C. fumosus* (Müller, 1895) um eine Art handelt, die eine Präkloakal-Grube besitzt und wahrscheinlich ausschließlich im Norden Sulawesis beheimatet ist. Die Art ist durch einen weiblichen Holotypus (NMB-REPT 2662) definiert. Belege in naturhistorischen Sammlungen, die unter dem Namen *C. fumosus* verzeichnet sind, jedoch von Lokalitäten außerhalb Sulawesis stammen, sind falsch identifiziert und repräsentieren möglicherweise unbeschriebene Arten.

Schlüsselwörter: *Cyrtodactylus klakahensis* **sp. nov.**, *C. fumosus*, *C. marmoratus*, Lacertilia, Gekkonidae, Bogenfingergeckos, Ost-Java, Indonesien, Große Sunda Inseln, Morphologie

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Introduction

The genus *Cyrtodactylus* Gray, 1827 currently comprises ~200 recognized species and thus is the most species-rich group within the Gekkota (Shea *et al*. 2011; Wood *et al*. 2012; Oliver *et al*. 2014; Riyanto *et al*. 2014; Uetz & Hošek 2015). On mainland Asia, the genus occurs in India, Nepal, Bhutan, and on the Tibetan plateau, and has a continuous range from the southern foothills of the Himalayas towards the southeast into Myanmar, Laos, Thailand, Cambodia, Vietnam, and Peninsular Malaysia. *Cyrtodactylus* is also found in Sri Lanka, the Andaman Islands, and virtually across the entire Malay Archipelago east across New Guinea to the Solomon Islands, with a small number of species also found in northern Australia, in the Kimberley Region of Western Australia and in northern Queensland (e.g., Bauer & Henle 1994; Youmans & Grismer 2006; Rösler & Glaw 2008; Shea *et al*. 2011; Bauer & Doughty 2012; Wood *et al*. 2012; Oliver *et al*. 2014).

Recently, Riyanto *et al*. (2014) listed three *Cyrtodactylus* species, *C. marmoratus* Gray, 1831, *C. fumosus* (Müller, 1895), and *C. semiadii* Riyanto *et al*., 2014 for Java, an island in the Greater Sunda Archipelago covering an area of about 130,000 km^2 (Whitten *et al*. 1996). We here describe a new species of *Cyrtodactylus* from Klakah, Lumajang Regency, East Java, on the basis of material collected by the *Deutsche Limnologische Sunda-Expedition* (German Limnological Sunda Expedition) of 1928/29. The four specimens (two males, one female, one juvenile) are housed in the collection of the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany (SMF) and were initially identified as *Gymnodactylus* (= *Cyrtodactylus*) *fumosus* by Mertens (1934). Based on our examination of the type specimen of *C. fumosus* and additional vouchers from North Sulawesi, the Javanese specimens are clearly distinct from *C. fumosus*.

Material and methods

For each specimen of the new species (*n* = 4) as well as for all material used for comparison (*n* = 56), we recorded data for 28 eidonomic characters (see Table 1 for definitions and abbreviations). Of these, 14 were metric and 14 meristic. We also calculated the following ratios: ArmL/SVL, LegL/SVL, HeadL/SVL, HeadW/HeadL, SnoutL/HeadL, SnoutL/OrbD, and MentalL/MentalW. All measurements were taken to the nearest 0.1 mm using digital calipers. Rows of enlarged scales between the precloacofemoral scale rows and the cloaca, forming distinct chevrons, are referred to as 'posterior precloacal scales' (new name proposed herein). Scale counts and observations of external morphology were made using dissecting microscopes. Characters occurring bilaterally were measured or counted on the right side of specimens, unless stated otherwise; for labial scales, we provide scale counts for both sides (the prefixes 'R' and 'L' are used to distinguish characters counted on the right and left side, respectively). For descriptions of pattern and coloration, we apply the terminology of Köhler (2012). Numbers in parentheses behind the respective capitalized color name refer to the coding therein.

While *Cyrtodactylus klakahensis* **sp. nov.** clearly differs from all known congeners, we limited our comparisons to species occurring in the Greater Sunda Islands (including Sulawesi) and Lesser Sunda Islands only. Comparisons were made with material housed in the collections of AMNH, BMNH, MCZ, MTKD, NMB, RMNH, SMF, ZMA (now in Naturalis, Leiden; RMNH), ZRC, and ZSM (abbreviations follow Sabaj Pérez [2014]), as well as with relevant literature sources (e.g., original descriptions and descriptions in broader taxonomic accounts).

Results

Cyrtodactylus klakahensis sp. nov.

English: Klakah bent-toed gecko; German: Klakah Bogenfinger-Gecko
Chresonym: *Cyrtodactylus fumosus*—Mertens 1934, *Archiv für Hydrobiologie*: 689
Figures 1–3; Table 2 & 3

Holotype. SMF 22476 (Figures 1 & 3A–C; Table 2), an adult male, collected in 1928 or 1929 by members of the *Deutsche Limnologische Sunda-Expedition* at Klakah, Lumajang Regency, Jawa Timur Province, Java, Indonesia.

Paratypes. SMF 22477 (Figure 2A; Table 2), an adult male; SMF 22478 (Figure 2B; Table 2), an adult female; and SMF 22479 (Figure 2C; Table 2), an unsexed juvenile. All specimens have the same collection information as the holotype.

TABLE 1. Metric and meristic characters with abbreviations used in this study.

Character	Abbreviation	Definition
Snout-vent length	SVL	from tip of snout to cloaca
Axial length	AxialL	from axilla to groin
Tail length	TailL	length of original tail, from cloaca to tip of tail
Arm length	ArmL	from insertion of antebrachium with body wall to claw of longest finger
Leg length	LegL	from insertion of femur with body wall to claw of longest toe
Head length	HeadL	from tip of snout to articulation of quadrate bone
Head width	HeadW	measured at level of ear openings
Head height	HeadH	measured at level of ear opening
Snout length	SnoutL	from tip of snout to anterior margin of orbit
Orbit-ear length	OrbEarL	from posterior margin of orbit to anterior margin of ear opening
Orbital diameter	OrbD	from anterior to posterior margin of orbit
Ear length	EarL	from anterior to posterior margin of ear opening
Mental length	MentalL	maximum length of mental shield
Mental width	MentalW	maximum width of mental shield
Dorsal tubercles	DTR	number of tubercle rows on dorsum at midbody, counted in one row between lateral folds
Paravertebral tubercles	PVT	number of tubercles counted in a longitudinal row between posterior insertion of fore limb and anterior insertion of hind limb
Ventral scales	VS	number of ventral scales at midbody, counted in one row between lateral folds
Precloacofemoral scales	PFS	number of enlarged precloacofemoral scales, counted along lowest, pore-bearing row
Precloacofemoral pores	PFP	number of precloacofemoral pores
Postcloacal tubercles	PCT	number of postcloacal tubercles
Subdigital lamellae under 4th toe	LT_4	subdigital scales under 4th toe, counted from first enlarged scale (true lamellae) on lower side of toe to scale proximal to apical scale
Supralabial scales 1	$SupraLab_1$	labial scales of upper jaw, beginning with first enlarged scale bordering rostral shield, ending with last enlarged scale bordering labial angle
Supralabial scales 2	$SupraLab_2$	labial scales of upper jaw, beginning with first enlarged scale bordering rostral shield, ending with enlarged scale below anterior margin of orbit
Infralabial scales	InfraLab	labial scales of lower jaw, beginning with first scale bordering mental shield, ending with last enlarged scale bordering labial angle
Internasal scales	InterNas	number of scales between rostronasals, bordering rostral shield
Supraciliar scales	SC	number of enlarged scales extending from anterior-ventral to posterior-medial edge of orbit
Interorbital scales	IOS	number of scales counted in one row between medial edges of orbits across occiput
Gular scales	GulS	number of gular scales bordering pair of 1st postmentals (excluding enlarged second 2nd postmentals)

TABLE 2. Metric (in mm) and meristic data for the type series of *Cyrtodactylus klakahensis* **sp. nov.** Abbreviations are defined in Table 1.

	Holotype SMF 22476	Paratype SMF 22477	Paratype SMF 22478	Paratype SMF 22479
Sex	male	male	female	unsexed juvenile
SVL	68.1	61.1	67.2	37.2
AxialL	31.9	27.3	28.7	14.0
ArmL	25.9	21.7	24.1	13.6
LegL	36.3	28.9	34.0	16.8
HeadL	18.1	16.8	16.6	10.4
HeadW	10.6	10.4	10.5	6.1
HeadH	7.0	7.2	8.3	4.2
SnoutL	7.6	7.0	7.9	4.2
OrbEarL	5.9	5.6	6.7	2.9
OrbD	3.7	3.4	3.4	1.9
EarL	1.3	1.3	1.4	0.5
DTR	19	17	17	15
PVT	26	29	33	26
VS	38	36	36	35
PFS	40	38	38	38
PFP	37	38	0	0
$LT_{4\ (proximal)}$	9	7	7	8
$LT_{4\ (distal)}$	11	10	10	9
LT_4	20	17	17	17
$SupraLab_1$	R10 L10	R11 L10	R10 L11	R11 L10
$SupraLab_2$	R6 L5	R5 L5	R5 L6	R5 L6
InfraLab	R9 L9	R9 L10	R8 L10	R9 L8
GulS	4	4	4	4

Definition. *Cyrtodactylus klakahensis* can be distinguished from all other congeners occuring in the Greater Sunda Islands (including Sulawesi) and Lesser Sunda Islands by the following combination of characters: (1) a deep precloacal groove in males, (2) three rows of enlarged precloacofemoral scales, of which the third row bears 37–38 pores in males, (3) three or four rows of posterior precloacal scales, (4) raised and strongly keeled dorsal tubercles in 15–19 rows at midbody, (5) an indistinct lateral fold, (6) 17–20 subdigital lamellae under the 4th toe, and (7) subcaudal scales which are not transversely enlarged.

Comparison with other species. The new species can be readily distinguished from the Greater Sunda Island congeners *Cyrtodactylus batik* Iskandar *et al*., 2011, *C. consobrinus* (Peters, 1871), *C. ingeri* Hikida, 1990, *C. jellesmae* (Boulenger, 1897), *C. lateralis* (Werner, 1896), *C. malayanus* (de Rooij, 1915), *C. matsuii* Hikida, 1990, *C. semiadii* Riyanto *et al*., 2014, *C. quadrivirgatus* Taylor, 1962, *C. wallacei* Hayden *et al*., 2008, and *C. yoshii* Hikida, 1990, and from the Lesser Sunda Island species *C. darmandvillei* (Weber, 1890), *C. gordongekkoi* (Das, 1993), *C. laevigatus* Darevsky, 1964, and *C. wetariensis* (Dunn, 1927) by the presence of a deep precloacal groove in males, bearing five pores. Data in Table 3 allow a detailed comparison of *C. klakahensis* with all other Sundanese bent-toed geckos, and additional characters to distinguish the new species from taxa without a precloacal groove are listed therein.

In the following comparisons with species that also possess a precloacal groove, including *Cyrtodactylus agamensis* (Bleeker, 1860), *C. baluensis* (Mocquard, 1890), *C. cavernicolus* Inger & King, 1961, *C. celatus* Kathriner *et al*., 2014, *C. fumosus*, *C. marmoratus*, *C. psarops* Harvey *et al*. 2015, *C. pubisulcus* Inger, 1958, *C. semicinctus* Harvey *et al*. 2015, and *C. spinosus* Linkem *et al*., 2008, the characters for *C. klakahensis* are provided in parentheses. *Cyrtodactylus agamensis* (data from Rösler *et al*. 2007, based on the single known specimen, an adult female) possesses 67 (35–38) VS; 26 (17–20) LT_4; 54 enlarged PFS (38–40); and a single enlarged scale in the precloacal groove (five scales in the precloacal groove). *Cyrtodactylus baluensis* (data from Hikida 1990 and obtained from specimens listed in the Appendix) possesses precloacal scales that are separated from the femoral scales (enlarged PFS in both sexes); 4–10 precloacal- and 9–11 femoral pores in males (37–38 PFP in a continuous series in males); no posterior precloacal scales (posterior precloacal scales present); and enlarged subcaudals (enlarged subcaudals absent). *Cyrtodactylus cavernicolus* (data from Grismer & Leong 2005) possesses 51–58 (35–38) VS; 22–26 (17–20) LT_4; no enlarged femoral scales (enlarged PFS in three rows present in both sexes); no femoral pores (pores, including those on the femur, present in males); and dorsal bands (dorsal blotches). *Cyrtodactylus celatus* (data from Kathriner *et al*. 2014; Rösler & Kaiser, in press.; and obtained from specimens listed in the Appendix) is a small-sized species with adult SVL of 38.4−43.6 mm (61.1−68.1 mm) that possesses no femoral pores (pores, including those on the femur, present in males). *Cyrtodactylus fumosus* (data obtained from specimens listed in the Appendix) possesses widely scattered, roundish, flat, and smooth dorsal tubercles in 4–7 rows at midbody (closely arranged, trihedral, raised, and strongly keeled dorsal tubercles in 15–19 rows at midbody); no or a low number of scattered tubercles on the limbs (limbs strongly tuberculated); a total number of 16 pores, ten of which are precloacal pores, separated from three femoral pores by ten enlarged pore-less scales[1] in males (37–38 PFP in a continuous series in males); and an ear opening forming a horizontal cleft[2] (ear opening vertically elongated). *Cyrtodactylus marmoratus* (data from Rösler *et al*. 2007 and obtained from specimens listed in the Appendix) possesses 38–47 (35–38) VS; 48–56[3] (38–40) enlarged PFS; 45–53[4] (37–38) PFP in males; and pores present in females (no pores present in females). Based on our examinations, *C. marmoratus* also lacks posterior precloacal scales (posterior precloacal scales present), possesses a different arrangement of postmental and gular scales, and has differently shaped postcloacal tubercles. The reader is referred to Figure 3 for a comparison of the shape and arrangement of dorsal tubercles at midbody, the precloacal region in males, and the postmental and gular scale pattern between *C. klakahensis*, *C. fumosus*, and *C. marmoratus*. *Cyrtodactylus psarops* possesses weakly keeled dorsal tubercles in 23–26 rows at midbody (strongly keeled tubercles in 15–19 rows at midbody); tubercles often present on the brachium (tubercles on brachium absent); 38–49 (35–38) VS; 28–32 (37–38) PFP in males; a single, greatly enlarged, pore-bearing scale at the apex of the pore-bearing scale series (apical scale of pore-series not greatly enlarged); no posterior precloacal scales (posterior precloacal scales present); and a single (2–3) PCT. *Cyrtodactylus pubisulcus* (data from Hikida 1990; Das & Jim 2000; and obtained from specimens listed in the Appendix) possesses 37–58 (35–38) VS; no enlarged femoral scales (enlarged PFS present); no femoral pores (pores, including those on the femur, present in males); and no posterior precloacal scales (precloacal scales present). *Cyrtodactylus semicinctus* possesses weakly keeled dorsal tubercles in 24–27 rows at midbody (strongly keeled tubercles in 15–19 rows at midbody); and a single, greatly enlarged, pore-bearing scale at apex of the pore-bearing scale series (apical scale of pore-series not greatly enlarged). *Cyrtodactylus spinosus* (data from Linkem *et al*. 2008) possesses 38–44[5] (35–38) VS; no femoral pores (pores, including those on the femur, present in males); and lateral and caudal spines (lateral and caudal spines absent).

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[1] Boulenger (1897) provided a count of 42 PFP for *C. fumosus*. We re-examined the material used by Boulenger, which is clearly conspecific with the type specimen housed in NMB, and found that his single adult male specimen (BMNH 1896.12.9.3, from Rurukan, North Sulawesi) does not possess a continuous series of PFP. De Rooij (1915) provided a count of 42–52 PFP, but included data of specimens from Sulawesi (*C. fumosus*), Halmahera (identified as *C. philippinicus* [Steindachner, 1867] by Boettger [1900] and subsequently described as a new taxon currently known as *C. halmahericus* [Mertens, 1929]), and Java (misidentified *C. marmoratus*) in her definition of *C. fumosus* (see Brongersma 1934). De Rooij's (1915) count of 42–52 PFP for *C. fumosus* is often cited in the literature (e.g., Oliver *et al*. 2009; Chan & Norhayati 2010; Grismer *et al*. 2012), although this count is incorrect as demonstrated by our examination and literature survey (see also Remarks on the taxonomy of *C. fumosus*).

[2] De Rooij (1915) and Brongersma (1934) attributed the shape of the ear-opening to the state of preservation. We examined well preserved specimens of *C. fumosus sensu stricto* that exhibited a horizontal, slit-shaped ear opening, indicating that this character is taxonomically informative.

[3] Although Rösler *et al*. (2007) provided a maximum count of 52 PFS for the type series, the lectotype of *C. marmoratus* (RMNH.RENA 2710a.1) possesses 56 PFS.

[4] Rösler *et al*. (2007) provided a count of 45–50 PFP for male *C. marmoratus*, with the lectotype stated to have 45 pores. However, the lectotype possesses 52 PFP.

[5] Linkem *et al*. (2008; Table 1) listed 38−44 VS for *C. spinosus* (counts listed for individual specimens), while in their comparative table (Table 2) they provided a range of 40−43 VS.

TABLE 3. Characters used to distinguish *Cyrtodactylus klakahensis* **sp. nov.** from congeneric species occurring in the Sunda Islands (including Sulawesi). The presence of a diagnostic character is coded as '1', the absence of a character is coded as '0'. For taxa possessing precloacofemoral scales (= scales in a continuous series; column entitled '9'), precloacal- and femoral scales (separated from each other by infrascales) are coded 'n/a' (columns entitled '7' and '8'). Numbers at the head of the table correspond to characters as follows: 1 = tubercles on forelimbs, 2 = tubercles on hindlimbs, 3 = tubercles on head, 4 = number of ventral scales, 5 = enlarged subcaudals, 6 = number of subdigital lamellae under 4th toe, 7 = enlarged precloacal scales (and number of pores in parentheses if present; if pores are present in one sex only, this is indicated either by '♂' or '♀'), 8 = enlarged femoral scales (and number of pores in parentheses if present; if pores are present in one sex only, this is indicated either by '♂' or '♀'), 9 = enlarged precloacofemoral scales (and number of pores in parentheses if present; if pores are present in males only this is indicated by '♂'), 10 = pores in a continuous series, 11 = precloacal groove present (if a groove is present in males only, this is indicated by '♂'), 12 = pattern of dorsum (bd = banded; bl = blotched; mo = mottling; pl = patternless; st = striped). If data for a character are not available, this is indicated by a '?'. Where derived from the literature ('Lit.' column), references are abbreviated by letters as follows: A = this publication; B = Rösler *et al.* 2007; C = Grismer & Leong 2005; D = Manthey & Grossmann 1997; E = Iskandar *et al.* 2011; F = Inger & King 1961; G = Kathriner *et al.* 2014; H = Rösler & Kaiser, in press.; I = Hikida 1990; J = de Rooij 1915; K = Brongersma 1934; L = Boulenger 1897; M = Das 1993; N = Youmans & Grismer 2006; O = Auffenberg 1980; P = Darevsky 1964; Q = Werner 1896; R = Das 2010; S = Harvey *et al.* 2015; T = Inger 1958; U = Riyanto *et al.* 2014; V = Linkem *et al.* 2008; W = Taylor 1962; X = Hayden *et al.* 2008; Y = Dunn 1927. Under the column heading '*n*' we provide the number of adult specimens we examined personally.

Taxon	SVL in adults	1	2	3	4	5	6	7	8	9	10	11	12	Lit.	*n*
klakahensis	**61–68**	**1**	**1**	**1**	**35–38**	**0**	**17–20**	**n/a**	**n/a**	**1 (37–38, ♂)**	**1**	**1**	**bl**	**A**	**4**
agamensis	50	1	1	1	67	0	26	n/a (?^{a})	n/a (?^{a})	1 (?^{a})	?	1	bl	B	-
baluensis	71–95	1	1	1	36–46	1	19–23	1 (9–11, ♂)	1 (4–10, ♂)	0	0	0	bl	A, C, D	9
batik	103–113	1	1	1	48–57	1	24–27	1	0	0	0	0	bd	E	-
cavernicolus	64–81	0	1	1	51–58	0	22–26	1 (4, ♂)	0	0	0	1	bd	C, F	-
celatus	38–44	1	1	1	34–42	0	15–18	1 (4, ♂)	0	0	0	1 (♂)	bl	A, G, H	3
consobrinus	97–125	1	1	1	58–71	1	22–28	1 (8–11, ♂)	0/1 (0–6, ♂)	0	0	0	bd	A, C, D, I	2
darmandvillei	80–82	1	1	1	34–36	1	23–24	n/a	n/a	1	0	0	bl	A, J, K	2
fumosus	57–78	1	1	1	37–50	0	17–23	n/a (10, ♂)	n/a (3, ♂)	1	0	1 (♂)	bl	A, L	3
gordongekkoi	71–73	1	1	1	30	0	22–23	n/a	n/a	1	0	0	bl	A, M	2
ingeri	65–76	1	1	1	40–43	1	23–27	1 (8, only ♂♂ known)	0	0	0	0	bl	I, N	-
jellesmae	42–64	1	1	1	40–47	0	16–19	1	0	0	0	0	bl	A, L	3
laevigatus	38–47	0	1	0	30–34	0	10–15	?	0/1	?	0	0	mo, pl	A, E, O, P	5
lateralis	65–85	1	1	1	60–64	0	21–22	1 (13, ♂)	0	0	0	0	bl	C, D, Q	-
malayanus	70–83	1	1	1	58–62	1	21–23	1 (8–10)	0	0	0	0	bd	C, I, N	-

...continued on next page

TABLE 3 (continued)

Taxon	SVL in adults	1	2	3	4	5	6	7	8	9	10	11	12	Lit.	*n*
marmoratus	45–82	0	1	1	38–47	0	19–24	1 (16, ♀)	1 (6–7, ♀)	1 (45–53, ♂)	0 (♀)/1	1	bl	A, B	2
matsuii	105	1	1	1	48–51	0	22	0 (7–8, ♂)	0	0	0	0	bl	I, N, R	-
psarops	?[b]	1	1	1	38–49	0	18–22	n/a (?[c],♀)	n/a (?[c],♀)	1 (28–32, ♂) (0–29,♀)	0 (♀)/1	1	bl	S	-
pubisulcus	51–74	0/1	1	1	37–58	0	16–23	1 (7–9, ♂)	0	0	0	1	bl	A, I, N, T	10
semiadii	40–47	?	1	0	35–36	0	14–15	0	0	0	0	0	bl	U	-
semicinctus	?[b]	0	1	1	33–44	0	19–22	n/a	n/a	1 (36–38, ♂) (0–19,♀)	1	1	bl	S	-
spinosus	70–83	1	1	1	38–44	0	19–21	1 (12–13, ♂)[d]	1 (?[e])	0	0	1 (♂)	bd	V	-
quadrivirgatus	51–71	1	1	1	34–42	0	19–20	n/a (3–4, ♂)	n/a	1	0	0	bl, st	D, N, W	-
wallacei	92–114	1	1	1	45–49	1	17–25	1	0	0	0	0	bd, bl	X	-
wetariensis	42–67	1	1	1	36–42	0	15–22	n/a (11, ♂)	n/a (12–16, ♂)	1	0	0	bl	A, Y	4
yoshi	75–96	1	1	1	50–58	0	25–30	0 (8–12, ♂, absent or indistinct in ♀♀)	0	0	0	0	bl	C, I	-

[a] *Cyrtodactylus agamensis* is known from a single female only (see Rösler *et al*. 2007). Hence, it is not known at present if males possess pores.

[b] Harvey *et al*. (2015) did not provide ranges for adult specimens of *C. psarops* and *C. semicinctus*.

[c] In female *C. psarops*, pores can either be arranged continuously, discontinuously, or can be absent altogether. Harvey *et al*. (2015) only provided counts for total pore numbers, but failed to indicate individual counts for the pore-bearing parts of separated pore series.

[d] In their diagnosis and Table 1, Linkem *et al*. (2008) listed 12–13 precloacal pores for *C. spinosus*, whereas in their Table 2, they listed only 8–12 precloacal pores.

[e] According to the diagnosis in Linkem *et al*. (2008), *C. spinosus* lacks femoral pores; it was listed as possessing 4–7 femoral pores in their Table 2.

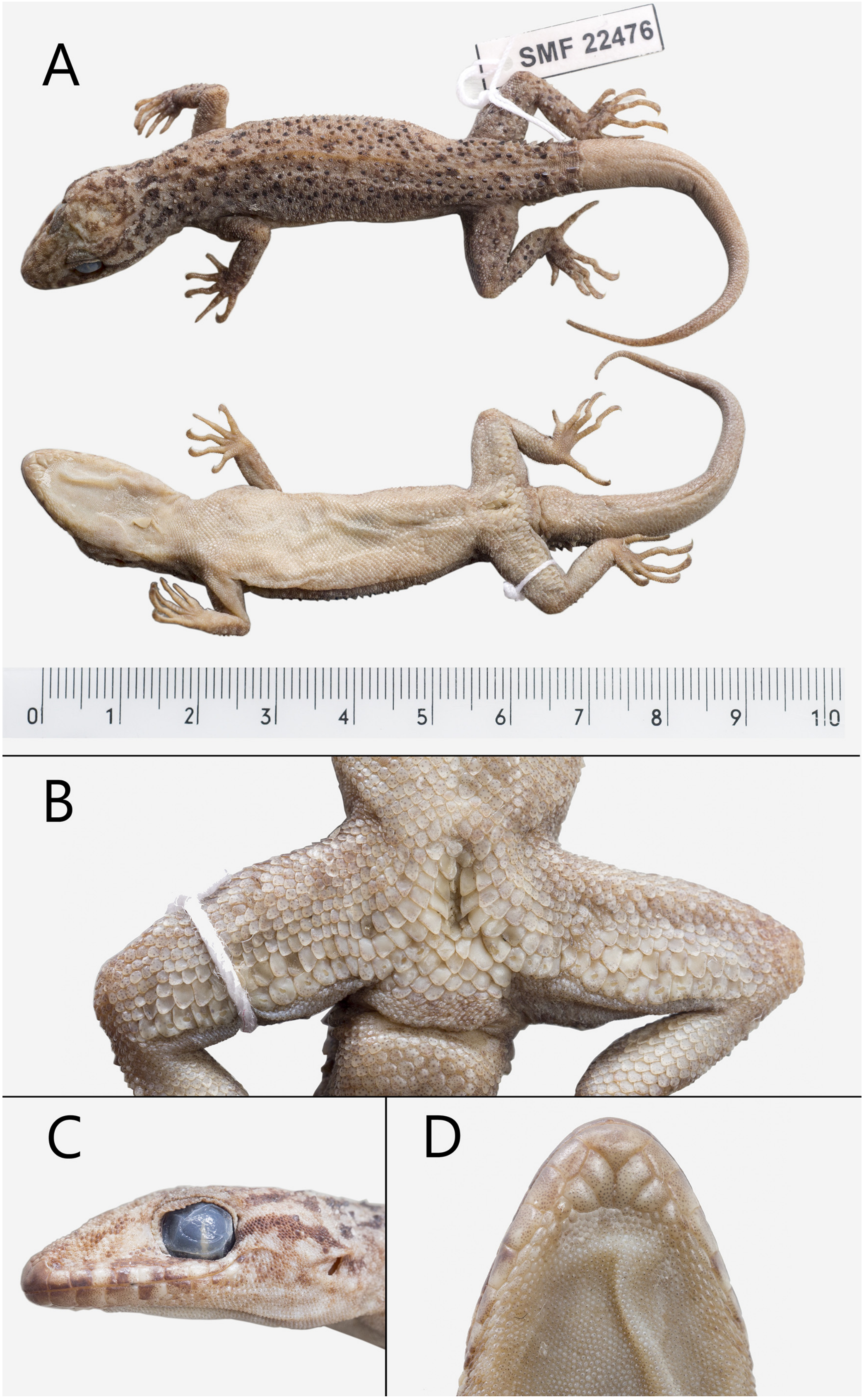

FIGURE 1. Morphological features of the holotype of *Cyrtodactylus klakahensis* **sp. nov.** (SMF 22476). (A) Dorsal and ventral view of the body. (B) Precloacal region showing precloacofemoral scales (bearing precloacofemoral pores) and posterior precloacal scales. (C) Lateral view of the left side of the head. (D) Ventral view of the head, showing pattern of postmental and gular scales. Photos by Sven Mecke.

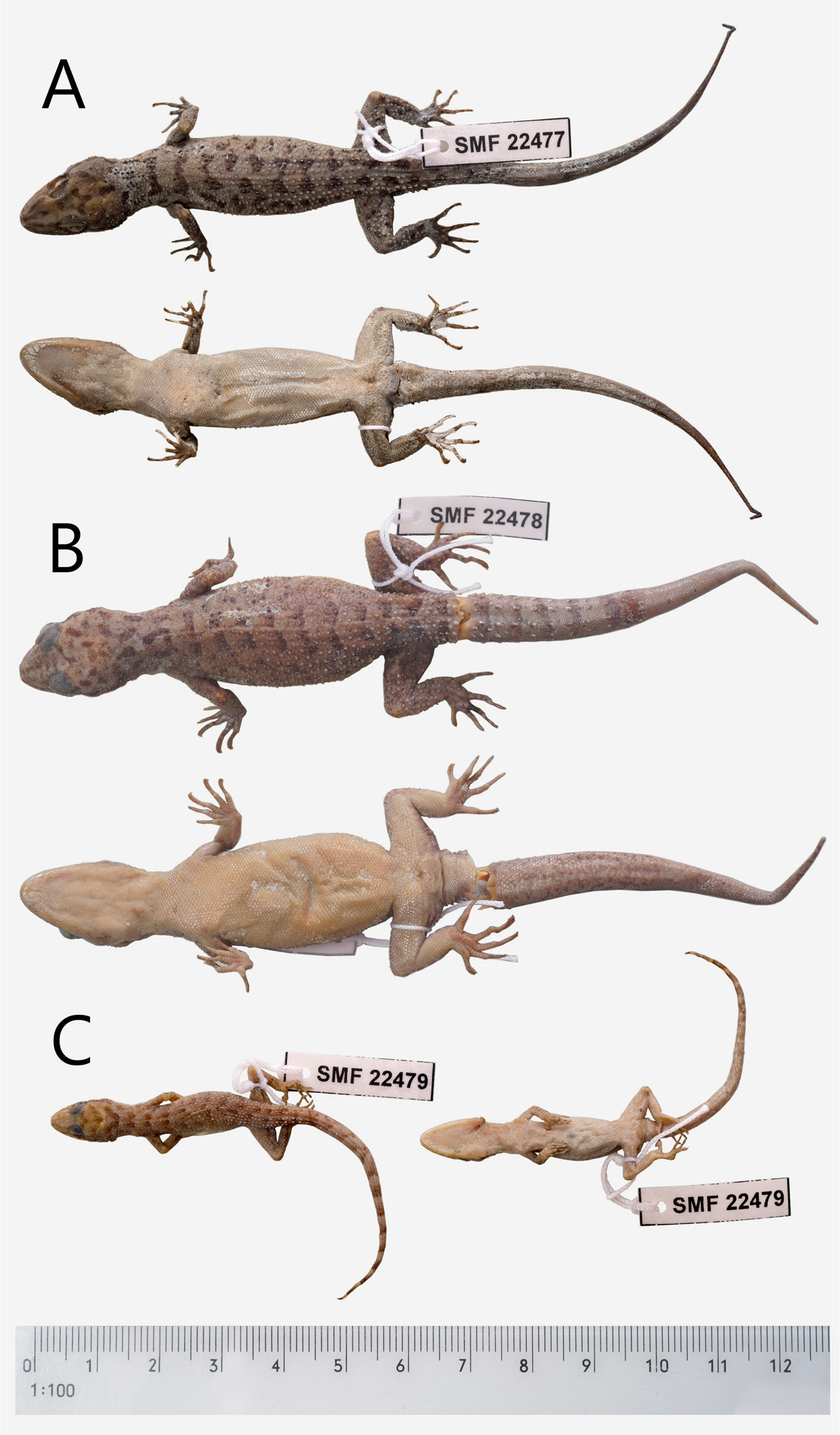

FIGURE 2. Paratype series of *Cyrtodactylus klakahensis* **sp. nov.** in dorsal and ventral view. (A) SMF 22477, an adult male. (B) SMF 22478, an adult female. (C) SMF 22479, an unsexed juvenile specimen. Photos by Sven Mecke.

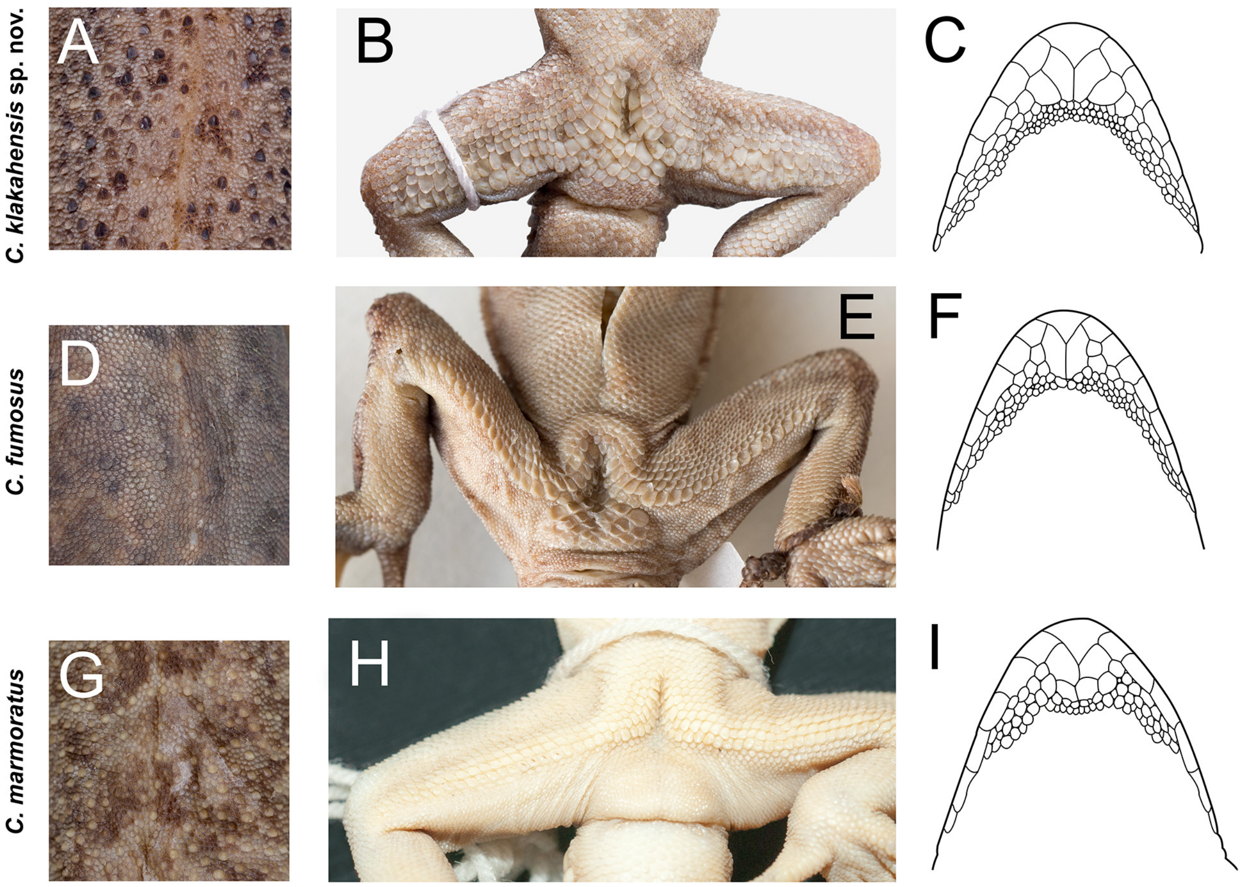

FIGURE 3. Comparison of the shape and arrangement of dorsal tubercles at midbody, the precloacal region in males, and the postmental and gular scale pattern between *Cyrtodactylus klakahensis* **sp. nov.**, *C. fumosus*, and *C. marmoratus*. *Cyrtodactylus klakahensis* **sp. nov.**: A) Closely arranged, trihedral, raised, and strongly keeled dorsal tubercles at midbody; B) eidonomy of precloacofemoral scales (three series), precloacal groove, and posterior precloacal scales; C) gular region, showing the presence of enlarged 2nd postmentals (photos and drawings of SMF 22476, holotype). *Cyrtodactylus fumosus*: D) Widely scattered, roundish, flat, and smooth dorsal tubercles at midbody; E) eidonomy of precloacofemoral scales (only one series distinctly enlarged), precloacal groove, and posterior precloacal scales; F) gular region, indicating the absence of enlarged 2nd postmentals (D, F = NMB-REPT 2662, holotype; E = BMNH 1896.12.9.3). *Cyrtodactylus marmoratus*: G) Closely arranged, slightly raised and keeled dorsal tubercles at midbody; H) eidonomy of precloacofemoral scales (three series) and precloacal groove, with posterior precloacal scales absent; I) gular region, indicating the absence of enlarged 2nd postmentals and the presence of a single pair of enlarged gular scales bordering the single pair of enlarged postmentals posteriorly (G = MTKD 8903; H, I = RMNH.RENA 2710a.1, lectotype). Photos by Sven Mecke; line drawings by Felix Mader (based on photos by Sven Mecke).

Description of the holotype. General habitus, metrics (in mm) and ratios. Adult male; SVL = 68.1; AxialL = 31.9; TailL = 61.7 (tail regenerated); ArmL = 25.9; LegL = 36.3; HeadL = 18.1; HeadW = 10.6; HeadH = 7.0; SnoutL = 7.6; OrbEarL = 5.9; OrbD = 3.7; EarL = 1.3; head length moderate (HeadL/SVL = 0.27); head rather wide (HeadW/HeadL = 0.59), clearly depressed between eyes, distinct from neck; snout rather elongate (SnoutL/HeadL = 0.42), much longer than OrbD (SnoutL/OrbD = 2.10), canthus rostralis distinct; fore- and hindlimbs of moderate size (ArmL/SVL = 0.38; LegL/SVL = 0.53), without webbing between digits; relative length of fingers = IV > III > V > II > I, relative length of toes = IV > III > V > II > I.

Scalation. Dorsal scales rounded and granulate, interspersed with distinctly enlarged, trihedral, raised, strongly keeled, and irregularly arranged dorsal tubercles (Figure 3A); 19 DTR; 26 PVT; latero-dorsal tubercles most strongly keeled, tubercles on lateral portion of the trunk and PVT smaller and feebly keeled; tubercles on base of the tail largest, strongly keeled, pointed and elongate, in eight rows (the longer part of the tail is regenerated, without tubercles present); tubercles on forelimbs small, most prominent on the antebrachium; tubercles on hindlimbs similar in size and shape to latero-dorsal tubercles.

Ventral scales distinctly larger than dorsals, juxtaposed; 38 VS; three series of enlarged PFS, lowest series possessing 40 scales, bearing 37 pores; pore series interrupted by a single, enlarged, pore-less PFS on the left femur (PFS at level of this pore-less scale irregularly arranged and/or smaller; due to an aberration likely caused by an injury); scales immediately posterior to the precloacal groove (posterior precloacal scales) enlarged, arranged in a chevron-like shape consisting of three series (from anterior to posterior: nine scales/ seven scales/ three scales) (Figures 1B & 3B); two domed PCT; number of lamellae under fingers: I 11, II 12, III 14, IV 15, V 15; number of lamellae under toes: I 14, II 16, III 18, IV 20, V 19.

Rostral shield rectangular, about 0.6 time high as wide, partly divided by a suture dorsally, in contact with 1st SupraLab, two rostronasals and a single InterNas; nostril surrounded by rostral, 1st SupraLab, three post-nasals, and a single rostro-nasal; R10 L10 SupraLab_1, R6 L5 SupraLab_2, separated from the orbit by 2–3 rows of small granular scales; R9 L9 InfraLab, bordered by two rows of scales larger than granular scales on the throat; cephalic scales small, rounded, granulate and juxtaposed; tubercles on occiput and neck raised, bearing an apex; 43 IOS; 26 SC; mental triangular, wider than long (MentalL/MentalW = 1.4); one pair of enlarged 1st postmentals, followed by a pair of enlarged 2nd postmentals (Figure 3C); pair of 1st postmentals bordered by mental, 1st InfraLab, enlarged 2nd postmentals, and four GulS (Figure 3C); scales on throat minute, rounded.

Coloration. In preservative, ground color of dorsal surface of head and body Drab (19); head with indistinct Walnut Brown (27) colored reticulum; a Burnt Sienna (38) stripe running from the posterior border of the orbit to a point above the ear opening; light Pale Buff (1) labial scales and postmentals strongly stippled with darker color; dorsum with irregular, faint Warm Sepia (40) blotches, most visible on neck and at level of posterior margin of the forelimbs, between hindlimbs and base of tail; ground color of dorsal surface of limbs like body; venter, throat and lower surface of limbs uniformly Pale Buff (1), heavily dotted and stippled with dark markings of different size; color of regenerated tail Pale Pinkish Buff (3).

Variation. Paratypes similar to holotype except as follows: Paratype SMF 22477 (adult male; Figure 2A) with 17 DTR; 29 PVT; dorsal scales on original part of tail arranged in whorls, each ending in a row of four tubercles; 36 VS; a series of 38 PFS bearing 38 PFP in a continuous series; posterior precloacal scales arranged in a chevron-like shape consisting of four series of scales (from anterior to posterior: nine scales/ nine scales/ six scales/ three scales); three domed PCT; number of lamellae under fingers: I 14, II 14, III 14, IV 15, V 15 (counted on left side of the body; some fingers on right side damaged); number of lamellae under toes: I 12, II 15, III 16, IV 17, V 15; R11 L10 SupraLab_1, R5 L5 SupraLab_2; R9 L10 InfraLab; 27 SC; a single InterNas; a second dark stripe running from nostril to occiput, interrupted only by the orbit; a dark V-shaped collar present, followed by nine pairs of dark paravertebral blotches, larger than lateral ones, which may be fused to form bars anteriorly.

Paratype SMF 22478 (adult female; Figure 2B) with 17 DTR; 33 PVT; dorsal scales on original part of tail arranged in whorls, each ending in a row of four to six tubercles; 36 VS; 38 PFS, lacking pores; no sign of a precloacal groove; posterior precloacal scales arranged in a chevron-like shape consisting of three series of scales (from anterior to posterior: nine scales/ seven scales/ five scales); two domed PCT; number of lamellae under fingers: I 13, II 14, III 18, IV 16, V 13; number of lamellae under toes I 13, II 15, III 19, IV 17, V 19; R10 L11 SupraLab_1, R5 L6 SupraLab_2; R8 L10 InfraLab; 39 IOS; 33 SC; three InterNas; eight pairs of dark paravertebral blotches, which may be fused to form bars; original part of tail with six Burnt Sienna (38) colored bands.

Paratype SMF 22479 (unsexed juvenile; Figure 2C) with 15 DTR; dorsal surface on entirely original tail with scales arranged in whorls, ending in a row of tubercles, tubercles present on proximal quarter of tail only; 35 VS; 38 slightly enlarged PFS, lacking pores; no sign of a precloacal groove; posterior precloacal scales arranged in a chevron-like shape consisting of three series of scales (from anterior to posterior: eight scales/ eight scales/ five scales); two domed PCT; number of lamellae under fingers: I 14, II 15, III 17, IV 18, V 15; number of lamellae under toes: I 12, II 14, III 16, IV 17, V 15; R11 L10; SupraLab_1, R5 L6 SupraLab_2; R9 L8 InfraLab; 36 IOS; 28 SC; a single InterNas; a second dark stripe running from nostril to occiput, interrupted only by the orbit; a dark Verona Brown (37) V-shaped collar present; tail with 15 Verona Brown (37) colored bands, becoming Burnt Sienna (38) distally.

Etymology. The specific epithet is a Latinized, toponymic adjective referring to the type locality Klakah (Lumajang Regency, Jawa Timur Province, Java, Indonesia) of the new species.

Distribution and Natural History. *Cyrtodactylus klakahensis* is currently only known from its type locality, Klakah, Lumajang Regency, Jawa Timur Province, Java, Indonesia (Figure 4). Klakah is located in the lowlands (elevation ca. 200 m) between the Tengger and Iyang-Argapura mountain massifs. Although the species range is probably not restricted to Klakah, it may exhibit a relatively limited distribution in central Jawa Timur Province and therefore should be regarded as endemic to the region, until evidence to the contrary becomes available.

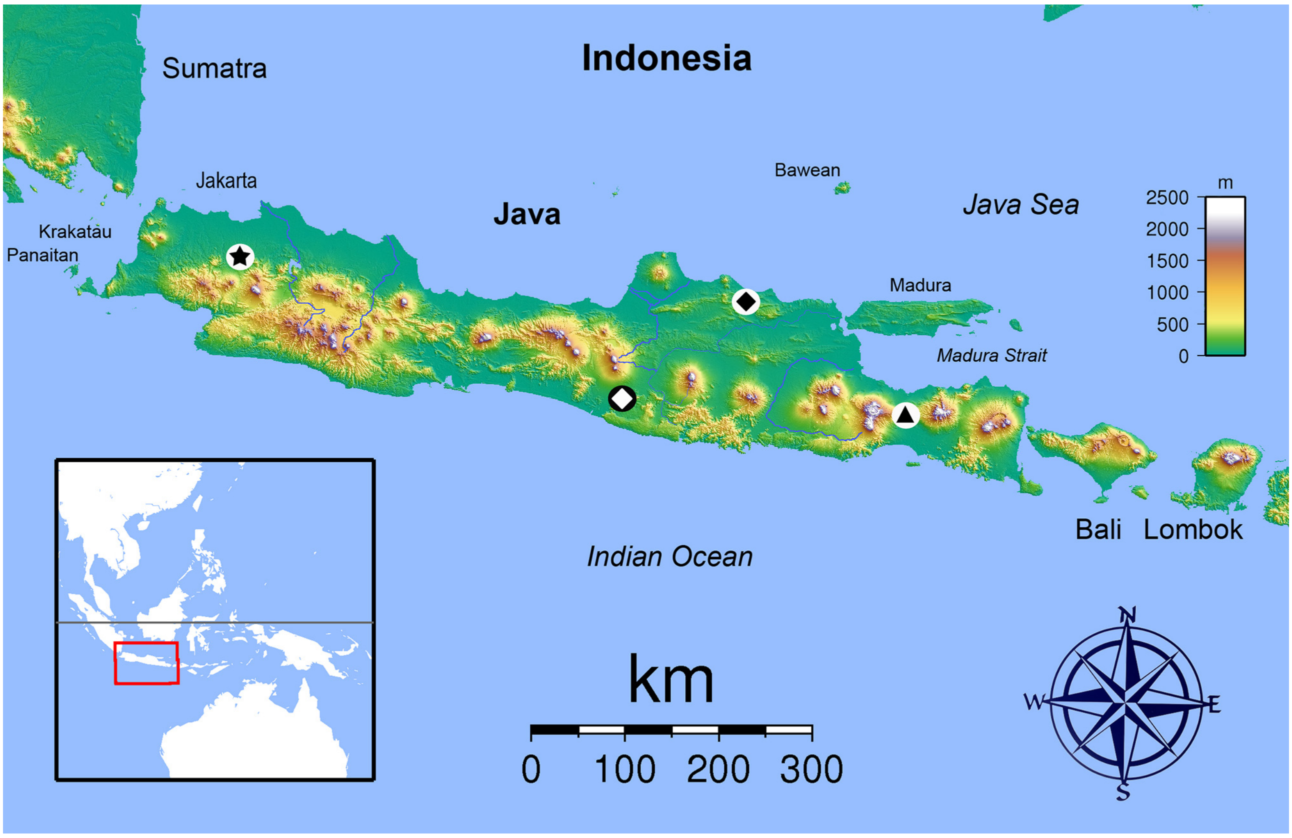

FIGURE 4. Map of Java illustrating the type-, potential type-, and paratype localities of *Cyrtodactylus* spp. The black triangle marks the type locality of *C. klakahensis*. The black diamond marks the type locality of *C. semiadii* (paratype locality identified by a white diamond). The exact type locality of *C. marmoratus* in Java is unknown, but the type specimens were, in all probability, collected from western Java. The potential type locality (indicated by a black star) may lie within the mountainous area around Bogor, but a revision of the *C. marmoratus* species-complex is needed to narrowly restrict the type locality of *C. marmoratus sensu stricto*. Base map modified from Wikipedia by Sven Mecke.

Remarks on the taxonomy of *Cyrtodactylus fumosus*. The bent-toed gecko species *Cyrtodactylus fumosus* (proposed vernacular name: Sulawesi bent-toed gecko) was described by Friedrich ('Fritz') Müller (1834–1895) based on a single adult female (NMB-REPT 2662; Figure 5) collected by Karl Friedrich ('Fritz') Sarasin (1859–1941) and Paul Benedict Sarasin (1856–1929) in the "Bulawa Mountains" (North Sulawesi, elevation ca. 1200 m) (Müller 1895; the 1894 volume was issued in 1895). In his second article published in the *Verhandlungen der naturforschenden Gesellschaft Basel* (Reptilien und Amphibien aus Celebes, part II), Müller (1895b) mentioned a second specimen of the species (NMB-REPT 2663) from "Masarang" but referred to NMB-REPT 2662 as "*Original-Exemplar*" (i.e., the holotype). We therefore recognize NMB-REPT 2662 as the only type specimen (see Brongersma 1934; Kramer 1979; Koch 2012) in disagreement with de Rooij (1915:17) who referred to an unspecified number of type specimens in a footnote. Boulenger (1897) provided a more detailed description of *C. fumosus* based on four specimens, including NMB-REPT 2662–63 and two additional North Sulawesi specimens donated by Paul Sarasin, BMNH 1895.2.27.7 and BMNH 1896.12.9.3, and corrected the type locality from Boelawa Mountains (= Huidu Matabulawa) to Bone Mountains (= Pegunungan Bone). De Rooij (1915) recorded *C. fumosus* for Java based on a single specimen but Brongersma (1934) subsequently referred to this apparently misidentified voucher as *C. marmoratus* and restricted *C. fumosus* to Sulawesi. Mertens (1934) once again listed *C. fumosus* as occuring on Java (Klakah, Lumajang) and clearly indicated that this assignment would be provisional with the genus being in need of a revision. Several subsequent authors have listed *C. fumosus* as part of the Javanese herpetofauna (e.g., Manthey & Grossmann 1997; Hayden *et al*. 2008; Oliver *et al*. 2009; Das 2010; Riyanto *et al*. 2014) but these records seem to be either based on erroneous data provided in the literature (e.g., de Rooij 1915; Das 2010) and/or misidentified specimens. Linkem *et al*. (2008) did not consider *C. fumosus* a valid

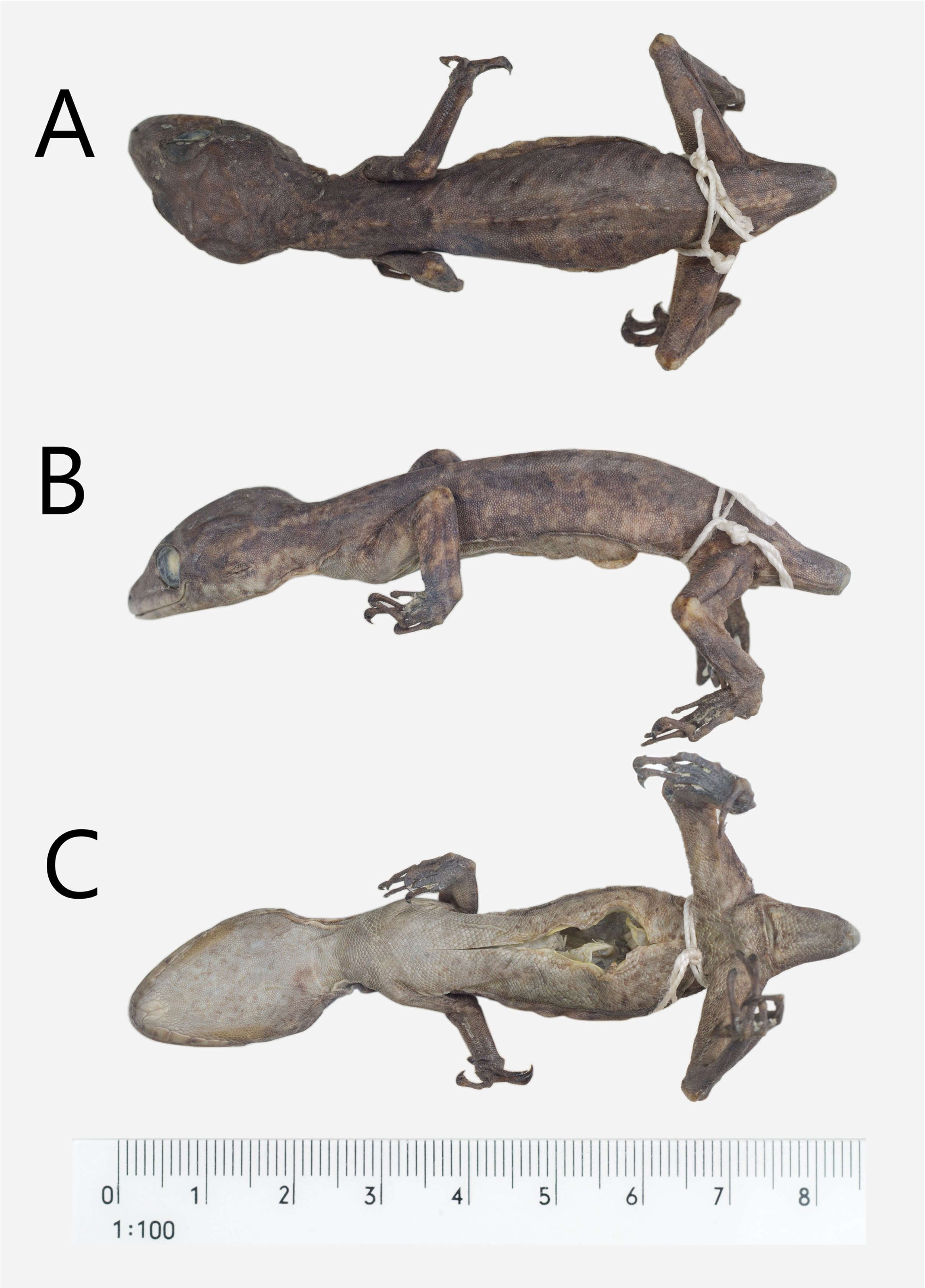

FIGURE 5. Holotype of *Cyrtodactylus fumosus* (NMB-REPT 2662; adult female) in (A) dorsal, (B) lateral, and (C) ventral view. Photos by Sven Mecke.

species, stating that it had been synonymized with *C. marmoratus*. However, Brongersma (1934) did not synonymize *C. fumosus* with *C. marmoratus* but indicated both taxa were distinct (see also Brongersma 1953; Koch 2012).

There is considerable confusion in the literature as to whether *Cyrtodactylus fumosus* possesses a precloacal groove in males. *Cyrtodactylus fumosus* was referred to as a species lacking a precloacal groove by Rösler *et al.* (2007), Grismer & Norhayati (2008), Welton *et al.* (2009), Chan & Norhayati (2010), and Grismer *et al.* (2012). Boulenger (1897), who examined *C. fumosus* specimens from North Sulawesi (Bone Mountains, Masarang, Rurukan; all collected by Fritz and Paul Sarasin), reported that male individuals of this species did possess a precloacal groove. We examined the adult male specimen (BMNH 1896.12.9.3) used by Boulenger for his species account of *C. fumosus* and confirm the presence of a precloacal groove in this species. A precloacal groove, however, may be only weakly defined in subadult male specimens, as seen in NMB-REPT 2663.

It appears that several species may be masquerading under the name *Cyrtodactylus fumosus*, both in the Greater and Lesser Sunda Islands (Riyanto *et al.* 2014; pers. obs.). Above, we were able to demonstrate unequivocally that the specimens from Klakah, Lumajang Regency, Java, originally referred to as *C. fumosus* by Mertens (1934), represent a new species. The populations on Bali referred to as *C. fumosus* by Mc Kay (2006) and additional forms from Java are likely also new species (Mecke *et al.*, in prep., Riyanto *et al.*, in prep.). Based on a photograph of a strongly tuberculated individual of *C.* cf. *fumosus* in Koch (2012: 151) from North Sulawesi, we assume that Sulawesi *C. fumosus* populations may represent a species complex as well. The taxon is in dire need of a revision, with a thorough re-description of *C. fumosus sensu stricto* currently underway (Hartmann *et al.*, in prep.).

Discussion

Despite its large size (ca. 130,000 km^2), the island of Java is home to only three described *Cyrtodactylus* species (*C. marmoratus*, *C. semiadii*, and *C. klakahensis*). Our examinations of museum specimens have revealed that the diversity of bent-toed geckos in Java is significantly underestimated, perhaps owing to a lack of comprehensive survey work in the past and neglect from taxonomists. For the description of some of these unrecognized species, redescriptions of *C. marmoratus* and *C. fumosus* are crucial, as these names have frequently been applied to a number of undescribed species, some of which are likely not even closely related.

The discovery of *Cyrtodactylus klakahensis* in an area near Bromo Tengger Semeru National Park further emphasizes the need for survey efforts targeting East Java Province as a major center of Southeast Asian endemism and biodiversity (e.g., Natus 2005; Hong *et al.* 2011). The Tengger and Iyang-Argapura mountain massifs, and surroundings are home to a highly endemic flora in diverse habitats (e.g., Whitten *et al.* 1996; Wikramanayake *et al.* 2002; Hakim & Miyakawa 2013), and Natus (2005) identified several endemism centers for terrestrial vertebrates (birds and mammals) in East Java. This may indicate that the area is also worth exploring further from a herpetological perspective. Among reptiles, the snake *Tetralepis fruhstorferi* Boettger, 1892 is so far the only known species endemic in the Tengger Mountains. We anticipate that additional new reptile and amphibian species will eventually be discovered in East Java as taxonomic museum and field work continues. The description of *C. klakahensis* underscores the high biotic diversity of the Tengger and Iyang-Argapura mountain massifs and their surroundings, and confirms their obvious conservation value.

Our observations are not limited to the eastern portion of Java Island and recent taxonomic research on Javanese reptiles by ourselves and colleagues has already resulted in the description of several new taxa. These include, among snakes, a new species of *Cylindrophis* (Kieckbusch & Mecke *et al.*, accepted) and *Dendrelaphis underwoodi* van Rooijen & Vogel, 2008, among skinks, the species *Carlia nigrauris* Zug, 2010 and *Eutropis macrophtalma* (Mausfeld & Böhme, 2002), and among geckos *Cyrtodactylus semiadii*. The fact that such distinctive species are still being described serves to underline both the diversity of the Javanese herpetofauna and the need of further taxonomic research.

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APPENDIX. Specimens examined for comparison.

Cyrtodactylus baluensis.—**Indonesia**: *Kalimantan Timur Province*: "Mount Tibang" (= Bukit Batu Tiban): MCZ Herp R-22626.—**Malaysia**: *Sarawak* (*Borneo*): Mount Kinabalu (= Gunung Kinabalu): MCZ Herp R-39036; Mount Kinabalu: "Kaddmayan River", near Kiau: MCZ Herp R-43474; Kenokok: MCZ Herp R-43475; Kiau (= Kampung Kiau): MCZ Herp R-43477, R-163132; "Mahunbayon": MCZ Herp R-43473, R-163646; "Penokok River" (= alternative spelling of Kenokok River), near Kiau: MCZ Herp R-43476.

Cyrtodactylus celatus.—**Indonesia**: *Nusa Tenggara Timur Province*: West-Timor: Ofu: ZSM 556/2002, Soe: NMB-REPT 12789, "Djamplong, 55 kilometers by road from Kupang" ("Djamplong" = Tjamplong or Camplong): BMNH 1926.10.30.45 (holotype).

Cyrtodactylus consobrinus.—**Malaysia**: *Sarawak* (*Borneo*): Labang Camp on Sungei Seran, Bintulu District, Fourth Division: MCZ Herp R-102031; Mount Matang, First Division: MCZ Herp R-55124; "Semerjoh Forest Reserve, First Division, 12.5 miles from Kuching": MCZ Herp R-160784.

Cyrtodactylus darmandvillei.—**Indonesia**: *Nusa Tenggara Timur Province*: Flores: Sikka: ZMA.RENA. 10943–44 (syntypes).

Cyrtodactylus fumosus.—**Indonesia**: *North Sulawesi Province*: "Bone Mountains" (= Pegunungan Bone): NMB-REPT 2662 (holotype); "Masarang": NMB-REPT 2663; Rurukan: BMNH 1895.2.27.7, 1896.12.9.3.

Cyrtodactylus gordongekkoi.—**Indonesia**: *Nusa Tenggara Timur Province*: Lombok: Vicinity of Sendanggila Falls, ca. 0.5 kilometers south of Senaru village: ZRC 2.3380 (holotype), ZRC 2.3381 (paratype).

Cyrtodactylus jellesmae.—**Indonesia**: *North Sulawesi Province*: "Kema": NMB-REPT 2659 (paralectotype); "Buol": NMB-REPT 2660 (lectotype); "Masarang Mountains": NMB-REPT 2661 (paralectotype).

Cyrtodactylus laevigatus laevigatus.—**Indonesia**: *Nusa Tenggara Timur Province*: Komodo: Loho Liang: FLMNH 28910–12.

Cyrtodactylus laevigatus uniformis.—**Indonesia**: *Nusa Tenggara Timur Province*: Flores: FLMNH 32596 (holotype), FLMNH 32597 (paratype).

Cyrtodactylus marmoratus.—**Indonesia**: Java: RMNH.RENA 2710a.1 (lectotype), RMNH.RENA 2710a.2 (paralectotype).

Cyrtodactylus cf. *marmoratus*.—**Indonesia**: Java: MTKD 8903–06.

Cyrtodactylus pubisulcus.—**Malaysia**: *Sarawak* (*Borneo*): Baram River (= Sungai Baram): SMF 8222–23; Labang Camp on Sungai Seran, Bintulu District, Fourth Division: AMNH R111888; Tubau Camp on Sungai Pesu, Bintulu District, Fourth Division: AMNH R11889–95; "Tandjong Datu", First Division (= Tanjung Datu National Park): MCZ Herp R-79197.

Cyrtodactylus cf. *quadrivirgatus*.—**Indonesia**: *Sumatera Utara* (*Sumatra*): MCZ Herp R-7502; "Asahan": SMF 8225.

Cyrtodactylus sadleiri.—**Australia**: Christmas Islands (south of Java): NMB-REPT 2658.

Cyrtodactylus wetariensis.—**Indonesia**: *Maluku Province*: Wetar: near Uhak, north coast of Wetar: AMNH R32162, 32164 (paratypes), 32165 (holotype), MCZ Herp R-26998–99 (paratypes).

5.3 Paper 4

Mecke, S., Kieckbusch, M., Hartmann, L. & Kaiser, H. (2016): Historical Considerations and Comments on the Type Series of *Cyrtodactylus marmoratus* Gray, 1831, with an Updated Comparative Table for the Bent-toed Geckos of the Sunda Islands and Sulawesi. *Zootaxa*, **4175**(4): 353–365.

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Historical considerations and comments on the type series of *Cyrtodactylus marmoratus* Gray, 1831, with an updated comparative table for the bent-toed geckos of the Sunda Islands and Sulawesi

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Abstract

Cyrtodactylus marmoratus Gray, 1831, a species of bent-toed gecko exhibiting a precloacal groove in males, was described on the basis of specimens collected by Heinrich Kuhl and Johan Conrad van Hasselt in Java, Greater Sunda Islands, Indonesia. Kluge (1985) subsequently designated a lectotype for *C. marmoratus* from a series of these specimens (i.e., syntypes), now housed in the herpetological collection at Naturalis (formerly the Rijksmuseum van Natuurlijke Historie; RMNH), Leiden, the Netherlands. Our work at Naturalis shows that the type series of *C. marmoratus* at RMNH actually comprises two sets of specimens, and that examination of specimens from one set or the other by different authors, including Kluge (1985), is responsible for some confusion surrounding the type series of this species. As a consequence, we present relevant morphological data for all 14 specimens constituting the type series of *C. marmoratus* at RMNH for the first time. The type status of two specimens of *C. marmoratus* in the collection at the Muséum National d'Histoire Naturelle, Paris, France, remains unresolved at present. Owing to the inconsistent naming and application of terms for some key characters (e.g., groove, sulcus, pit, hollow, depression) used in the diagnoses of *Cyrtodactylus* species, we here propose a set of novel and useful definitions that are supported by photographs. We also illustrate the sexually dimorphic expression of this character in *C. marmoratus*. Finally, we present a revised comparative table for the bent-toad geckos of the Sunda Islands and Sulawesi.

Key words: *Cyrtodactylus marmoratus*, bow-fingered geckos, Reptilia, Squamata, Gekkonidae, type specimens, paratypes, precloacal morphology

Introduction

Hartmann *et al.* (2016), as part of their recent description of *Cyrtodactylus klakahensis* Hartmann, Mecke, Kieckbusch, Mader & Kaiser, 2016, provided some further insights into the taxonomy of *C. marmoratus* Gray, 1831 and *C. fumosus* (Müller, 1895), two species hitherto considered to have fairly wide distributions in the Indonesian archipelago. Since this publication, we have uncovered additional information regarding the type series of *C. marmoratus* and some other species from the Sunda Islands and Sulawesi, which will be critical to the impending descriptions of additional species in the region (Awal Riyanto, in litt.; our unpubl. data). Furthermore, reporting on these new insights now also allows us to make some additions and corrections to the comparative table of Hartmann *et al.* (2016: Table 3) and prevent the perpetuation of omissions and errors in the next series of species descriptions from this region.

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Material and methods

Vouchers used to obtain data for our tables are listed in the Appendix. Measurements and scale counts follow Hartmann *et al.* (2016), unless stated otherwise. Comparative material is housed in the collections of the AMNH, BMNH, FLMNH, MCZ, MTD, NMB, RMNH, SMF, ZMA (now in Naturalis, Leiden; RMNH), ZRC, and ZSM (abbreviations follow Sabaj Pérez [2014]).

Results and discussion

A type series with two accession numbers

In a footnote referring to their comparison section (page 556: footnote 4), Hartmann *et al.* (2016) provided some meristic data for the lectotype of *Cyrtodactylus marmoratus* (RMNH.RENA 2710a.1), which differed from the values presented by Rösler *et al.* (2007). However, due to unclear numbering of specimens, it appears that Rösler *et al.* (2007) did not actually present data for RMNH.RENA 2710a.1, the lectotype, but for what they referred to as "RMNH 2710/1," a specimen they correctly called a paralectotype (Rösler *et al.* 2007: 206, Fig. 11). We compared our data for the lectotype of *C. marmoratus* to the data of Rösler *et al.* (2007), because we believed their notation "RMNH 2710/1" to be a variant of 2710a.1. This was an error on our part, rooted in the way the name-bearing specimens of *C. marmoratus* were partitioned at some point in the past, and in the unfortunate circumstance that the authors who collected data for two scientific articles covering *C. marmoratus* used only one set of specimens each, and moreover examined a different part of the type series.

Gray (1831) based his description of *Cyrtodactylus marmoratus* on a series of bent-toed geckos collected by Heinrich Kuhl (1797–1821) and Johan Conrad van Hasselt[1] (1797–1823) in Java and now housed in the collection of the Naturalis Museum (formerly the Rijksmuseum van Natuurlijke Historie, abbreviated RMNH) in Leiden, The Netherlands. Gray had examined these personally while visiting the RMNH collection (see Kluge 1985). Kluge (1985) subsequently designated an adult male (RMNH.RENA 2710a.1) as lectotype of *C. marmoratus*, rendering all other specimens of the original type series paralectotypes. The lectotype, now kept separately, came from a jar cataloged as RMNH.RENA 2710a, which contained a series of six specimens that Kluge considered to be the syntypes of *C. marmoratus*. Kluge listed no other types, even though a series of specimens cataloged under accession number RMNH.RENA 2710 existed.

Unfortunately, Rösler *et al.* (2007) based their species account of *Cyrtodactylus marmoratus* on specimens in the jar Kluge (1985) had not considered. The jar identified as RMNH.RENA 2710 contains eight specimens also collected by Kuhl and Van Hasselt in Java, and, in light of Kluge's (1985) paper, Rösler *et al.* (2007) correctly referred to them as paralectotypes (see below). Unaware that the reports by Kluge (1985) and Rösler *et al.* (2007) dealt with two distinct sets of specimens, we (Hartmann *et al.* 2016) felt it necessary to correct the counts made by Rösler *et al.* (2007) on the specimen they referred to as "RMNH 2710/1" (properly cited as RMNH.RENA 2710.1), which we thought must be the lectotype RMNH 2710a.1. We were then unaware (and we suppose Kluge was as well) that the type series of *C. marmoratus* at RMNH consisted of two sets of specimens under different catalogue numbers. Although Rösler *et al.* (2007: 205) listed the lectotype under its correct accession number in their note section for *C. marmoratus*, they appear not to have examined it, and therefore did not mention it specifically in their measurements and proportion section and their appendix. We feel that in a case such as this, where a divided type series exists but where only a single set (or subset of it) was examined in a study of broader implications, a direct reference to the other set(s) of the series is critical to prevent confusion. This appears especially important in the case an accession number itself gives no clear indication regarding partitioning. We assume that Kluge (1985) and Rösler *et al.* (2007), just like we ourselves, were stymied by the accession number scheme historically employed at the RMNH.

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[1] In the literature, Van Hasselt's second Christian name is often quoted as "Coenraad." Klaver (2007:43), however, demonstrated the proper name to be "Conrad."

What constitutes the entire type series?

We have now examined the entire type series of *Cyrtodactylus marmoratus* housed in the RMNH collection and note that all but three specimens had no individual labels, including all specimens in the jar labeled RMNH.RENA 2710. We were able to confidently identify the specimens enumerated by Rösler *et al*. (2007) as “RMNH 2710/1, 2710/2, and 2710/3” based on data and a photograph provided by these authors. These specimens have now received labels that correspond to the numbering of Rösler *et al*. (2007), identifying them as RMNH.RENA 2710.1, 2710.2, and 2710.3, respectively. Although, neither Kluge (1985) nor Rösler *et al*. (2007) explicitly stated that the type series of *C. marmoratus* at RMNH consisted of specimens in more than a single jar, Brongersma (1934) already reported on two series of specimens of *C. marmoratus* collected by Kuhl and Van Hasselt in Java (RMNH.RENA 2710, 2710a) but did not refer to them as types. We may assume that both sets of specimens (RMNH.RENA 2710 and 2710a), with the same data and collectors, were seen by Gray when he visited the RMNH in the late 1820s (Hoogmoed 1973). Absent any indication to the contrary, all must be regarded as types. By the time of Gray’s visit, all material collected by Kuhl and Van Hasselt had been received in Leiden (Marinus Hoogmoed, in litt.), and both collectors had died (Klaver 2007). We present relevant morphological data for all 14 specimens of the RMNH type series in Table 1.

Brongersma (1934: 169) also referred to specimens of *Cyrtodactylus marmoratus* in the Muséum National d’Histoire Naturelle (jar number MNHN 2331) as syntypes (“collected in Java by Kuhl & Van Hasselt and preserved in the Paris Museum”[2]), whereas Guibé (1954) did not refer to these specimens at all in his catalogue of the lizard types in the collection of MNHN. Kluge (1985) stated that the specimens in the MNHN collection could not be treated as types without further consideration. Brygoo (1990) considered them types for four reasons:

(1) Duméril & Bibron (1836) and Duméril & Duméril (1851) stated that the Paris Museum received these two specimens from the Leiden collection (= RMNH);

(2) they were received prior to 1836 (the publication date of Duméril & Bibron’s third volume of their *Erpétologie Générale*);

(3) Duméril & Bibron (1836) referenced Kuhl’s unpublished manuscript (that contains a description of *C. marmoratus*) and Gray’s (1831) valid species description;

(4) in his published catalogue, Gray (1845: 173) listed two specimens (*a*, *b*) that the Natural History Museum, London (BMNH) received from RMNH as well.

We dispute this assertion for the following reasons:

(1) In the 1820s and 1830s, the RMNH sent specimens to various museum collections, with vouchers of *Cyrtodactylus marmoratus* evidently transferred to the following institutions: BMNH—Gray (1845); MNHN—Brongersma (1934), Marinus Hoogmoed & Esther Dondorp, in litt.; NMW—Marinus Hoogmoed & Esther Dondorp, in litt.; SMF—Mecke & Kieckbusch, pers. obs. In the absence of records of an accession date for the Paris specimens (there are no extant records indicating the arrival of these specimens at MNHN; Nicolas Vidal, in litt.), there is no unique way by which these can be reliably connected to the collection made by Kuhl and Van Hasselt or the types in the RMNH.

(2) Depending on the year when these specimens were sent, they need not necessarily have been collected by Kuhl and Van Hasselt. After Kuhl’s and Van Hasselt’s deaths, there was a steady stream of young researchers (most of them dying very quickly after their arrival in the tropics) being sent out to Indonesia (e.g., Heinrich Boie, Heinrich Christian Macklot, Salomon Müller; and always via the main trading port of Batavia, now Jakarta, on Java) under the auspices of the Natuurkundige Commissie voor Nederlandsch Indië, and all material they collected went to the RMNH. There, specimens were partly or wholly accessioned, and then exchanges with other museums took place (Marinus Hoogmoed, in litt.).

(3) The references listed in Duméril & Bibron (1836) appear irrelevant to the question of type specimens in this case, given that these are merely taxonomic references associated with the species as a whole, and not with individual specimens.

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[2] Brongersma (1934), obviously unaware of Gray’s species description, incorrectly attributed the authorship of *C. marmoratus* to Duméril & Bibron (1836), who worked at MNHN at the time when Kuhl and Van Hasselt material would have arrived in Paris (see Kluge 1985). Under this assumption it appears logical that Brongersma (1934) did not consider the specimen series RMNH.RENA 2710 and 2710a to be type material.

(4) The fact that Gray (1845) listed specimens of *Cyrtodactylus marmoratus* in the collection of the Natural History Museum, London (BMNH) indicates that these are most likely specimens that Gray had seen during his visit to Leiden and which were subsequently transferred to the BMNH (see Hoogmoed *et al*. 2010: 9 for a similar example). These specimens may be part of the original syntype series and hence paratypes. This information, however, lends no support to the assertion of type status for the MNHN specimens. If the MNHN specimens, now registered under the accession number MNHN 1994.0734 (Nicolas Vidal, in litt.), did once belong to the RMNH 2710/2710a series, Gray may have seen them either in Leiden (still as part of 2710 or 2710a) or in Paris in 1829 (see Bour 2006), depending on when the two specimens were sent to Paris. We feel that the MNHN specimens (and all other specimens of *C. marmoratus* that originated in Leiden) should not be regarded paralectotypes by default in the absence of specific indication of either collectors (which would have to be Kuhl and Van Hasselt) or an accession date; additional evidence is needed to confirm their status, but based on the archival research in Paris such evidence is likely not forthcoming (Nicolas Vidal, in litt.). We therefore follow Kluge (1985) to state that further consideration is required. Additional research on specimens of *C. marmoratus* that originated from Leiden is currently in preparation.

Of pores, grooves, sulci, pits, hollows, and depressions

Whereas Kluge (1985) counted 53 pores for the lectotype of *Cyrtodactylus marmoratus* (RMNH.RENA 2710a.1), we (Hartmann *et al*. 2016) reported 52. We re-examined the specimen and here correct the count to 56 pores, some barely visible. We also examined the two adult females from the type series (RMNH.RENA 2710.3, 2710a.6) and additional female specimens of that taxon, which show no sign of a precloacal groove or "shallow pit" as reported by Rösler *et al*. (2007) and possess a precloacal region largely different from that of males, which possess a groove. Rösler *et al*. (2007), however, referred to both expressions as "preanal pits." We refer the reader to Fig. 1 for a comparison of the precloacal region of a male and a female specimen of *C. marmoratus*.

It appears that the terms 'groove,' 'sulcus,' 'pit,' 'hollow,' and 'depression' are sometimes used interchangeably in the relevant literature but may also be used to refer to different expressions of depressed precloacal areas. These terms, used in combination with 'shallow' and 'deep' (as e.g., 'shallow sulci,' 'shallow pits,' or 'shallow depressions'), render this useful diagnostic character quite subjective. Harvey *et al*. (2015) divided this key character into two major categories based on their appearance, a longitudinal groove *vs*. a triangular depression, but neglecting the often used term 'pit.' We propose the following terminology: (1) A 'depression' can be of any shape and the term should be used as a higher category for the narrower terms 'groove' and 'pit.' A depression could therefore be present in the form of a grove or a pit, with the latter terms mutually exclusive. (2) A 'groove' is always longitudinal and relatively narrow. As part of a groove some or all of the scales (which are often pore-bearing) on the left and right side of the posterior-most, enlarged precloacal scale series are in contact with each other or only narrowly separated. This type of depression may have the shape of a slit (or sulcus) along its entire length, with the posterior-most precloacal scales often sunk deeply into the depression, being barely visible. Alternatively, these enlarged scales are arranged in the shape of an inverse 'Y' with the depression broadening posteriorly (Fig. 2A–C). (3) The term 'pit' (= 'hollow' *sensu* Hikida 1990) is used to refer to a triangular depression (*sensu* Harvey *et al*. 2015) with most or all of the scales (which are often pore-bearing) on the left and right side of the posterior-most, enlarged precloacal scale series widely separated from each other (Fig. 2D & E). Attribution of depressions to either a groove or a pit might be challenging, since transitional expressions may exist and/or because the shape of a depression may be affected by preservation. For these reasons, researchers should always depict the precloacal region of the bent-toed gecko taxa in question in order to give others a better idea of the described structures. The following species of *Cyrtodactylus* from the Sunda Island and Sulawesi possess a precloacal groove in adult males: *C. agamensis* (Bleeker, 1860); *C. cavernicolus* Inger & King, 1962; *C. celatus* Kathriner, Bauer, O'Shea, Sanchez & Kaiser, 2014; *C. fumosus* (Fig. 2C); *C. klakahensis* (Fig. 2B); *C. lateralis* (Werner, 1896); *C. marmoratus* (Fig.1A); *C. pubisulcus* Inger, 1957 (Fig. 2A); and *C. semicinctus* Harvey, O'Connell, Barraza, Riyanto, Kurniawan & Smith, 2015. The following species possess a precloacal pit in adult males: *C. baluensis* (Mocquard, 1890; Fig. 2D); *C. consobrinus* (Peters, 1871; Fig. 2E); *C. psarops* Harvey, O'Connell, Barraza, Riyanto, Kurniawan & Smith, 2015; *C. spinosus* Linkem, McGuire, Hayden, Setiadi, Bickford & Brown, 2008; and *C. yoshii* Hikida, 1990 (see also Table 2). Determination of the presence/absence of this character in *C. malayanus* (De Rooij, 1915) warrants further examination. The following species lack a depression: *C. batik* Iskandar, Rachmansah & Umilaela 2011; *C. darmandvillei* (Weber, 1890); *C. gordongekkoi* (Das, 1994); *C. hitchi*; *C. ingeri* Hikida, 1990; *C. jellesmae*; *C. laevigatus* Darevsky, 1964; *C. matsuii* Hikida, 1990; *C. petani*; *C. semiadii* Riyanto, Bauer & Yudha, 2014; *C. quadrivirgatus* Taylor, 1962; *C. wallacei* Hayden, Brown, Gillespie, Setiadi, Linkem, Iskandar, Umilaela, Bickford, Riyanto, Mumpini & McGuire, 2008; and *C. wetariensis* (Dunn, 1927; Fig. 2F).

TABLE 1. Metric (in mm) and meristic data from the type series of *Cyrtodactylus marmoratus* in the RMNH.RENA collection. RMNH.RENA 2710a.1 is the lectotype of *C. marmoratus*. RMNH.RENA 2710a.1–a.6 and RMNH.RENA 2710.1–3 are adults, 2710.4–8 are juveniles. Characters are abbreviated as follows: ArmL = arm length, AxialL = length from axilla to groin, DTR = dorsal tubercle rows, FP = femoral pores (number provided only when pore-bearing femoral scales are separated from pore-bearing precloacal scales by InfraS or when pores on the thigh are present only; a continuous pore series is referred to as PFP), GulS = gular scales (including second postmentals if present), HeadL = head length, HeadH = head height, HeadW = head width, InfraLab = infralabial scales, InfraS = infrascales (number of enlarged poreless scales separating pore-bearing precloacal from pore-bearing femoral scales), IOS = interorbital scale rows, LegL = leg length, LT_4 = subdigital scales/lamellae under fourth toe, OrbD = orbital diameter, PCT = postcloacal tubercles, PFP = precloacofemoral pores, PFS = precloacofemoral scales, PP = precloacal pores (number provided only when pore-bearing precloacal scales are separated from pore-bearing femoral scales by InfraS or when pores in the precloacal region are present only; a continuous pore series is referred to as PFP), PVT = paravertebral tubercles, SC = supraciliaries, SnoutL = snout length, SupraLab = supralabial scales, SVL = snout-vent length, TailL = tail length, VS = ventral scales. Regenerated tails were not measured with the condition abbreviated as 'reg.'. If data for a character are not available, this is indicated by a hyphen (-). A question mark (?) indicates an uncertainty in the absence/presence of a character. For specimens possessing precloacofemoral pores (= pores in a continuous series, including indistinct pores and primordia), precloacal- and femoral pores (separated from each other by infrascales) are coded as 'n/a'. In juvenile specimens pores are either located in the precloacal region only or run onto the legs. Discrepancies between the data for 2710.1–8 presented below and the data for this series presented by Rösler *et al*. (2007) may be due to different data collection methods.

Character	2710a.1 ♂	2710a.2 ♂	2710a.3 ♂	2710a.4 ♂	2710a.5 ♂	2710a.6 ♀	2710.1 ♂	2710.2 ♂	2710.3 ♀	2710.4 ♀	2710.5 ♂	2710.6 ♂	2710.7 ?	2710.8 ♂
SVL	73.3	69.7	73.8	73.7	75.1	85.7	75.1	75.6	69.0	48.6	50.0	43.9	42.0	42.8
AxialL	31.0	30.3	32.5	29.6	31.2	40.1	33.4	37.5	31.8	23.4	23.1	19.6	17.1	18.5
TailL	71.6	76.0	reg.	72.7	reg.	reg.	reg.	reg.	reg.	49.5	51.0	42.0	43.6	reg.
ArmL	25.5	26.1	25.9	25.0	25.7	31.5	27.2	25.3	24.4	17.3	16.8	15.8	12.3	14.1
LegL	33.6	32.0	32.1	31.7	36.5	36.2	35.6	34.5	31.3	23.8	22.5	20.5	18.6	19.9
HeadL	20.0	19.0	20.6	20.5	20.9	22.1	21.7	21.8	18.4	13.8	14.7	12.9	12.7	12.4
HeadW	14.0	13.5	13.7	14.1	14.5	16.2	14.2	14.0	13.2	9.9	9.9	8.1	8.0	8.2
HeadH	8.7	8.5	9.2	9.3	8.5	10.7	9.8	9.4	7.9	6.2	6.5	5.4	5.6	5.7
SnoutL	8.0	7.8	8.3	8.5	8.1	9.2	8.3	8.8	7.6	5.5	6.1	5.3	4.8	5.1
OrbD	4.8	3.9	4.1	4.4	4.4	4.9	4.7	4.1	3.7	3.4	3.1	3.2	2.9	2.9
DTR	11	17	16	13	17	19	15	13	15	15	17	18	18	-
PVT	26	24	26	28	22	24	26	25	23	25	26	29	26	27
VS	46	40	42	38	38	40	34	45	41	39	37	-	43	38
PFS	57	55	59	52	50	51	50	54	52	49	51	-	-	42
PFP	56	52	57	49	45	0	45	50	0	24	?	26	-	43
PP	n/a	n/a	n/a	n/a	n/a	20	n/a	n/a	16	n/a	18	n/a	-	n/a
FP	n/a	n/a	n/a	n/a	n/a	9/9	n/a	n/a	11/9	n/a	n/a	n/a	-	n/a
InfraS	n/a	n/a	n/a	n/a	n/a	1/3	n/a	n/a	2/1	n/a	?	n/a	n/a	n/a
PCT	1	2	1	1	2	2	2	3	3	2	2	1	2	2
SupraLab	9	8	10	13	9	10	10	10	10	10	12	10	9	11
InfraLab	9	9	9	9	9	10	9	9	7	9	9	9	9	8
SC	31	30	29	33	27	34	32	31	30	27	30	35	31	31
IOS	47	46	-	38	44	45	51	43	39	49	48	-	46	42
GulS	6	6	6	8	5	9	6	8	6	8	7	8	7	6
LT4	22	20	20	20	18[a]	19[a]	22	22	21	23	21	22	17[a]	21

[a] Following Hartmann *et al*. (2016) we counted subdigital scales underneath the fourth toe beginning with the first notably enlarged/ transversely widened scale (lamellae), which is usually located at the toe joint. In three specimens with < 20 subdigital scales, a few of the proximal scales were fragmented (or similar to plantar scales). If these are included in the count, the following values are obtained: 2710a.5 = 21 LT_4, 2710a.6 = 22 LT_4, 2710.7 = 20 LT_4.

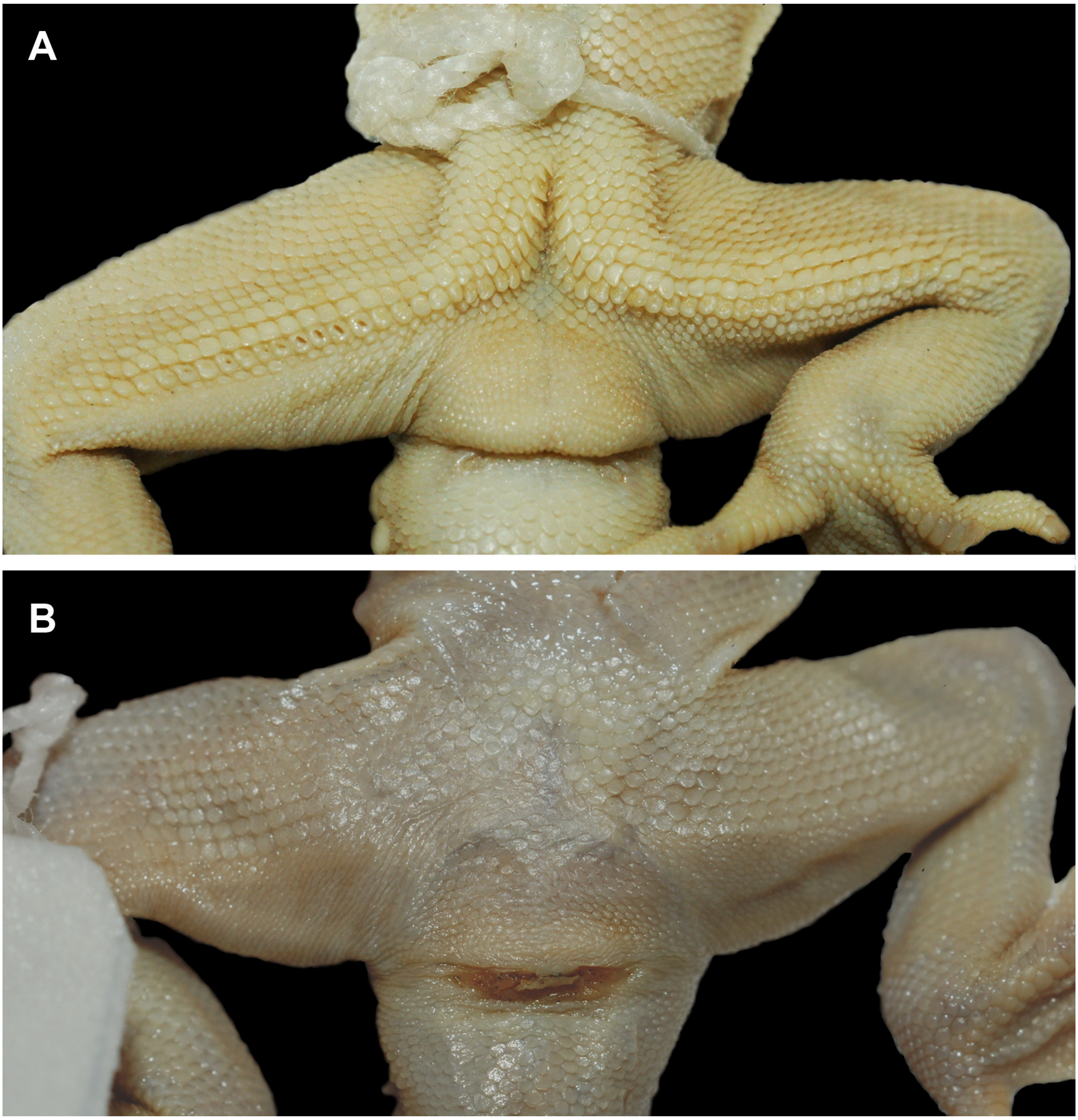

FIGURE 1. Precloacal region of *Cyrtodactylus marmoratus*. (A) Lectotype of *C. marmoratus* (RMNH.RENA. 2710a.1; adult male) with a precloacal groove as typical for males of that species. (B) Paralectotype of *C. marmoratus* (RMNH.RENA. 2710.3; adult female) lacking a precloacal depression as typical for females of that species. Photographs are not to scale. Plate prepared by Max Kieckbusch based on photographs by Sven Mecke.

Correction and update of the comparative table in Hartmann *et al.* (2016)

While our research on bent-toed geckos from the Sunda Islands, Sulawesi, and the Moluccas continues (Mecke *et al.* in press, in prep.), we noticed some inaccuracies in our previously published comparative table (Hartmann *et al.* 2016: Table 3), pertaining largely to the presence/absence of a precloacal depression in males *vs*. females. We herein correct these inaccuracies and take the opportunity to complement the earlier table by including the recently described *Cyrtodactylus hitchi* Riyanto, Kurniati & Engilis, 2016 and *C. petani* Riyanto, Grismer & Wood, 2015, and by adding new data for several species (e.g., *C. jellesmae* [Boulenger, 1897] and *C. marmoratus*). Furthermore, we here exclude the following characters from our table: tubercles on hind limbs and tubercles on head. A re-evaluation of the literature cited in the reference section and a re-examination of relevant bent-toed gecko specimens revealed that tubercles are invariably present on the head (at least on the occiput) and the hind limbs of *Cyrtodactylus* from the Sunda Islands and Sulawesi. Thus, these characters are of no importance for diagnosis and/or taxonomy. The presence/absence of tubercles on the upper arm (brachium) seems to be a more important character for differentiating species than the tuberculation of the whole forelimb, since tubercles on the forearm (antebrachium) are usually present. Hence, we exchanged 'tubercles on forelimbs' for 'tubercles on the upper arm (brachium).' We also ascertained that only adult specimens were included in our comparison. Lastly, we supplemented our table by adding a column to provide information on the distribution of the species involved. Below we present a corrected and updated comparative table (Table 2) for the bent-toed geckos of the Sunda Islands and Sulawesi.

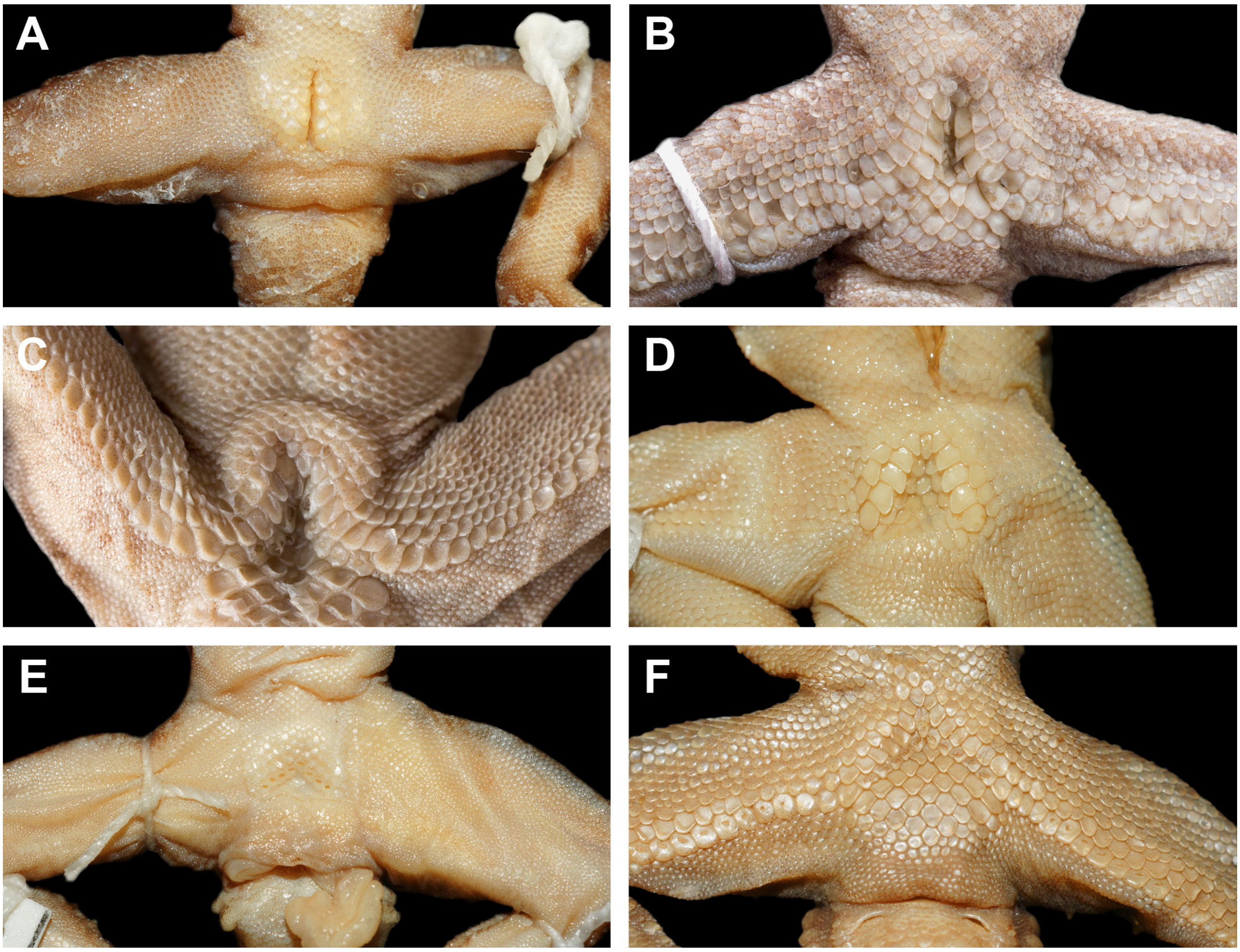

FIGURE 2. Precloacal regions of six Sundanese and Sulawesi species of *Cyrtodactylus* showing differences in the expression of a precloacal depression in adult males. (A) *C. pubisulcus* (AMNH R111889) possessing a slit-like precloacal groove, with the pore-bearing scales sunk deeply into the depression and not visible. (B) *C. klakahensis* (SMF 22476; holotype) possessing a slit-like precloacal groove, with the pore-bearing scales sunk deeply into the depression and barely visible. (C) *C. fumosus* (BMNH 1896.12.9.3) possessing a precloacal groove, with the enlarged pore-bearing scales arranged in the shape of an inverse 'Y' with the groove broadening posteriorly. (D) *C. baluensis* (MCZ.Herp R-39036) possessing a precloacal pit, with the pore-bearing scales from the left and right side of the posterior-most precloacal scale series arranged in the shape of an inverse 'V' and widely separated from each other, creating a depression in the form of an acute triangle. (E) *C. consobrinus* (MCZ.Herp R-102031) possessing a precloacal pit in the form of an obtuse triangle. (F) *C. wetariensis* (AMNH R32165; holotype) lacking a precloacal depression. Photographs are not to scale. Plate prepared by Max Kieckbusch based on photographs by Sven Mecke.

TABLE 2. Characters used to distinguish *Cyrtodactylus* species occurring in the Sunda Islands and Sulawesi. The presence of a diagnostic character is coded as '1', the absence of a character is coded as '0'. For taxa possessing precloacofemoral scales (= scales in a continuous series; column entitled '7'), precloacal- and femoral scales (separated from each other by infrascales) are coded as 'n/a' (columns entitled '5' and '6'). Numbers at the head of the table correspond to characters as follows: 1 = tubercles on upper arm (brachium), 2 = number of ventral scales, 3 = enlarged subcaudals, 4 = number of subdigital scales/lamellae under 4th toe, 5 = enlarged precloacal scales (the number of pores is given in parentheses and includes primordia; if pores are present in one sex only, this is indicated either by '♂' or '♀'), 6 = enlarged femoral scales (the number of pores is given in parentheses and includes primordia; if pores are present in one sex only, this is indicated either by '♂' or '♀'), 7 = enlarged precloacofemoral scales (the number of pores is given in parentheses and includes primordia; if pores are present in males only this is indicated by '♂'), 8 = precloacal and femoral pores in a continuous series, 9 = expression of precloacal depression (N = no depression, G = groove, P = pit; if a depression is present in males only, this is indicated by '♂'), 10 = pattern of dorsum (bd = banded; bl = blotched; mo = mottled; pl = patternless; st = striped). If data for a character are not available, this is indicated by a question mark (?). The abbreviation 'Dist.' stands for 'Distribution' and indicates the island(s) on which a respective taxon occurs. Where derived from the literature ('Lit.' column), references are abbreviated by letters as follows: A = this publication; B = Rösler *et al.* 2007; C = Youmans & Grismer 2006; D = Manthey & Grossmann 1997; E = Hikida 1990; F = Iskandar *et al.* 2011; G = Inger & King 1961; H = Kathriner *et al.* 2014; I = Rösler & Kaiser 2016; J = De Rooij 1915; K = Brongersma 1934; L = Boulenger 1897; M = Das 1993; N = Riyanto *et al.* 2016; O = Malkmus *et al.* 2002, P = Auffenberg 1980; Q = Darevsky 1964; R = Werner 1896; S = Harvey *et al.* 2016; T = Das 2010; U = Riyanto *et al.* 2015; V = Harvey *et al.* 2015; W = Inger 1958; X = Riyanto *et al.* 2014; Y = Linkem *et al.* 2008; Z = Taylor 1962; Aa = Grimser *et al.* 2012; Ab = Hayden *et al.* 2008; Ac = Dunn 1927. Under the column heading '*n*' we provide the number of adult specimens we examined personally.

Taxon	SVL (mm)	1	2	3	4	5	6	7	8	9	10	Dist.	Lit.	*n*
agamensis	50	0	67	?	26	n/a (?[a])	n/a (?[a])	1 (?[a])	?	G (♂)[a] ? (♀)	bl	Sumatra	A, B	1
baluensis	71–95	0/1	36–46	1	19–23	1 (9–11, ♂; absent or indistinct in ♀♀)	1 (4–10, ♂)	0	0	P (♂)	bd, bl	Borneo	A, C, D, E	8
batik	103–113	1	48–57	1	24–27	1	0	0	0	N	bd	Sulawesi	F	-
cavernicolus	64–81	0	51–58	0	22–26	1 (4, ♂)	0	0	0	G (♂) ? (♀)	bd	Borneo	C, E, G	-
celatus	38–44	0	34–42	0	15–18	1 (4, ♂)	0	0	0	G (♂)	bl	Timor	A, H, I	3
consobrinus	97–125	1	58–71	1	22–28	1 (8–11, ♂; absent or indistinct in ♀♀))	1 (0–6, ♂); 0/1 ♀	0	0	P (♂) ? (♀)	bd, mo	Sumatra, Borneo	A, C, D, E	2
darmandvillei	80–82	1	34–36	1	23–24	n/a	n/a	1	0	N	bl	Flores, Rinca, Komodo	A, J, K	2
fumosus	57–78	0	37–50	1	17–23	n/a (10–11, ♂)	n/a (3, ♂)	1	0	G (♂)	bl	Sulawesi	A, L	4
gordongekkoi	71–73	0	30	0	22–23	n/a	n/a	1	0	N	bl	Lombok	A, M	2
hitchi	62–79	?	39–45	1	18–21	1	0	0	0	N	bd	Sulawesi	N	-
ingeri	65–76	?	40–43	1	23–29	1 (7–9, only ♂♂ known)	0	0	0	N	bd, bl	Borneo	C, E, O	-
jellesmae	58–70	0/1	40–54	0	16–23	1	0	0	0	N	bl	Sulawesi and offshore islands[b]	A, F, L	9
klakahensis	61–68	0	35–38	0	17–20	n/a	n/a	1 (37–38, ♂)	1	G (♂)	bl	Java	A	3
laevigatus	38–47	0	30–34	0	10–15	?	0/1	?	0	N	mo, pl	Flores, Komodo	A, F, P, Q	5

…continued on the next page

TABLE 2. (Continued)

Taxon	SVL (mm)	1	2	3	4	5	6	7	8	9	10	Dist.	Lit.	*n*
lateralis	65–93	1	51–66	0	18–24	1 (9–13, ♂) (0–15, ♀)	0/1	0	0	G (♂)	bl	Sumatra	C, D, R, S	-
malayanus	70–83	1	58–62	1	21–23	1 (8–10, ♂)	0	0	0	P?	bd	Borneo?	C, E, J, T	-
marmoratus	69–86	0	34–47	0	18–24	n/a (16–20, ♀)	n/a (9–11, ♀)	1 (43–57)	0 (♀)/1	G (♂)	bl	Java	A, B	14
matsuii	105	?	48–51	0	22	0 (7–8, ♂)	0	0	0	N	bd, bl	Borneo	C, E, O, T	-
petani	45–57	0	30–35	0	17–18	n/a	n/a	1 (31–35, ♂)	1	N[c]	bl	Java	U	1
psarops	?[d]	0/1	38–49	0	18–22	n/a (?[e],♀)	n/a (?[e],♀)	1 (28–32, ♂) (0–29,♀)	0 (♀)/1	P (♂)	bd, bl	Sumatra	V	1
pubisulcus	56–74	0	37–58	0	16–23	1 (7–9, ♂)	0	0	0	G	bd, bl, st	Borneo	A, C, E, W	8
semiadii	40–47	?	35–36	0	14–15	0	0	0	0	N	bl	Java	X	-
semicinctus	?[d]	0	33–44	0	19–22	n/a	n/a	1 (36–38, ♂) (0–19,♀)	1	G (♂)	bd, bl	Sumatra	V	-
spinosus	70–83	?	38–44	0	19–21	1 (12–13, ♂)[f]	1 (?[g])	0	0	P (♂)	bd	Sulawesi	Y	
quadrivirgatus	51–71	1	34–42	0	19–20	n/a (0–4)[h]	n/a	1	0	N	bl, st	Sumatra	C, D, Z, Aa	-
wallacei	92–114	1	45–49	1	17–25	1	0	0	0	N	bd, bl	Sulawesi	Ab	-
wetariensis	58–67	0	36–38	0	20–22	n/a (11, ♂)[i]	n/a (12–16, ♂)[i]	1	0	N	bl	Wetar	A, Ac	3
yoshii	75–96	1	50–58	0	25–30	0 (8–12, ♂; absent or indistinct in ♀♀)	0	0	0	P(♂)	bl	Borneo	C, E	-

[a] While visiting the RMNH, we discovered in the herpetological collection a male specimen of *C. agamensis*. This is only the second specimen known of that species, with a detailed description of the female holotype provided by Rösler *et al.* (2007). We did not examine the male specimen in detail (i.e., we did not gather metric and meristic data), but we can certainly report the presence of a precloacal groove. Pores were present as well, but we are unfortunately not able to report on their expression (e.g., a continuous or discontinuous series).

[b] *C. jellesmae* occurs as far north as Talaud (Koch *et al.*, 2009).

[c] Riyanto *et al.* (2015) provided inconsistent data on whether a precloacal groove is present in male specimens of *C. petani*. However, Awal Riyanto (in litt.) confirmed that male *C. petani* lack a precloacal groove or pit, as is also evident from their Fig. 4A.

[d] Harvey *et al.* (2015) did not provide ranges for adult specimens of *C. psarops* and *C. semicinctus*.

[e] In female *C. psarops*, pores (primordia) can either be arranged continuously, discontinuously, or can be absent altogether. Harvey *et al.* (2015) only provided counts for total pore numbers, but failed to indicate individual counts for the pore-bearing parts of separated pore series.

[f] In their diagnosis and Table 1, Linkem *et al.* (2008) listed 12–13 precloacal pores for *C. spinosus*, whereas in their Table 2 they listed only 8–12 precloacal pores. In their Table 1, these authors also listed precloacal pores for individual females, although females are described as lacking pores in their variation section.

[g] According to the diagnosis in Linkem *et al.* (2008), *C. spinosus* lacks femoral pores; it was listed as possessing 4–7 femoral pores in their Table 2.

[h] Taylor (1962), in his description of *C. quadrivirgatus*, reported males and females to usually possess four precloacal pores or primordia but failed to indicate if a sexual dimorphism for this character exists. Manthey & Grossmann (1997) reported the presence of three or four pores in males only, whereas e.g., Youmans & Grismer (2006) and Grismer *et al.* (2012) provided a range of 0–4 precloacal pores for the species, again without reporting on the likely occurrence of a sexual dimorphism.

[i] A female specimen (MCZ Herp R-26998), also collected by the Douglas Burden East Indian Expedition (1926), has nine precloacal pores, and no femoral pores on the right and two on the left thigh.

Variation in the pore series of adult *Cyrtodactylus marmoratus*

While all male specimens of *Cyrtodactylus marmoratus* we personally examined had a continuous pore series (precloacofemoral pores), female specimens appear to be more variable in this respect (Table 2). Of the five adult females examined, two had precloacal pores only (ZMA.RENA 15945, SMF 92361), in two specimens the femoral pores were separated from the precloacal pores by infrascales (RMNH.RENA 2710.3, 2710a.6; paralectotypes), and one specimen had a continuous series of pores (precloacofemoral pores; MTKD 8094). The pattern observed is similar to that reported for *C. psarops*, where adult male specimens possess continuous pore series, whereas female specimens show much variation in this character.

Brongersma (1953) also reported variation in pore and infrascale numbers in male specimens of *Cyrtodactylus marmoratus*, assuming this would be the result of an ontogenetic change. While ontogenetic variation or even variation in adult male specimens of this species appears to be possible, it is likely that Brongersma (1953) combined data from different Javanese taxa masquerading under the name *C. marmoratus*. Recent descriptions of new bent-toed geckos from Java (Riyanto *et al*. 2014, 2015; Hartmann *et al*. 2016) indicate that the diversity of this group of geckos in Java is largely underestimated.

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APPENDIX. Specimens examined for this study.

Cyrtodactylus agamensis.—**Indonesia**: no specific locality data available but collected by P. Bleeker, the describer of the taxon: RMNH.RENA 3965.

Cyrtodactylus baluensis.—**Indonesia**: *Kalimantan Timur Province*: "Mount Tibang" (= Bukit Batu Tiban): MCZ Herp R-22626.—**Malaysia**: *Sarawak* (*Borneo*): Mount Kinabalu (= Gunung Kinabalu): MCZ Herp R-39036; Mount Kinabalu: "Kaddmayan River", near Kiau: MCZ Herp R-43474; Kiau (= Kampung Kiau): MCZ Herp R-43477, R-163132; "Mahunbayon": MCZ Herp R-43473, R-163646; "Penokok River" (= alternative spelling of Kenokok River), near Kiau: MCZ Herp R-43476.

Cyrtodactylus celatus.—**Indonesia**: *Nusa Tenggara Timur Province*: West-Timor: Ofu: ZSM 556/2002, Soe: NMB-REPT 12789, "Djamplong, 55 kilometers by road from Kupang" ("Djamplong" = Tjamplong or Camplong): BMNH 1926.10.30.45 (holotype).

Cyrtodactylus consobrinus.—**Malaysia**: *Sarawak* (*Borneo*): Labang Camp on Sungei Seran, Bintulu District, Fourth Division: MCZ Herp R-102031; "Semerjoh Forest Reserve, First Division, 12.5 miles from Kuching": MCZ Herp R-160784.

Cyrtodactylus darmandvillei.—**Indonesia**: *Nusa Tenggara Timur Province*: Flores: Sikka: ZMA.RENA. 10943–44 (syntypes).

Cyrtodactylus fumosus.—**Indonesia**: *North Sulawesi Province*: "Bone Mountains" (= Pegunungan Bone): NMB-REPT 2662 (holotype); "Masarang": NMB-REPT 2663; Rurukan: BMNH 1895.2.27.7, 1896.12.9.3.

Cyrtodactylus gordongekkoi.—**Indonesia**: *Nusa Tenggara Timur Province*: Lombok: Vicinity of Sendanggila Falls, ca. 0.5 kilometers south of Senaru village: ZRC 2.3380 (holotype), ZRC 2.3381 (paratype).

Cyrtodactylus jellesmae.—**Indonesia**: *Central Sulawesi Province*: Malakosa, Kuala Navusu: AMNH R142969–70, 14296972–73; Tolai, Sungai River: AMNH R142974; *North Sulawesi Province*: Buol: NMB-REPT 2660 (lectotype); Mount Masarang: NMB-REPT 2661 (paralectotype); Pulau Biaro: MCZ 171466; *South Sulawesi Province*: Lowah (Muara Loa): MCZ 25337.

Cyrtodactylus klakahensis.—**Indonesia**: *Jawa Timur Province*: Lumajang, Klakah: SMF 22476 (holotype); SMF 22477–78 (paratypes).

Cyrtodactylus laevigatus laevigatus.—**Indonesia**: *Nusa Tenggara Timur Province*: Komodo: Loho Liang: FLMNH 28910–12.

Cyrtodactylus laevigatus uniformis.—**Indonesia**: *Nusa Tenggara Timur Province*: Flores: FLMNH 32596 (holotype), FLMNH 32597 (paratype).

Cyrtodactylus marmoratus.—**Indonesia**: Java: RMNH.RENA 2710.1–8 (paralectotypes), RMNH.RENA 2710a.1 (lectotype), RMNH.RENA 2710a.2–6 (paralectotypes), MTKD 8903–05; *Jawa Tengah Province*: "Goewa Djatidjadjar, Jdjoe, Bagelen" (= Gua Jatijajar, Kebumen): ZMA.RENA 15945; Karangpucung: SMF 92361

Cyrtodactylus petani.—**Indonesia**: *Jawa Timur Province*: "Toeloeng Agoeng" (= Tulungagung): ZMA.RENA 11353.

Cyrtodactylus psarops.—**Indonesia**: *Lampung Province* (*Sumatra*): "Wai Lima, Lampangs" (= Lampung): ZMA.RENA 14652

Cyrtodactylus pubisulcus.—**Malaysia**: *Sarawak* (*Borneo*): Baram River (= Sungai Baram): SMF 8223; Tubau Camp on Sungai Pesu, Bintulu District, Fourth Division: AMNH R111889–93, 111895; "Tandjong Datu", First Division (= Tanjung Datu National Park): MCZ Herp R-79197.

Cyrtodactylus wetariensis.—**Indonesia**: *Maluku Province*: Wetar: near Uhak, north coast of Wetar: AMNH R32164 (paratype), 32165 (holotype), MCZ Herp R-26998 (paratype)

5.4 Paper 5

Mecke, S., Hartmann, L. (joint first authors), Mader, F., Kieckbusch, M. & Kaiser, H. (2016): Redescription of *Cyrtodactylus fumosus* (Müller, 1895) (Reptilia: Squamata: Gekkonidae), with a Revised Identification Key to the Bent-toed Geckos of Sulawesi. *Acta Herpetologica*, **11**(2): 151–160.

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Redescription of *Cyrtodactylus fumosus* (Müller, 1895) (Reptilia: Squamata: Gekkonidae), with a revised identification key to the bent-toed geckos of Sulawesi

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Abstract. The binominal *Cyrtodactylus fumosus* has frequently been used for populations of bent-toed geckos occurring on some Indonesian islands, including Java, Bali, Sulawesi, and Halmahera. Unfortunately, incorrect usage of this name for different geographic lineages has resulted in confusion about the true identity of *C. fumosus*. Examination of the type specimen and additional specimens from Rurukan and Mount Masarang, North Sulawesi Province, Indonesia, revealed that this population is distinct from other forms heretofore called '*fumosus*' by a combination of unique morphological characters. In order to stabilize the taxonomy of *C. fumosus* sensu stricto, and to prevent further confusion, we provide a comprehensive redescription of this species, whose distribution we herein restrict to North Sulawesi. *Cyrtodactylus fumosus* is one of the most distinctive species among the six bent-toed geckos recorded from Sulawesi, and it differs from Sulawesi congeners by the presence of (1) precloacofemoral scales, including three pore-bearing scales on each thigh, separated from 10 or 11 pore-bearing scales in the precloacal region by 9-11 interscales in males, (2) a precloacal groove in adult males, (3) flat dorsal tubercles in 4-7 irregularly arranged longitudinal rows at midbody, and (4) a distinct lateral fold lacking tubercles. We also provide a revised identification key to the bent-toed gecko species of Sulawesi.

Keywords. *Cyrtodactylus fumosus*, *C. marmoratus*, Lacertilia, bent-toed geckos, reptiles, North Sulawesi, Indonesia, morphology.

INTRODUCTION

The bent-toed gecko fauna of Sulawesi consists of six species, including *Cyrtodactylus batik* Iskandar et al., 2011; *C. fumosus* (Müller, 1895); *C. hitchi* Riyanto et al., 2016; *C. jellesmae* (Boulenger, 1897); *C. spinosus* Linkem et al., 2008; and *C. wallacei* Hayden et al., 2008. Two of these, *C. fumosus* and *C. jellesmae* have been reported from North Sulawesi Province, Indonesia (e.g., Boulenger, 1897; Koch et al., 2009; Iskandar et al., 2011; Koch, 2012). *Cyrtodactylus fumosus* was described by Müller (1895a) based on a single specimen (NMB-REPT 2662; adult female), collected by Paul Benedict Sarasin (1856-1929) and Karl Friedrich ("Fritz") Sarasin (1859-1942) in the

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"Boelawa Mountains" (= Huidu Matabulawa) of northern Sulawesi. Following its original description, *C. fumosus* was also reported from localities outside of Sulawesi (e.g., De Rooij, 1915; Mertens, 1929, 1934; Manthey and Grossmann, 1997; McKay, 2006; Oliver et al., 2009; Das, 2010; Koch, 2012; De Lisle et al., 2013; Riyanto et al., 2013, 2015), leading to the perception of a wide distribution and a rather inconsistent or even erroneous definition of the taxon, since the name became applied to bent-toed gecko species not representing *C. fumosus* sensu stricto (see Hartmann et al., 2016). Boulenger (1897) was the only author who provided a detailed, though not entirely correct (see Hartmann et al., 2016: footnote 1), species account for *C. fumosus* sensu stricto, based on specimens from North Sulawesi.

The recent identification of new species from the Sunda Islands masquerading under the name *C. fumosus* (Riyanto et al., 2015; Hartmann et al., 2016) and re-examination of *C. fumosus* specimens from North Sulawesi, however, show that the taxonomy of *C. fumosus* is in disarray, and this makes it necessary to properly redescribe this conspicuous taxon based on a multitude of eidonomic characters, some of which have never been provided in the literature. Whereas Hartmann et al. (2016) already published remarks on the taxonomy of *C. fumosus* and provided selected comparative morphological data for this species, a comprehensive redescription of *C. fumosus* is necessary to stabilize the taxonomy of a species that has experienced prominent use in the literature, but whose identity has regularly been misconstrued. This redescription, featured below, can serve as solid basis for the delineation and description of additional new species of bent-toed geckos currently recognized as *C. fumosus*, and allows the correction of comparative literature data.

MATERIALS AND METHODS

Our redescription of *Cyrtodactylus fumosus* is based on the examination of four specimens of that taxon, including the holotype (NMB-REPT 2662) and three additional specimens (NMB-REPT 2663; BMNH 1895.2.27.7, 1896.12.9.3). For each specimen used in the redescription, we recorded data for 31 eidonomic characters (see Table 1 for definitions and abbreviations). Of these, 14 were metric and 16 meristic. We also calculated the following ratios: AxialL/SVL, ArmL/SVL, LegL/SVL, HeadL/SVL, HeadW/HeadL, SnoutL/HeadL, SnoutL/OrbD, and MentalH/MentalW. All measurements were taken to the nearest 0.1 mm using digital calipers. Scale counts and observations of external morphology were made using a dissection microscope. Characters occurring bilaterally were measured or counted on the right side of specimens, unless stated otherwise; for femoral pores, interscales, and labial scales, we provide counts for both sides of the body (the prefixes "R" and "L" are used to distinguish characters counted on the right or left side, respectively). In our diagnosis, ranges are followed by means ± standard deviations. For descriptions of pattern and coloration we apply the terminology of Köhler (2012). Numbers in parentheses behind the respective capitalized color name refer to the coding therein. The terminology used to distinguish between different depressed precloacal areas follows Mecke et al. (2016). Drawings are based on photographs of ethanol-preserved specimens and were prepared using the program CorelDraw Graphics Suite X3. Museum abbreviations follow Sabaj Pérez (2014).

RESULTS

***Cyrtodactylus fumosus* (Müller, 1895)** (Figs 1; 2)

Gymnodactylus fumosus Müller, 1895a: 833 (holotype NMB-REPT 2662; type locality: "*Boelawa Gebirge*," Sulawesi, elevation 1200 m)
Gymnodactylus fumosus—Müller, 1895b: 865
Gymnodactylus fumosus—Boulenger, 1897: 204
Gymnodactylus fumosus (part.)—De Rooij, 1915: 16
Gymnodactylus fumosus—Brongersma, 1934: 168
Gymnodactylus fumosus—Brongersma, 1953: 172
Gymnodactylus fumosus—Kramer, 1979: 160
Cyrtodactylus fumosus (part.)—Manthey and Grossmann, 1997: 222
Cyrtodactylus fumosus (part.)—Grismer, 2005: 429
Cyrtodactylus fumosus (part.)—Grismer and Leong, 2005: 588
Cyrtodactylus fumosus (part.)—Biswas, 2007: 19
Cyrtodactylus fumosus (part.)—Hayden et al., 2008: 109
Cyrtodactylus fumosus (part.)—Rösler and Glaw, 2008: 14
Cyrtodactylus fumosus (part.)—Chan and Norhayati, 2010: 50
Cyrtodactylus fumosus (part.)—Das, 2010: 209
Cyrtodactylus fumosus (part.)—Iskandar et al., 2011: 65
Cyrtodactylus fumosus (part.)—Koch, 2012: 161
Cyrtodactylus fumosus—Hartmann et al., 2016: 556
Cyrtodactylus fumosus (part)—Riyanto et al., 2016: 69
Cyrtodactylus fumosus—Mecke et al., 2016: 356

Holotype: NMB-REPT 2662 (Fig. 1A and Table 2; Hartmann et al. 2016: Fig. 5): adult female (SVL = 77.8 mm) collected by Paul and Fritz Sarasin in 1894; terra typica: "*Boelawa Gebirge*" (= Huidu Matabulawa), corrected to "Bone Mountains" (= Pegunungan Bone, North Sulawesi Province, Indonesia) by Boulenger (1897).

Referred specimens: NMB 2663 (Fig. 1B): Mount Masarang; BMNH 1895.2.27.7 (Fig. 1C; same specimen figured in Boulenger, 1897: Plate VII, Fig. 2), 1896.12.9.3 (Fig. 1D): Rurukan.

Definition: *Cyrtodactylus fumosus* is a moderately-sized bent-toed gecko species (maximum SVL = 78 mm)

Table 1. Metric and meristic characters with abbreviations used in this study.

Character	Abbreviation	Definition
Snout-vent length	SVL	From tip of snout to cloaca
Axial length	AxialL	From axilla to groin
Tail length	TailL	From cloaca to tip of tail
Arm length	ArmL	From insertion of brachium into body wall to claw of longest finger
Leg length	LegL	From insertion of thigh into body wall to claw of longest toe
Head length	HeadL	From tip of snout to articulation of quadrate bone with lower jaw
Head width	HeadW	Measured at level of ear openings
Head height	HeadH	Measured at level of ear openings
Snout length	SnoutL	From tip of snout to anterior margin of orbit
Orbit-Ear distance	OrbEarD	From posterior margin of orbit to anterior margin of ear opening
Orbital diameter	OrbD	From anterior to posterior margin of orbit
Ear length	EarL	From anterior to posterior margin of ear opening
Mental length	MentalL	Maximum length of mental shield
Mental width	MentalW	Maximum width of mental shield
Dorsal tubercle rows	DTR	Number of longitudinal tubercle rows on dorsum at midbody, counted in one row between lateral folds
Paravertebral tubercles	PVT	Number of tubercles counted in a longitudinal row between posterior insertion of forelimb and anterior insertion of hindlimb
Ventral scales	VS	Number of ventral scales at midbody, counted in one row between lateral folds
Precloacofemoral scales	PFS	Number of enlarged precloacofemoral scales, counted along lowest, pore-bearing series
Femoral pores	FP	Number of femoral pores on enlarged scales on thigh
Interscales[a]	InterS	Number of enlarged poreless scales between series of pore-bearing precloacal scales and series of pore-bearing femoral scales on thigh
Precloacal pores	PP	Number of precloacal pores situated in precloacal groove
Postcloacal tubercles	PCT	Number of postcloacal tubercles
Subdigital lamellae under 4th toe	LT_4	Number of subdigital scales under 4th toe, counted from first enlarged scale (lamellae) on lower side of toe to scale proximal to apical scale
Supralabial scales 1	SupraLab_1	Number of labial scales of upper jaw, beginning with first enlarged scale bordering rostral shield, ending with last enlarged scale bordering labial angle
Supralabial scales 2	SupraLab_2	Number of labial scales of upper jaw, beginning with first enlarged scale bordering rostral shield, ending with enlarged scale below anterior margin of eye
Infralabial scales	InfraLab	Number of labial scales of lower jaw, beginning with first scale bordering mental shield, ending with last enlarged scale bordering labial angle
Internasal scales	InterNas	Number of scales between rostronasals, bordering rostral
Supraciliar scales	SC	Number of enlarged scales extending from anterior-ventral to posterior-dorsal edge of orbit
Interorbital scales	IOS	Number of scales counted in a row between the medial edges of orbits across head
Gular scales	GulS	Number of gular scales bordering pair of first postmentals

[a] Rösler et al. (2007); Hartmann et al. (2016); and Mecke et al. (2016) referred to interscales as "infrascales."

that can be readily distinguished from all other congeners occurring in the Greater and Lesser Sunda Islands, Sulawesi, and the Maluku Islands by the following combination of characters: (1) a single series of precloacofemoral scales, including three pore-bearing scales on each thigh, separated from 10 or 11 pore-bearing scales in the precloacal region by 9-11 interscales in males (Fig. 2A), (2) a precloacal groove in adult males (Fig. 2A), (3) posterior precloacal scales (Fig. 2A), (4) flat and smooth (unkeeled) dorsal tubercles in 4-7 irregularly arranged longitudinal rows at midbody (Fig. 2B), (5) a distinct lateral fold lacking tubercles, (6) 37-50 longitudinal rows of ventral scales at midbody, (7) 17-23 scales under 4th toe, and (8) a horizontal slit-like ear opening.

Comparisons: Characters distinguishing *Cyrtodactylus fumosus* from all other species of *Cyrtodactylus* occurring on the Sunda Islands and Sulawesi were provided by Mecke et al. (2016: Table 2). Here, our comparisons are limited to Sulawesi taxa, with characters of *C. fumosus* provided in parentheses. *Cyrtodactylus batik* can be

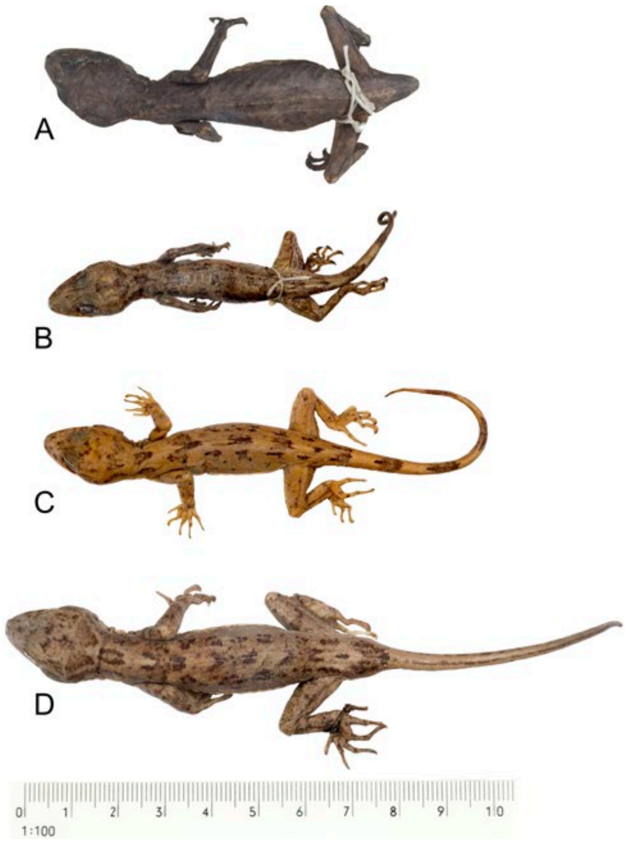

Fig. 1. Dorsal views of the known specimens of *Cyrtodactylus fumosus*: (A) NMB-REPT 2662 (holotype, adult female); (B) NMB-REPT 2663 (subadult male); (C) BMNH 1895.2.27.7 (adult female); (D) BMNH 1896.12.9.3 (adult male). Photographs by Sven Mecke. BMNH 1895.2.27.7 is also figured (in dorsal view) in Boulenger (1897: Plate VII, Fig. 2).

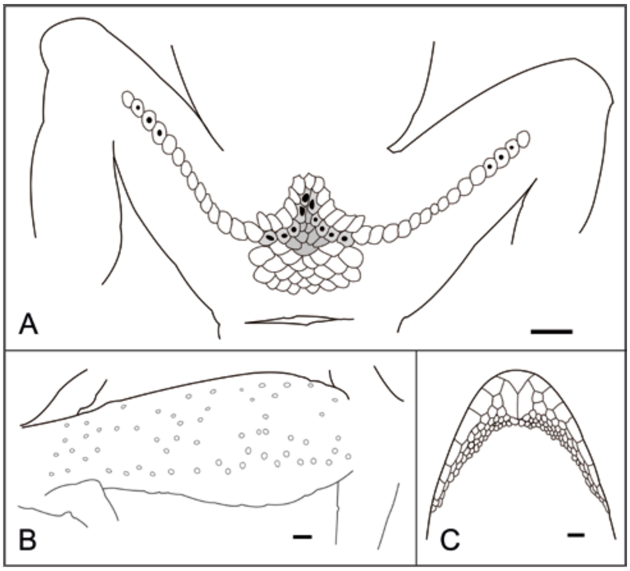

Fig. 2. Diagnostic characters of *Cyrtodactylus fumosus*. (A) Precloacofemoral region (with pore-bearing precloacal scales and groove shaded in grey) of a male specimen (BMNH 1896.12.9.3), showing precloacal and femoral pores. Scale bar equals 2 mm (B) Dorsum, showing tubercles (holotype NMB-REPT 2662). Scale bar equals 2 mm. (C) Ventral side of anterior part of head (holotype NMB-REPT 2662). Scale bar equals 1 mm. Drawings prepared by Felix Mader based on photographs by Sven Mecke.

distinguished from *C. fumosus* by a larger size of adults with a maximum SVL of 115 mm (78 mm); the absence of PFS (PFS present); the absence of PP and FP in both sexes (PP and FP present in males); the absence of a precloacal depression in both sexes (precloacal groove present in males); 23-26 slightly keeled DTR (4-7 unkeeled DTR); the presence of tubercles on the lateral skin fold (tubercles on lateral skin fold absent); 24-27 LT$_4$ (17-23 LT$_4$); and the presence of transversely enlarged subcaudal scales in a single row (enlarged, paired median subcaudals) (Iskandar et al., 2011; Riyanto et al., 2016). *Cyrtodactylus hitchi* can be distinguished from *C. fumosus* by the absence of PFS (PFS present); the absence of PP and FP in both sexes (PP and FP present in males); the absence of a precloacal depression in both sexes (precloacal groove present in males); the presence of 18-20 keeled DTR (4-7 unkeeled DTR); the presence of tubercles on the lateral skin fold (tubercles on lateral skin fold absent); and the presence of transversely enlarged subcaudal scales in a single row (enlarged paired median subcaudals) (Riyanto et al., 2016). *Cyrtodactylus jellesmae* can be distinguished from *C. fumosus* by the absence of PFS (PFS present); the absence of PP and FP in both sexes (PP and FP present in males); the absence of a precloacal depression in both sexes (precloacal groove present in males); the presence of 13-22 raised DTR (4-7 flat DTR); the presence of tubercles on the lateral skin fold (tubercles on lateral skin fold absent); and the absence of enlarged subcaudal scales (enlarged paired median subcaudals present) (Boulenger, 1897; Mecke et al., 2016, pers. obs.). *Cyrtodactylus spinosus* can be distinguished from *C. fumosus* by the absence of a continuous series of enlarged precloacal and femoral scales (PFS present); by widely spaced femoral scales (femoral scales juxtaposed); the presence of a shallow precloacal pit in males (deep precloacal groove in males); the presence of lateral and caudal spines (spines absent); and the presence of a prehensile tail (tail not prehensile) (Linkem et al., 2008; Harvey et al., 2016). *Cyrtodactylus wallacei* can be distinguished from *C. fumosus* by a larger size of adults, reaching a maximum SVL of 114 mm (78 mm); the absence of PFS (PFS present); the absence of PP and FP in both sexes (PP and FP present in males); the absence of a pre-

Table 2. Metric (in mm) and meristic data for the known specimens of *Cyrtodactylus fumosus*. Abbreviations are defined in Table 1. Characters occurring bilaterally were measured or counted on the right side of specimens, unless stated otherwise; for femoral pores, interscales, and labial scales we provide counts for both sides of the body (the prefixes "R" and "L" are used to distinguish characters counted on the right and left side, respectively). n/a = not applicable. Our metric data of BMNH 1895.2.27.7, the only known specimen with an original tail (TailL = 67.1), well agree with the measurements listed by Boulenger (1897), who also provided a drawing of a specimen (Plate VII, Fig. 2) identifiable as BMNH 1895.2.27.7.

	NMB-REPT 2662 (holotype)	NMB-REPT 2663	BMNH 1895.2.27.7	BMNH 1896.12.9.3
Sex	Female	Male	Female	Male
SVL	77.8	56.6	60.7	77.5
AxialL	35.2	22.2	28.3	31.4
ArmL	35.7	22.1	24.9	32.9
LegL	43.9	29.6	32.9	42.0
HeadL	21.3	15.7	16.8	20.4
HeadW	14.2	10.6	11.9	14.5
HeadH	9.2	7.0	6.7	9.5
SnoutL	8.8	6.9	7.7	9.4
OrbEarD	6.6	4.1	4.3	6.3
OrbD	5.2	3.6	4.0	4.1
EarL	1.2	1.2	2.0	2.3
DTR	5	7	4	6
PVT	13	16	14	18
VS	38	37	47	50
PFS	46	45	46	39
FP	0	R3 L3	0	R3 L3
InterS	n/a	R10 L9	n/a	R10 L11
PP	0	11	0	10
$\text{LT}_{4\ (\text{proximal})}$	7	8	10	9 (L)
$\text{LT}_{4\ (\text{distal})}$	10	11	13	12 (L)
LT_4	17	19	23	21 (L)
SupraLab_1	R12 L12	R13 L13	R11 L12	R11 L12
SupraLab_2	R6 L5	R6 L6	R6 L6	R6 L6
InfraLab	R9 L11	R10 L10	R11 L10	R8 L8
GulS	9	8	7	8

cloacal depression in both sexes (precloacal groove present in males); and the presence of 23-25 slightly keeled, trihedral DTR (4-7 unkeeled and flat DTR) (Hayden et al., 2008).

Description of the holotype. General habitus, metrics, and ratios: Adult female; SVL = 77.8 mm; AxialL = 35.2 mm; TailL (broken, only tail stump present) = 8.7 mm; ArmL = 35.7 mm; LegL = 43.9 mm; HeadL = 21.3 mm; HeadW = 14.2 mm; HeadH = 9.2 mm; SnoutL = 8.8 mm; OrbEarD = 6.6 mm; OrbD = 5.2 mm; EarL = 1.2 mm; head rather short (HeadL/SVL = 0.27) and wide (HeadW/HeadL = 0.67), clearly depressed between eyes, distinct from neck; snout rather elongate (SnoutL/HeadL = 0.41), longer than OrbD (SnoutL/OrbD = 1.69), canthus rostralis distinct; fore- and hindlimbs of moderate size (ArmL/SVL = 0.46; LegL/SVL = 0.56), without webbing between digits; relative length of fingers = IV > III > V > II > I; relative length of toes = IV > III > V > II > I; lateral skin fold distinct, lacking tubercles.

Scalation: Dorsal scales granulate, interspersed with slightly enlarged, flat, roundish and irregularly arranged dorsal tubercles (Fig. 2B), 5 DTR; 13 PVT; tubercles on occiput, neck, and hindlimbs similar in shape to those on dorsum (no tubercles present on the forelimbs).

Thirty-eight VS, distinctly larger than those on dorsum, juxtaposed; a single series of 46 poreless PFS; enlarged posterior precloacal scales present, arranged in a chevron-like shape consisting of five series of scales (from anterior to posterior: 10/ 8/ 7/ 6/ 2 scales); 2 flat PCT; number of lamellae under fingers: I 12, II 16, III 16, IV 18, V 16; number of lamellae under toes: I 13, II 15, III 17, IV 17, V 16.

Rostral shield rectangular, 2.2 times as wide as high, partly divided by a median, vertical furrow, in contact with 1st SupraLab, 2 rostro-nasals and a single InterNas; naris surrounded by rostral, 1st SupraLab, a single rostronasal, and three post-nasals; R12 L12 SupraLab_1, R6 L5 SupraLab_2, separated from orbit by three rows of small granular scales; R9 L11 InfraLab; cephalic scales small, rounded, granulate and juxtaposed; tubercles on occiput and neck flat and unkeeled; 40 SC; 46 IOS; mental triangular, wider than long (MentalW/MentalL = 1.7); one pair of enlarged 1st postmentals, enlarged 2nd postmentals absent (Fig. 2C); pair of 1st postmentals bordered by mental, 1st InfraLab, and 9 GulS (Fig. 2C); scales on throat minute and rounded.

Coloration: Natural color and pattern altered due to preservation. Ground color of dorsum Cinnamon-Drab (50); head darker than dorsum, Burnt Umber (48) in color, with indistinct Warm Sepia (40) stripe running from posterior border of orbits along neck, forming a collar at level of posterior margin of forelimbs; labial scales Buff (5), stippled with darker color, with stipples most concentrated at edges of some scales; dorsum with irregular, faint Dark Drab (45) blotches, not arranged in distinct pairs, most visible on vertebral region between forelimbs and on mid-dorsum; ground color of dorsal surface of limbs similar to ground color of dorsum; limbs with diffuse Dark Drab (45) markings; venter, throat and lower surface of limbs uniformly Smoke Grey (266), heavily dotted; color of dorsal and ventral surfaces of tail stump similar to dorsal and ventral ground color, respectively.

Intraspecific variation: Our assessment of the variation is based on the holotype and three additional specimens from North Sulawesi (one adult and one subadult male, one adult female) unless stated otherwise. Measurements (in mm) are listed as range followed by mean ± standard deviation provided in parentheses: SVL = 56.6-77.8 (68.2 ± 11.1); AxialL = 22.2-35.2 (29.3 ± 5.5); TailL (original tail) = 67.1 (n = 1); ArmL = 22.1-35.7 (28.9 ± 6.4); LegL = 29.6-43.9 (37.1 ± 6.9); HeadL = 15.7-21.3 (18.6 ± 2.7); HeadW = 10.6-14.5 (12.8 ± 1.9); HeadH = 6.7-9.5 (8.1 ± 1.5); SnoutL = 6.9-9.4 (8.2 ± 1.1); OrbEarD = 4.1-6.6 (5.3 ± 1.3); OrbD = 3.6-5.2 (4.2 ± 0.7); EarL = 1.2-2.3 (1.7 ± 0.6). Ratios: AxialL/SVL = 0.39-0.47 (0.43 ± 0.03); ArmL/SVL = 0.39-0.46 (0.42 ± 0.03); LegL/SVL = 0.52-0.56 (0.54 ± 0.02); HeadL/SVL = 0.27-0.28 (0.27 ± 0.01); HeadW/HeadL = 0.67-0.71 (0.69 ± 0.02); SnoutL/HeadL = 0.41-0.46 (0.44 ± 0.02); SnoutL/OrbD = 1.69-2.29 (1.96 ± 0.25); RostralW/RostralH = 1.53-2.18 (1.91 ± 0.28); MentalW/MentalL = 1.29-1.83 (1.64 ± 0.24).

Scale counts are listed as range followed by mean ± standard deviation provided in parentheses: DTR = 4-7 (5.75 ± 1.3); PVT = 13-18 (15.25 ± 2.2); VS = 37-50 (43 ± 6.5); PFS = 39-46 (44 ± 3.4), only a single series present; enlarged posterior precloacal scales consisting of 5 or 6 series; PCT = 2-3, flat in shape; LT_4 = 17-23 (19 ± 2.8); SupraLab_1 = 11-13 on right side of head and 12-13 on left side of head; InfraLab = 8-11 on right side of head and 8-11 on left side of head; SC = 32-40 (33.5 ± 4.4); IOS = 45-49 (47.3 ± 2.1); GulS = 7-9.

Furthermore, all specimens possess a distinct lateral skin fold lacking tubercles and a horizontal, slit-like ear opening. A distinctive row of 5 or 6 tubercles on the dorsal surface of the upper leg is present in three specimens (absent in the holotype). Specimens with unregenerated tails possess two strongly enlarged median subcaudal rows. Unlike female specimens, male specimens of *Cyrtodactylus fumosus* (n = 2) possess three pore-bearing scales on each thigh, separated from 10 or 11 pore-bearing precloacal scales by 9-11 InterS. A distinct precloacal groove is fully developed in adult males (n = 1) only. Data of measurements and scale counts for the main characters of the holotype and additional specimens used for the diagnosis are provided in Table 2.

Ground color of dorsal surface of body, head, and tail varies considerably between the specimens available to us and appears to depend on the respective preservation method. Hence, ground color of dorsal surface varies from Cinnamon (255) over Cinnamon-Drab (50) to Drab (19), with the specimens housed in NMB being darker than the ones housed in BMNH; dorsum with 4-7, sometimes indistinct, Warm Sepia (40) blotches; original tail (n = 1) with six Warm Sepia (40) blotches; regenerated tail of one specimen (BMNH 1896.12.9.3) possesses three indistinct, partially interrupted, Warm Sepia (40) lines, running from base to tip of tail; dorsal surface of limbs and head with diffuse Warm Sepia (40) or Dark Drab (45) markings; venter, lower surface of limbs, and throat uniformly Pale Buff (1) or Smoke Grey (266 and 267). See Fig. 1 for coloration and pattern of preserved specimens.

Distribution and natural history: Although the name *Cyrtodactylus fumosus* has frequently been applied to bent-toed gecko populations from Java, Bali, Halmahera, and the entire island of Sulawesi (e.g., De Rooij, 1915; Grismer, 2005; Das, 2010; De Lisle et al., 2013; Riyanto and Mumpini, 2013; Riyanto et al., 2015), *C. fumosus* sensu stricto is only known from the four specimens featured herein, all of which were collected in North Sulawesi (Müller, 1895a, b; Boulenger, 1897; see Fig. 3). The occurrence of *C. fumosus* on Lembeh Island, off the coast of northern Sulawesi (Grismer, 2005: Appendix 1, Grimser and Leong, 2005: Appendix 1), appears to be based on misidentified specimens, since the data (including key characters for diagnosis) provided by Grismser (2005: Table 2) and Grismer and Leong (2005: Table 2) do not match those of *C. fumosus* sensu stricto as reported herein. Moreover, the data provided by Grismer (2005) and Grismer and Leong (2005: Table 2) seem to be partly based on the erroneous description of *C. fumosus* provided by De Rooij (1915) (see Hartmann et al., 2016).

According to the data provided by Müller (1895a, b), specimens of *Cyrtodactylus fumosus* sensu stricto were collected at elevations 1200-1260 m, in a terrain that is, based on satellite images (Google Earth, viewed on 24 January 2016), covered with montane rainforest. Although there are only limited data available on the natural history of *C. fumosus*, we believe the species to be restricted to montane rainforest habitats in North Sulawesi. The distribution of *C. fumosus*, as currently known, overlaps with the range of *C. jellesmae*, the only other species of *Cyrtodactylus* known from North Sulawesi. Figure 3 shows the distribution of the six bent-toed geckos currently known from Sulawesi.

Remarks on the identity of Cyrtodactylus fumosus *from Java*: Hartmann et al. (2016) discussed the status of *Cyrtodactylus fumosus* populations outside of Sulawesi and came to the conclusion that these records were based on erroneous data provided in the literature (e.g., De Rooij, 1915) and/or misidentified specimens. Recently, Riyanto et al. (2015) applied the name *C. fumosus* to populations of bent-toed geckos from Java, which are unequivocally identifiable as belonging to the *C. marmoratus* (Gray, 1831) complex. These authors largely based their

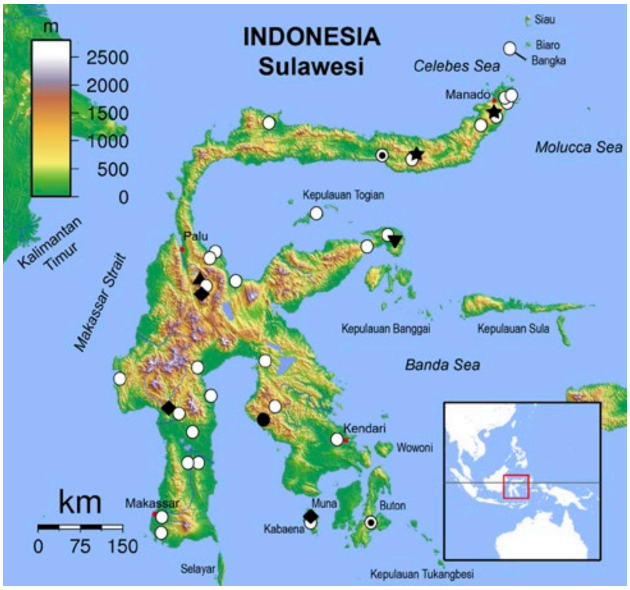

Fig. 3. Map of Sulawesi showing the distribution of the six species of *Cyrtodactylus* currently recognized from this island: *Cyrtodactylus batik* (inverted black triangle), *C. fumosus* (black star), *C. hitchi* (black circle), *C. jellesmae* (white circle), *C. spinosus* (black triangle), and *C. wallacei* (black diamond). Records are based on specimens listed in the appendices and data provided in Hayden et al. (2008), Linkem et al. (2008), Iskandar et al. (2011), Wanger et al., (2011), Koch (2012), Riyanto et al., (2016). A white circle with a black dot represents a photo-voucher for *C. jellesmae* available to us. Base map modified from Wikipedia © Sadalmelik / Wikimedia Commons / CC-BY-SA-3.0 by Max Kieckbusch.

assumption on De Rooij (1915), who mainly distinguished between *C. fumosus* and *C. marmoratus* by a continuous or discontinuous pore series, respectively. However, De Rooij (1915) largely based her definition of *C. fumosus* on Boulenger (1897), who erroneously reported this species to have a continuous pore series, and her personal examination of specimens housed in the collections of BMNH and SMF, which are conspecific with *C. halmahericus* (Mertens, 1929) (see Hartmann et al., 2016: Footnote 1). *Cyrtodactylus halmahericus*, unlike *C. fumosus*, possesses a continuous pore series in males (a redescription of *C. halmahericus* is currently underway).

Whereas the lectotype of *C. marmoratus* (RMNH. RENA 2710a.1; adult male), all other adult male paralectotypes housed in RMNH (RMNH.RENA 2710a.2-a.5, 2710.1-2), and several other adult male specimens we have examined personally, possess a continuous series of pores (precloacofemoral pores), this character may vary ontogenetically (Brongersma, 1953, pers. obs.), between sexes (Rösler et al.; 2007, Mecke et al., 2016), and between *C. marmoratus* sensu stricto and morphologically similar species masquerading under this name. *Cyrtodactylus fumosus* can be easily distinguished from *C. marmoratus* as currently defined by the following characters: (1) a discontinuous series of precloacal (10 or 11) and femoral pores (three on each thigh) in males, (2) the absence of pores in females, (3) the presence of posterior precloacal scales, (4) the presence of widely scattered, roundish, flat, and smooth dorsal tubercles in 4-7 rows at midbody (11-19 in the type series of *C. marmoratus* at RMNH), (5) 14-18 paravertebral tubercles (22-29 in in the type series of *C. marmoratus* at RMNH), and enlarged paired median subcaudals (enlarged subcaudals absent in *C. marmoratus*).

It is obvious that the male specimen (MZB.Lace 12903) identified as *Cyrtodactylus fumosus* by Riyanto et al. (2015) and depicted in their Fig. 4B is not conspecific with *C. fumosus*, because it possesses a continuous pore series and lacks posterior precloacal scales. The precloacofemoral region of that specimen rather matches that of *C. marmoratus* sensu stricto (see Hartmann et al., 2016: Fig. 3H, Mecke et al., 2016: Fig. 1A). Since Riyanto et al. (2015) failed to properly identify *C. fumosus* and *C. marmoratus*, their comparative Table 3 should not be used for the identification of these taxa. The example well demonstrates the importance of examining relevant type specimens before taxonomic decisions are made.

DISCUSSION

The phylogenetic affinities of *Cyrtodactylus fumosus* remain unclear. The presence of pores, a precloacal depression in males, and posterior precloacal scales are shared with other species of *Cyrtodactylus* from the region, e.g., *C. halmahericus* (Halmahera) and *C. klakahensis* Hartmann et al., 2016 (eastern Java), with which it may be closely allied[1]. By contrast, *C. fumosus* might represent an offshoot of an exclusive clade containing Sulawesi bent-toed geckos only.

Results of studies on Sulawesi amphibians and reptiles suggest that this island is herpetogeographically complex, supporting taxa of both Sundaic and Australopapuan affinities (Koch, 2011, 2012), including endemics (e.g., How and Kitchener, 1997; Whitten et al., 2001; Koch, 2011, 2012).

The restriction of *Cyrtodactylus fumosus* to Sulawesi underscores that this island holds a significant amount

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[1] *Cyrtodactylus petani* Riyanto et al., 2015 also shares with *C. fumosus* the presence of pores and posterior precloacal scales. Riyanto et al. (2015) provided inconsistent data on whether a precloacal groove is present in male specimens of *C. petani*. However, male *C. petani* lack a precloacal groove or pit (Awal Riyanto, in litt.; Mecke et al., 2016).

of endemism. The species is apparently only found in the mountains of North Sulawesi Province, and such a limited range exemplifies that isolated geographic features in this region (e.g., mountain ranges) may be the key locales for such endemism. According to Koch (2012: Table 11) more than 20 amphibians and reptiles (including candidate species) are endemic to northern Sulawesi. Most of these appear to be endemic to offshore islands, but we hypothesize that the North Sulawesi mountain ranges may harbor a higher number of endemic herpetofaunal taxa than generally assumed as well.

We disagree with Iskandar et al. (2011), who considered that the Sulawesi herpetofauna is impoverished compared to other regions in Southeast Asia, largely due to natural factors alone. The high rate at which new amphibian and reptile species are being discovered on Sulawesi contradicts this hypothesis, and the relatively low diversity may simply reflect the limited amount of fieldwork conducted there to date. Since 2000, 16 reptile species have been described from Sulawesi (e.g., *Tropidophorus baconi* Hikida et al., 2003; *Calamaria butonensis* Howard and Gillespie, 2007; *Rabdion grovesi* Amarasinghe et al., 2015), a number that equals ~15% of the reptiles known from this island. The number of described species of *Cyrtodactylus* in Sulawesi alone increased by 200% during the last decade. Preliminary examination of preserved bent-toed geckos from Sulawesi in museum collections suggests that at least one undescribed species of bent-toed gecko is present on the island. Photographic images of specimens in life available to us indicate that a further three species of *Cyrtodactylus* from Sulawesi are yet to be described. Therefore we agree with e.g., Linkem et al. (2008), and Koch (2011, 2012), who considered the herpetological diversity of Sulawesi to be underestimated.

KEY TO THE SPECIES OF THE GENUS *CYRTODACTYLUS* OF SULAWESI

This key is applicable to identify adult bent-toed geckos based on non-sexually dimorphic characteristics, although characters present in males only may accompany a choice.

1a Long spines on lateral fold and lateral portion of tail present; tail prehensile **C. spinosus**
1b Long spines on lateral fold and lateral portion of tail absent; tail not prehensile **2**
2a Enlarged precloacofemoral scales present in both sexes, bearing a total number of 16 or 17 pores in males, 10 or 11 of which are precloacal pores and 3 of which are femoral pores; pore-bearing scales separated by 9-11 enlarged interscales; precloacal groove present in males; no tubercles on lateral fold **C. fumosus**
2b Enlarged precloacofemoral scales; pores; precloacal groove; and tubercles on lateral fold absent **3**
3a Enlarged median subcaudals absent **C. jellesmae**
3b Enlarged median subcaudals present **4**
4a Enlarged subcaudals in multiple rows **C. wallacei**
4b Enlarged subcaudals in a single row for most of the tail's length **5**
5a 24-27 lamellae under 4th toe; SVL in adults 103-113 mm **C. batik**
5b 18-21 lamellae under 4th toe; SVL in adults 62-79 mm **C. hitchi**

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APPENDIX

Specimens examined for diagnosis and comparison

Cyrtodactylus fumosus.—**Indonesia**: *North Sulawesi Province*: Bone Mountains (Pegunungan Bone, 1200 m a.s.l.): NMB 2662 (holotype); Mount Masarang: NMB 2663; Rurukan: BMNH 1895.2.27.7, 1896.12.9.3.

Cyrtodactylus halmahericus.—**Indonesia**: *North Maluku Province*: North Halmahera: MCZ Herp R-19279, SMF 8230 (paratype); Central Halmahera: Oba (Payahe): SMF 8232 (paratype); Soah Konorah (Soakonora): SMF 8233 (holotype).

Cyrtodactylus jellesmae.—**Indonesia**: *Central Sulawesi Province*: Malakosa, Kuala Navusu: AMNH R142969-73; Tolai, Sungai River: AMNH R142974; *North Sulawesi Province*: Kema: NMB-REPT 2659 (paralectotype); Buol: NMB-REPT 2660 (lectotype); Mount Masarang: NMB-REPT 2661 (paralectotype); Pulau Biaro: MCZ 171466; *South Sulawesi Province*: Lowah (Muara Loa): MCZ 25337.

Cyrtodactylus klakahensis.—**Indonesia**: *Jawa Timur Province*: Lumajang, Klakah: SMF 22476 (holotype); SMF 22477-79 (paratypes).

Cyrtodactylus marmoratus.—**Indonesia**: Java: RMNH.RENA 2710.1-8 (paralectotypes), RMNH.RENA 2710a.1 (lectotype), RMNH.RENA 2710a.2-6 (paralectotypes), MTKD 8903-05, SMF 8218; West Java: RMNH.RENA 9847, ZMA.RENA 15387 (three specimens); *Jawa Barat Province*: Garoet (Garut Regency): RMNH.RENA 9846 (three specimens), RMNH.RENA 10114 (two specimens), Kamodjang (Kawah Kamojang): RMNH.RENA 9849; *Jawa Tengah Province*: "Goewa Djatidjadjar Jdjoe Bagelen" (= Gua Jatijajar, Kebumen); Karangpucung: SMF 92361; *Jawa Timur Province*: Malang: RMNH.RENA 9848 (two specimens).

Cyrtodactylus petani.—**Indonesia**: *Jawa Timur Province*: Toelong Agoeng (Tulungagung Regency): ZMA.RENA 11353.

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Errata to

Mecke, S., Hartmann, L., Mader, F., Kieckbusch, M., Kaiser, H. (2016): Redescription of *Cyrtodactylus fumosus* (Müller, 1895) (Reptilia: Squamata: Gekkonidae), with a revised identification key to the bent-toed geckos of Sulawesi. Acta Herpetologica 11(2): 151-160.

In Acta Herpetologica 11(2), Mecke et al. (2016) redescribed *Cyrtodactylus fumosus* (Müller, 1895) (Reptilia: Squamata: Gekkonidae) and provided an identification key to the bent-toed geckos of Sulawesi. After the publication of this article it came to our attention that some aspects of this paper have to be corrected as follows:

- page 152, MATERIAL AND METHODS section, left column, lines 5 and 6: "…we recorded data for 31 eidonomic characters…" should read "…we recorded data for 30 eidonomic characters…"
- page 153, Table 2, Definition of "precloacal pores." In this definition we mention that we counted the number of precloacal pores situated in the precloacal groove. However, precloacal pores may not be situated in a groove. Non-adult males of *Cyrtodactylus fumosus* do possess pores, but their groove might not be fully developed (see p. Mecke et al. 2016: 156)
- page 156, right column, paragraph 2. The author "Mumpini" is correctly spelled "Mumpuni" (see also page 160, left column, first reference).
- page 156, right column, paragraph 3: "…were collected at elevations 1200-1260 m…" should read "…were collected at elevations of 1200-1260 m…"
- page 158, KEY TO THE SPECIES OF THE GENUS *CYRTODACTYLUS* OF SULAWESI. As stated in our comparisons (page 153-155), the species *Cyrtodactylus batik*, *C. hitchi*, *C. jellesmae*, and *C. wallacei* possess tubercles on the lateral fold. An error regarding this characteristic in the named species occurs in choice 2b of our key:
  "2b Enlarged precloacofemoral scales; pores; precloacal groove; and tubercles on lateral fold absent.......3"
  should read:
  "2b Enlarged precloacofemoral scales, pores, and precloacal groove absent; tubercles on lateral fold present..3"

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5.5 Paper 6

Kieckbusch, M., **Mecke, S.** (joint first authors), Hartmann, L., Ehrmantraut, L., O'Shea, M. & Kaiser, H. (2016): An Inconspicuous, Conspicuous New Species of Asian Pipesnake, Genus *Cylindrophis* (Reptilia: Squamata: Cylindrophiidae), from the South Coast of Jawa Tengah, Java, Indonesia, and an Overview of the Tangled Taxonomic History of *C. ruffus* (Laurenti, 1768). *Zootaxa*, **4093**(1): 1–25.

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An inconspicuous, conspicuous new species of Asian pipesnake, genus *Cylindrophis* (Reptilia: Squamata: Cylindrophiidae), from the south coast of Jawa Tengah, Java, Indonesia, and an overview of the tangled taxonomic history of *C. ruffus* (Laurenti, 1768)

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Abstract

We describe a new species of *Cylindrophis* currently known only from Grabag, Purworejo Regency, Jawa Tengah Province (Central Java), Java, Indonesia. *Cylindrophis subocularis* **sp. nov.** can be distinguished from all congeners by the presence of a single, eponymous subocular scale between the 3rd and 4th or 4th and 5th supralabial, preventing contact between the 4th or 5th supralabial and the orbit, and by having the prefrontal in narrow contact with or separated from the orbit. We preface our description with a detailed account of the tangled taxonomic history of the similar and putatively wide-ranging species *C. ruffus*, which leads us to (1) remove the name *Scytale scheuchzeri* from the synonymy of *C. ruffus*, (2) list the taxon *C. rufa* var. *javanica* as *species inquirenda*, and (3) synonymize *C. mirzae* with *C. ruffus*. We provide additional evidence to confirm that the type locality of *C. ruffus* is Java. *Cylindrophis subocularis* **sp. nov.** is the second species of Asian pipesnake from Java.

Key words: *Cylindrophis subocularis* **sp. nov.**, *C. ruffus*, Serpentes, Cylindrophiidae, Asian pipesnakes, species complex, morphology, Central Java, Indonesia, Greater Sunda Islands

Zusammenfassung

Wir beschreiben eine neue Art der Gattung *Cylindrophis*, die gegenwärtig nur aus Grabag, Purworejo, Jawa Tengah (Zentral-Java), Java, Indonesien, bekannt ist. *Cylindrophis subocularis* **sp. nov.** unterscheidet sich von allen anderen Arten dieser Gattung durch das Vorhandensein einer einzelnen, namensgebenden Subokular-Schuppe, die sich zwischen das dritte und vierte oder das vierte und fünfte Supralabial-Schild schiebt, und den Kontakt zwischen dem vierten oder fünften Supralabiale und dem Auge verhindert. Zudem steht das Präfrontale in minimalem Kontakt mit dem Auge oder ist von diesem separiert. Wir stellen unserer Beschreibung einen detaillierten Überblick über die verworrene Taxonomie-Geschichte der ähnlichen und scheinbar weit verbreiteten Art *C. ruffus* voran, was uns dazu veranlasst (1) den Namen *Scytale scheuchzeri* aus der Synonymie von *C. ruffus* herauszunehmen, (2) *C. rufa* var. *javanica* als *species inquirenda* zu betrachten, und (3) *C. mirzae* mit *C. ruffus* zu synonymisieren. Wir liefern weitere Hinweise für die Berichtigung der Typuslokalität von *C. ruffus* auf Java. Bei *Cylindrophis subocularis* **sp. nov.** handelt es sich um die zweite auf Java vorkommende Asiatische Walzenschlange.

Schlüsselwörter: *Cylindrophis subocularis* **sp. nov.**, *C. ruffus*, Serpentes, Cylindrophiidae, Asiatische Walzenschlangen, Art-Komplex, Morphologie, Zentral-Java, Indonesien, Große Sundainseln

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Introduction

The genus *Cylindrophis*. The henophidian snake genus *Cylindrophis* Wagler, 1828 currently comprises 13 secretive, semifossorial species, including *C. aruensis* Boulenger, 1920; *C. boulengeri* Roux, 1911; *C. burmanus* Smith, 1943; *C. engkariensis* Stuebing, 1994; *C. isolepis* Boulenger, 1896; *C. jodiae* Amarasinghe *et al*., 2015; *C. lineatus* Blanford, 1881; *C. maculatus* (Linnæus, 1758); *C. melanotus* Wagler, 1828; *C. mirzae* Amarasinghe *et al*., 2015; *C. opisthorhodus* Boulenger, 1897; *C. ruffus* (Laurenti, 1768); and *C. yamdena* Smith & Sidik, 1998 (see Wallach *et al*. 2014; Amarasinghe *et al*. 2015). These snakes are collectively referred to as Asian pipesnakes due to their cylindrical appearance, with a body of near-uniform diameter. Members of the genus are small- to medium-sized (total length 125–857 mm), rather stout-bodied snakes that may be defined on the basis of the following eidonomic characters: (1) a relatively blunt head with minute eyes, head not distinct from neck, bearing a mental groove; (2) absence of true gastrosteges, with ventral scales only slightly larger than or equal in size to dorsal scales; (3) presence of a pair of pelvic spurs (= cloacal spurs) in both sexes; (4) a very short tail, often with conspicuous ventral coloration; and (5) contrasting light and dark ventral blotching (e.g., de Rooij 1917; Smith 1943; Taylor 1965; Greene 1973; pers. obs.). The conspicuous ventral color pattern plays a vital role in the defensive behavior of *Cylindrophis* species. When threatened, pipesnakes will flatten the posterior portion of their body and arch it above the ground to display their ventral pattern, while the head remains concealed among the body coils (e.g., Flower 1899; Barbour 1912; Smith 1927, 1943; Campden-Main 1970; Deuve 1970; Greene 1973).

Distribution. *Cylindrophis* is a widely distributed genus (Flower 1899; de Rooij 1917; Smith 1943; Lal Hora & Jayaram 1949; Taylor 1965; Campden-Main 1970; Deuve 1970; McDowell 1975; in den Bosch 1985; Stuebing 1991; Adler *et al*. 1992; Iskandar 1998; Zug *et al*. 1998; McDiarmid *et al*. 1999; Orlov *et al*. 2000; de Lang 2011) with species occurring from Sri Lanka (one species) throughout the continental and insular parts of Southeast Asia (12 species currently recognized). In Southeast Asia the genus is distributed from southern China and Hong Kong through Vietnam, Laos, Cambodia, Thailand, Myanmar, Peninsular Malaysia, and Singapore including Singapore, south to the Greater Sunda Islands (Borneo, Sumatra, Java, as well as some of their offshore islands), Sulawesi, the Lesser Sunda Islands (Lombok, Komodo, Flores, Sumbawa, Timor), and east to the Maluku Islands (Halmahera, Wetar, Damar, Babar, and into the Tanimbar Archipelago); the eastern distributional limit, the Aru Islands, was considered questionable by Iskandar (1998). However, within this vast range, smaller-scale zoogeographic patterns, phylogenetic relationships, and even the true species richness of the genus remain poorly known.

Many species of *Cylindrophis*, especially those from the eastern end of the distribution (e.g., *C. aruensis*, *C. boulengeri*, *C. isolepis*, *C. yamdena*), are known from very few specimens (McDowell 1975; Iskandar 1998; Smith & Sidik 1998). This is likely due to both the remoteness of the eastern Indonesian islands and the secretive lifestyle of these snakes, and *Cylindrophis* diversity in this region may still be underestimated. Even on Borneo, an island with a relatively well-studied herpetofauna (Das 2004), Stuebing (1994) discovered *C. engkariensis*, a species with a potentially very restricted range. More recently, Amarasinghe *et al*. (2015) described two new species (one from Singapore and one from Vietnam) that had been masquerading under the name *C. ruffus*. However, the descriptions and redescriptions (including of *C. ruffus*) presented by these authors contain some inaccuracies, including descriptive errors, which unfortunately increase the complexity of an already intricate taxonomic situation.

The problematic nature of *Cylindrophis ruffus*. Compared with other members of the genus, the species *Cylindrophis ruffus sensu historico* (e.g., Schlegel 1837b, 1837−1844; de Rooij 1917; Smith 1943; for a definition of the term *sensu historico* see below) exhibits an extraordinarily wide distribution, extending from mainland Southeast Asia across most parts of the Greater Sunda Islands into eastern Java (de Rooij 1917; Smith 1943; Taylor 1965; McDiarmid *et al*. 1999; Wallach *et al*. 2014). It was already identified as a species complex (Smith & Sidik 1998) and it appears to include several undescribed taxa (Amarasinghe *et al*. 2015; Mecke *et al*., in prep.). Despite its redescription by Amarasinghe *et al*. (2015), both the morphological definition and the geographic range limits of *C. ruffus sensu stricto* remain unsettled. *Cylindrophis ruffus sensu historico* appears to be common, frequently encountered (Smith 1943; Taylor 1965; Campden-Main 1970; Kupfer *et al*. 2003), and well represented in museum collections, but a comprehensive taxonomic revision of this group has never been conducted. While it is evident that the taxonomy of *C. ruffus* is flawed, its complex taxonomic history, the absence of a type specimen, and an incorrect type locality ("Surinami") have stood in the way of developing a stable taxonomic hypothesis (Boie 1827; Schlegel 1837a, b; McDiarmid *et al*. 1999; Wallach *et al*. 2014). Furthermore, due to the age of available museum specimens in general, and of type material in particular, it is only through a thorough morphological study encompassing the entire range and variation of *C. ruffus* that its taxonomy can be resolved.

History necessitates three working definitions of *Cylindrophis ruffus.* As part of our comprehensive review of the genus *Cylindrophis*, we examined several hundred museum specimens listed by the available collection data as *C. ruffus*. We noted that, given the long history of *C. ruffus* in the literature and the morphological diversity of examined specimens, three definitions of *C. ruffus* as a taxonomic unit became necessary to permit a complete understanding of how different authors through time dealt with the taxon. Our most inclusive definition for the taxon is '*C. ruffus sensu historico*[1],' which includes all forms historically considered to be part of *C. ruffus* at one time or another, but before the revision of Amarasinghe *et al.* (2015). This definition includes *C. burmanus* as well as the forms that were recently described as *C. jodiae* and *C. mirzae* by Amarasinghe *et al.* (2015); it essentially covers forms from all over Southeast Asia and into the Indonesian archipelago. The second, more specific definition is '*C. ruffus sensu lato*,' which excludes *C. burmanus* and *C. jodiae*, but still includes the weakly defined *C. mirzae* as well as populations from Borneo, Java, Sumatra, and Peninsular Malaysia. Specimens north of Peninsular Malaysia belong either to *C. burmanus* or *C. jodiae* (pers. obs.). Our third definition is '*C. ruffus sensu stricto*,' by which we refer to the true species *C. ruffus*.

An unusual population from Java. As we progressed with our study, we noticed that a particular specimen series was sufficiently different from *C. ruffus sensu historico* to warrant recognition as a distinct species, even while our review of *C. ruffus* was still in progress. Specifically, our work in the collections at the Naturalis Biodiversity Center in Leiden, the Netherlands (formerly the Rijksmuseum van Natuurlijke Historie; RMNH), the Natural History Museum in Vienna, Austria (NMW), and the Museum für Naturkunde Berlin, Germany (ZMB), revealed several specimens labeled as *C. ruffus* that had apparently been collected at a single, isolated locality on the Indonesian island of Java, and which allowed easy differentiation from all other forms of *Cylindrophis* by a unique character: the presence of a subocular scale. We here describe this species, which is currently only known from Grabag, Purworejo Regency, Jawa Tengah Province (Central Java), Indonesia, and provide an historical overview of *C. ruffus* taxonomy.

Material and methods

Morphological characters. For each specimen of the new species ($n = 8$) and all specimens used for comparison ($n = 451$), we recorded data for 52 morphological characters. Of these, 37 were metric, eight meristic, and seven qualitative. In the list below, character names are provided in bold, followed by their definitions.

The following metric characters were obtained (characters used for the calculation of ratios are abbreviated for convenience): **snout-vent length** (SVL), measured from tip of snout to cloaca; **tail length** (TL), measured from cloaca to tip of tail; **body diameter** (BD), calculated as the mean of body height and body width at midbody; **head length** (HL), measured from tip of snout to articulation of quadrate bone; **head width** (HW), measured at level of anterior margin of parietals; **snout length** (SL), measured from tip of rostral to anterior margin of orbit; **snout width** (SW), measured at level of nares; **eye diameter** (ED), measured as length of orbit; **interorbital distance** (IOD), measured as shortest distance between orbits across head; **naso-orbital distance** (NOD), measured from posterior margin of naris to anterior margin of orbit; **internarial distance**, measured between interior margins of nares; **length of prefrontal-eye contact** (PrefO), measured at prefrontal margin bordering orbit. We also measured the following **head scale characters** (dimensions of these scale characters are expressed as the maximal length, height, or width): rostral height and width; nasal length and height; prefrontal length and width; frontal length and width; parietal length and width; supraocular length and width; postocular length and height; anterior temporal length and height; upper posterior temporal length and height; mental height and width; anterior chin shield length and width; posterior chin shield length and width; and mental groove length. SVL and TL were measured to the nearest 1 mm by gently straightening the respective specimen along a metric ruler. All other metric characters were measured to the nearest 0.1 mm under a stereomicroscope using digital calipers and a measuring magnifier. We also calculated the following ratios: TL/SVL, BD/SVL, HL/SVL, HW/HL, SL/HL, SW/SL, ED/HL, IOD/HL, NOD/HL, and PrefO/ED.

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[1] The term *sensu historico* has been used by scholars in the classical sciences (specifically of the languages of Ancient Greece and Ancient Rome) to indicate that a term is used within an historical context, as opposed to a direct translation. We borrow this term to distinguish between a taxon as historically defined and one based on the most current taxonomy.

The following meristic characters were counted: number of **dorsal scale rows**, counted in an inverse 'V' shape (to include all dorsal scales developmentally associated with a single pair of ribs) at (A) one head length behind head, (B) at midbody, and (C) one head length before cloaca (displayed in a formula as A/B/C); **ventrals**, beginning with the gular scale bordered by posterior chin shields; **subcaudals**, counted from cloaca to end of tail, excluding terminal spine (this count included, if present, a single row of multiple small scales bordering cloaca, counted as one subcaudal); **postoculars**; **temporals**, including (a) number of anterior temporals and (b) number of posterior temporals, expressed in a formula as a + b; number of **supralabials**; number of **infralabials**; and **number of light transverse ventral blotches** present along body, beginning with first blotch behind head to last blotch anterior to cloaca. Head scales occurring bilaterally were counted on (a) the right and (b) the left side of the body. We use the formula a|b when counts are different on either side of the body; a single value for a bilaterally occurring head scale character indicates that counts on both sides of the body resulted in an identical value.

The system of counting ventral scales described by Dowling (1951) is not applicable to anilioid snakes (Aniliidae, Anomochilidae, Cylindrophiidae, Uropeltidae) because these, unlike more advanced snakes, have no true gastrosteges and no preventral scales. Gower & Ablett (2006) therefore proposed a ventral-counting system for these snakes that includes every scale between the mental and cloacal scute. We did not apply their system, because all members of the genus *Cylindrophis* possess a mental groove formed by the first pair of infralabials and two pairs of enlarged chin shields, with the latter morphologically distinct from the smaller scales bordering them posteriorly. Consequently, ventral scales were counted from the first unpaired scale positioned medially behind the mental groove to the, often slightly enlarged, scale anterior to the divided cloacal scute.

In terms of qualitative characteristics, we recorded the specific **supralabials contacting the orbit**; the specific **infralabials contacting the chin shields**; the **condition of the cloacal scute** (divided or entire); and **pattern and coloration** of head, dorsum, venter, and tail. For descriptions of pattern and coloration we applied the terminology of Köhler (2012). Numbers in parentheses behind the respective capitalized color name refer to the coding therein. Sex was determined by the presence of testes or ovaries and oviducts and only if ventral incisions into the body cavity already existed.

Comparative material. Comparative morphological data were obtained primarily from museum specimens examined by the authors. Only for comparisons with *Cylindrophis aruensis* and *C. yamdena* did we use data from the original species descriptions or other relevant literature.

We compared the new species to 451 specimens from across the range of *Cylindrophis*, housed in the following collections (abbreviations follow Sabaj Pérez [2014]): AMNH, MHNG, MTD (= MTKD), NMB, NMBE, NMW, RMNH, SMF, ZMA (now in Naturalis, Leiden; RMNH), ZMB, ZMH, and ZRC. Since the examined material used for species delineation included (1) very distinct species not easily confused with the new species, and (2) 231 specimens of *C. ruffus sensu lato*, our Appendix includes only a relevant subsample of museum specimens used for direct comparisons herein, most notably specimens of *C. ruffus sensu lato* from Java, including 53 specimens with precise localities (e.g., towns, regencies) and 60 lacking exact locality data (specimens labelled only as collected on 'Java'). Although *C. mirzae* might ultimately be considered a valid species, we herein refrain from differentiating between *C. mirzae* and *C. ruffus* for reasons outlined in the taxonomic history section.

Statistical analyses. Since our new species is sufficiently distinct from congeneric taxa by a multitude of characters (see Results: Comparisons), and with a revision of *C. ruffus* in progress, our statistical analyses for this study focused exclusively on revealing characters to distinguish between the new species and *C. ruffus* from Java (the type locality of *C. ruffus*; see Results: History leads to the type locality of *Cylindrophis ruffus*). Meristic characters that were constant between the groups or exhibited two expressions only were excluded from all statistical analyses.

For statistical tests, the data analysis software R (R-Core Team, version 3.1.3) was used. The normality assumption for individual variables (i.e., of the metric and meristic characters, and ratios defined above) was tested with a Shapiro-Wilk statistic. Prior to variance analyses (see below), tested metric variables were adjusted to the mean SVL across all groups, in order to minimize variance due to possible ontogenetic variation between different populations (e.g., Thorpe 1975, 1983; Turan 1999; Vogel *et al.* 2007; van Rooijen & Vogel 2008, 2010, Mecke *et al.* 2013). The equation for the adjustment of data follows Vogel *et al.* (2007), van Rooijen & Vogel (2008, 2010), and Mecke *et al.* (2013):

$$Y_{adj} = Y_i - ß * (SVL_i - SVL_{mean})$$

In this formula, Y_{adj} is the value of the respective, allometrically adjusted variable of the i^{th} specimen, Y_i is the original value of this variable of the i^{th} specimen, β is the pooled regression coefficient of Y against SVL, SVL_i is the SVL of the i^{th} specimen, and SVL_{mean} is the overall mean SVL of all specimens.

Subsequently, adjusted metric characters, meristic characters, and ratios were tested for statistically significant differences between the two *Cylindrophis* forms occurring on Java (our new species and *C. ruffus sensu lato*). We used one-way ANOVA (analysis of variance) if a variable fulfilled normal distribution, and a Mann-Whitney U-test if a variable was not normally distributed. When the respective statistical test yielded significant outputs (i.e., statistically confirming differences between the two compared forms), these are shown in the Results section with superscripted asterisks indicating probability levels as follows: * < 0.05; ** < 0.01; *** < 0.001.

Results

Comments on the taxonomic history of *Cylindrophis ruffus* (Laurenti, 1768)

Early beginnings: Johann Jakob Scheuchzer's (1672–1733) *Physica Sacra Illustrata*. Scheuchzer (1735) was probably the first author who, in his pre-Linnæan treatise entitled *Physica Sacra Illustrata*, depicted snake specimens referable to *Cylindrophis ruffus sensu historico*, presenting three different illustrations (Tabulae DCXXIX-F, DCLX-3, DCCXLVIII-6; illustrated in Fig. 1A–C herein) of specimens from the Linck collection (Merrem 1820; Boie 1827; Wagler 1828–1833; see also Bauer & Wahlgren [2013] for an overview of the Linck collection). A precise identification of the specimens depicted, including their allocation to *C. ruffus*, *C. burmanus*, or *C. jodiae*, however, is difficult.

Albertus Seba (1665–1736) and his Cabinet of Natural Curiosities. In the second volume of his *Thesaurus*, Seba (1735: Tabulae VII-3, XXV-1; illustrated in Fig. 1D–E herein), described and figured two snakes based on specimens housed in his cabinet of natural curiosities. These were identified as the taxon *Cylindrophis ruffus* by subsequent authors (e.g., Merrem 1820). Seba's short diagnosis indicates that both snakes originated on Ambon, an island in the Moluccas. However, in the main description (following the diagnosis) and referring to Tabula XXV-1 (illustrated in Fig. 1E herein), Seba (1735: 26) assigned a larger area of distribution to the respective specimen, namely "Les Grandes & […] les Petites Indes" [i.e., Asia and the American Continents]. Since the figures in Seba leave little doubt as to the identity of the specimens (*C. ruffus sensu historico*), it is evident that they must have originated in Asia. The taxon, however, does not appear to occur on Ambon (de Lang 2013), an island with a five-centuries-long history of commercial and strategic importance for Europe, with specimens both collected or merely shipped from there (e.g., Weijola & Sweet 2015).

Laurens Theodorus Gronovius (1730–1777) and the first detailed account of *Cylindrophis ruffus*. In his *Musei Ichthylogici*, a detailed, descriptive catalogue of fish, amphibian, and reptile specimens housed in his Leiden cabinet of curiosities, Gronovius (1756) introduced under the heading "6. ANGUIS squamis abdominalibus CLXXIX, & squamis caudalibus VII" [6. SNAKE with 179 ventral scales and seven subcaudal scales] a taxon that Merrem (1820) listed as *Tortrix rufa* (= *Cylindrophis ruffus*). Gronovius's fairly detailed description of his species "6. ANGUIS" (Gronovius 1756: 54; see also Adler *et al.* 1992) matches *C. ruffus sensu historico*, based on the following morphological characters: 179 ventrals; seven subcaudals; small eyes; ventrals slightly enlarged, hexagonal; stout, short, conical tail; reddish coloration with white transverse ventral bands. Although Gronovius stated that his specimen originated in "Surinamam" [sic] [= Suriname], a thorough literature survey revealed that there is no snake taxon known from Suriname (nor a species from outside Asia) that would match his description. The only Asian species matching the listed characteristics are *C. ruffus sensu lato* and *C. jodiae*, and we therefore conclude that Gronovius's specimen must have been collected in Asia.

Josephus Nicolaus Laurenti (1735–1805) and the species description of *Cylindrophis ruffus*. The valid species name *ruffa* was coined by post-Linnæan author Laurenti in 1768, who placed this taxon from a location he listed as "Surinami" (Laurenti 1768: 71) into the genus *Anguis* Linnæus, 1758. As was common practice during

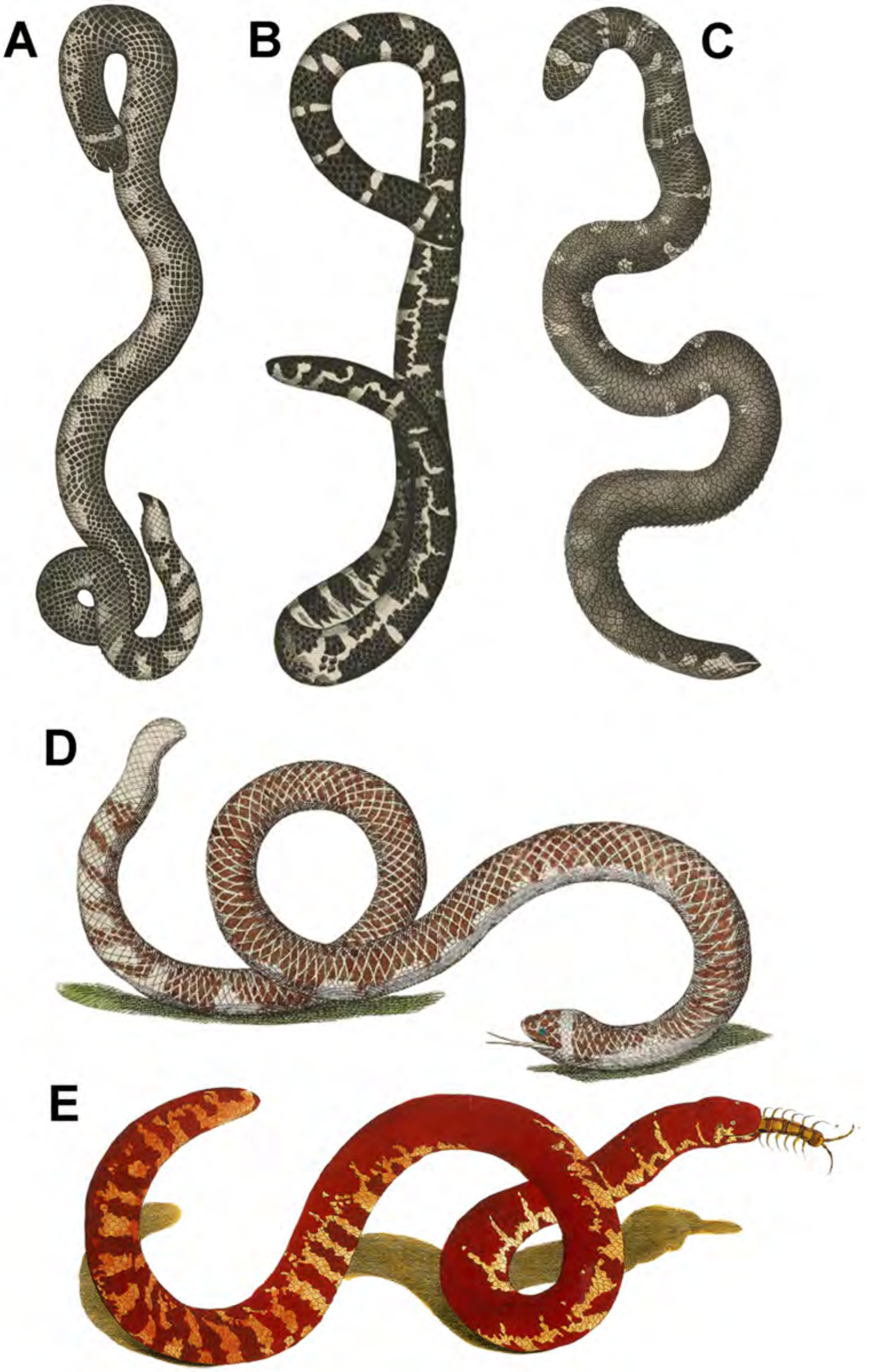

FIGURE 1. Historical drawings of *Cylindrophis ruffus sensu historico*. Illustrations from: (A–C) Scheuchzer (1735); and (D–E) Seba (1735). Illustrations are not to scale. Plate prepared by Hinrich Kaiser and Mark O'Shea.

that time, Laurenti only provided exceedingly short descriptions of the known amphibian and reptile species that, taken on their own, would hardly permit a proper diagnosis of specific taxa. However, in the case of his taxon *Anguis ruffa*, Laurenti (1768: 139) stated "*hospitatur in Museo Gronoviano*" [housed in the collection of Gronovius], thereby apparently referring to Gronovius's 1756 catalogue (and hence to *Anguis* species number 6). A comparison of Gronovius's and Laurenti's texts shows that Laurenti's description is, by virtue of its wording, a shortened version of that provided by Gronovius, with both authors providing the same erroneous information regarding the specimen's provenance. This leaves little doubt that the species identity of Laurenti's *A. ruffa* is the same as *Anguis* species number 6 of Gronovius (1756). It is unfortunate that the type specimen of *A. ruffa* appears to be lost (Iskandar & Colijn 2002). Gronovius's private collection was partly incorporated into the collection at the BMNH (e.g., dried fish-skins; Gray 1854), but the rest of his collection probably became dispersed. His herpetological collection cannot be traced to any larger museum collection extant today (Aaron M. Bauer, in litt.).

Johann Friedrich Gmelin (1748–1804) and his new species name. In his enhanced edition of the Linnæan *Systema Naturae*, Gmelin (1789) listed *Anguis rufus* (*nomen emendatum*) and attributed this taxon to Laurenti (1768). Gmelin (1789) also coined a new species name, *A. striatus*, and attributed this species to the pre-Linnæan Gronovius by referencing the publication of the latter, directly referring to *Anguis* species number 6 ("A. *Gron. mus*. 2. *p*. 53. *n*. 6."). Since Laurenti (1768) clearly refers to Gronovius (1756) in his description of *A. ruffa* as well, the connection between the descriptions published by Gmelin (1789), Laurenti (1768), and Gronovius (1756) leaves little doubt, that *A. striatus* can be regarded as an objective junior synonym of *Cylindrophis ruffus*. Daudin (1803) also listed Gmelin's accounts of *A. striatus* and *A. rufus*, and Gronovius's description of *Anguis* species number 6 in his references for his description of *Eryx rufus* (*comb. nov.* for *Anguis ruffa* Laurenti, 1768).

Contributions by Patrick Russell (1726–1805). Russell (1801) used the preoccupied name *Anguis scytale* Linnæus, 1758 (current name *Anilius scytale*) to refer to a *Cylindrophis ruffus* specimen he received from Java (Russell 1801: Plate XXVII; illustrated in Fig. 2A herein). Hence, *Anguis scytale* Russell, 1801 is a junior homonym of *Anilius scytale* (Linnæus, 1758) and a subjective junior synonym of *C. ruffus* (Laurenti, 1768).

George Shaw (1751–1813) and the confusion over *Anguis scytale*. Shaw (1802) depicted a *Cylindrophis ruffus* specimen as part of his description of *Anguis Corallina*, using a figure (Shaw 1802: Fig. 131; illustrated in Fig. 2B herein) undoubtedly based on Seba (1735: Tabula XXV-1; see Fig. 1E herein). In his references prefacing the description of *A. Corallina*, Shaw listed Gmelin (1789), although in his own account of *A. corallinus* (*nomen emendatum*) Gmelin referenced Laurenti (1768) as his source for that name. Laurenti (1768), Gmelin (1789), and Shaw (1802) list the same plate in Seba (1735: Tabula LXXIII-2) as a reference. Alas, the specimen in this Tabula is not a *Cylindrophis* at all, but an individual of *Anilius scytale* (a South American species), and hence, Laurenti's *Anguis corallina* and Gmelin's *A. corallinus* have been regarded as synonyms of *Anilius scytale* (e.g., Wallach *et al.* 2014). We agree and therefore do not follow Boulenger (1893) in regarding Shaw's *Anguis Corallina* as synonymous with *C. rufus* (*nomen emendatum*). We believe that the *C. ruffus* figure in Shaw (1802), the sole indication supporting synonymy of *C. ruffus* with *A. Corallina*, was used by mistake; it does not correspond to Seba's Tabula LXXIII-2.

Blasius Merrem (1761–1824) and the problem with *Scytale scheuchzeri*. In his *Versuch eines Systems der Amphibien*, Merrem (1820) listed *Tortrix rufa* (*nomen emendatum*) and described a new species, *Scytale scheuchzeri*. As part of this description, Merrem referred to an illustration in Scheuchzer (1735: Tabula 647-1; illustrated in Fig. 2C herein). The name *S. scheuchzeri* was considered synonymous with *Cylindrophis ruffus* by subsequent authors (e.g., Boie 1827; Schlegel 1837b; Duméril & Bibron 1844; Gray 1849; McDiarmid *et al.* 1999; Bauer & Wahlgren 2013; Wallach *et al.* 2014). However, it is evident from both Scheuchzer's illustration and Merrem's description of his genus *Scytale* (non *Scytale* Latreille in Sonnini and Latreille, 1802) that *S. scheuchzeri* is not conspecific with *C. ruffus*. Despite similarities in coloration, the specimen depicted by Scheuchzer has enlarged gastrosteges and a tapering tail. Merrem (1820) also listed enlarged gastrosteges in his generic description of *Scytale*. Hence, the name *S. scheuchzeri* does not refer to an anilioid snake but most likely to a colubroid snake, and we therefore remove this name from the synonymy of *C. ruffus*.

Contributions by Friedrich Boie (1789–1870) and Hermann Schlegel (1804–1884). Boie (1827) was the first author to correct the distribution of *Cylindrophis ruffus* (under the name *Tortrix rufa*) to Java (not Schlegel 1837a, b, as commonly believed[2]; see e.g., Wallach *et al.* 2014). Schlegel (1837a: 128) then revised the distribution of *C. ruffus* (as *T. rufa*) to "*Java et de Célèbes*" [Java and Sulawesi], but already indicated that the Sulawesi form was distinct, later (1837b: 11) referring to it as *Tortrix melanota* (= *C. melanotus*; see also Wallach *et al.* 2014). Schlegel (1837b) provided distribution records for the genus *Cylindrophis* (as *Tortrix*) from

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[2] Both Amarasinghe *et al.* (2015) and Uetz & Hošek (2015) list Schlegel (1844) as the reference for the type locality correction for *C. ruffus* to Java. However, Schlegel (correctly cited as 1837−1844), in the explanatory text supplementing the plates in his *Abbildungen Neuer oder Unvollständig Bekannter Amphibien*, does not provide such a correction (but see Schlegel 1837a, b).

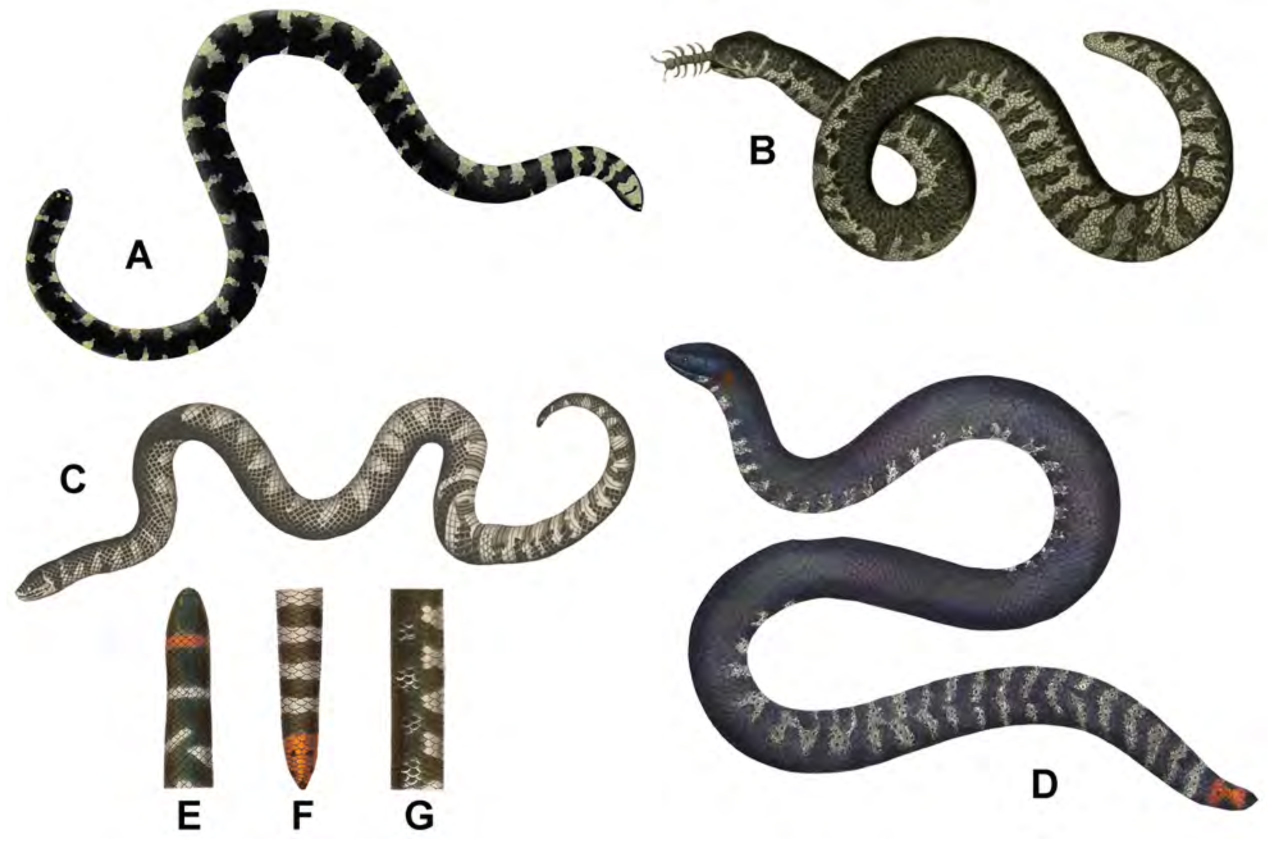

FIGURE 2. Historical drawings of *Cylindrophis ruffus sensu historico* (A, B & D−G) and *Scytale scheuchzeri* (C). Illustrations from: (A) Russell (1801); (B) Shaw (1802); (C) Scheuchzer (1735); (D) Wagler (1828–1833); and (E–G) Schlegel (1837–1844). Illustrations are not to scale. Plate prepared by Hinrich Kaiser and Mark O'Shea.

India: (1) "Tranquebar" (Tharangambadi, State of Tamil Nadu, SE India; see Russell 1801: 33), which was an important seaport during Russell's time; and (2) "Bengale" (NE India and Bangladesh). However, Smith (1943) indicated that the genus *Cylindrophis* did not occur on the Indian subcontinent, and hence the distributional records listed above appear to be in error and a reflection of maritime trade routes as opposed to natural distribution.

Johann Georg Wagler (1800–1832) and *Cylindrophis resplendens*. A new species from Java was described and figured by Wagler (1828–1833: Tabula V-1; illustrated in Fig. 2D herein) under the name *Cylindrophis resplendens* Wagler, 1828. Although Wagler (1828–1833) provided a figure of *C. resplendens* in life (see Fig. 2D herein), capably illustrated by Kaspar Georg Karl Reinwardt (1733–1854) (see also Schlegel 1837b), in the *Observationes* following the species description, he explicitly referenced Russell (1801) for additional illustrations of that taxon.

Cylindrophis resplendens, the type species of the genus *Cylindrophis* (Wallach *et al*. 2014), has since been synonymized with *C. ruffus* (e.g., Schlegel 1837b; Duméril & Bibron 1844; Gray 1849; Boulenger 1893; Smith 1943; McDowell 1975; McDiarmid *et al*. 1999; Wallach *et al*. 2014; Amarasinghe *et al*. 2015). Wagler's description of *C. resplendens* was based on specimens housed in the "*Museo Parisiensi*" [now MNHN], "*Lugdunensi Bat*." [now RMNH], and "*in collectione mea*" [in my collection; probably referring to the ZSM collection]. One or more type specimens may still exist in the collection of the MNHN, but we failed to locate specimens from the time of the original description matching Wagler's Tabula V-1 in the collections of either RMNH or ZSM.

John Edward Gray (1800–1875) and *Cylindrophis rufa* var. *javanica*, the name of a taxon from Borneo. Gray (1849: 112) described *Cylindrophis rufa* var. *javanica* in a simple two-line listing for a single specimen from Borneo (not from Java, as stated by Amarasinghe *et al*. 2015), donated by Sir James Brooke (1803–1868), the first

White Rajah of Sarawak. This specimen is still extant in the collection of the BMNH[3]. Gray (1849) referred to figures in Schlegel (1837–1844: Plate 33, Figs 5–10; illustrated in Fig. 2E–G herein), which according to Schlegel's own statement were drawn from a single Javanese specimen. However, Schlegel (1837–1844) also mentioned similarities between the Java "race" (Schlegel's term) and a specimen the RMNH received from Borneo. This may have led Gray, who was clearly familiar with Schlegel's works, to apply the geographically incongruous name *javanica* (referring to the island of Java) to a specimen from a locality on Borneo. Gray's taxon was synonymized with *C. ruffus* by Amarasinghe *et al.* (2015).

Malcom Arthur Smith (1875–1958) and a valid species from Myanmar. Smith (1943) described a subspecies of *Cylindrophis ruffus* from "Tenasserim and Burma as far North as Myitkyina" (today's Myanmar) as *C. rufus burmanus*. This taxon was accepted as a subspecies with the spelling *C. r. burmanicus* (*nomen emendatum*) by Lal Hora & Jaya Ram (1949), and in its original form by Taylor (1965). McDiarmid *et al.* (1999) and Wallach *et al.* (2014) included subspecies in their synonymy lists of species, but these lists allow no conclusion regarding the validity of the listed subspecies. Recently, Amarasinghe *et al.* (2015: 41) raised *C. r. burmanus* to species level (see also Iskandar & Colijn 2002) and provided a redescription of that species based on "the presumed type series." However, among the six paralectotypes designated by Amarasinghe *et al.* (2015) is one specimen (cited as ZMB 3094) that these authors considered to "probably" be a paralectotype, based on Iskandar & Colijn (2002). The ZMB accession number of this specimen actually identifies a neotropical frog (Frank Tillack, in litt.) and hence cannot possess "the same characters as the lectotype" (Amarasinghe *et al.* 2015: 41). Iskandar & Colijn (2002) stated that ZMB 3094 originated at "Bhamo," Myanmar. The only *Cylindrophis* specimen from Bhamo housed in the ZMB collection has the accession number ZMB 11619, and it was collected by Leonardo Fea (1852–1903) in the late 1880s. We doubt that this specimen could have belonged to the original type series used by Smith (1943) to define *C. r. burmanus*. We consider the designation of ZMB 3094 as a paralectotype of *C. burmanus* to be invalid.

Amarasinghe *et al.* (2015) also presented conflicting data on the shape of the collar of *Cylindrophis burmanus*. In their Table 2 (see also their Figs. 2 & 3), the band around the neck was listed as "dorsally interrupted" in that species, yet it was described as complete when referring to *C. burmanus* in their diagnoses of both *C. ruffus* ("a complete and narrow ring encircling the nape in *C. burmanus*," p. 38) and *C. burmanus* ("a complete and narrow ring encircling the nape," p. 41). As seen in the illustration of the *C. burmanus* lectotype (Amarasinghe *et al.* 2015: Fig. 3A), the band is actually separated by a single, dark brown vertebral scale. Our unpublished data show that this character is quite variable in both *C. burmanus* and Javanese *C. ruffus* and not useful to diagnose either taxon. Likewise, there is incongruity in the description of the pattern of dorsal blotches in *C. burmanus*. Whereas in their Table 2 Amarasinghe *et al.* (2015) indicated that *C. burmanus* had alternating dorsal blotches, they also stated that the species had paired (or "constant"; their term, p. 41) dorsal blotches. In a group of snakes where the true level of intra- and interspecific morphological variability has not been fully explored, such contradictions may lead to a similar level of instability as has resulted from the original descriptions (Laurenti 1768; Smith 1943).

History leads to the type locality of *Cylindrophis ruffus*. As a consequence of our careful review of the historical literature, we agree with Amarasinghe *et al.* (2015) that the type locality of *Cylindrophis ruffus sensu stricto* should be restricted to Java. The taxonomic history of the species shows that specimens in historical times were most often collected on Java (e.g., Russell 1801; Boie 1827; Wagler 1828–1833; Schlegel 1837–1844), which was an important trading hub for the Dutch Empire. With the establishment of the Dutch East India Company (in Dutch: Vereenigde Oostindische Compagnie, VOC) in Batavia (now Jakarta) in 1611, trade to Europe from Southeast Asia became heavily influenced by shipping conducted on behalf of the VOC (Boxer 1965). After the disbanding of the VOC in 1799, the various administrations of the Netherlands continued trading with their Southeast Asian colonies during the Napoleonic upheaval, although contacts with these colonies were often

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[3] In his published snake catalogue, Gray (1849) listed six specimens of *C. rufa*, three (*a–c*) from Penang (presented by General Hardwicke), one (*d*) from Borneo listed as "Var. 1. *Javanica*" (presented by Sir James Brooke), and two additional ones (*e–f*) listed as "Var. 2." without providing a Latin name. However, in the extant handwritten catalogue at the BMNH, the entry for the particular specimen from Borneo presented by Sir James Brooke, is found under the number IV.23.2.*a*, which is also how it is listed in the collection's online database. We have ascertained that the specimen identified in the collection by a jar label as IV.23.2.*a* ("Penang. Gen. Hardwicke") is unquestionably conspecific with *C. jodiae* and therefore cannot have originated on Borneo. Furthermore, the specimen in the jar labelled "IV.23.2.*d*. Borneo. Sir J. Brooke" possesses large blotches on the prefrontals, as mentioned in Gray's description. The error is therefore not in Gray's published snake catalogue, but appears to be an error that might have happened when the entries in Gray's catalogue were transferred to the extant BMNH catalogue. Thus, the holotype of *C. rufa* var. *javanica* really does have the number IV.23.2.*d*. It is not currently indicated as a type specimen in the BMNH collection.

blockaded by the British. Shortly after The Netherlands were annexed by France in 1810, the last Dutch colony in Southeast Asia, Java, fell to Britain in 1811. However, the Netherlands regained independence and became a kingdom in 1813, restoring their authority over the islands of Southeast Asia in 1816. The Dutch presence lasted until a protracted dispute with Indonesia in the 1960s[4], and trade continued throughout this time (e.g., Motadel 2014).

As highlighted above, the pipesnake specimen on which Laurenti (1768) based his description was housed in Gronovius's extensive natural history collection located in Leiden. Laurens Theodorus Gronovius and his father, Jan Frederik Gronovius (1686–1762), were both renowned naturalists who were tied into early global trade, and both would have received specimens from America and Asia via their trade connections (e.g., Margócsy 2014). Based on the historic and economic circumstances that place Java as the nexus of Dutch trade with Southeast Asia, along with the fact that Javanese *Cylindrophis* are the form most reliably described and illustrated in historical accounts, we regard the type locality restriction Java as conforming with Recommendation 76A.1.4 of the *International Code on Zoological Nomenclature* (ICZN 1999). For a neotype designation (Mecke *et al*., in prep.), we believe that the type locality should be further restricted to northwestern Java, where the main trade port was located at the time the original type specimen would have been collected (before 1756); most other parts of Java remained undeveloped during that time as indicated by historic maps (e.g., "Nouvelle Carte de l'Isle de Java" by Baussard 1756).

Amarasinghe *et al*. (2015) offered another hypothesis to demonstrate that the original type specimen originated in Java: the possible confusion between the town of Batavia, Saramacca District, Suriname, and Batavia (Jakarta), Java Island, Indonesia. While this is an interesting hypothesis, historical evidence appears to contradict this line of reasoning. Firstly, shipments of specimens to private collectors in Leiden from mid-18th century Suriname would have included only the name of the colony (i.e., Suriname) and possibly the main port (Paramaribo), but not the name of a strategically irrelevant, small settlement (Marinus Hoogmoed, in litt.). Secondly, the settlement in present-day Suriname near the confluence of the Coppename and Saramacca Rivers called Batavia was founded only in 1790 (Anonymous 2015), several decades after the specimens Laurenti described would have had to have reached Leiden in order to become integrated into Gronovius's collection. Thus, it appears that the problem with the type locality of *C. ruffus sensu stricto* really is a documentation error and not due to confusion with the geographic identity of a place.

Synonyms. Based on the careful survey of early literature accounts and descriptions, we have determined that the following names are synonyms of *Cylindrophis ruffus* (with type locality in Java): (1) *Anguis striatus* Gmelin, 1789 and, until evidence to the contrary becomes available, (2) *A. scytale* Russell, 1801, and (3) *C. resplendens* Wagler, 1828. Gray's (1849) *C. rufa* var. *javanica* should be regarded as *species inquirenda* until a formal revision of *C. ruffus* is conducted. Gray's name *javanica* would be available for the purposes of nomenclature for a *Cylindrophis* species from Borneo, and if combined with the masculine generic name would need to be emended to *javanicus*. Even though *C. engkariensis* and *C. lineatus* are Bornean taxa, they are clearly distinct from *C. ruffus* and from the *javanica* type specimen held at the BMNH (BMNH IV.23.2.*d*.) and therefore not impacted by the availability of the name *javanica*.

Comments on Amarasinghe *et al.* (2015). In their recent publication, Amarasinghe *et al*. (2015) redescribed *Cylindrophis ruffus* based on 14 specimens from Java. However, the characters used in their diagnosis do not allow either unequivocal species identification, nor are they suitable to establish stable species boundaries. Our unpublished data from 113 Javanese specimens indicate that *C. ruffus sensu lato* includes sympatric forms with specimens that (1) possess 19 or 21 dorsal scale rows at midbody, (2) show great variability in the number of ventrals (179−225), (3) have either a complete or interrupted collar, and (4) may or may not possess dorsal blotches that are, if present, either paired or alternating, and either complete or interrupted. We are currently in the process of determining the taxonomic status of Javanese *C. ruffus* populations (Mecke *et al*., in prep.) and to resolve which of these forms are conspecific with the specimen described by Gronovius (1756).

Amarasinghe *et al*. (2015) also described two new species of *Cylindrophis*, *C. jodiae* and *C. mirzae*. This publication exists in two versions, an earlier one, in which Fig. 8 lists the names of the new species as *C. jodii* and *C. mirzai*, and a revised version in which these errors have been corrected. These versions are otherwise

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[4] Indonesia gained independence in 1949 after a period of Japanese occupation during World War II (1942–45), but Dutch New Guinea did not become part of Indonesia until international pressure and Indonesian military infiltration forced the Netherlands to relinquish control in 1962 (Gruss 2005).

indistinguishable, and it appears that the revised version was simply exchanged on the journal's website for the one with the errors. This is evident from the URL[5] used to download the revised file. However, having been validly published in the first version of the paper, the names *C. jodii* and *C. mirzai* must be considered objective junior synonyms of *C. jodiae* and *C. mirzae*, respectively.

While the pholidotic characters of *Cylindrophis jodiae*, a species widely distributed on mainland Southeast Asia (pers. obs.), conform to our unpublished data, qualitative color characters vary both intraspecifically and ontogenetically (Kieckbusch *et al*., unpublished data). The definition of *C. mirzae*, on the other hand, appears to be problematic. One of the key characteristics listed by Amarasinghe *et al*. (2015: Table 3) to differentiate *C. mirzae* from *C. ruffus* was an invariable dorsal scale row count of 21 at midbody in *C. mirzae*. However, some specimens we have examined from Singapore (the type locality of *C. mirzae*) have 19 dorsal scale rows, and the ratio of Singaporean specimens with 21 vs. 19 scale rows in our data set is 8:8, with both forms possessing a similar range of ventrals. In their Table 3, Amarasinghe *et al*. (2015) also list color pattern characteristics to distinguish *C. mirzae* from *C. ruffus*. A complete narrow nape band and complete narrow dorsal crossbands, however, can occur in specimens from Singapore with either 19 or 21 dorsal scale rows. These bands may also be interrupted in either 19- or 21-row specimens, and are hence not useful to distinguish among species. Furthermore, *C. ruffus* with collection localities on Java (the type locality of that species) may have 19 or 21 dorsal scale rows at midbody, and these forms are equally variable in dorsal color pattern as specimens from Singapore. While we agree with Amarasinghe *et al*. (2015) that *C. ruffus sensu stricto* is a taxon with an invariable number of middorsal scale rows, and that forms with 19 dorsal scale rows should be distinct at species level from those with 21 rows (this difference being the main character these authors used to differentiate *C. mirzae* from *C. ruffus*), the lack of a type specimen for *C. ruffus* makes it at this point uncertain whether the 19-row or the 21-row morphotype represents *C. ruffus sensu stricto*, and this hinders a diagnosis and renders their definitions of both *C. mirzae* and *C. ruffus* unsuccessful. Lastly, Amarasinghe *et al*. (2015: 38) stated that "*C. ruffus* could extend beyond Java, e.g., Borneo and Peninsular Malaysia," which would include Singapore and overlap with the distribution of *C. mirzae*, but they failed to demonstrate this zoogeographical scenario using voucher specimens. Given the problems outlined above, we see no alternative than to place *C. mirzae* in the synonymy of *C. ruffus* until it can be unequivocally defined and differentiated from that species.

Species description

Having ascertained the history of *Cylindrophis ruffus sensu historico* in general, and the history and morphology of *C. ruffus sensu lato* in particular, we are confident when we propose that a population from south-central Java with morphological features that allow unequivocal identification should be recognized taxonomically. We formally describe this species below.

Cylindrophis subocularis sp. nov.

(Figs. 3–5; Table 1)

Holotype. RMNH.RENA 8785 (Figs. 3–4; Table 1), an adult female, collected in Grabag, Purworejo Regency (formerly Koetoardjo), Central Java Province (Jawa Tengah), Java, Indonesia, by Felix Kopstein in February 1937. The original label for this specimen states "Grabag, Koetoardjo, Midden Java. +10 m."

Paratypes. All RMNH.RENA specimens were collected by Kopstein at the type locality. RMNH.RENA 8958 (Fig. 5A), a gravid female, was collected in October 1937; RMNH.RENA 8959 (Fig. 5B), an adult female, was collected in November 1937; RMNH.RENA 11257 (Fig. 5C), an adult male, was collected in August 1937; RMNH.RENA 11263 (Fig. 5D), an adult male, was collected in August 1937; RMNH.RENA 47929 (Fig. 5E), an adult male, was collected in November 1937. NMW 21559.1 (Fig. 5F), an unsexed adult specimen from Java (no precise locality provided), was also collected by Kopstein, presumably during 1937, but the date is unknown.

Referred specimen. ZMB 53459, an unsexed adult with no further collection data.

Definition. A species of the genus *Cylindrophis* that can be readily distinguished from all congeners by the following combination of characters: (1) presence of a single subocular scale, positioned between 3rd and 4th or 4th

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[5] A Google search for the paper by Amarasinghe *et al*. (2015) by title leads to a downloadable pdf at the URL http://fds.lib.harvard.edu/fds/deliver/51488619/nsd_014410685_corrected.pdf. This URL features the term "corrected," implying that an uncorrected version existed for download at least temporarily.

and 5th supralabial, contacting postocular and separating 4th or 5th supralabial from orbit (Fig. 4B); (2) prefrontal in very narrow contact with or separated from orbit; (3) 19 smooth dorsal scale rows at midbody; (4) 6–7 supralabials; (5) 6–7 infralabials; (6) 190–196 ventrals; (7) 6–7 subcaudals; (8) 40–48 transverse light ventral blotches, and (9) light blotches on lateral surfaces of prefrontals (Fig. 3A, 4A & B).

FIGURE 3. Holotype of *Cylindrophis subocularis* **sp. nov.** (RMNH.RENA 8785) in (A) dorsal and (B) ventral view. Numbered units on ruler are in centimeters. Photos by Sven Mecke.

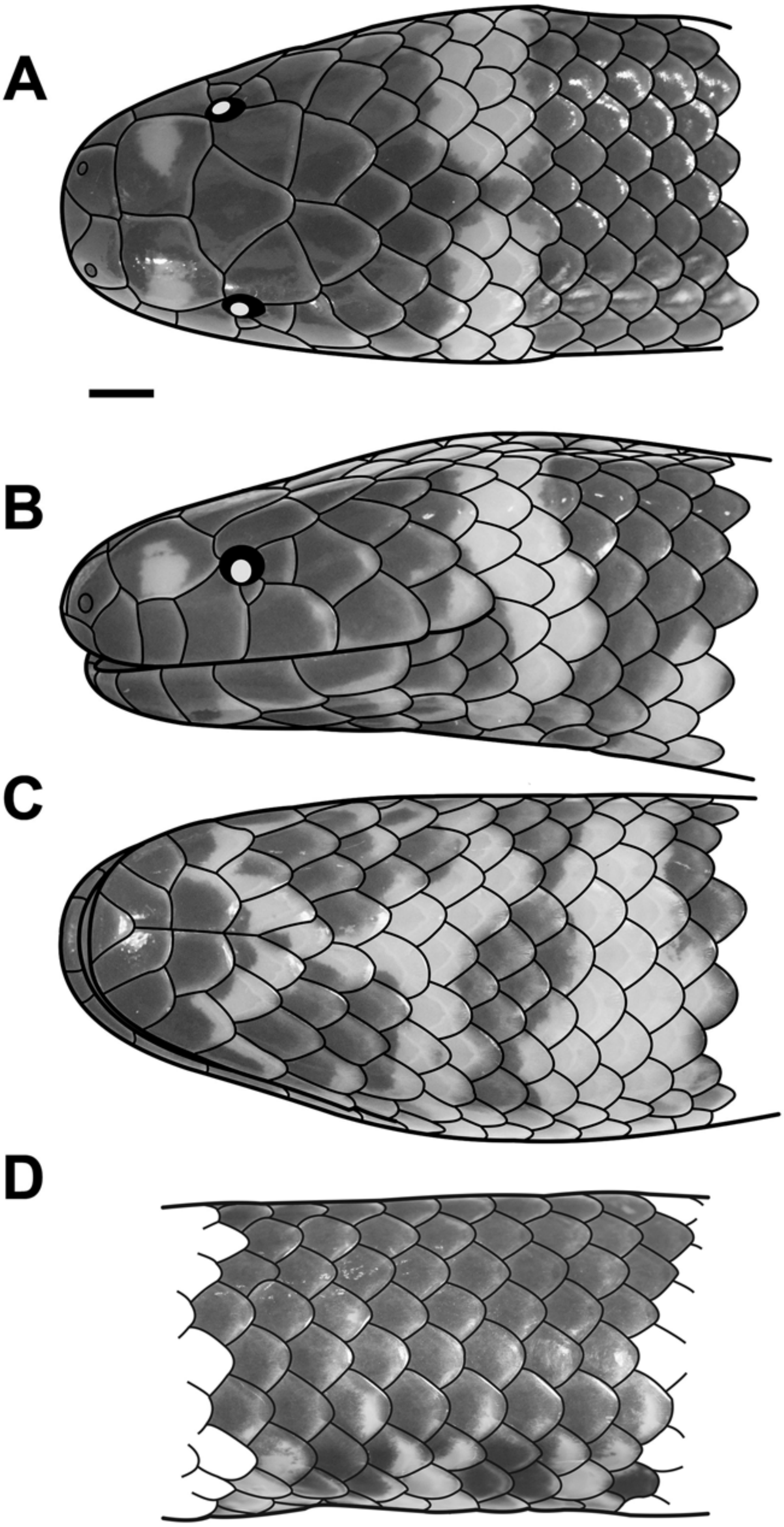

FIGURE 4. Holotype of *Cylindrophis subocularis* **sp. nov.** (RMNH.RENA 8785). (A) Dorsal, (B) lateral, and (C) ventral view of the head. (D) Lateral view of a midbody section (left side). Scale bar = 2.0 mm. Drawings by Felix Mader based on photographs by Sven Mecke.

FIGURE 5. Paratypes of *Cylindrophis subocularis* **sp. nov.** in dorsal view. (A) RMNH.RENA 8958; (B) RMNH.RENA 8959; (C) RMNH.RENA 11257; (D) RMNH.RENA 11263; (E) RMNH.RENA 47929; (F) NMW 21559.1. All RMNH specimens were collected at the type locality, Grabag, Purworejo (formerly Koetoardjo) Regency, Central Java Province (Jawa Tengah), Java, Indonesia. NMW 21559.1 is from Java, Indonesia, without detailed locality data. Numbered units on ruler are in centimeters. Photos by Sven Mecke.

Comparisons. *Cylindrophis subocularis* **sp. nov.** can be easily distinguished from all congeners by the presence of a single subocular, positioned between the 3rd and 4th (rarely between the 4th and 5th)[6] supralabial, contacting the postocular and separating the 4th (or 5th) supralabial from the orbit (e.g., Fig. 4B). In the following comparisons, ranges are followed by mean ± standard deviation and sample size (*n*), with the measures and counts for *C. subocularis* provided in parentheses. Whenever range and mean ± standard deviation are not provided, the respective character was invariable within a species.

Cylindrophis aruensis possesses 23 (19, *n* = 8) dorsal scale rows at midbody and 173–182 (190–196, 193.7 ± 2.0, *n* = 8) ventrals (Boulenger 1920; McDowell 1975; Amarasinghe *et al*. 2015). *Cylindrophis boulengeri*

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[6] While the general, relative position of the subocular is fixed, it may be bordered by the 4th and 5th supralabial, resulting from a vertical division of the 3rd upper labial.

possesses 197–204, 200.3 ± 3.5, $n = 3$ (190–196, 193.7 ± 2.0, $n = 8$) ventrals; and wavelike markings on supralabials, which may run onto prefrontals (uniformly dark supralabials and light blotches on prefrontals). *Cylindrophis burmanus* possesses 201−210, 208.3 ± 7.7, $n = 6$ (190–196, 193.7 ± 2.0, $n = 8$) ventrals. *Cylindrophis engkariensis* possesses 17, $n = 1$ (19, $n = 8$) dorsal scale rows at midbody; 230[7], $n = 1$ (190–196, 193.7 ± 2.0, $n = 8$) ventrals; rugose (smooth) dorsals on tail; a dorsal pattern of two paravertebral rows of spots (dorsal pattern of transverse, light, dorsolateral blotches); and uniformly colored prefrontals (light blotches on prefrontals). *Cylindrophis isolepis* possesses 21, $n = 2$ (19, $n = 8$) dorsal scale rows at midbody; and nasals separated by rostral (nasals in contact). *Cylindrophis jodiae* possesses 21, $n = 77$ (19, $n = 8$) dorsal scale rows at midbody; and wavelike markings on supralabials (uniformly dark supralabials). *Cylindrophis lineatus* possesses 21, $n = 1$ (19, $n = 8$) dorsal scale rows at midbody; 210[8], $n = 1$ (190–196, 193.7 ± 2.0, $n = 8$) ventrals; 9, $n = 1$ (6–7, 6.6 ± 0.5, $n = 8$) subcaudals; and a dorsal pattern of stripes (dorsal pattern of transverse, light, dorsolateral blotches). *Cylindrophis maculatus* does not possess light blotches on prefrontals (present); has a relatively longer snout, with SL/IOD = 1.03–1.25, 1.13 ± 0.06, $n = 34$ (0.94–1.03, 1.00 ± 0.03, $n = 7$); and a dorsal pattern of reddish-brown, large and round blotches (dorsal pattern of transverse[9], light, dorsolateral blotches). *Cylindrophis melanotus* (including its synonyms *Tortrix rufa* var. *celebica* Schlegel, 1844, *T. rufa* var. *celebensis* Gray, 1849[9], *C. celebensis* Smith, 1927, and *C. heinrichi* Ahl, 1933) possesses 230–268, 245.3 ± 10.5, $n = 35$ (190–196, 193.7 ± 2.0, $n = 8$) ventrals; and predominantly light-colored supralabials, including a characteristic dark bar running down the supralabials below eye (completely dark supralabials and light blotches on prefrontals). *Cylindrophis opisthorhodus* possesses 23, $n = 6$ (19, $n = 8$) dorsal scale rows at midbody; and has a light dorsum with dark speckles forming two paravertebral rows and occasionally a discontinuous vertebral line (dorsal pattern of transverse, light, dorsolateral blotches). *Cylindrophis ruffus sensu lato* (including its synonyms *Anguis striatus* Gmelin, 1789, *A. scytale* Russell, 1801, *C. resplendens* Wagler, 1828, and *C. mirzae*), and *C. rufa* var. *javanica* Gray, 1849 (inferred from the relevant descriptions, drawings, figures, or examination of type material) do not have a subocular scale (present). Javanese *C. ruffus sensu lato* have the prefrontal usually in broad contact with the orbit (Fig. 6; Table 1), with PrefO/ED = 0.28–0.60, 0.38 ± 0.08, $n = 51$ (prefrontal in narrow contact with or separated from the orbit [Fig. 4B]; with PrefO/ED = 0.0–0.27, 0.11 ± 0.11, $n = 8$); results of Mann-Whitney U-test: $Z = 0.29$, $p < 0.001^{***}$. *Cylindrophis yamdena* possesses 21 (19, $n = 8$) dorsal scale rows at midbody, and a pale light dorsum without any pattern (Smith & Sidik 1998) (dorsal pattern of transverse, light, dorsolateral blotches).

Description of the holotype: metrics (in mm) and pholidosis. An adult female; SVL 385; tail very short, TL 10 (2.6 % of SVL); head not distinct from body; body cylindrical, body diameter 12.0 (3.1 % of SVL); head rounded in dorsal view; HL 11.9 (3.1 % of SVL); HW 8.7 (73.1 % of HL); snout rounded in dorsal and lateral view; SL 5.1 (42.8 % of HL); SW 3.4 (66.7 % of SL); ED 1.3 (10.9 % of HL); pupil round; IOD 5.0 (42.0 % of HL); NOD 3.7 (31.1 % of HL); PrefO/ED 0.04; internarial distance 2.5; pelvic spurs not visible externally but hidden in pouches situated laterally of cloacal plate, covered by scales; 21/19/17 dorsal scale rows, scales smooth, apical pits absent; 196 ventrals; six subcaudals + one terminal spine; cloacal plate divided; rostral clearly visible from above, triangular, wider than high (rostral height 2.0, rostral width 2.2); two pentangular nasals, height 1.9, length 2.6; nasal suture sinistral in respect to prefrontal suture; naris positioned close to the suture of nasal with first supralabial; postnasal absent; loreal absent; prefrontal in contact with 2nd and 3rd supralabial; preocular absent; rectangular subocular scale present, length 1.0, height 0.9; one pentangular postocular (length 1.1, height 1.4); temporal formula 1 + 2, anterior temporal larger than each posterior temporal (anterior temporal length 2.5, height 2.6; upper posterior temporal length 2.6, height 2.1); 6|7 supralabials: on right side of head: 1st smallest, 3rd largest, 2nd, 4th, 5th, and 6th equal in size, 2nd and 3rd in contact with prefrontal, 3rd in contact with orbit; on the left side: 1st smallest, 3rd largest, 4th, 5th, and 6th equal in size, 2nd, 3rd and 7th equal in size, 2nd, 3rd, and 4th in contact with prefrontal, 4th in contact with orbit; six infralabials, 3rd in contact with first pair of chin shields; first pair of infralabials in contact, preventing contact of mental with first pair of chin shields; mental triangular, wider than high, width 2.2, height 1.5; two pairs of chin shields, anterior chin shield length 2.1, width 2.0, posterior chin shield length 2.6, width 1.3; mental groove present, length 3.5; one hexagonal prefrontal, length 2.9, width 3.2; one pentangular supraocular, length 2.7, width 2.6; frontal rectangular, length 3.2, width 3.8; one pentagonal parietal, length 2.9, width 2.7.

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[7] Stuebing (1994) reported 234 ventrals for the holotype of *C. engkariensis*. A re-examination of the specimen by one of us (HK) showed that there are only 230 ventrals present.

[8] Blanford (1881) reported 215 ventrals for *C. lineatus* and Smith & Sidik (1998) provided a ventral range of 210−215.

[9] *Tortrix rufa* var. *celebensis* Gray, 1849 is a *nomen emendatum* for *T. rufa* var. *celebica* Schlegel, 1844 and should currently be regarded a junior synonym of *Cylindrophis melanotus* Wagler, 1828. It is also a junior secondary homonym of *C. celebensis* Smith, 1927.

TABLE 1. Data for the individual type specimens of *Cylindrophis subocularis* **sp. nov.**, and a comparison of this species with *C. ruffus sensu lato* from Java (data of specimens with precise collection locality shown only). Metric characters are given in mm. Ranges are followed by mean ± standard deviation (indicated in parentheses). An 'X' indicates a fusion between the subocular and the postocular.

	RMNH.RENA 8785	RMNH.RENA 8958	RMNH.RENA 8959	RMNH.RENA 11257
Status	Holotype	Paratype	Paratype	Paratype
Sex	F	F	F	M
SVL	385	394	326	451
TL	10	9	10	11
Dorsals	21/19/17	21/19/18	20/19/18	21/19/17
Ventrals	196	194	192	195
Subcaudals	6	7	7	7
Supralabials	6|7	6	6	6
Infralabials	6	6	7	6
Ventral bands light	43	40	48	43
Ventral bands dark	43	40	48	43
Subocular scale length	1.0|0.8	0.8|1.0	0.6|0.9	1.6|1.8
Subocular scale height	0.9|0.6	0.6|1.1	0.6|0.9	1.7|1.9
PrefO/ED	0.04	0	0.02	0.27

TABLE 1. (continued).

	RMNH.RENA 11263	RMNH.RENA 47929	NMW 21559	*C. ruffus sensu lato* (*n* = 53)
Status	Paratype	Paratype	Paratype	
Sex	M	M	unsexed	-
SVL	331	353	288	148–737 (356.1±143.8)
TL	7	10	10	4–19 (9±3.3)
Dorsals	21/19/17	20/19/17	21/19/17	19–23/19–21/15–19
Ventrals	196	194	190	179–225 (194.5±8.9)
Subcaudals	7	7	6	5–7 (5.9±0.7)
Supralabials	6	7	6	6
Infralabials	6	6|7	6	6
Ventral bands light	40	43	45	33–59 (45.9±6.0)
Ventral bands dark	40	43	44	32–59 (45.2±5.8)
Subocular scale length	X|1.3	1.0|1.1	1.1|1.1	-
Subocular scale height	X|1.0	1.0|0.9	0.9|1.0	-
PrefO/ED	0.25	0.21	0	0.28–0.6 (0.38±0.08)

Description of the holotype: coloration and pattern in preservative (after 78 years in ethanol). Dorsal surface of head Sepia (279) with a Pale Buff (1) blotch on each prefrontal, extending from center of scale at about half scale's width to lateral edge of scale; most upper head scales with lighter edges; supralabials Sepia (279); ventral surface of head Sepia (279) with lighter edges of scales and a Pale Buff (1) 'X'-shaped marking beginning at level of lower edges of 3rd infralabial, extending to throat (Fig. 4C); neck with a two scale broad Pale Buff (1) collar, interrupted medially in vertebral region, located one dorsal scale behind parietals; dorsal surfaces of trunk and tail Burnt Umber (48); dorsal surface of trunk with paired, occasionally slightly alternating, transversely arranged Pale Buff (1) blotches, approximately one scale broad, well-developed anteriorly and posteriorly, very faint or absent at central part of trunk; dorsal surface of tail with a Pale Buff (1) band that continues to the ventral surface, demarcating a Raw Umber (48) tail tip; ventral surface of trunk Raw Umber (280), with 43 transverse, alternating ventrolateral Pale Buff (1) blotches (two ventral scales broad at midbody); cloacal region and ventral surface of tail Pale Buff (1), with a Raw Umber (280) tail tip (from 4th subcaudal to terminal caudal spine), and Raw Umber (280) blotches on scales covering the cloacal spurs.

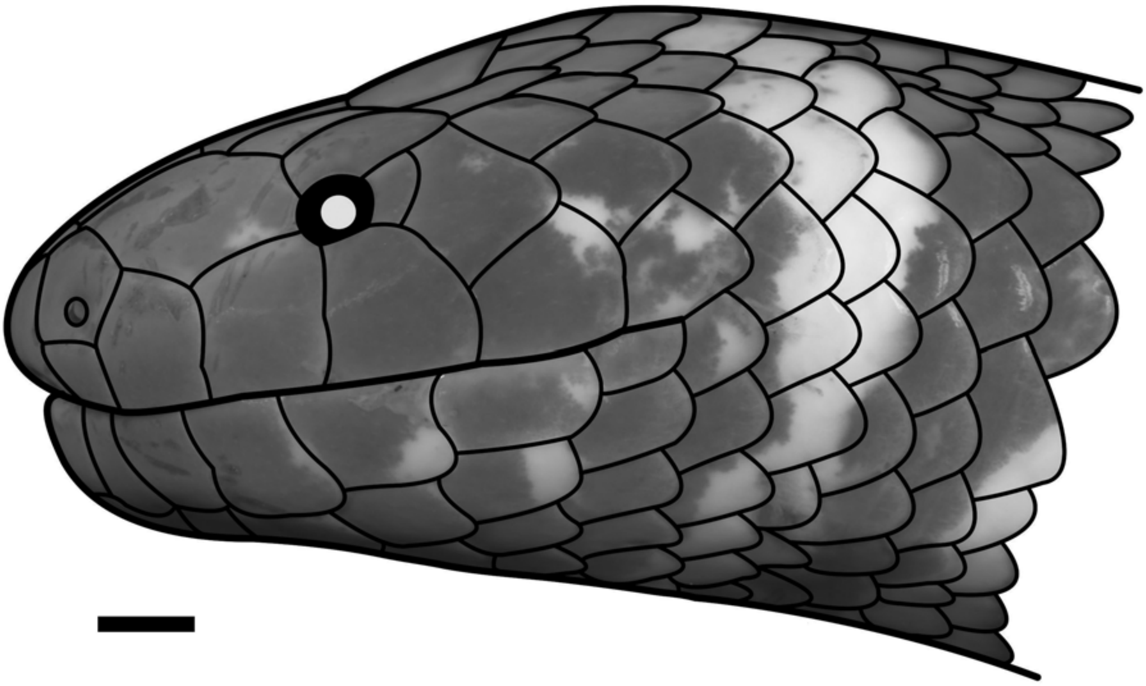

FIGURE 6. Head of a *Cylindrophis ruffus sensu lato* specimen from Bogor, Java (SMF 16980), in lateral view. Note the broad contact of the prefrontal with the orbit. Scale bar 2.0 mm. Drawing by Felix Mader based on a photograph by Gunther Köhler.

Intraspecific variation. Our assessment of the variation is based on the holotype and six paratypes (three males, three females, one unsexed specimen; Figs. 3 & 5; Table 1), with measurements provided in mm and listed including range and mean ± standard deviation and specimen numbers (*n*) in parentheses: SVL 288–451 (361.1 ± 53.7, *n* = 7); TL 7–11 (9.6 ± 1.3, *n* = 7); 21/19/17 (*n* = 5), 20/19/18 (*n* = 1), and 20/19/17 (*n* = 1) dorsal scale rows; 190−196 (193.8 ± 2.2, *n* = 7) ventrals; 6–7 (6.7 ± 0.5, *n* = 7) subcaudals; six (*n* = 5), seven (*n* = 1) or 6|7 (*n* = 1) supralabials; six (*n* = 5), seven (*n* = 1), or 6|7 (*n* = 1) infralabials; 4th supralabial in contact with orbit in specimens with seven supralabials (*n* = 2); subocular present on both sides of head in all specimens (*n* = 7); subocular may be fused with postocular (*n* = 1); subocular in contact with postocular, orbit and 3rd and 4th supralabial (in the case of the presence of six supralabials) or 4th and 5th supralabial (in the case of the presence of seven supralabials); subocular size: length on right side of head 0.6–1.6 (1.0 ± 0.3, *n* = 6) and 0.8–1.8 (1.1 ± 0.3, *n* = 7) on left side, height 0.6–1.7 (0.9 ± 0.4, *n* = 6) on right and 0.6–1.9 (1.0 ± 0.4, *n* = 7) on left side of head; 40–48 (43.1 ± 2.8, *n* = 7) alternating, light ventral blotches, two ventrals wide at midbody, three ventrals wide at midbody in a single specimen; light blotches on lateral surfaces of prefrontals might be fused into a bar running across the snout; light 'X'-shaped marking on ventral surface of head might be dissolved into a reticulated pattern.

Etymology. The specific epithet *subocularis* is a compound adjective of *sub* (Latin: 'under,' 'beneath') and *ocularis* (Latin: 'pertaining to the eye'), referring to the presence of a subocular scale in the new species.

Distribution and natural history. The new species is only known from Grabag on the south coast of Purworejo Regency, Central Java Province, Java, Indonesia (Fig. 7). The type locality in the South Central Java basin area is enclosed by mountain ranges to the north, west, and east, which include active volcanoes (Darman & Sidi 2000).

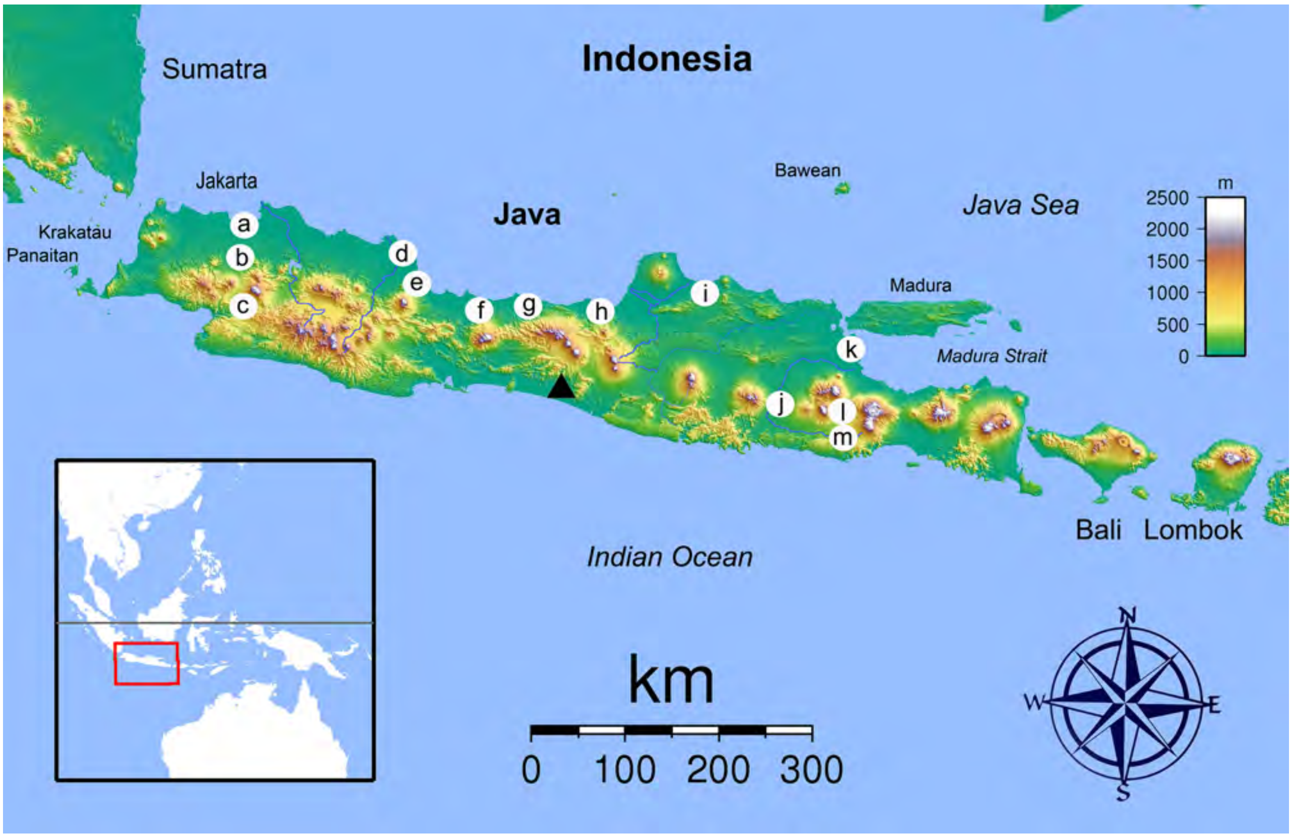

FIGURE 7. Distribution map of *Cylindrophis subocularis* **sp. nov.** and *C. ruffus sensu lato* on Java, Indonesia. The black triangle marks the type locality of *C. subocularis* **sp. nov.** at Grabag. The white circles with letters identify localities of examined specimens of *C. ruffus sensu lato*, including (a) Jakarta (Batavia), (b) Bogor (Buitenzorg), (c) Sukabumi (Soekaboemi), (d) Indramayu (Indramajoe), (e) Cirebon (Cheribon), (f) Kagok, Tegal, (g) Pekalongan, (h) Semarang (Samarang), (i) Rembang, (j) Kediri, (k) Surabaya (Surabaja, Soerabaja), (l) Mount Arjuno (Ardjoeno), (m) Malang (Malary/ Malang?), and (n) Tengger Mountains. Note that not all locality data of museum vouchers provided necessarily correspond to towns and their environs but may refer to district names at the time of specimen collection. Locality names in parentheses refer to historical names provided on museum labels or in museum catalogues. Base map modified from Wikipedia © Sadalmelik / Wikimedia Commons / CC-BY-SA-3.0 by Sven Mecke.

During the geological history of Sundaland, Java was connected to the islands of Borneo and Sumatra (Voris 2000; Sathiamurthy & Voris 2006; Wilting *et al*. 2012), and according to Natus (2005) many elements of the Javanese terrestrial vertebrate fauna descended from Bornean and Sumatran lineages that migrated to Java during or even before the Pleistocene and Holocene. Natus (2005) also identified eight endemism centers for terrestrial vertebrates in Java (Natus 2005: Fig. 4.22), which can be divided into two major groups: the lowlands in the northwest (immediately adjacent to Sumatra) and the eastern parts of Java, and the highlands of the Neogene-Quaternary volcanic arc that stretches longitudinally through the centre of Java. The South Central Java basin, however, has long been isolated to the north by the central volcanic chain (based on the maps presented in Sathiamurthy & Voris 2006) that may have largely prevented immigration events to the south, leading to vicariant evolution. Although the range of *Cylindrophis subocularis* is probably not restricted to Grabag, it may indeed exhibit a relatively limited distribution in the South Central Java basin and therefore should be regarded as a regional endemic.

Based on the lifestyle of congeneric species, we assume that *Cylindrophis subocularis* is semifossorial and preys mainly on elongate vertebrates (e.g., fishes, caecilians, skinks, and snakes: Schmidt 1928; Taylor 1965; Pauwels *et al*. 2000; Kupfer *et al*. 2003; pers. obs.), which are subdued by constriction (Greene 1983). Both the limited distribution and the secretive semifossorial lifestyle of *C. subocularis* may explain its apparent rarity in museum collections.

One specimen of the new species (RMNH.RENA 8958) contains eggs covered by a thin membrane. An incision into the membrane of one of the largest eggs (length 26.8 mm, width 13.3 mm) revealed the presence of an embryo (approximately at developmental stage 26–27, following Zehr 1962). We believe that this observation confirms that *Cylindrophis subocularis* is a viviparous species (*sensu* Blackburn 1994), with viviparity being the reproductive strategy for most, if not all, *Cylindrophis* species (de Rooij 1917; Smith 1943; McDowell 1975; Blackburn 1985; Brischoux *et al*. 2011). We also found one specimen of the closely related *C. ruffus* from Java (NMW 21558.6) that contains fully developed embryos. No further information is available on the biology of *C. subocularis*.

Remarks. While we discovered six of the seven type specimens of *Cylindrophis subocularis* in the collection of the RMNH, all of which were collected by Felix Kopstein (1893−1939) and accompanied by precise collection locality data, a single specimen was found in the collection of the NMW. For this specimen (NMW 21559.1) the collection locality is limited to "Java," but the specimen label lists Felix Kopstein as the collector of the specimen. Based on specimen labels in the RMNH, Kopstein collected *Cylindrophis* specimens at other localities in Java, such as at "Indramajoe" (Indramayu, on the north coast of Central Java). We have examined these, as well as 113 additional Javanese specimens, and all lack a subocular scale and have the prefrontal usually in broad contact with the orbit. We believe that NMW 21559.1 is part of the series Kopstein collected on the south coast of Central Java, but deposited mostly in Leiden, with the single specimen deposited in the Vienna collection[10]. We discovered an additional specimen of *C. subocularis* in the Berlin collection (ZMB 53459). In the absence of a listed collection locality and collector's name, we chose not to include this specimen in our type series.

Two specimens (RMNH.RENA 47931–32, formerly RMNH.RENA 8785.80–81) from the same original jar (jar number 8785) as the holotype (RMNH.RENA 8785, formerly RMNH.RENA 8785.51) and supposedly also collected at Grabag, are not conspecific with *Cylindrophis subocularis*. In the original catalogue of the herpetological section of the RMNH, we found the following entry:

> "*De fles [8785] bevat nu 3 ex, zij zijn bewerkt door E.M.J. Jaspars en door hem voorzien van de nrs. 51, 80, 81. Mogelijk zijn de nrs 80 en 81 door bewerker bij vergissing in deze fles ondergebracht en zijn zij afkomstig van Buitenzorg [Bogor], Java.*"
>
> [The jar [8785] now contains three specimens; they were examined by E.M.J. Jaspars and labeled with the numbers 51, 80, 81. Potentially, the numbers 80 and 81 have been misplaced in the jar by the researcher and they may have originated in Buitenzorg [Bogor], Java.]

We agree with the catalogue entry that RMNH.RENA 47931–32 (formerly RMNH.RENA 8785.80–81) were most likely misplaced in the jar; these specimens strongly resemble *Cylindrophis ruffus* from Bogor (n = 9) in having no subocular and the prefrontal in broad contact with the orbit, PrefO/ED = 0.42 and 0.47 respectively (vs. subocular present and prefrontal in narrow contact with or separated from the orbit in *C. subocularis*, PrefO/ED = 0.0–0.27, 0.11 ± 0.11, n = 8). An additional specimen (RMNH.RENA 11255), with greatly damaged anterior head scalation, but lacking a subocular scale, was supposedly also collected at the type locality of *C. subocularis*. Due to the consistent presence of a subocular scale in the Grabag population, we have reasonable grounds to believe that RMNH.RENA 11255 is also not conspecific with the new species. We believe that RMNH.RENA 11255 was most likely also misplaced or erroneously labeled, as was the case with RMNH.RENA 47931–32.

Discussion and outlook

Species of *Cylindrophis* have generally been described from small series of specimens collected at remote localities (e.g., Roux 1911; Boulenger 1920; Stuebing 1994; Smith & Sidik 1998) or, especially in the early days of taxonomy, were described using insufficient or unsuitable characters (e.g., Laurenti 1768; Wagler 1828–1833). Taking into account the distribution of the morphologically variable taxon *Cylindrophis ruffus sensu lato* (Java, Borneo, Sumatra, Singapore and Peninsular Malaysia), which heretofore had been considered even more widely

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[10] It is perhaps incongruous that an Austrian naturalist with ties to the NMW would not deposit a majority of specimens at what was essentially his home institution (without formal ties). It is possible that Kopstein had designs on an appointment at the RMNH, and he perhaps sent a significant number of specimens there to court favor. Unfortunately for Kopstein, he died before his appointment might have become reality (Marinus Hoogmoed, in litt.).

distributed, it appears that the diversity of *Cylindrophis* in general, and of forms hidden under the name *C. ruffus* in particular, is still significantly underestimated. While *C. ruffus* has long been identified as a species complex in need of a thorough and comprehensive revision, including the designation of a neotype (Mecke *et al.*, in prep.), we feel it necessary to caution against taxonomic studies of such historically difficult taxa without a solid basis of comparative material, without a wide range of characteristics used, and when personally unfamiliar with relevant specimens. While a general aim of these studies is to achieve greater taxonomic stability, the example of *C. mirzae* shows that, even with the best intentions, a small data set may yield an unsatisfactory result.

Cylindrophis subocularis is superficially similar to other forms currently referred to as *C. ruffus sensu lato*. It is, however, 'inconspicuously conspicuous,' because it is easily diagnosed by its unique pholidotic characters: the presence of a subocular and the prefrontal in narrow contact with or separated from the orbit. The former character has been considered of broad taxonomic importance in snake systematics and has readily been used to identify distinct species (e.g., Schätti 1987; Dowling & Price 1988[11]; O'Shea 1998, 1999; Murphy *et al.* 2005). We are confident that the subocular scale in *C. subocularis* represents a true, distinctly differentiated scale and not an aberrant horizontal division of the 4th or 5th supralabial (in specimens with six or seven supralabials respectively). In contrast to developmental aberrations in head scales, which usually occur only on one side of the head, the subocular occurs bilaterally in all specimens in precisely the same position below the orbit. This convincingly demonstrates that the occurrence of a subocular scale in the genus *Cylindrophis* is a stable character found only in a single, probably isolated population and does not represent a sporadic aberration found across the genus. Moreover, the scale is always of the same rectangular shape and is clearly independent of the supralabial below it. In one specimen (RMNH.RENA 11263), the subocular is fused with the postocular on the right side of the head, but still clearly separated from the supralabial, which supports the concept of this scale as an independent, bilaterally occurring pholidotic character. During our examination of *Cylindrophis* specimens from the entire range of the genus (451 specimens), we found ten specimens (2.2 %) with aberrant head scale conditions, of which seven (70 %) were unilateral anomalies of bilaterally occurring scales and three (30 %) were aberrant divisions or fusions of azygous head scales. Unilateral anomalies of bilaterally occurring scales included deformations and were never found to occur in a single population with any specific frequency.

Cylindrophis subocularis is one of several poorly known species with a rather restricted area of distribution, and in that it is similar to *C. aruensis*, *C. boulengeri*, *C. engkariensis*, *C. isolepis*, and *C. yamdena*. As outlined above, the new species is only known from eight specimens collected almost 80 years ago, six of which were evidently collected at a single locality in southern Java. Although it appears to be generally accepted that the Javanese herpetofauna is relatively well studied compared to the herpetofaunas of the other Greater Sunda Islands (e.g., Teynié *et al.* 2010), we argue that historic and recent research has mostly been conducted along the north coast and the western and eastern parts of the island. Hence, species diversity for the whole of Java may still be underestimated. The recent discovery of new bent-toed gecko species (genus *Cyrtodactylus*) in Java (Riyanto *et al.* 2014, 2015; Hartmann & Mecke *et al.*, 2016) indicates that new species, some of which have a rather limited area of distribution, are still being identified.

It is uncertain at this time whether *Cylindrophis subocularis* exhibits a wider distribution than the single collection locality would indicate, or is truly a localized endemic. Herpetological surveys of southern coastal localities in Java are required to investigate the taxon's distribution and population size, and to assess any potential threats that may impact its conservation status. It may be noted that Central Java has little remaining forest, and that the long history of deforestation and intensification of agriculture along the south-central coast potentially led to local species extinctions in the region (Whitten *et al.* 1996). As the almost 80-year-old type series of *C. subocularis* is unsuitable to obtain molecular data, it would be desirable to obtain fresh tissue samples for molecular genetic approaches to investigate its phylogenetic affinities, especially in relation to *C. ruffus sensu lato*.

During our work with specimens of *Cylindrophis*, we have progressively been able to recognize morphological and ontological patterns in these snakes that would not be recognizable when working with only a few selected specimens, let alone only type specimens. Detailed revisions of the *C. ruffus* and the *C. melanotus* complexes, including the description of new species, are ongoing and will be published elsewhere (Kieckbusch *et al.* & Mecke *et al.*, in prep.).

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[11] Dowling & Price (1988) called suboculars "lorilabial scales."

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APPENDIX. Specimens examined for comparison.

Cylindrophis burmanus.—**Myanmar**: *Kachin State*: Bhamo: NMB-REPT 479, NMW 21552.3–4, ZMB 11619, ZMH R06256; *Rakhine State*: “Aracan”: MTKD 14867.

Cylindrophis boulengeri.—**Indonesia**: *Maluku Province*: Wetar Island: without precise locality data: RMNH.RENA 5529A.168, 5529B.169; Ilwaki: Wetar Island, SMF 16996 (holotype).

Cylindrophis engkariensis.—**Malaysia**: *Sarawak* (*Borneo*): Second Division, Lubok Antu District, Lanjak-Entimau, headwaters of the Engkari River, Nanga Segerak: ZRC 2.3398 (holotype).

Cylindrophis isolepis.—**Indonesia**: *South Sulawesi Province*: Jampea Island: RMNH.RENA 11269A.171, 11269B.72.

Cylindrophis jodiae.—**Malaysia**: *Kedah State*: NMW 39624.2; Penang: NMW 21570.1, 21570.4. **Thailand**: no precise locality data: NMW 21556.4, ZMH R09798–99, R09801–02, MTKD 24126–27, SMF 16987, 16991, ZMB 30205, 52611; *Bangkok Province*: Bangkok: MHNG 1335.17, NMW 21561, 21562.1−4, 21563.1−2, 21564.1−11, SMF 58675, 58679, 61903, 64838, ZMB 4394, 4545, 58428, ZMH R09794, ZRC 2.4583; *Chiang Mai Province*: MTKD 39216; Dangrek Mountains: Phu Khi (Pu-Kin, Don-Rek): NMW 21556.2, 21569.1−3; Don Pia Fei Mountains: NMW 21565.1−6, 21566.1−6; Muang Pou Vieng (Pu Wieng): NMW 21567.1−2; *Phang Nga Province*: Khaolak-Luk National Park: ZMB 55188; *Phetchaburi Province*: Puek Tian: NMW 21569.1–3; *Saraburi Province*: Saraburi: MHNG 1471.30, MHNG 1530.9. **Vietnam**: no precise locality data: NMBE 1015768−69; *Ho-Chi-Minh Province*: Ho-Chi-Minh City: NMBE 1015764–66, ZMB 31123, 50774; “South Vietnam”: MHNG 1325.30, 1551.18–20.

Cylindrophis lineatus.—**Singapore** (in error): AMNH R-12872.

Cylindrophis maculatus.—**Sri Lanka** (occasionally labeled as “Ceylon”): without specific localities: MHNG 762.65, 1199.44, 2745.34, MTKD D14873–76, NMW 21574.1–5, NMW 21575.1–2, RMNH.RENA 160–63, SMF 16995, ZMB 1456, 18550, 18551.A–B, 24125, 49460, 77698, ZMH R09785, R09792, R09795–96. *Central Province*, Kandy District, Peradenyia: ZMB 31506. *Sabaragamuwa Province*: Kitulgala: MHNG 2156.29; Ratnapura: MHNG 2156.30. *Western Province*: near Colombo: MHNG 1199.30–32.

Cylindrophis melanotus.—**Indonesia:** *North Maluku Province*: Bacan Island: SMF 16975; Halmahera: ZMB 34313 (holotype of *Cylindrophis heinrichi* Ahl, 1933)); Sanana Island (Soela-Sanana): RMNH.RENA 5104.176. *Central Sulawesi Province*: Poso: ZMA.RENA 11453.117–19; Lake Wawontoa: ZMB 62929. *South Sulawesi Province*: Lake Tempe: ZMA.RENA 11464.116; Makale: RMNH.RENA 11274.88; “Patmmang” (possibly Ujung Pandang, today’s Makassar): NMW 21571.1–3. *North Sulawesi Province*: Lake Moat: ZMB 50020; Manado: RMNH.RENA 19.82, 173.18B, 174.18A, 5459.41–42; without precise locality data: RMNH.RENA 5461.34–40, ZMA.RENA 11451.112–15. *Southeast Sulawesi Province*: Buton Island, Bau Bau: RMNH.RENA 11265.87; Kolaka: RMNH.RENA 11276.89. Mainland Sulawesi (occasionally labeled as “Celebes”): without precise locality data: RMNH.RENA 17.83–84, 17.86, ZMA.RENA 11459.120, ZMB 1450, 4049 (potential holotype of *Tortrix rufa* var. *celebica* Schlegel, 1844).

Cylindrophis opisthorhodus.—**Indonesia**: *East Nusa Tenggara Province*: Flores Island: SMF 23301, ZMB 33787. *West Nusa Tenggara Province*: Lombok Island: SMF 23299, ZMA.RENA 12135, 14082; Sumbawa Island: SMF 23300.

Cylindrophis ruffus sensu lato.—Indonesia: without precise locality data: ZMH R09749, R09786, R09793, R09797. “East coast of Borneo”: RMNH.RENA 3924.15–17. “Java”: MHNG 2745.35–38, MTKD D5614–15, D7071, D14868–72, NMW 13835–36, 21558.1, 21558.3, 21558.6, 21558.8, 21559.2–14, NMBE 1015767, RMNH.RENA 1.65–68, 46, 47927–28, SMF 16976–78, 16981–82, 16984–86, 16990, ZMA.RENA 10495, 11452.145, 11467.151–53, 14460, ZMB 1455, 4908, 13129, 29696. “South Java”: ZMB 14443, 58433. “Sumatra”: NMW 21550.4–5. *Aceh Province* (Atje), Sumatra: NMW 21550.2. *Bangka-Belitung Islands Province*: Bangka Island: ZMA.RENA 10487, 23068, 23070; Belitung Island: ZMA.RENA 11471.177–79. *Central Java Province*: Kagok, Tegal: ZMA.RENA 11455.155; Pekalongan: ZMA.RENA 11468.157; Rembang: RMNH.RENA 11252.105; Semarang (Samarang): RMNH.RENA 5.60–61, ZMA.RENA 11461.158, ZMB 14351, 58429–30. *Central Kalimantan Province* (Borneo): Muara Teweh: NMW 21554.6. *East Java Province*: without precise locality data: RMNH.RENA6928.52–55; Kediri: ZMA.RENA 11462.159, 11454.146–50; Malang (Malary): NMW 21558.4–5; Mount Arjuno (Ardjoeno): RMNH.RENA 11260.108–09, 11261.93–94; Surabaya (Surabaja, Soerabaja): RMNH.RENA 5791.49, 5999.58–59, 11251, 11252.105, ZMA.RENA 11457.154; Tengger Mountains: NMB-REPT 471–73. *Jakarta Province* (Java): Jakarta (historically: Batavia): MTKD D14750, NMB-REPT 20441. *North Sumatra Province*: Langkat: RMNH.RENA 6349.25–26; Tanah Merah, Bindjey Estate: ZMH R09751–52. *Riau Province* (Sumatra): Rantau Island: RMNH.RENA 8185.13; Sungai Lala: ZMH R09787. *South Sumatra Province*: Tanjung Enim: ZMA.RENA 11458.126. *Sultanate of Deli* (Sumatra): NMW 21550.1, 21550.3, 21568.1–6, RMNH.RENA 6968.27–33, ZMA.RENA 10490, 11463.125, 11465.127, 11466.124. *Sultanate of Serdang* (Sumatra): ZMA.RENA 11460.123. *West Java Province*: Bogor (historically: Buitenzorg): NMB-REPT 462–70, RMNH.RENA 11256.110, 11258.92, 11272.98, SMF 16979–80, 16992–94, ZMB 20525; Cirebon (Cheribon): ZMA.RENA 11469.129–33; Indramayu (Indramajoe): RMNH.RENA 8956.56, 8972.62–64; Itjabe: MHNG 676.67; Sukabumi (Soekaboemi): ZMA.RENA 11456.156. *West Kalimantan Province* (Borneo): Badau: NMW 21554.5; Landak: ZMA.RENA 10488, 23064; Pontianak: RMNH.RENA 8234.2–3, 8264.5–6, 8264.8–11, 8264.14. Malaysia: *Johor State*: no precise locality data: AMNH R-12873; Johor Bahru: ZRC 2.3009–10. *Kelantan State*: Kuala Lebir: ZRC 2.3011. *Penang State*: no precise locality data: NMW 21570.2–3; *Sarawak* (*Borneo*): Baram: NMW 21554.1; Sungai Tangap, Niah: AMNH R-111923. Singapore: no precise locality data: ZMH R09788–89, ZRC 2.3017–20, ZRC 2.3021, ZRC 2.3023, ZRC 2.6907; Bukit Timah Road: ZRC 2.3022; Sembawang: Naval Base: ZRC 2.3029.

5.6 Paper 7

Mecke, S., Kieckbusch, M., O’Shea, M. & Kaiser, H. (2016): First Record of the Poorly Known Skink *Sphenomorphus oligolepis* (Boulenger, 1914) (Reptilia: Squamata: Scincidae) from Seram Island, Maluku Province, Indonesia. *Asian Herpetological Research*, **7**(1): 64–68.

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SHORT NOTES

First Record of the Poorly Known Skink *Sphenomorphus oligolepis* (Boulenger, 1914) (Reptilia: Squamata: Scincidae) from Seram Island, Maluku Province, Indonesia

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Abstract Based on four specimens discovered in the collection of The Natural History Museum, London, United Kingdom, we present a new distribution record for the skink *Sphenomorphus oligolepis* for Seram Island, Maluku Province, Indonesia. This find constitutes the westernmost record for the species and extends its range by over 800 km. The species was heretofore only known from apparently isolated mainland New Guinean populations.

Keywords Scincidae, Lygosominae, *Sphenomorphus oligolepis*, new record, Seram, Maluku Islands, Indonesia, Wallacea

1. Introduction

Sphenomorphus oligolepis (suggested common name: MIMIKA FOREST SKINK) is a member of the *S. maindroni* group (sensu Greer and Shea, 2004). It is a poorly known skink with apparently disjunct populations on mainland New Guinea and has experienced a very limited treatment in the scientific literature (e.g., de Rooij, 1915; Greer, 1973; Greer and Shea, 2004). The species has been reported from the Mimika River (the type locality; Boulenger, 1914) and the Lorentz River, Papua Province, Indonesia (de Rooij, 1915), and more recently from several localities in Papua New Guinea (see Greer, 1973: Figure 8), including Bikim, Matkomrae, and Mendua (Western Province); Soliabeda (Simbu Province), and Oroi (Gulf Province). Additional specimens housed in the Museum of Comparative Zoology, Cambridge, Massachusetts, USA (MCZ) and the Bernice P. Bishop Museum, Honolulu, Hawaii, USA (BPBM) were collected in Gulf Province at Kikori (MCZ R-150879) and Weiana (MCZ R-101484), and in Morobe Province at Aseki (BPBM Herp-17441–48; 19103–09), with a single voucher collected at Timika, Papua Province, Western New Guinea, Indonesia (BPBM Herp-42441). The westernmost record of *S. oligolepis* known to date is the type locality, and the species has never been recorded from localities other than on mainland New Guinea. Here we report a first record of *S. oligolepis* from Seram Island, Maluku Province, Indonesia (for a distribution map see Figure 1).

2. Material and Methods

During a taxonomic investigation of skinks in the collection of The Natural History Museum, London, United Kingdom (BMNH), two of the authors (HK and SM) discovered four specimens of a scincid lizard from Seram Island, Maluku Province, Indonesia, labeled "*Sphenomorphus* sp. A" (BMNH 1998.299–303; Figure 2).

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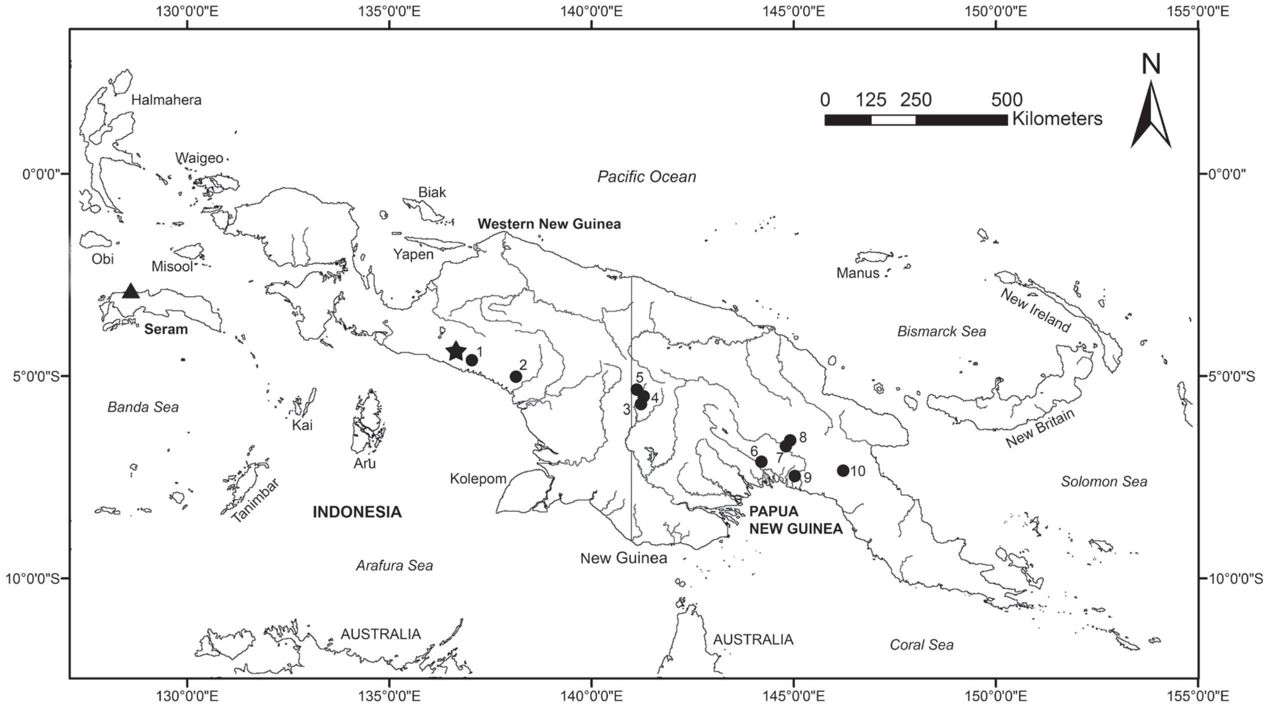

Figure 1 Distribution of *Sphenomorphus oligolepis* in New Guinea and in the Moluccas (black symbols). The type locality of the species (Mimika River, West Papua, Indonesia; BMNH 1946.8.3.47–48) is indicated by a star. The triangle denotes the new distribution record for Seram Island, Maluku Province, Indonesia (BMNH 1998.299–302). Numbers accompanying black circles identify the following known localities for *S. oligolepis*: (1) Lorentz River (de Rooij, 1915), (2) Timika, Nayaro Settlement (BPBM Herp-42441), (3) Matkomrae (MCZ R-130716), (4) Menuda (MCZ R-130717), (5) Bikim (MCZ R-130718), (6) 30 km N, 14 km W Kikori (MCZ R-150879), (7) Weiana (MCZ R-101484), (8) Soliabedo (MCZ R-118857), (9) Oroi (MCZ R-109330–45, 118854–56; WAM R-67631–32), (10) Aseki (BPBM Herp-17441–48; 19103–09). Map prepared by Sven Mecke.

The four specimens had been caught by Paul Edgar and Ronald Lilley in pitfall traps in a lowland rainforest (elevation ca. 50 m) near Solea, northwestern Seram, in late August and early September 1987, during a herpetofaunal survey of the island. Climate data for the collection locality and survey methods were summarized in detail by Edgar and Lilley (1993).

Comparative measurements and scale counts (Table 1) of "*Sphenomorphus* sp. A" and other museum specimens examined were performed according to the following protocol. Measurements were taken on the right side of the body to the nearest 0.1 mm using digital calipers. Eidonomic characters (abbreviations provided in parentheses) used include snout-vent length (SVL), measured from tip of snout to cloaca; tail length (TailL), measured from cloaca to tip of tail; arm length (ArmL), measured from axilla to tip of longest finger; leg length (LegL), measured from point of posterior body insertion to tip of longest toe; head length (HeadL), measured from tip of snout to anterior edge of ear opening, head width (HeadW), measured at widest point of head; number of scales rows at midbody (MBSR), number of nuchal scales (NS), number of paravertebral scales (PVS), counted in one row beginning with the first nuchal scale to the first scale fully anterior to the rear edge of the hindlimbs; number of supralabials (SupraLab); number of supracilaries (SupraCil), and the number of enlarged lamellae under the 4th toe (4TLam), counted as all scales wider than the plantar scales distal to the cleft between the 3rd and 4th digits. We also calculated the following ratios: ArmL/SVL, LegL/SVL, HeadL/SVL. Greer (1973) found female specimens of *S. oligolepis* to be gravid at a minimal SVL of 43.0 mm. Hence, we assume that the four unsexed specimens from Seram (minimal SVL 48.0 mm) are adults.

3. Results and Discussion

The four specimens could be easily identified as members of the *Sphenomorphus maindroni* group (sensu Greer and Shea, 2004; 22 species recognized) by the presence of a post-supraocular scale. While the highest species diversity of the *S. maindroni* group is found in New Guinea, members of this assemblage also occur in the Bismarck Archipelago and the Solomon Islands, the southern part of the Philippines, Palau, and some of the Moluccan Islands

Table 1 Morphometric (in mm) and meristic data of the four specimens of *Sphenomorphus oligolepis* from Seram Island, Maluku Province, Indonesia (BMNH 1998.299–302), and of the two syntypes of this species (BMNH 1946.8.3.47–48). Only characters that allow comparison with data in the relevant literature are shown. When meristic characters occurring bilaterally where different on both sides of the body, this is indicated by the letters 'R' (right) and 'L' (left). Otherwise the respective character is represented by a single value. When tails were found to be partly regenerated, this is indicated by a superscript 'R' after TailL. Numbers in square brackets show sample sizes (individuals) or cases, if the superscript 'C' is used. Numbers in parentheses refer to mean values or, when underlined, modal values.

SPECIMEN OR REFERENCE	CHARACTERS													
	SVL	TailL	ArmL	ArmL/SVL	LegL	LegL/SVL	HeadL	HeadL/SVL	HeadW	MBSR	NS	SupraLab	SupraCil	4TLam
BMNH 1998.299	48.8	31.5^{R}	7.7	0.16	11.3	0.23	8.0	0.16	6.1	24	3R 0L = 3 total	7	7	9R 10L
BMNH 1998.300	48.0	47.2^{R}	5.8	0.12	10.6	0.22	7.8	0.16	6.1	24	4 = 8 total	7	6R 7L	9
BMNH 1998.301	50.6	broken	7.0	0.14	10.8	0.22	7.7	0.15	6.0	24	0	7	7	9R 10L
BMNH 1998.302	49.5	41.4^{R}	6.9	0.14	11.9	0.24	8.1	0.14	6.1	28	0	7	7	9R 10L
BMNH 1946.8.3.47 (syntype)	54.5	57.5^{R}	7.5	0.14	12.0	0.22	8.6	0.16	6.8	24	3R 3L = 6 total	7	7	10
BMNH 1946.8.3.48 (syntype)	53.5	tail-stump	7.5	0.14	12.0	0.23	8.6	0.16	6.3	24	4R 3L = 7 total	7	7	11
Boulenger, 1914	55.0	60^{R}	10.0	-	13.0	-	12.0[a]	-	-	24	6–10 total	-	7	12–13
Greer, 1973	max. 55.0; gravid ♀♀ 43.0–53.0	-	-	-	-	-	-	-	-	24–28 (26)	-	6–7	-	9–12
Greer and Shea, 2004	51–55 [5]	-	-	-	-	-	-	-	-	24–28 (26.6) [5]	5–13 total (8.2) [5]	7 (see key)	-	9–12 [9^{C}]

[a] Boulenger measured HeadL from the tip of the snout to the occipital condyle (Boulenger 1885).

(Greer and Shea, 2004).

Identification of the four *Sphenomorphus* specimens from Seram as *S. oligolepis* was confirmed eidonomically, based on the descriptions in Boulenger (1914), de Rooij (1919), Greer (1973), and the diagnostic characters presented by Greer and Shea (2004), who also provided a key to the members of the *S. maindroni* group. We also examined the syntypes of *S. oligolepis* (BMNH 1946.8.3.47–48; Figure 3) for direct comparison.

In overall eidonomy (size, body proportions, scalation, general aspects of coloration), the specimens from Seram conform to the descriptions of *Sphenomorphus oligolepis* as presented in the relevant literature (Boulenger, 1914; de Rooij, 1915; Greer, 1973; Greer and Shea 2004). Morphometric and meristic data for the specimens (Table 1) show that they fall well within the range of *S. oligolepis*, although the data available in the literature are quite limited. The Seram specimens are also diagnosable as *S. oligolepis* using the identification key of Greer and Shea (2004). In addition, the last supralabial scale in the Seram specimens is divided, as is typical for *S. oligolepis* (Glenn Shea, in litt.). Moreover, eidonomic data of the *Sphenomorphus* specimens from Seram also conform to those of the syntypes of *S. oligolepis* (Table 1)[1]. We therefore conclude that the Seram specimens provisionally labeled "*Sphenomorphus* sp. A" are members of this species, which is hereby recorded for the first time as part of the Seram herpetofauna. This record for *S. oligolepis* is the westernmost record for the species, and the first non-New Guinean; it is the first from the biogeographic region known as Wallacea.

Sphenomorphus oligolepis is readily distinguishable from *S. undulatus*, the only other species of the *S. maindroni* group known from Seram (de Rooij, 1915; Dunn, 1927; Edgar and Lilley, 1993) by separated prefrontal scales (vs. prefrontals in medial contact in *S. undulatus*), a single infralabial in contact with the postmental (vs. two infralabials in contact with the

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[1] Data on the number of PVS in *S. oligolepis*, although available for most other *S. maindroni* group members, are not provided in the relevant literature. Although our examination of the Seram specimens yielded PVS counts different from those of the type specimens of *S. oligolepis* (63–69 in the Seram specimens, and 57 and 58 in the type series of *S. oligolepis*), Glenn Shea examined 38 specimens of *S. oligolepis* and obtained a PVS range of 55–73 (Glenn Shea, unpubl. data), indicating that this character is much more variable than in the type series.

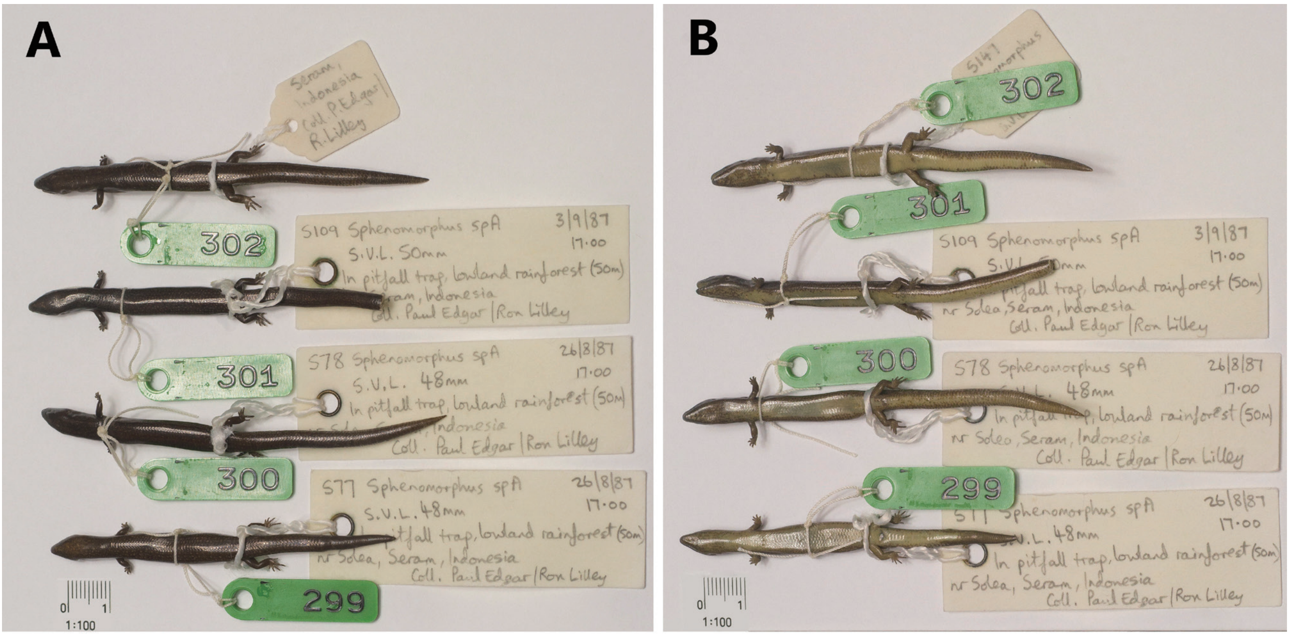

Figure 2 *Sphenomorphus oligolepis* (BMNH 1998.299–302) from Seram Island, Maluku Province, Indonesia. (A) Specimens in dorsal view. (B) Specimens in ventral view. Scale = 10 mm. Photos by Thomas Beitz.

postmental in *S. undulatus*), and a much lower number of 4TLam (9–12 vs.17–23 in *S. undulatus*) (see Greer and Shea, 2004: Table 2 and Key to Species; pers. obs.).

The species (listed as "*Sphenomorphus* sp. A") was reported to be diurnal and fossorial by Edgar and Lilley (1993). According to these authors, on Seram it was found in lowland rainforest (50 m) and in forest above 700 m, but no voucher specimens were obtained from the higher locality. In a lowland rainforest near Solea, northwestern Seram, *S. oligolepis* occurs in syntopy with three species of geckos, a dibamid, five skinks, two blindsnakes, one colubrid snake, and one elapid snake species (Edgar and Lilley, 1993: Table 4).

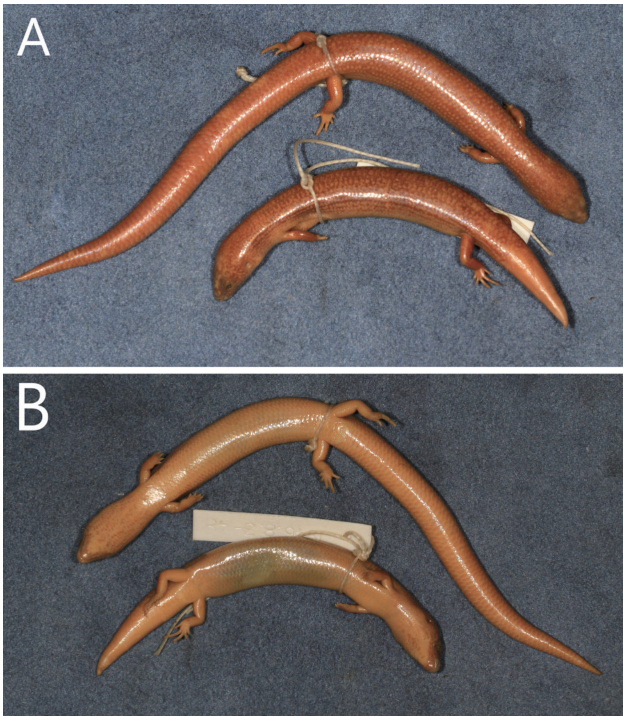

Figure 3 Syntypes of *Sphenomorphus oligolepis* (BMNH 1946.8.3.47–48) in (A) dorsal and (B) ventral view. Photos by Mark O'Shea.

Sphenomorphus oligolepis appears to be a widely, though not necessarily continuously, distributed species in southern New Guinea (distribution extends ~1200 km from west to east; Figure 1), where it has been found in lowland rainforests and freshwater swamp forests (elevations 0–550 m), but also at higher elevations in the lower montane southeastern Papuan rainforests (elevations up to 1250 m). It might be expected that the species also occurs in the lowland rainforests of the 'neck' of the Vogelkop Peninsula (West Papua Province, Indonesia), and further range extensions in the western part of New Guinea can be expected. These would fill the largest known distribution gap for *S. oligolepis* (linear distance of > 800 km; Figure 1).

It should be noted that many mainland New Guinean lizard taxa have rather discontinuous distribution patterns, often with larger gaps between isolated populations (see distribution maps provided by Allison and Kraus, 2011). Obvious distribution gaps might be the result of a true spatial separation of single species (intraspecific allopatry) or represent potential interspecific barriers between similar looking, though different taxa (interspecific allopatry in an undiscovered biodiversity). However, distribution gaps might rather reflect an undersampling bias.

Some of these taxa with spatially separated populations are also found on islands west of New Guinea, including Seram. Examples may be the gecko *Cyrtodactylus papuensis*, and the skinks *Eugongylus rufescens*, *Sphenomorphus muelleri*, *Sphenomorphus undulatus*, and *Tiliqua gigas* (Brongersma, 1953; de Rooij, 1915; Dunn, 1927; Shea, 2000).

The absence of records of *Sphenomorphus oligolepis* between the type locality and Solea, Seram (including the 'neck' of the Vogelkop Peninsula and eastern Seram) may be explained by an undersampling bias resulting from (1) under-collection in areas potentially difficult to access; and (2) the semifossorial habit of this taxon, which makes it difficult to find individuals (especially by expeditions not primarily focusing on herpetofauna species and if no pitfall traps were used). Voucher specimens were thus almost exclusively collected by experienced herpetologists (Fred Parker, Allen Allison) and predominantly during more recent expeditions to Papua New Guinea.

The presence of *Sphenomorphus oligolepis* in Seram increases to three the number of *Sphenomorphus* skinks known from this island and, together with recent species descriptions from the region (e.g., Harvey *et al*., 2000; Oliver *et al*., 2009; Vogel and van Rooijen, 2008; Weijola and Sweet, 2010; Ziegler *et al*., 2007), demonstrates how little is known about the herpetofauna of the Moluccas (Maluku and North Maluku Provinces).

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5.7. Conclusions

Taxonomic research should ideally be driven by comparative approaches based on physical objects – including all relevant types – and detailed literature studies, both of which are time-consuming and rather complex tasks, especially when dealing with widely distributed taxa that were described a long time ago or multiple times using different names. It is therefore hardly surprising that previous taxonomic studies on *Cyrtodactylus* geckos from the Malay Archipelago (e.g., Das 1993; Oliver *et al*. 2009; Iskandar *et al*. 2011; Kathriner *et al*. 2014; Riyanto *et al*. 2014) and on the genus *Cylindrophis* (Stuebing 1994; Smith & Sidik 1998; Amarasinghe *et al*. 2015) accumulated relatively little new information on the widely distributed taxa dealt with in this chapter. In fact, the taxonomy of *Cyrtodactylus fumosus* and *C*. *marmoratus*, as well as of *Cylindrophis ruffus*, had remained largely unchanged since De Rooij (1915, 1917) published her influential work *The Reptiles of the Indo-Australian Archipelago*.

This gap of comprehensive knowledge created a source of substantial problems for research, especially because our understanding of the taxonomy and distribution of these taxa relied on the perpetuation of errors with respect to their identity. Taxonomic knowledge, including names as key identifiers, is the “access point” to the biological information needed for any kind of meaningful comparative studies on *Cyrtodactylus* and *Cylindrophis*. Mixing taxa and not adequately resolving their taxonomy results in incorrect interpretations and is a waste of resources.

The results of the publications presented in this chapter provide several new findings regarding the taxonomy and distribution of the examined species, with inaccuracies and errors from different references – including some concerning the terminology and definition of characters – described and clarified. I was able to show that the names *Cyrtodactylus fumosus* and *Cylindrophis ruffus* were (and still are; see Outlook) applied to several species. Only bent-toed geckos from northern Sulawesi mountain ranges (Sulawesi Utara Province, Indonesia) represent true *Cyrtodactylus fumosus*, whereas the taxonomy of *Cylindrophis ruffus* and its allies was shown to be even more complex. The level of variation for characters within *Cylindrophis* was hitherto unknown, which led to rather imperfect treatments based on pattern and other poorly understood features (Amarasinghe *et al*. 2015). In paper 6, I was able to demonstrate that pattern (e.g., the shape of the nuchal bands) varies intraspecifically and is of no taxonomic value. In addition, in this chapter new species masquerading under the mentioned names were described based on solid characters. Interestingly, both new species were described from Java, an island generally assumed to be relatively well studied from a herpetological point of view (e.g., Teynié *et al*. 2010). These findings, including the descriptions of many other new species in recent years (e.g., Zug 2010; Riyanto *et al*. 2014, 2015), indicate that herpetofaunal species richness in Java is still underestimated and that further taxonomic and systematic research is urgently needed. Knowledge deficits also became apparent regarding the exact distribution of *Sphenomorphus oligolepis*, with the distributional area significantly extended westwards based on records from Seram, Indonesia. Essential for all presented research was the examination of the relevant type material and topotypic specimens, some of which were described in detail for the first time (e.g., papers 4 & 5).

Providing a detailed taxonomic history of the taxa in question is certainly also a significant contribution and this allowed me to clarify misapplications of names and confirm identifications and/or geographic origins of important specimens. Only by clarifying the taxonomic history of *Cylindrophis ruffus* in detail, was I able to fix the type locality of this species to Java (paper 6). A previous attempt for a type locality fixation by Amarasinghe *et al*. (2015) failed because the necessary background information had not been adequately portrayed.

With the natural habitat (i.e., tropical rainforests) in Southeast Asia undergoing dramatic changes (e.g., Arunarwati Margono *et al*., 2014), it is very important to improve our knowledge of the forest-dwelling and more secretive reptiles in order to accurately identify these taxa. A reliable species determination, which is only possible once their alpha taxonomy is adequately resolved, is essential for the evaluation of potential threats and, if necessary, effective protection and management programs. Detailed morphological information is scarce for many of the species in question, and original descriptions are sometimes minimal and lack suitable drawings. This includes the descriptions by Laurenti (1768) and Müller (1895), which were the key references to trace the current taxonomy of *Cyrtodactylus fumosus* and *Cylindrophis ruffus* back to its beginnings. Only by tracking the past, can taxonomy be adequately resolved and enable meaningful future research, including biodiversity studies and nature conservation.

The unrivaled advantage of the studies I presented herein lies with the large number of museum specimens, including all relevant type material that were directly examined and used for comparison, allowing me to detect geographical patterns but also previously unrecognized features for the differentiation of taxa. In some *Cyrtodactylus* geckos, this included the recognition of enlarged scales posterior to the precloacal scales referred to as “posterior precloacals” in paper 3. Unlike the limited and erroneous differentiation between *Cyrtodactylus fumosus* and *C. marmoratus* by

De Rooij (1915), which depended primarily on the number of femoral pores in male specimens (papers 3–5), I was able to demonstrate that at least five characters were available to allow unequivocal delineation of these species (paper 5). The new species described appear to be restricted range endemics, only known from a few specimens collected during the first half of the 20th century. In light of this, the taxonomic studies presented in chapter 5 may serve as a key example to highlight the great, yet widely underestimated value of museum collections for research, which permit a detailed and comprehensive approach that is difficult to take when using today's standard procedures of molecular taxonomy/phylogenetics alone (see chapter 7 – "The Value of Natural History Collections for Biodiversity Research")

6 Ecology of Selected Southeast Asian Amphibians and Reptiles (Feeding and Reproductive Biology)

Figure 1a from Döring & Mecke *et al*. (2017): Food spectrum analysis of the Asian toad, *Duttaphrynus melanostictus* (Schneider, 1799) (Anura: Bufonidae), from Timor Island, Wallacea. *Journal of Natural History*, **51**(11–12): 1–17 (paper 11, this chapter). The figure shows an unvouchered *D*. *melanostictus* specimen from the park grounds of the Timor Lodge Hotel, Dili, Dili District, Timor-Leste.

6.1 Introduction

More than 800 amphibian species are known to inhabit Southeast Asia (Frost 2018), with new taxa being described at a rapid rate. The current decade has seen a dramatic increase in the appearance of publications related to the taxonomy of amphibians in the Malay Archipelago alone. Long-recognized centers of diversity (e.g., Sumatra, Borneo, Java, Bali, and Sulawesi) were explored intensively and yielded many new taxa (e.g., Matsui *et al*. 2011, 2013 a, 2013 b, 2014; Iskandar *et al*. 2014; Riyanto & Kurniati 2014; Hamidy & Kurniati 2015; Dehling 2015; Dehling *et al*. 2016; Wostl *et al*. 2017), including *Limnonectes larvaepartus* Iskandar, Evans & McGuire, 2014, the only known frog that gives birth to tadpoles (Iskandar *et al*. 2014). For amphibian taxonomy and systematics in the Malay Archipelago, these are exciting times.

Unfortunately, amphibians are now at greater peril than at any time in recent geological history, a situation chronicled in a number of books (Lanoo 2005; Stuart *et al*. 2008; Collins & Crump 2009). Habitats in Southeast Asia are being lost at an alarming rate because of expanding human populations and generally favorable economic conditions fostering development (e.g., Rowley *et al*. 2010; Hughes 2017). Infectious diseases, particularly the amphibian chytrid fungus *Batrachochytrium dendrobatidis* and the only recently discovered *B. salamandrivorans*, threaten to have serious impacts worldwide (e.g., Gilbert *et al*. 2012; Olson *et al*. 2013; Moriguchi *et al*. 2015). The saturation of aquatic habitats with a host of lethal and sublethal toxic substances from human endeavors is also highly problematic, as it affects amphibians due to their permeable skin and generally biphasic life cycles (e.g., Collins & Crump 2009). New threats, such as the effects of global climate change, further imperil amphibians, especially those with limited distributions and limited dispersal capabilities (see Bickford *et al*. 2010 and Rowley *et al*. 2010 for the impact of climate change on Southeast Asian amphibians).

Threats also emanate from proliferating, non-indigenous species, affecting both, native amphibians and their habitats (e.g., Bradford 1989; Bradford *et al*., 1993; Fisher & Shaffer 1996; Kiesecker & Blaustein 1997; Cox 1999; Goodsell & Kats 1999; Adams 2000; Gillespie 2001; Lever 2003; Kraus 2009). Sometimes, the invasive taxon can be an amphibian as well, as in the case of the cane toad (*Rhinella marina*) that was accidentally as well as intentionally introduced into tropical environments around the world (e.g., Lever 2001; Turvey 2013). Originally from Central and South America, cane toads are, due to their large size, high mobility, generalized feeding habit, and high reproductive capabilities, extremely successful invaders and a threat to biodiversity, as described most notably for their presence in Australia[3], (e.g., Schwarzkopf & Alford 1996; Lever 2001; Philips *et al*. 2007; Shine 2010, 2012).

The Asian toad (*Duttaphrynus melanostictus* complex sensu Wogan *et al*. 2016[4]) is one of 26 "species" comprising the genus *Duttaphrynus* Frost *et al*., 2006 (Frost 2018). The dorsal and lateral surfaces of its head are covered with several black-tipped bony ridges (cranial crests); the rough skin on the back is covered with numerous black-tipped warts. Because of these characteristics, *D. melanostictus* is also known as the black-spined toad (e.g., Manthey & Grossmann 1997; Kaiser, H. *et al*. 2011a). The taxon is abundant and widespread across subtropical and tropical Asia, naturally occurring from Pakistan through the Indian subcontinent and southern China into Mainland Southeast Asia and the Greater Sunda Islands (see Manthey & Grossmann 1997; Van Dijk *et al*. 2004; Daniels 2005). The species has recently become naturalized in Madagascar (Kolby 2014; McClelland *et al*. 2015), the Andaman and Nicobar Islands (Das 1999), Borneo (fide Inger & Stuebing 2005), Lombok (Trainor 2009), Sulawesi (Malkmus 1993), several islands of the Moluccas (Van Dijk *et al*. 2004), Western New Guinea (Menzies & Tapilatu 2000), and Timor (Trainor 2009; Kaiser, H. *et al*. 2011a).

Duttaphrynus melanostictus is a human commensal that is found in diverse altered habitats (e.g., coffee plantations, rice paddies, towns, roadsides), and rarely encountered in natural environments. It is also one of the few species of amphibians that is commonly encountered in larger cities (Manthey & Grossmann 1997; Daniels 2005; Van Dijk *et al*. 2004; Kaiser, H. *et al*. 2011a). As *D. melanostictus* shares some characteristics with the cane toad (see above), concerns were raised that the Asian toad may have a negative impact on small vertebrates, such as frogs and lizards, through direct predation (Trainor 2009: Timor; McClelland *et al*. 2015: Madagascar). However, little is known about its ecology, including food habits, within its natural range (Berry & Bullock 1962; Mathew 1999; Yap 2015), and nothing is known about the ecology of naturalized Asian toad populations elsewhere. Because of this lack of data, recent calls for the rapid eradication of naturalized Asian toad populations (e.g., Kolby 2014) appear panicked and not rooted in evidence.

In chapter 6, I caution against countermeasures to eradicate naturalized populations of *Duttaphrynus melanostictus* unless they are based on sufficient data basis, considering

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[3] *Rhinella marina* feeds on a variety of prey items, including vertebrates (Hinckley 1963; Evans & Lampo 1996; Crossland 2000; Crossland *et al*. 2011; Reed *et al*. 2007; Markula *et al*. 2016; Shine 2010).

[4] According to Wogan *et al*. (2016), *Duttaphrynus melanostictus* represents a species complex, consisting of three deeply divergent clades.

any parallels drawn between the Asian toad and the truly invasive cane toad inappropriate. Recent reports on the spread of the introduced and now abundant Asian toad in Timor-Leste (Trainor 2009; Kaiser, H. *et al.*, 2011a, b; O'Shea *et al.* 2012; Sanchez *et al.* 2012; papers 1 & 9 herein [see chapters 4 & 6]), along with an observation of this toad species feeding on the blind snake *Indotyphlops braminus* (Daudin, 1803) presented in this chapter, prompted the collection of > 80 toad specimens from selected localities in Timor-Leste to carry out a food spectrum analysis. This analysis is presented in chapter 6 and was aimed at determining if *D. melanostictus* regularly consumes small vertebrates, identifying the consumed prey, examining if differences between the food of toads from different localities in Timor-Leste exist, and comparing the food spectrum between the introduced Timorese toad population and populations from its natural range. During the preparations necessary to obtain gut contents for this food spectrum analysis, an optimal incision for opening the abdominal cavity in preserved anurans was developed, which is presented in a separate publication in this chapter.

The ecology of Southeast Asia's amphibians remains poorly studied, and the same applies to the reptiles found in this region. Night skinks of the genus *Eremiascincus* were collected during most field trips to Timor-Leste, but their status and identity has been the source of some confusion (see paper 1, chapter 4, which also presents an account for the genus). Since a comprehensive study on *Eremiascincus* is currently underway (Mecke *et al.*, in prep.), with new species under description (Mecke & Doughty, in press), and due to the fact that taxonomic as well as phylogenetic analyses based on morphology and genetic data can be significantly improved by supplemental information from ecological, ethological, and reproductive data (see Salthe 1967; Scholz 1995; In den Bosch & Zandee 2001; Haddad *et al.* 2005), several live specimens of a taxon referred to as *Eremiascincus* 'Ermera' in paper 1 were collected in the field in 2012, transported to Germany, and housed in a terrarium at the Philipps-Universität Marburg in order to make observations in captivity. These resulted in unexpected findings. In chapter 6, I provide a report on the first captive breeding of an *Eremiascincus* species from the Lesser Sunda Islands and outline the current knowledge of reproduction in the genus.

The publications presented in this chapter are twofold, dealing with the feeding biology of a toad species introduced to Timor and the reproductive biology of an endemic Timorese scincid lizard. Both studies evolved from the survey work presented in chapter 4 (paper 1), however, with research questions that could not be solved in the field or by examining the outer anatomy of the taxa in question.

6.2 Paper 8

Mecke, S. [and 11 co-signatories] (2014): Review Risks Before Eradicating Toads. *Nature* **511**: 534.

Correspondence

Review risks before eradicating toads

Jonathan Kolby and colleagues call for swift eradication of the invasive Asian common toad *Duttaphrynus melanostictus* from Madagascar (*Nature* **509,** 563; 2014). We caution against disproportionate countermeasures that are not founded on proper data and assessment. These could have detrimental effects on local ecosystems that are comparable to the threat posed by the toads themselves.

Draining potential breeding ponds, for example (see *Nature* http://doi.org/ts3; 2014), could have an impact on local fauna or even on entire ecosystems. This approach would probably fail anyway because larvae of *D. melanostictus* can survive in streams, puddles and brackish waters. Also, efforts by amateur conservationists and locals to destroy toad spawn and larvae could jeopardize native frog species if people do not identify tadpoles or juveniles correctly (see, for instance, R. Somaweera *et al. Biol. Conserv.* **143,** 1477–1484; 2010).

We consider the parallels drawn by Kolby and colleagues between *D. melanostictus* and the invasive cane toad (*Rhinella marina*) to be inappropriate. Invasion potential and the effects of alien species are hard to predict without sufficient data. To confirm a genuine biological invasion, information first needs to be collected on the toads' range extension and the impact on local flora and fauna. Before implementing countermeasures, any negative effects should be evaluated. This calls for rapid assessment of the practical difficulties, risks and prospects of success.

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**On behalf of 12 correspondents (see go.nature.com/wj2aju for full list).*

Supplementary information to: Review risks before eradicating toads

Full list of co-signatories to a Correspondence published in Nature ***511,*** *534 (2014);*
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6.3 Paper 9

O'Shea, M., Kathriner, A., **Mecke, S.**, Sanchez, C. & Kaiser, H. (2013): 'Fantastic Voyage': A Live Blindsnake (*Ramphotyphlops braminus*) Journeys through the Gastrointestinal System of a Toad (*Duttaphrynus melanostictus*). *Herpetology Notes*, **6**: 467–470.

Herpetology Notes, volume 6: 467-470 (2013) (published online on 18 October 2013)

'Fantastic Voyage': a live blindsnake (*Ramphotyphlops braminus*) journeys through the gastrointestinal system of a toad (*Duttaphrynus melanostictus*)

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Abstract. We report an unusual predator-prey interaction between the Common Asian toad, *Duttaphrynus melanostictus*, and the Brahminy blindsnake, *Ramphotyphlops braminus*, as observed in Manufahi District, Timor-Leste. The live blindsnake was found emerging headfirst from the cloaca of the toad, with about one-third of its body length still inside. This interaction may indicate that indiscriminate foraging by invasive toads could endanger small vertebrate prey, while it appears that the physiology and habits of blindsnakes may allow them on occasion to elude predation in an unexpected manner.

Keywords. *Duttaphrynus melanostictus,* Bufonidae, *Ramphotyphlops braminus,* Typhlopidae, Timor-Leste, predation, diet, invasive species.

Introduction

Timor is the largest island of the Outer Banda Arc of the Indo-Australian Archipelago, a chain of diverse islands situated off the northern coast of Western Australia. With coastlines on the Savu and Timor Seas, the country of Timor-Leste (total surface area 15,410 km^2) comprises the eastern half of Timor, the Oecusse exclave on the northern coast of Indonesian West Timor, and the islands of Ataúro and Jaco (Kaiser et al., 2011a). A Portuguese colony for almost five centuries, Timor-Leste, also known as East Timor, has had a traumatic and bloody history, including an exploitative colonial period, occupation by Japan during the Second World War, and, most recently and most seriously, annexation by Indonesia (1975–99). Timor-Leste finally became fully independent in 2002, but only since mid-2008 have the political circumstances stabilized.

As a consequence of its geography and its history, Timor has had many diverse human visitors. It was settled during prehistoric times by waves of Melanesians, Polynesians, and Malays from New Guinea, Australia, southern China, and Southeast Asia, each bringing their baggage, chattels, and agricultural practices, including rice farming, an industry established in the region thousands of years ago (Chi and Hung, 2008). Indonesian and Chinese traders came and went, some settling into the communities or establishing their own. Colonization during the 16th Century brought the Dutch to the west and Portuguese and Indians from Goa to the east, while wars in the 20th Century brought the Japanese, Australians, and Indonesians. The uneasy peace in 1999 brought many more nationalities to the shores of East Timor, first the Australian-led multinational InterFET[1] task force, comprising troops from 19 countries sent to separate the warring factions from 1999–2000, and then an interim administration (UNTAET[2]), which controlled peacekeeping from 2000 until independence in 2002. These initiatives were followed by UNMIT[3] from 2006–12, which again involved large numbers of personnel and large quantities of equipment arriving from distant shores. Colonization, trade, agriculture, war, and peace

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[1] InterFET = International Force for East Timor

[2] UNTAET = United Nations Transitional Administration in East Timor

[3] UNMIT = United Nations Integrated Mission in Timor-Leste

all resulted not only in a mixing of humans on the island of Timor, but also in the introduction of numerous alien species. The ongoing Reptile and Amphibian Survey of Timor-Leste (Kaiser et al., 2011a; O'Shea et al., 2012) has so far confirmed the presence of six species of amphibians (of which at least three may have been introduced), three species of freshwater turtles (two introduced), 44 species of lizards (at least eight species, or 18% introduced), and 12 species of snakes (several possibly introduced).

During the latest phase of our survey (21 June–9 July 2012), we observed a curious interaction between two certainly non-native species: the Common Asian toad, *Duttaphrynus melanostictus* (Schneider, 1799), and the Brahminy blindsnake, *Ramphotyphlops braminus* (Daudin, 1803). The toad is locally known as *manduku interfet* or 'InterFET toad' due to the locally held belief that its arrival was mitigated by the first wave of peacekeeping forces (Kaiser et al., 2011a). The species has established itself widely across western and central mainland Timor-Leste (Trainor, 2009; Kaiser et al., 2011a,b, 2012; O'Shea et al., 2012), to altitudes of 1225 m, although it has yet to be documented from the easternmost part of the country (Lautém District). The Brahminy blindsnake, a parthenogenetic species, is ideally suited to colonize new habitats and its colloquial name, 'flower pot snake,' is an indication for how it has become the most widely distributed non-native snake species in the world (O'Shea, 2007). It has spread throughout the entire island of Timor, occurring at altitudes up to 1495 m in Timor-Leste (carried to this locale in plant pots destined for the Portuguese Governor's garden; O'Shea et al., unpubl. data).

Materials and Methods

The toad was discovered serendipitously by lifting a rock destined to become a doorstopper at the facility where we were assembling a specimen preparation area during a recent herpetofaunal survey in Timor-Leste (see Kaiser et al., 2011a for detailed methodology). Measurements of snout–vent length (SVL) and total length (TL) were taken to the nearest 1 mm using a ruler. Specimens have been deposited in the United States National Museum of Natural History (USNM).

Results and Discussion

At 1230 h on 3 July 2012 a *Duttaphrynus melanostictus* (SVL 58 mm; USNM 565895) was discovered under a rock in the grounds of the Convent of St. Antony d'Lisboa, at Fatucahi Suco, Manufahi District, southern Timor-Leste (9.03789°S, 125.98622°E, datum: WGS84; elev. 38 m). Protruding headfirst from its cloaca was a *Ramphotyphlops braminus* (SVL 103 mm, TL 106 mm; USNM 565896) with approximately 60% of the snake visible. When the toad hopped to escape, the blindsnake was carried along with it.

Both specimens were captured together and photographed (Fig. 1A), and after a few minutes the struggling toad completely expelled the blindsnake (Fig. 1B). Even though the blindsnake appeared passive during the encounter, it was not possible to determine with certainty whether the expulsion was due to digestive or cloacal activity of the toad or exertions from the blindsnake. Both animals were again photographed alongside a ruler (Fig. 1C). The blindsnake was clearly alive when it emerged, based on the visibility of both heartbeat and circulation when viewed ventrally using a strong light, and it still made weak movements until at least 2100 h. The following morning we found that it had died, and we vouchered it. While we do not collect specimens of *D. melanostictus* as a matter of course, the unusual circumstances under which we found this specimen made it an exception.

The only possible scenario leading up to this unusual circumstance is that the toad had predated the blindsnake, gulping it down with great speed and minimal jaw pressure, enabling the snake to survive and enter the digestive tract essentially unharmed. The blindsnake, as a species adapted to a light-restricted fossorial lifestyle, presumably continued on its *Fantastic Voyage*[4] through the digestive tract of the toad, either passively and propelled by the toad's digestive musculature, or by actively working its way through the toad, until it again emerged into daylight from the cloaca of the toad. It is a testament to the hardiness of the species that the blindsnake succumbed only after more than 7.5 h post-exposure, due to either the chemicals produced by the toad's digestive tract, from anoxia (Pizzatto et al., 2012), or from a combination of the two.

The blindsnake's escape is curious, however, since toads are generally known as voracious and effective carnivores of a great diversity of prey. While we appreciate that the blindsnake in this instance did not survive its passage through the toad, its overall condition upon emergence leaves us with the impression that safe passage may be possible. We have been unable to find

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[4] *Fantastic Voyage* is the title of a 1966 science fiction movie starring Stephen Boyd, Raquel Welch and Donald Pleasence, in which a specially designed nuclear submarine, the *Proteus*, and its crew are shrunk to 0.001 mm in size so that they may be injected into the circulatory system of a scientist.

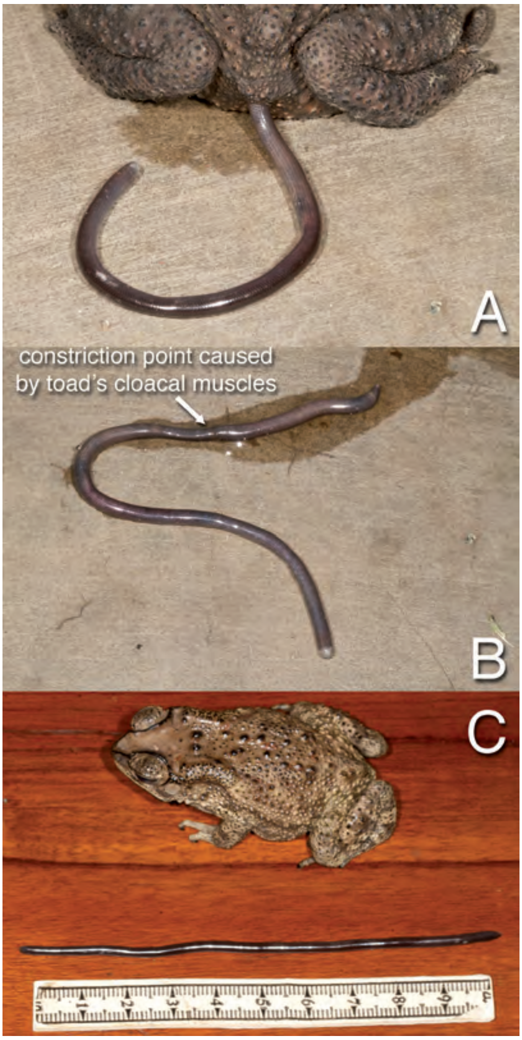

Figure 1. Participants in the ‘Fantastic Voyage’ of a Brahminy blindsnake (*Ramphotyphlops braminus*) through the digestive system of a Common Asian toad (*Duttaphrynus melanostictus*) in Timor-Leste. (A) In this image taken immediately after the discovery of the toad, ca. 40% of the blindsnake is still inside the toad. There were no visible signs of discomfort on the part of the toad. (B) After it completely emerged from the toad, the blindsnake did not move noticeably, but physiological functions (blood flow, heartbeat) could be observed. The body of the snake showed a constriction where the toad’s cloacal muscles had most recently held it. (C) Relative dimensions of toad and blindsnake shown to illustrate that the blindsnake was considerable longer than the toad in body length.

either anecdotal or documented observations of any other prey emerging alive from a toad’s digestive tract. The toad appeared to be none the worse for wear by the passage of a relatively large organism through its entire alimentary system.

Whereas prey selection among bufonid toads in nature is usually restricted to invertebrates, there are reports that one species, the cane toad *Rhinella marina* (Linnaeus, 1758), sometimes takes vertebrate prey. Such reports need to be carefully evaluated, however, because they may depend on the geographic location of the observation. It appears that *R. marina* takes vertebrate prey opportunistically but rarely, and reportedly only in locations where it is introduced (e.g., Shine, 2010; Stammer, 1981); in their broad-based study in the toad’s native range on Barro Colorado Island, Panamá, Zug and Zug (1979) found no vertebrate prey in toad stomachs. Two reports from introduced cane toad populations document predation of typhlopid snakes by *R. marina*, for tropical northern Australia (*Anilios guentheri, A. unguirostris,* introduced *Ramphotyphlops braminus*: Pizzatto et al., 2012) and the Philippines (*Typhlops*: Rabor, 1952). These cases show that certainly for the large species *R. marina*, consumption of blindsnakes may be part of that species’ opportunistic feeding routine, even though some blindsnakes were reported to have been regurgitated alive (Rabor, 1952) or found dead but undigested in the toads’ guts or in fecal matter (Pizzatto et al., 2012). A possible simple explanation for the regurgitation of blindsnakes by toads is perhaps the inability of toads to distinguish between a blindsnake and an earthworm. The question therefore remains whether there is generally any tangible nutritional gain for toads by including blindsnakes, or other vertebrate prey, in their diet.

Unlike for *R. marina* there are no previous reports of the invertebrate generalist *D. melanostictus* preying upon vertebrates (Berry & Bullock, 1962). Even the large (70–100 mm) river toad, *Phrynoidis aspera* (Gravenhorst, 1829), is not documented as taking vertebrate prey (Berry, 1970). In the specific case we observed, and akin to the circumstances of *R. marina*, introduced *D. melanostictus* are perhaps more likely to ingest vertebrate prey than they are in their native range. Nevertheless, we believe ours is the first observation of *D. melanostictus* predating a vertebrate prey species, and it is simultaneously the first account of a living blindsnake passing completely through the digestive tract of a potential predator.

As an introduced species in Timor-Leste, *D. melanostictus* may cause similar, though perhaps less severe, ecological problems than those caused by the introduced, physically larger cane toad *R. marina* in New Guinea, Australia, and other non-native locations.

Among the key issues are the following (see Shine, 2010 for a broader discussion): (1) toads may be consumed and subsequently poison naïve vertebrate predators (potentially including humans); (2) because of their very generalized habitat needs and considerable tolerance for adverse environmental conditions, toads and their tadpoles may outcompete native anurans and their tadpoles; (3) toads can prey upon local terrestrial invertebrates and, given our finding for *D. melanostictus*, perhaps vertebrates, thus upsetting the ecological balance; (4) the predatory pressure of a fast-growing and fast-expanding toad population may endanger rare species (perhaps including small vertebrates) and remove prey species for other amphibians and reptiles.

Our observation might also provide an alternative explanation for the presence of blindsnakes in the nests of owls (Gehlbach and Baldridge, 1987). In addition to the deliberate transportation of live blindsnakes to the nest in the owl's beak as prey for its young, blindsnakes may be transported to the nest while in the owl's digestive tract and escape from its would-be predator *in situ*. While it would require additional observations to determine whether a blindsnake such as *R. braminus* is capable of surviving the digestive chemistry or oxygen-deficient alimentary system of a homeotherm, such occurrences may be rare and extreme, just like the arboreal climbing abilities of blindsnakes reported by Vanzolini (1970).

Acknowledgments. We thank Their Excellencies Prime Minister Xanana Gusmão and Minister Ágio Pereira for their continuing active support of our research in the beautiful country of Timor-Leste. We are also grateful to Claudia Abate-Debat, Senior Advisor in the Prime Minister's Office, for her help in making connections and facilitating many aspects of our work. We very much appreciate the support and friendship of Manuel Mendes, Head of the Department of National Parks, through whose office we obtained necessary permits. We are very thankful for the warm welcome and hospitality of the residents at the Franciscan Convent of St. Antony d'Lisboa, and particularly the kind assistance of Father Cornelius and Father Hendrik. We thank Paulo Pinto for heeding our call for a field assistant at the last minute; we salute his courage in adverse circumstances, and we applaud his willingness to learn on the go and his exceptional work ethic. At the USNM, Jeremy Jacobs and Steve Gotte have always made every effort to get our collections accessioned and cataloged, and their help is very much appreciated. This paper is Contribution No. 11 from the Tropical Research Initiative at Victor Valley College.

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6.4 Paper 10

Döring, B., **Mecke, S.** (joint first authors), Mader, F. & Kaiser, H. (2016): A Proposed Optimal Incision Method to Obtain Gut Contents from Preserved Anurans. *Amphibia-Reptilia*, **37**(4): 437–440.

Amphibia-Reptilia 37 (2016): 437-440

Short Notes

A proposed optimal incision method to obtain gut contents from preserved anurans

Britta Döring[1,*], Sven Mecke[1,*,**], Felix Mader[2], Hinrich Kaiser[3,4]

Abstract. Information on the diet of anuran species based on gut content analyses have been published by numerous researchers, yet the details of the incision method used to open the abdominal cavity of preserved specimens in preparation for such examinations are rarely explained in the presented methods. Our objective is to formally propose an optimal incision into the pleuroperitoneal cavity of liquid-preserved anuran specimens to gain access to and permit easy removal of parts of the digestive tract in preparation for food spectrum analyses. In our experience, this U-shaped cut is easy to perform and teach. It also provides better access to the pleuroperitoneal cavity than a small ventrolateral incision and is less destructive than the classic textbook medial “double T-incision” routinely listed in dissection protocols.

Keywords: anatomy, Anura, food spectrum analysis, gut content analysis, incision, invasive method.

Gut content analysis is an important and efficient tool for determining the diet of amphibians, including anurans. Publications on feeding habits of anurans based on gut content analysis of preserved specimens, however, usually lack information on the type of incision used to open the abdominal cavity, and hence there is no defined consensus on the most appropriate method to use for this purpose (Berry and Bullock, 1962; Zug and Zug, 1979; Vences et al., 1999; Cogălniceanu et al., 2000; Dos Santos et al., 2003; Maneyro et al., 2004; Moseley et al., 2005; Da Silva et al., 2009; Yousaf et al., 2010; Da Silva et al., 2011; Crnobrnja-Isailović et al., 2012; Olson and Beard, 2012; Sugai et al., 2012; Almeria and Nuñeza, 2013; Luría-Manzano and Gutiérrez-Myén, 2014).

During a preliminary study on celiotomies performed on liquid-preserved anuran specimens as part of a broader study (food spectrum analysis of *Duttaphrynus melanostictus*; Döring et al., accepted), we found one method to open the ventral body cavity particularly convincing: a U-shaped cut. This incision technique, that appears most useful when carrying out gut content analyses in preserved anurans, may be well known to some researchers and has already been in use (George Zug, in litt.). It has, however, not been previously described and compared to other incisions in the literature. We describe this U-incision method in the protocol below.

For performance of the U-incision, a rounded, transverse ventral cut at the lowest point in the curve of the U is made at the level of the anterior border of the hind leg insertion into the body wall to penetrate the skin and *musculus rectus abdominis* (fig. 1a). Subsequently, two parallel longitudinal cuts are made, beginning

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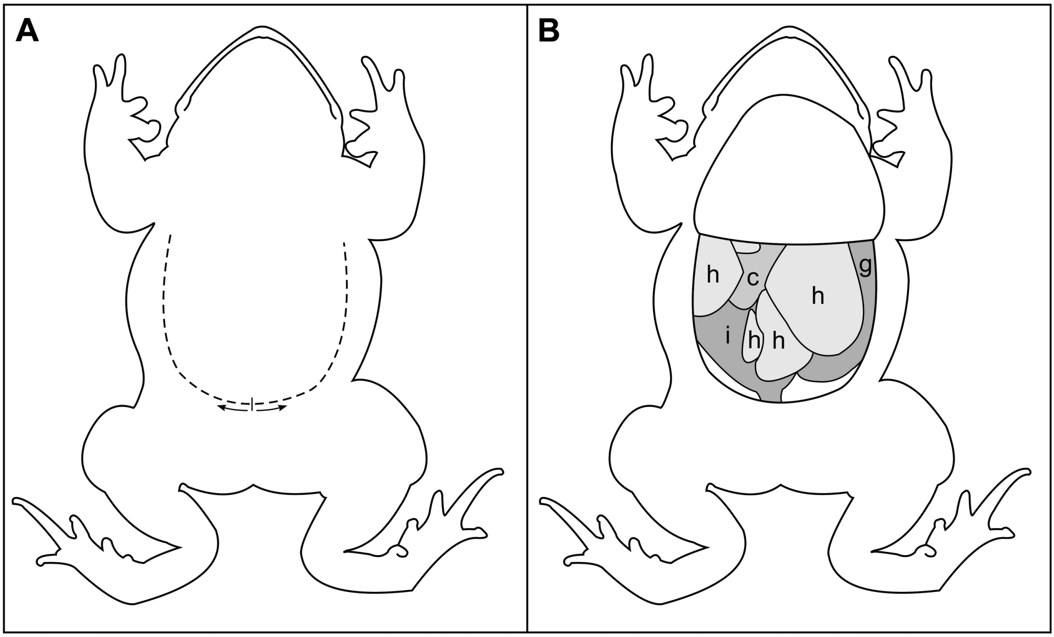

Figure 1. (A) Schematic representation of how to apply the U-incision to a liquid-preserved anuran specimen. (B) View into the body cavity after the single skin and muscle flap is reflected. c = cor (heart), h = hepar (liver), g = gaster (stomach), i = intestinum (intestine).

at the margins of the original incision in direction of the axils, resulting in a U-shaped cut (fig. 1a). After the incision is made, the single flap of skin and muscles is reflected and pinned to the front (in direction of the head) of the respective specimen to allow suitable exposure of the pleuroperitoneal cavity and the inner organs (fig. 1b). Removal of the stomach to analyse its contents does not necessitate the removal of the liver. The *vena abdominalis*, which runs along the inner surface of the abdominal muscles and enters the hepatic portal vein, slightly lifts the liver from its original position when the skin and muscle flap is reflected. This easily allows access to the entire stomach, with a cut necessary at its transition with the oesophagus and at its transition with the duodenum to remove the organ. Furthermore, the larger opening produced by the U-shaped cut also allows access to the lower guts, and thereby easy removal of the intestines is possible by a cut made at the transition of the rectum with the anus. In gravid females, eggs have to be removed prior to the removal of the guts. After completion of food item removal from the guts, the stomach and intestine are repositioned in the pleuroperitoneal cavity, with the stomach held in place by the liver when skin and muscles are flapped back to close the opening. Secure closure of the pleuroperitoneal cavity for the purpose of storage in a collection may be achieved by fixing the skin and muscle flap on each side of the body in vicinity of the hind legs using pins.

For the purpose of a gut content analysis, applying only a small ventrolateral incision does not provide access to all relevant organs. The classic textbook example to open the abdominal cavity in tetrapods is an incision (herein referred to as the double T-incision) along the mid-ventral line (slightly offset from the *linea alba*), beginning at the anterior border of the hind leg insertion into the body wall to a point posterior to the sternum. This mid-ventral cut is extended, using smaller cuts running in a lateral direction (at the level of the limbs), resulting in five separate cuts. This produces two skin flaps that can be reflected laterally and pinned (e.g., Jammes, 1904; Nierstrasz and Hirsch, 1930;

Boolootian and Heyneman, 1969; De Iuliis and Pulerà, 2007; Storch and Welsch, 2009).

The double T-incision, which some researchers have applied in the past to open the abdominal cavity of liquid-preserved anurans, is clearly more destructive than the proposed U-incision, since cutting affects the pectoral girdle and the muscles of the extremities as well as some of the inner organs, if the utmost possible insight into the body's interior is required. By using a double T-incision the resulting skin flaps need to be reflected laterally and pinned to keep the large pleuroperitoneal opening exposed. The U-incision makes specimen handling during examination of the inner body quite simple, since the large opening of the pleuroperitoneal cavity provides general orientation and accessibility to all relevant organs, and the single skin and muscle flap can easily be affixed to a dissection tray using a single pin, or can even simply be held with the fingers.

The level of organ exposure that is produced by the U-incision also provides an excellent view for photography, an important feature given that the morphology of various organs (e.g., liver shape; Hedges, 1989: fig. 12) has been shown to be useful for taxonomic purposes. In studies of eleutherodactylid frogs, Hedges and colleagues (e.g., Hedges, 1989; Hedges et al., 2008) extensively used liver shape as a taxonomic character, and their methodology called for the removal of the entire ventral surface, which would have been unnecessary if using a U-incision.

The U-incision, which is easy to perform and teach, might be a useful method for celiotomies in amphibian groups with relatively elongated body forms (newts and salamanders) as well, but the presence of elongated ribs inside the thorax does not allow an application on lizards. We argue that researchers in their studies should report on the respective incision method used, instead of only stating that an incision was made. This may contribute to the establishment of standardised incision methods in different animal groups.

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6.5 Paper 11

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Food spectrum analysis of the Asian toad, *Duttaphrynus melanostictus* (Schneider, 1799) (Anura: Bufonidae), from Timor Island, Wallacea

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ABSTRACT

The Asian toad, *Duttaphrynus melanostictus* (Schneider, 1799), is widespread throughout tropical Asia and very abundant where it occurs. It was relatively recently introduced to Timor, the second largest island in the biogeographic region called Wallacea. Timor Island shows an exceptionally high level of endemism in a wide range of faunal groups and there are concerns that *D. melanostictus* may have a negative impact on this diversity, including vertebrates, through direct predation. To evaluate the impact the diet of *D. melanostictus* might have on the local fauna, gut contents of 83 preserved toad specimens from five habitat types in Timor-Leste, a country occupying the eastern half of Timor Island, were examined. We identified 5581 prey items, comprising the following animal groups: annelids; snails and slugs; spiders and harvestmen; woodlice; millipedes and centipedes; grasshoppers, crickets and earwigs; termites; thrips and true bugs; beetles; ants; hymenopterans other than ants; true flies; butterflies; unidentified insects; and insect larvae. Small eusocial insects (ants and termites) constituted the major part of the diet (61.6% and 23.4%, respectively). No vertebrate prey was recorded. Prey item composition did not differ between habitats. The wide prey spectrum well indicates that *D. melanostictus* is a generalist invertebrate feeder, as other studies, from regions where this species occurs naturally, have already shown. Although the Asian toad seems to not generally prey on vertebrates, vertebrate species that are morphologically similar to invertebrates in their overall appearance may be consumed. Hence, a negative effect on some taxa (e.g. blindsnakes) may be possible. We also present some limited data on intestinal parasites occurring in *D. melanostictus*.

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Introduction

The Asian toad, *Duttaphrynus melanostictus* (Schneider, 1799) (Figure 1a), is one of the most widely distributed toad species in subtropical and tropical Asia and may represent a species complex (Wogan et al. 2016). The species is found from northern Pakistan throughout India, Sri Lanka, Nepal, Bhutan, Bangladesh, southern China, Myanmar, Laos, Vietnam, Cambodia and Thailand to Malaysia, Singapore, Java and Sumatra, and

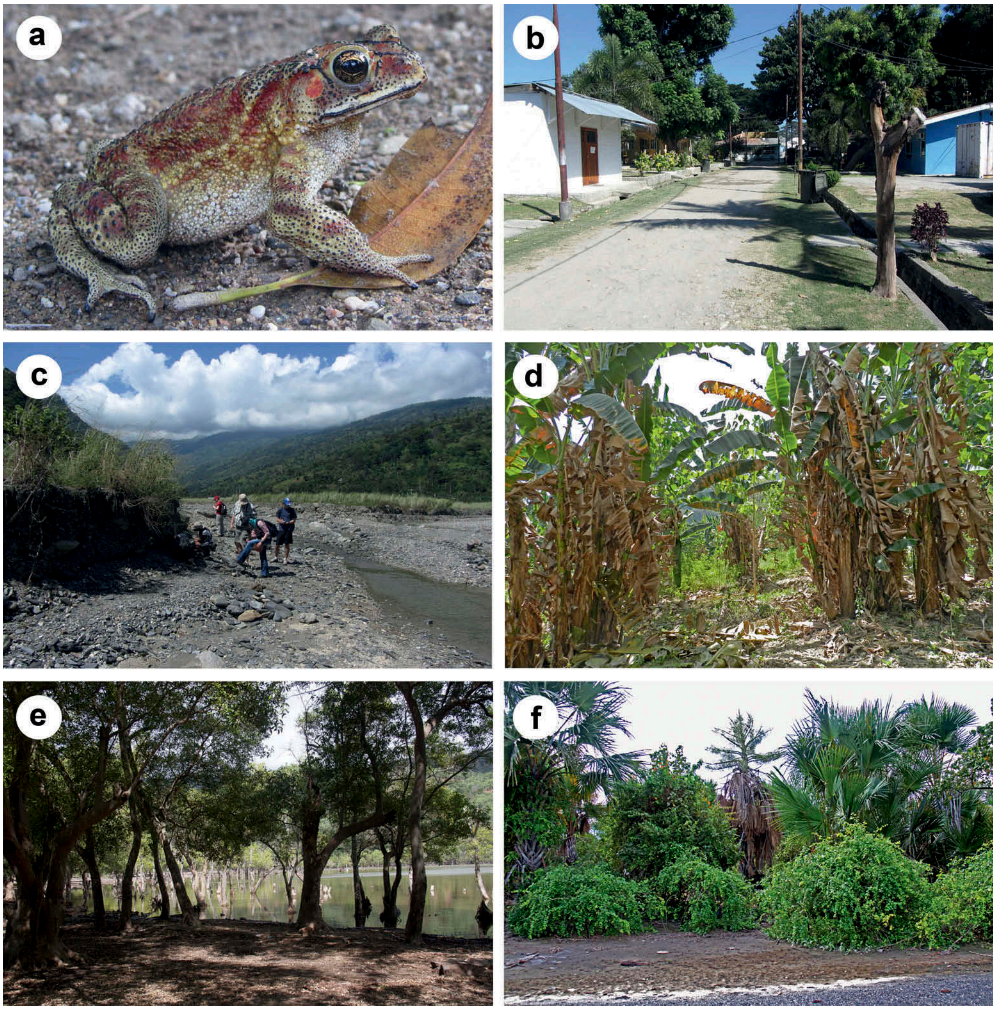

Figure 1. *Duttaphrynus melanostictus* and habitats in Timor-Leste sampled during June 2013. Habitat types are listed in the same order as they appear in Table 1. (a) Unvouchered *D. melanostictus* specimen from the park grounds of the Timor Lodge Hotel, Dili, Dili District. (b) Park grounds of the Timor Lodge Hotel, Dili, Dili District (Habitat I). (c) Dry riverbed at the confluence of the Comoro and Bemos rivers, 8 km south of the Comoro River bridge, Dili District (Habitat II). (d) Banana plantation south of the confluence of the Comoro and Bemos rivers, Aileu District (Habitat III). (e) Dry forest at the fringes of Lake Maubara, Liquiça District (Habitat IV). (f) *Corypha* forest west of Raeme, Liquiça District (Habitat V). Photographs (a–c) by Sven Mecke, (d) by Max Kieckbusch and (e–f) by Mark O'Shea.

represents the most common toad in cultural landscapes and urban areas (e.g. Manthey and Grossmann 1997; Van Dijk et al. 2004; Daniels 2005). *Duttaphrynus melanostictus* has been introduced to Madagascar (e.g. Kolby 2014; McClelland et al. 2015), the Maldives (Gardiner 1906), the Andaman and Nicobar Islands (Das 1999), Borneo (fide Inger and Stuebing 2005), Bali (Church 1960), Lombok (Trainor 2009), Sumbawa (McKay and Lilley 2012), Sulawesi (Malkmus 1993), the Moluccas (Van Dijk et al. 2004), Western New Guinea (Menzies and Tapilatu 2000) and Timor (Trainor 2009).

Timor Island is characterised by a remarkable variety and a high level of endemism among species (e.g. land snails, insects, frogs, lizards and snakes, birds – Trainor et al. 2008; Michaux 2010; Andersen et al. 2013; Köhler and Kessner 2014; O'Shea et al. 2015). The introduction of *Duttaphrynus melanostictus* to the island of Timor (which is politically divided between the sovereign states of Timor-Leste in the eastern half and Indonesia in the western half) raised concerns that *D. melanostictus* may have a negative impact on parts of this diversity, including small vertebrates, through direct predation (Trainor 2009). However, relatively little is known about the diet of *D. melanostictus* so far, with food spectrum analyses performed only using specimens collected in regions where the species occurs naturally (India – Mathew 1999; Malaysia – Yap 2015; Malaysia and Singapore – Berry and Bullock 1962).[1]

Members of the family Bufonidae Gray, 1825 usually prey on invertebrates such as small insects (e.g. Clarke 1974; Van Beurden 1980; Freeland 1984; Maragno and Souza 2011; Crnobrnja-Isailovic et al. 2012), and mainly on ants and/or beetles (e.g. Smith and Bragg 1949; Hamilton 1954; Moore and Strickland 1954; Bush 1959; Bush and Menhinick 1962; Cole 1962; Krakauer 1968; Berry 1970; Campbell 1970; Clarke 1974; Bailey 1976; Zug and Zug 1979; Mathew 1999; Smith et al. 2011; Yap 2015). However, one species, *Rhinella marina* (Linnaeus, 1758) is well documented to feed on larger prey items, including small vertebrates (e.g. tadpoles, toads, frogs, small snakes, birds and mammals – Hinckley 1963; Evans and Lampo 1996; Crossland 2000; Reed et al. 2007; Markula et al. 2010; Shine 2010; Crossland et al. 2011). The only other toad species known to occasionally and/or accidentally prey on vertebrates are *R. icterica* (Spix, 1824) (a bird – Camilotti and Barreto-Lima 2011), *R. jimi* (Stevaux, 2002) (a bat – da Silva et al. 2010), *Anaxyrus microscaphus* (Cope, 1867) (a teiid lizard and a toad – Ryan et al. 2016), *Incilius valliceps* (Wiegmann, 1833) (a spiny lizard and a toad – Campbell and Davis 1968) and *Duttaphrynus melanostictus* (blindsnakes – Hahn 1976; O'Shea et al. 2013).

Recent reports of the spread of the introduced and now abundant Asian toad in Timor-Leste[2] (Trainor 2009; Kaiser, Afranio Soares et al. 2011; Kaiser, Lopes Carvalho et al. 2011; O'Shea et al. 2012, 2013, 2015; Sanchez et al. 2012), along with its feeding on a vertebrate, the perianthropic blind snake *Indotyphlops braminus* (Daudin, 1803) (O'Shea et al. 2013; see also Hahn 1976), prompted us to collect 83 specimens of this exotic species from selected habitats in Timor-Leste to carry out a food spectrum analysis. Although the widespread *I. braminus* is, like *Duttaphrynus melanostictus*, not native to Timor, species that are potentially restricted to Timor have been identified in the blindsnake genera *Anilios* Gray, 1845 and *Sundatyphlops* Hedges et al. 2014 (the latter referred to as *Indotyphlops* spp. by O'Shea et al. 2015; Kaiser et al. in prep.) and, like other small vertebrates, could be included in the food spectrum of the Asian toad.

Our analysis was aimed at (1) determining if *Duttaphrynus melanostictus* regularly consumes small vertebrates, such as frogs and squamates; (2) identifying the consumed invertebrate prey; (3) examining whether differences between the food of toads from selected habitats in Timor-Leste exist; and (4) comparing the food spectrum between the introduced Timorese toad population and populations from its natural range, based on literature sources.

Material and methods

Study area and sampling

Eighty-three adult specimens of *Duttaphrynus melanostictus* (48 males: snout-vent length (SVL) 54.7–91.2 mm, mean and standard deviation 73.2 ± 8.4 mm; 35 females: SVL 50.5–118.1 mm, mean and standard deviation 78.0 ± 16.3 mm; see Appendix) were collected in the dry season (18–29 June 2013) during Phase VIII of the Amphibian and Reptile Survey of Timor-Leste, a project of the Tropical Research Initiative at Victor Valley College, Victorville, California, USA. Specimens were collected from five different habitat types (I–V) at four different localities in Timor-Leste (Figure 1b–f). Table 1 provides information on the habitat types, the collection localities and their geoposition, and the number of toads collected from each locality.

Specimens were collected in the evening at Habitat I and during the daytime at Habitats II–V. Shortly after capture, each individual was euthanised via intracardiac injection with a 5% procaine solution (Altig 1980), injected with 10% formalin through the body wall to halt digestion of the gut contents and subsequently fixed in 10% formalin. Specimens in 70% ethanol were deposited in the collection of the Division of Amphibians and Reptiles, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM).

Food spectrum analysis

For the food spectrum analysis, dissections were performed using a U-incision (Döring et al. 2016). Internal organs (i.e. stomach, intestine, rectum) were removed by cuts at the transition of the stomach with the oesophagus and at the transition of the rectum with the cloaca. In gravid females, eggs were removed prior to the removal of the

Table 1. List of habitat types and collection localities of specimens of *Duttaphrynus melanostictus* from Timor-Leste, with information on geoposition and number of toads collected.

Habitat number	Habitat type	Locality	District	Elevation (m)	GPS coordinates	Number of toads collected (*n*)
I	Park grounds	Timor Lodge Hotel, Dili	Dili	25	08°33'S, 125°31'E	18
II	Dry river bed	8 km south of Comoro River bridge, at confluence of Comoro and Bemos rivers	Dili	115	08°36'S, 125°31'E	13
III	Banana plantation	Confluence of Comoro and Bemos rivers	Aileu	115	08°36'S, 125°31'E	36
IV	Dry forest	Lake Maubara	Liquiça	7	08°36'S, 125°15'E	12
V	*Corypha* forest	West of Raeme	Liquiça	8	08°36'S, 125°16'E	4

organs. Stomach and intestine were separated by a cut at the furrow that characterises the transition from the stomach to the duodenum (pylorus), and intestine and rectum were separated at the junction between the sigmoid colon and the rectum (rectosigmoid). Stomach, intestine and rectum were slit open, and the contents removed using tweezers and by flushing the lumen using a pipette. The extracted contents were stored in 70% ethanol. For this purpose the contents of the different gut sections (stomach, intestine, rectum) of each specimen were transferred into separate Eppendorf tubes engraved with the respective USNM number and the abbreviation for stomach (S), intestine (G) or rectum (R). Gut contents were examined and identified under a dissection microscope (Leica Zoom 2000^{TM}), and divided into three major groups: (1) animal material; (2) plant material; and (3) miscellaneous material (e.g. small stones, plastic debris/microplastics). Animal material (prey items) was identified and assigned to one of the following groups based on the taxa found: (1) Annelida (annelids); (2) Gastropoda (snails and slugs); (3) Araneae and Opiliones (spiders and harvestmen); (4) Isopoda (woodlice); (5) Myriapoda (millipedes and centipedes); (6) Orthoptera and Dermaptera (grasshoppers and crickets, and earwigs); (7) Blattodea: Termitoidae (termites); (8) Thysanoptera and Hemiptera (thrips and true bugs); (9) Coleoptera (beetles); (10) Hymenoptera: Formicidae (ants, including winged specimens); (11) Hymenoptera: other; (12) Diptera (true flies); (13) Lepidoptera (butterflies); (14) unidentified insects; and (15) insect larvae.

We did not measure biomass or volume of prey, but quantified animal material based on the frequency of occurrence (the number of prey items), the most robust and interpretable measure of diet composition (Baker et al. 2013), which probably also allows the most reliable comparison across studies.

In the case of fragmentary prey items the number of specimens was counted based on the following criteria: (1) The number of annelids was recorded by the presence of fragments carrying a prostomium or periproct. If a fragment possessing a prostomium + a fragment with a periproct were found in a single toad, these were counted as a single specimen. (2) The number of gastropods was recorded by the presence of radulae and/or snail shells. If small, similar-looking shell fragments were found only, these were estimated to represent the remains of a single snail specimen. (3) The number of arthropods was recorded primarily based on the presence of head capsules (insects) or prosomas (spiders) to prevent counting a single individual twice.

Parasites

Intestinal parasites were counted and classified to the following higher taxonomic groups: Nematoda (roundworms), Cestoda (tapeworms), Trematoda (flukes), Acanthocephala (spiny-headed worms) and Turbellaria (flatworms). For each toad specimen, parasites were separated by intestinal section and stored in Eppendorf tubes with 70% ethanol (engraved as for prey). Eppendorf tubes with parasites received red markings to avoid confusion with gut content tubes.

Statistical analyses

The following percentage distributions were calculated using Microsoft Excel® 2007 (Microsoft Corporation, Redmond, Washington, USA): (1) empty stomachs, intestines and rectums as a percentage of the total number of toad specimens examined; (2) the percentage of each defined prey group among the total number of prey items identified from all toads; (3) the percentage of each defined prey group among the total number of prey items identified from toads from each habitat, respectively; (4) the percentage of toads that consumed small stones and plastic debris/microplastics; (5) the percentage of toads and organs (intestine and/or rectum) found to be infested with parasites, the percentage of each parasite group among the total number of toads and, for each habitat, the percentage of parasite groups among the total number of parasites identified.

Multivariate statistical analyses were performed using R version 3.1.3 (R Development Core Team 2012, Vienna, Austria). To test for differences in prey item composition in toads among the different habitats (see Table 1), we performed a non-metric multi-dimensional scaling analysis (NMDS) based on Bray-Curtis dissimilarities of prey item number from each toad (metaMDS, vegan package; Oksanen et al. 2012). We also tested for differences in prey item composition among habitats with an analysis of similarity (anosim, vegan package; Oksanen et al. 2012). We included both female and male toads in the analyses as preliminary tests for differences in total prey item number between sexes (tested with Mann-Whitney U-test) among all habitats and at each habitat yielded no statistical differences. Prey item communities did not differ between sexes either (tested with NMDS and anosim).

Results

Food spectrum

Of the 83 specimens of *Duttaphrynus melanostictus* examined, one had an entire empty gut (1.2%), eight had empty stomachs and intestines (9.6%), none had an empty intestine and rectum, one had an empty stomach and rectum (1.2%), four had empty stomachs only (4.8%), four had empty intestines only (4.8%) and none had an empty rectum only.

A total of 5581 prey items were identified. Gut contents consisted of prey items from 15 defined invertebrate groups, with ants identified as the most frequently consumed prey item (n = 3437, 61.6%; Table 2). Other groups included termites (n = 1307, 23.4%), beetles (n = 330, 5.9%), thrips and true bugs (n = 159, 2.9%), hymenopterans other than ants (n = 97, 1.7%), unidentified insects (n = 87, 1.6%), and millipedes and centipedes (n = 65, 1.2%). The remaining eight invertebrate groups accounted for < 1% each (see Table 2 for a more detailed listing). The mean number of prey items was 16 per stomach, 11 in the intestine and 44 for the rectum. The maximum number of prey items consumed was 819 (96 in the stomach, 131 in the intestine and 592 in the rectum) in a toad specimen collected in a banana plantation.

The largest proportion of ants was consumed by toads at Habitat II (89.4%), and of termites at Habitat IV (65.7%; Table 3). The largest proportion of beetles was consumed at Habitat V (12.2%), but the percentage of beetles varied between 3.0% and

Table 2. Analyses of prey items from specimens of *Duttaphrynus melanostictus* from Timor-Leste (n = 83).

	Percentage of toads in which prey type occurred				Total number of items recorded				Number of stomachs in which a stated number of item occurred								Number of intestines in which a stated number of item occurred								Number of rectums in which a stated number of item occurred							
									Number of items								Number of items								Number of items							
Prey items	Stomach	Intestine	Rectum	Entire gut	Stomach	Intestine	Rectum	Entire gut	1	2	3	4	5	6–10	11–20	20+	1	2	3	4	5	6–10	11–20	20+	1	2	3	4	5	6–10	11–20	20+
Annelida	6.0	1.2	–	6.0	11	1	–	12	3	1	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gastropoda	–	–	2.4	2.4	–	–	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–
Araneae and Opiliones	15.7	3.6	24.1	32.5	14	3	26	43	12	1	–	–	–	–	–	–	3	–	–	–	–	–	–	–	16	2	2	–	–	–	–	–
Isopoda	2.4	–	–	2.4	2	–	–	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Myriapoda	20.5	3.6	18.1	32.5	37	3	23	65	11	–	2	–	4	–	–	–	3	–	–	–	–	–	–	–	12	2	–	–	–	1	–	–
Orthoptera and Dermaptera	6.0	1.2	3.6	9.6	5	1	3	9	5	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–
Blattodea: Termitoidae	9.6	10.8	16.9	19.3	277	347	683	1307	–	–	2	–	–	2	1	3[a]	2	–	–	–	–	2	–	5[b]	1	–	2	2	–	1	3	5[c]
Thysanoptera and Hemiptera	20.5	15.7	30.1	43.4	61	33	66	159	9	4	–	–	1	2	–	1	10	–	–	2	–	–	1	–	17	2	2	1	–	2	1	–
Coleoptera	50.6	21.7	50.6	69.9	120	25	178	330	24	7	2	2	3	2	1	1	13	4	–	1	–	–	–	–	12	8	5	2	6	7	1	1
Hymenoptera: Formicidae	65.1	55.4	85.5	94.0	508	386	2527	3437	10	8	4	5	5	10	5	7[d]	14	6	7	4	2	6	3	4[e]	6	6	7	1	3	11	12	25[f]
Hymenoptera: other	10.8	2.4	15.7	24.1	51	2	44	97	4	1	1	–	–	1	–	1	2	–	–	–	–	–	–	–	8	2	1	–	–	–	2	–
Diptera	–	–	4.8	4.8	–	–	11	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	–	–	–	1	–	–
Lepidoptera	1.2	–	–	1.2	1	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Unidentified insects	15.7	10.8	30.1	49.4	25	13	47	87	9	1	–	2	–	1	–	–	6	2	1	–	–	–	–	–	12	9	–	3	1	–	–	–
Insect larvae	9.6	2.4	6.0	16.9	9	2	7	19	7	1	–	–	–	–	–	–	2	–	–	–	–	–	–	–	4	–	1	–	–	–	–	–

[a] Median (mdn) and range (r) of termites found in the three stomachs: mdn = 77; r = 71–91.

[b] Median (mdn) and range (r) of termites found in the five intestines: mdn = 34; r = 22–178.

[c] Median (mdn) and range (r) of termites found in the five rectums: mdn = 75; r = 27–378.

[d] Median (mdn) and range (r) of ants found in the seven stomachs: mdn = 24; r = 21–91.

[e] Median (mdn) and range (r) of ants found in the four intestines: mdn = 33; r = 22–128.

[f] Median (mdn) and range (r) of ants found in the 25 rectums: mdn = 48; r = 24–588.

Table 3. Analyses of prey items recorded in the entire guts of specimens of *Duttaphrynus melanostictus* (*n* = 83) from different habitats in Timor-Leste.

	Total number of prey items					Prey items per taxonomic group as a percentage of the total number of prey items per habitat				
	Habitat					Habitat				
Prey items	I	II	III	IV	V	I	II	III	IV	V
Annelida	12	–	–	–	–	1.0	–	–	–	–
Gastropoda	–	–	1	1	–	–	–	< 0.1	0.2	–
Araneae and Opiliones	4	7	31	1	–	0.3	1.3	1.0	0.2	–
Isopoda	2	–	–	–	–	0.2	–	–	–	–
Myriapoda	39	–	22	2	2	3.1	–	0.8	0.3	1.0
Orthoptera and Dermaptera	6	1	2	–	–	0.5	0.2	0.1	–	–
Blattodea: Termitoidae	568	–	194	426	119	45.6	–	6.6	65.7	58.0
Thysanoptera and Hemiptera	10	20	110	18	1	0.8	3.8	3.7	2.8	0.5
Coleoptera	128	16	111	50	25	10.3	3.0	3.8	7.7	12.2
Hymenoptera: Formicidae	365	474	2394	147	57	29.3	89.4	81.1	22.7	27.8
Hymenoptera: other	75	1	21	–	–	6.0	0.2	0.7	–	–
Diptera	–	–	10	–	1	–	–	0.3	–	0.5
Lepidoptera	–	–	–	1	–	–	–	–	0.2	–
Unidentified insects	37	10	38	2	–	3.0	1.9	1.3	0.3	–
Insect larvae	1	1	17	–	–	0.1	0.2	0.6	–	–

10.3% at the other habitats (Table 3). Aside from Habitat II, ants formed the major part of the diet of toads collected from Habitat III (81.1%), while termites were most frequently consumed by toads collected from Habitats I (45.6%), IV (65.7%) and V (58.1%). Whereas ants formed part of the diet of toads from all habitats, termites were absent in all toads from Habitat II. Results of the NMDS ordination (Figure 2; final stress = 0.152, linear fit R^2 = 0.91) and anosim (R = 0.1195, P = 0.01), however, revealed no overall differences in prey item composition among the habitats. It is evident from both the results of the statistical analyses and the ones summarised in Table 2 that termites were only taken by a few toads, but if present in a specific habitat and when they were consumed, they were found in large numbers in the digestive tract of individual toad specimens.

No vertebrate prey items were found. Seventy-two toads' guts contained plant material (small leaves and leaf fragments, twigs and seeds), and 79 yielded miscellaneous material (small stones: 95.2%, plastic debris: 10.8%). Plastic debris was, with a single exception (a toad from Habitat IV), only found in toads collected in heavily disturbed environments (Habitats I and III).

Parasites

Parasites were found in 77 toads (92.8%), comprising nematodes (85.5%), cestodes (27.7%), trematodes (20.5%), acanthocephalans (6.0%) and turbellarians (2.4%). These were exclusively found in the intestine (65 toads: 78.3%) and rectum (70 toads: 84.3%). Trematodes were only found in toads from Habitats I (66.7%) and III (11.1%). Turbellarians (*n*= 2) were only found in two toads from Habitat III (5.6%).

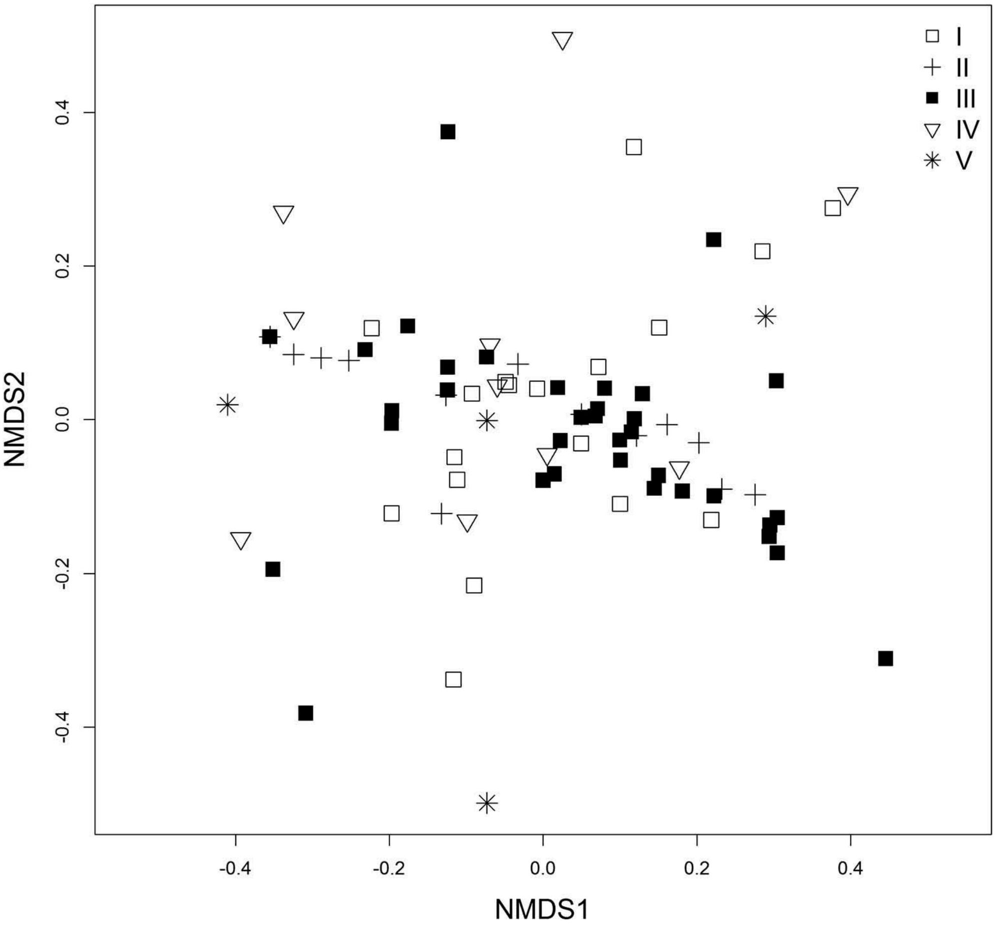

Figure 2. Ordination of non-metric multidimensional scaling analysis (NMDS) based on Bray-Curtis dissimilarities of the food item composition of toads from different habitats. I = park grounds of the Timor Lodge Hotel, Dili, Dili District; II = dry riverbed at the confluence of the Comoro and Bemos rivers, 8 km south of the Comoro River bridge, Dili District; III = banana plantation south of the confluence of the Comoro and Bemos rivers, Aileu District; IV = dry forest at the fringes of Lake Maubara, Liquiça District; V = *Corypha* forest west of Raeme, Liquiça District. Symbols close to each other in the ordination space are most similar. Their distribution well indicates that food composition does not differ between habitats.

Discussion

There were several limitations to our study, including the collection of adult Asian toads during a specific period of the year (the dry season in northern Timor-Leste) only. Thus, our results represent a snapshot in time. Food consumption, volume and composition may change over the course of the year, with seasonal variation reported by Mathew (1999), for toads collected in the Pathanamthitta District, Kerala State, India.

Our results show that the Asian toad in Timor-Leste preys on a wide variety of invertebrates, as other studies on the diet of *Duttaphrynus melanostictus* from regions within its natural range have already demonstrated (Berry and Bullock 1962; Mathew

1999; Yap 2015). No restricted specialisation appears to occur, but the number of ants and termites consumed is striking. Berry and Bullock (1962), Mathew (1999) and Yap (2015) demonstrated that small eusocial insects form the major component of the diet of *D. melanostictus*. In instances where a large number of small eusocial insects were recorded in single toads, it is likely that the respective toads lingered near an ant or termite column after being initially attracted by the column's continual movement. Such a feeding strategy was recently reported for the Australian frog *Platyplectrum ornatum* (Gray, 1842) and referred to by the author as 'blitz-feeding' (Mo 2015). While we encountered cockroaches, including their nymphs, in high numbers in Habitat I when collecting herpetofaunal specimens at night, none of these fast-moving insects was found to be part of the toads' diet.

No statistically significant differences were found in the invertebrate diet of toads between different habitats. Most ant species are ecological generalists found in diverse habitats, and thus it is not surprising that specimens of this successful insect group were found in the majority of toads (78 of 83; 94.0%) across all habitats sampled. Termites, however, were not found in the guts of toads from Habitat II, probably because this habitat, prone to flooding and erosion, does not favour the long-term establishment of termitaria, while ants may be abundant in this kind of habitat (Wishart 2000; Larned et al. 2007). Termites were found in 16.7% of the 18 toads from Habitat I (where ants were found in 100% of toads), 22.2% of the 36 toads from Habitat III (ants in 94.4%), 33.3% of the 12 toads from Habitat IV (ants in 83.3%) and 25.0% of the four toads from Habitat V (ants in 75.0%). Whenever termites were numerically dominant in the food spectrum of toads from a specific habitat, these were consumed in large numbers, but by only a few individual toads. This indicates that these toads were consuming termites from nests or shelter tubes, where these insects are abundant, shortly before the toad itself was collected. The feeding of *Duttaphrynus melanostictus* thus seems to depend on the abundance and availability of prey items, and on opportunistic encounters, a finding that is congruent with that of Berry and Bullock (1962). This indicates that *D. melanostictus* is a generalist feeder.

Although Timor harbours many native ant species (> 100; Trainor and Andersen 2010), some of which are endemic or likely endemic (Andersen et al. 2013), the impact of *Duttaphrynus melanostictus* on these insects through direct predation cannot be evaluated at present and further studies are required. Furthermore, it is not known how *D. melanostictus* and many other toad species that eat ants in abundance cope with the large amounts of formic acid their prey contains. There may be some special mechanism in toads to overcome the problem of potential chemical burns caused by formic acid.[3] Timor is also known for its highly endemic land gastropod fauna (e.g. Köhler and Kessner 2014), but snails and slugs were not found to be a major component in the diet of the Asian toad by us or other researchers (Berry and Bullock 1962; Mathew 1999; Yap 2015). Hence, we assume that the toad's impact on the gastropod fauna is negligible.

Plant material, small stones and plastic debris were likely taken in with invertebrate prey. A substantial amount of plant material in the guts of *Duttaphrynus melanostictus* was also reported by Berry and Bullock (1962) and Mathew (1999), and it is well known that the guts of other toad species can contain vegetation (e.g. Krakauer 1968; Campbell 1970; Clarke 1974; Zug et al. 1975; Zug and Zug 1979; Evans and Lampo 1996; Anderson et al. 1999; Reed et al. 2007; Crnobrnja-Isailovic et al. 2012). While small stones might have been ingested accidentally, it is also possible that deliberate ingestion of stones might aid in the mechanical breakdown of heavily chitinous prey items. The occurrence of plastic in the guts of *D. melanostictus* is unsurprising, since these toads, like many anurans, feed in a non-selective manner and are prone to ingesting plastic when residing in or near areas where human debris accumulates. Plastic was also reported in the guts of toads by Grant (1996; *Rhinella marina*) and Sabagh and Carvalho-e-Silva (2008; *R. icterica*). While the adverse effects of plastic debris consumption have been documented for marine animals (e.g. National Oceanic and Atmospheric Administration Marine Debris Program (USA) 2014), the effect on terrestrial animals has not yet been fully explored. As the most threatened vertebrate class, amphibians are exposed to a considerable number of environmental hazards (e.g. Stuart et al. 2004; Alford 2011; Bishop et al. 2012). The effects of ingested plastic may represent an additional negative factor that has not yet been quantified.

Vertebrate prey was not found in the guts of Asian toad specimens we collected (see also Berry and Bullock 1962; Mathew 1999; Yap 2015), despite the presence of small frogs and squamates at least in Habitats I, II and III. While the ingestion of an *Indotyphlops braminus* specimen by a *Duttaphrynus melanostictus* in Timor-Leste (O'Shea et al. 2013) appeared to be of an exceptional nature, Hahn (1976) previously reported on the consumption of this blindsnake by the Asian toad. Hahn (1976) collected 10 *D. melanostictus* specimens at Lundu, Sarawak, Malaysia, one of which regurgitated a blindsnake, and he found three additional blindsnakes in an undisclosed number of toad stomachs. While this one find may appear to represent a considerable rate of vertebrate predation, food spectrum analysis for which a larger number of Asian toads were examined in other surveys (Berry and Bullock 1962; Mathew 1999; Yap 2015) revealed no blindsnake specimens at all. Thus, it is most likely that Hahn (1976) serendipitously collected toads that had fed in a habitat with a high blindsnake encounter rate, and that availability and abundance of blindsnakes, as opposed to dietary preference on the part of *D. melanostictus*, can explain the high predation rate. Both Hahn (1976) and O'Shea et al. (2013) reported that the consumed snakes did not show much damage as a result of ingestion and passage into and out of the toad digestive system. It therefore appears that a blindsnake's hard, tightly imbricate scalation provides sufficient armour to protect the snake from digestion. Failure to digest prey means that the prey item does not contribute to the nutritional intake of the individual, and such prey is therefore a poor choice. Thus, consumption of blindsnakes by *D. melanostictus* is likely a consequence of the inability of toads to distinguish between blindsnakes (or other small, elongated vertebrates) and more suitable, similar-sized lookalikes (e.g. annelids, myriapods). We assume a greater impact on blindsnake species (some of which are localised endemics within the range of the Asian toad) by *D. melanostictus* is unlikely but not inconceivable. Blindsnakes, being largely fossorial, are rarely seen on the surface, usually only at night, and especially after rain (e.g. Cogger 2014). Their restricted habitat and specialised lifestyle may protect them against negative effects on the part of the Asian toad.

The success of *Duttaphrynus melanostictus* within its native and introduced range may be partly attributed to its generalist diet, including its ability to utilise human-dominated areas for foraging. These dietary attributes complement other characteristics of *D. melanostictus*, which makes it a successful invader of new habitats, such as being a habitat generalist in terms of reproductive requirements (e.g. Daniel 1963; Whitten et al. 1997; Saidapur and Girish 2001; O'Shea et al. 2012, 2015). Rather than direct predation on part of the Asian toad, niche overlap between this species (and/or its life stages) and Timor's native fauna may have a much greater impact that has yet to be investigated.

Notes

1. Jamdar and Shinde (2013) presented a gut content analysis of *Duttaphrynus melanostictus* from Aurangabad, Maharashtra, India. However, their article was printed in a 'predatory journal' (a journal that does not offer peer review but charges for article processing), the *Indian Journal of Scientific Research and Technology* (according to Beall's (2016) list of standalone journals), and contains sentences and paragraphs that are identical or similar to ones in Berry and Bullock (1962), who were not cited by Jamdar and Shinde (2013). This identifies Jamdar and Shinde's work as plagiarism. For this reason we do not consider their paper herein.
2. *Duttaphrynus melanostictus* presumably arrived in West Timor, Indonesia, around 1999–2000, entered Timor-Leste shortly afterwards (Trainor 2009) and was recorded in Timor-Leste's easternmost district (Lautém) for the first time in August 2014 (MCZ A-149329 from Com).
3. The myrmecophagous horned lizards (genus *Phrynosoma*) incapacitate their prey by binding them with mucus secreted by distinct papillae within their pharynx (Schwenk and Sherbrooke 2003). A similar mechanism may exist in toads that consume ants in high numbers, but this has not yet been documented.

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Appendix. Museum specimens examined

Duttaphrynus melanostictus

Timor-Leste: Timor Lodge Hotel, Dili, Dili District: USNM 581037–54; 8 km south of the Comoro River bridge, at the confluence of the Comoro and Bemos rivers, Dili District: USNM 581018–20, 581027–36; Confluence of the Comoro and Bemos rivers, Aileu District: USNM 581003–17, 581021–26, 581057–71; Lake Maubara, Liquiça District: USNM 581055–56, 581072–81; West of Raeme, Liquiça District: USNM 581083–86.

6.6 Paper 12

Mecke, S., Kieckbusch, M., Graf, T., Beck, L.A., O’Shea, M. & Kaiser, H. (2016): First Captive Breeding of a Night Skink (Scincidae: *Eremiascincus*) from Timor-Leste, Lesser Sunda Islands, with Remarks on the Reproductive Biology of the Genus. *Salamandra*, **52**(2): 178–188.

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First captive breeding of a night skink (Scincidae: *Eremiascincus*) from Timor-Leste, Lesser Sunda Islands, with remarks on the reproductive biology of the genus

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Abstract. We report two instances of captive breeding in a species of Timorese night skink (genus *Eremiascincus* Greer, 1979) in October and December 2012. Four and three neonates, respectively, with total lengths of ca 40 mm each, were discovered during routine maintenance of a terrarium, in which three adult animals (1 male, 2 females) were kept. The absence of eggshells in the terrarium and the unlikelihood of post-eclosion oophagy by the adults suggest that the reproductive mode of the species is viviparous. We also provide a summary of available information pertaining to the reproductive biology of other members of the genus *Eremiascincus*.

Key words. Reptilia, Squamata, Lygosominae, *Eremiascincus*, skink, reproductive mode, viviparity, Timor-Leste.

Zusammenfassung. Wir berichten über die Nachzucht einer Nachtskink-Art (Gattung *Eremiascincus* Greer, 1979) aus Timor-Leste. Bei Routinearbeiten im Terrarium der drei Adulti (1 Männchen, 2 Weibchen) wurden im Oktober und Dezember 2012 vier, beziehungsweise drei Jungtiere mit Gesamtlängen von je ca. 40 mm entdeckt. Da keine Eierschalen im Terrarium gefunden wurden und das Fressen der Schalen durch die Adulti nach dem Schlupf der Jungtiere unwahrscheinlich ist, liegt der Schluss nahe, dass es sich bei diesem Taxon um eine lebendgebärende Skinkart handelt. Wir präsentieren zudem eine aktuelle Übersicht zur Reproduktionsbiologie der Gattung *Eremiascincus*.

Schlüsselwörter: Reptilia, Squamata, Lygosominae, *Eremiascincus*, Skink, Reproduktionsmodus, Viviparie, Timor-Leste.

Introduction

Night skinks (genus *Eremiascincus* Greer, 1979) are small- to medium-sized skinks (max. SVL ca 125 mm) that inhabit tropical and subtropical environments in the Lesser Sunda Archipelago and Australia, where some taxa have also invaded the continent's central arid zone (Mecke et al. 2009, 2013). Four of the 14 *Eremiascincus* species hitherto described occur in the Lesser Sundas, including *E. antoniorum* (Smith, 1927), *E. butlerorum* (Aplin et al., 1993), *E. emigrans* (van Lidth de Jeude, 1895), and *E. timorensis* (Greer, 1990), all of which were previously assigned to the *Glaphyromorphus isolepis* group (Greer 1990). Evidence is currently emerging that *E. emigrans* may be a species complex (Mecke et al. unpubl. data) and many candidate taxa (both in the Lesser Sundas and Australia) still await scientific description.

Lesser Sundan *Eremiascincus* species possess smooth and very glossy scales, a cylindrical body with a long tail, and, in part (some Timor Island populations), a brightly-coloured venter (yellow, orange, pink). Bright ventral coloration is a character state that Timorese *Eremiascincus* have likely retained from a common ancestor; it is also found in *Hemiergis*, the putative sister group of *Eremiascincus* as inferred from molecular phylograms by Reeder (2003), Skinner (2007), and Rabosky et al. (2007). This conspicuous coloration begins either in the gular region or at the level of the forelegs. The majority of *Eremiascincus* species (all Australian members of the genus and the *Eremiascincus emigrans-butlerorum* group) appear to be lacking this distinctive feature, and the significance of the character, in terms of either its function in these crepuscular and nocturnal forms or its loss within the genus, is unknown at present. The dorsal ground colour of the Sundan taxa is brownish; the flanks are usually dark (especially in the anterior portion of the body) and spotted with white or cream. Some populations from Timor Island may ultimately be described as new species (Kaiser et al. 2011, 2013, O'Shea et al. 2015). One of these, an elongated, relatively short-legged taxon with a yellow venter, similar in overall morphology to *E. antoniorum*, occurs in the northwestern highlands of Timor-Leste (Ermera District) and is herein referred to as *Eremiascincus* "Ermera."

Since systematic and phylogenetic analyses based on morphology and/or genetic data can be significantly improved by supplemental information from ecological, ethological, or reproductive data (see Salthe 1967, Scholz 1995, in den Bosch & Zandee 2001, Haddad et al. 2005), we collected specimens of *Eremiascincus* "Ermera" in order to make observations on live specimens in captivity. We here report the first captive breeding of an *Eremiascincus* species from the Lesser Sunda Islands and outline the current knowledge of reproduction in the genus.

Materials and methods

During our herpetofaunal surveys in Timor-Leste (summarized in Kaiser et al. 2011, 2013, O'Shea et al. 2012, 2015, Sanchez et al. 2012), we collected specimens of *Eremiascincus* "Ermera," a little known cryptozoic skink species (Fig. 1A, B), from under rock piles and deadwood in a rainforest environment located at the Meleotegi River near Eraúlo, Ermera District, Timor-Leste (Fig. 1C). Voucher specimens for taxonomic work were collected in low numbers and euthanised by intracardiac injection of 5% procaine. Standards for processing (e.g., preparation and preservation methods) were summarized by Kaiser et al. (2011). Preserved specimens are housed in the United States National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM). Four live adult specimens were collected in February of 2012, transported to Germany, and housed in a terrarium at the Philipps-Universität Marburg (see Results and discussion – Husbandry). These individuals have received field numbers and we intend to deposit them in the USNM after their natural deaths.

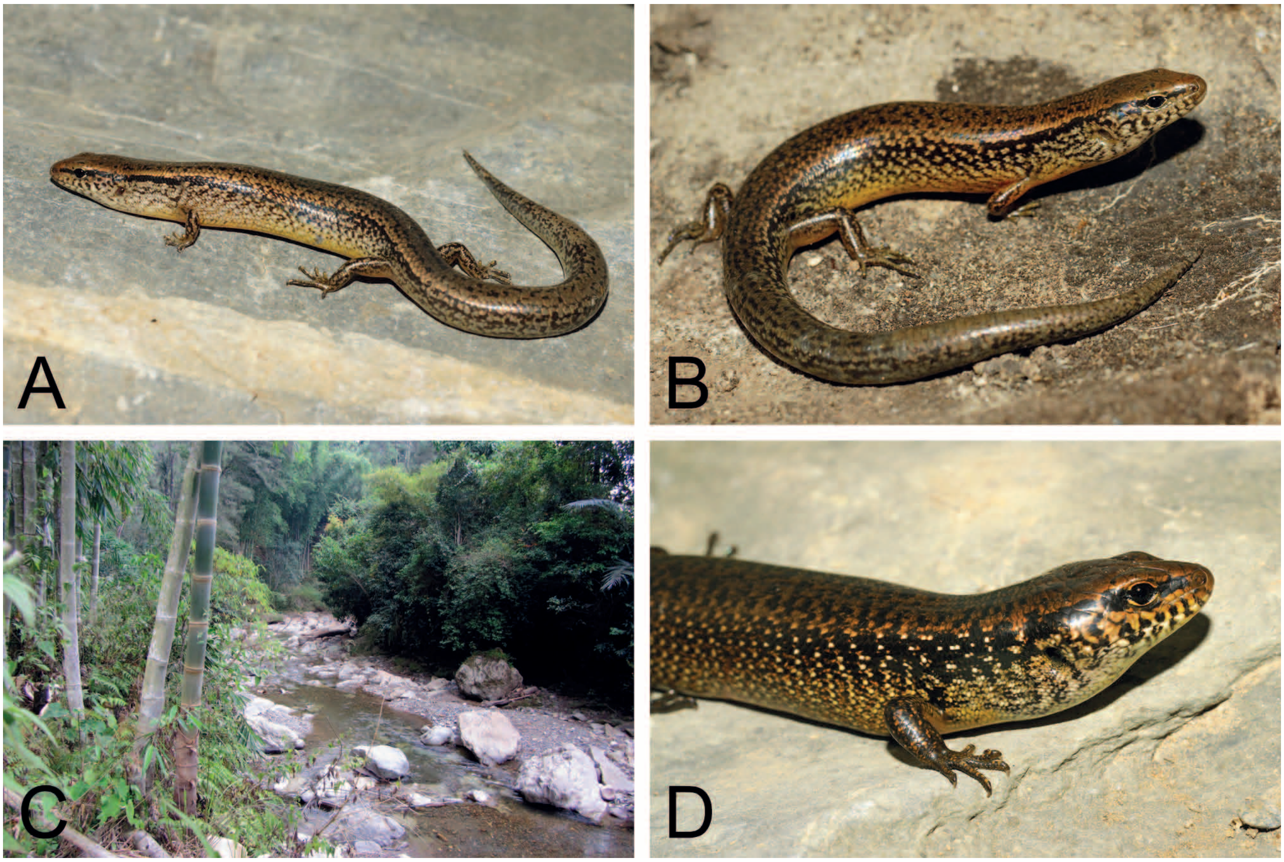

Figure 1. A + B) Lateral views of adult specimens of *Eremiascincus* "Ermera" from Ermera District, Timor-Leste; C) Rainforest habitat of *Eremiascincus* "Ermera" and *E. timorensis* at the Meleotegi River, near Eraúlo, Ermera District; D) Lateral view of an adult specimen of *Eremiascincus timorensis*. Photos by Sven Mecke.

Results and discussion

Habitat and natural history, husbandry, and captive breeding

Habitat and natural history. – *Eremiascincus* "Ermera" is known from only a single location in the evergreen, high mountain rainforest (altitude ca 1,200 m) at the Meleotegi River near Eraúlo, Ermera District, Timor-Leste (08°47' S, 125°27' E) and appears to be restricted to this habitat. The rainforest most likely represents a secondary forest that largely resembles an original old-growth stage. Human activities during the Second World War (as inferred from Japanese buildings in the area) may have altered at least part of this forest area that lies within a region also used for agricultural purposes, including plantations.

The area experiences an average annual precipitation of ca 2,600 mm, although strong intra-annual fluctuations in rainfall occur. Average humidity is > 70% during most months of the year, with average peak values of > 80%. Average temperatures throughout the year fluctuate between a minimum of ca 15°C and a maximum of 25°C, with maximum peak temperatures > 30°C. More detailed climate data can be found on the website of the Seeds of Life project hosted by the Ministry of Agriculture and Fisheries, Timor-Leste, at seedsoflifetimor.org.

The montane rainforest is home to four species of frogs (as of October 2012), including the introduced toad *Duttaphrynus melanostictus* (Schneider, 1799), a putatively new species of rice paddy frog (genus *Fejervarya*), the river frog *Limnonectes timorensis* (Smith, 1927), and the tree frog *Litoria everetti* (Boulenger, 1897). Lizards are more diverse, with at least seven species recorded (as of October 2012), including the agamid *Draco timoriensis* Kuhl, 1820, two putatively new four-fingered skink species (genus *Carlia*), the night skinks *Eremiascincus* "Ermera" and *E. timorensis*, the sun skink *Eutropis* cf. *multifasciata*, and two putatively new species of forest skinks (genus *Sphenomorphus*). Interestingly, no geckos or snakes have so far been recorded from this habitat.

Eremiascincus "Ermera" is a crepuscular and nocturnal skink that inhabits permanently humid microhabitats and its occurrence largely depends on substrate moisture (S. Mecke pers. obs.). Our experience indicates that during wet weather conditions, individuals can be found under rock piles at fairly high densities (up to four individuals per rock pile, depending on its size), whereas the species is less commonly encountered during dry periods. *Eremiascincus* "Ermera" specimens were encountered in close proximity to paths and the riverbed (most frequently under human-assembled rock piles), as well as in rainforest covering slopes (under dead wood). They were absent from the surrounding coffee plantations, an environment that largely lacks understorey and undergrowth. This species is found in syntopy with the larger Timor night skink (*E. timorensis*; Fig. 1D). In the event of an external threat, these semi-fossorial skinks attempt to burrow into the substrate by means of lateral undulation, which will often allow them to escape capture. Cursory observations during dissection revealed a food spectrum that appears to consist primarily of arthropods and their larvae.

Husbandry. *Eremiascincus* "Ermera" specimens were housed in a terrarium at the Philipps-Universität Marburg, Germany, where three animals (1 male, 2 females) are still in residence at the time of this writing. One animal died shortly after its arrival, although it was well nourished and had weathered the stress of transportation quite well; it is possible that intraspecific rivalry caused the animal's death. Antagonistic behaviour between these skinks, however, has never been observed, and we therefore had no reason to separate individuals. The unfortunate incident suggests that individuals of this taxon should probably best be kept in small groups of only a single male and one or two females. In spite of the loss of this specimen husbandry in general is progressing successfully and has resulted in captive-bred progeny.

The three adult night skinks have a mean snout–vent length (SVL) of 57 mm (individual lengths of 54, 56, and 60 mm). The individual with the greatest SVL has an original tail measuring 88 mm, whereas the tails in the other two specimens are partly regenerated and measure 78 mm (at 54 mm SVL) and 62 mm (at 56 mm SVL), respectively. All animals weigh close to 4.6 g. One individual is depicted in Fig. 2A.

The skinks are kept in a terrarium measuring 50 × 30 cm with height of 30 cm (Fig. 2B). A fertiliser-free, 5-cm peat-clay mix serves as a bottom substrate, which is richly structured with small rocks, dead wood, pieces of bark, leaf litter, and vegetation. Deadwood and pieces of bark are partly buried in the soil to provide refuges. The animals also burrow in more compact substrate, or "swim" through loose soil in the manner of some deserticolous, psammophilic reptiles. Some *Eremiascincus* species from Australia's arid zone are called "sand swimmers" for this reason (see Greer 1979), and Mecke et al. (2013) called them "Australische Sandfische," translating as "Australian sand fish" from German.

The rear wall of the terrarium consists of pieces of hollow clay tiles that are planted with epiphytic plants (*Tillandsia* spp., Bromeliaceae) and wandering jew (*Tradescantia zebrina*, Commelinaceae). The sidewalls are covered with corkboard. Plants covering the ground include bastard copperleafs (*Acalypha* cf. *chamaedryfolia*, Euphorbiaceae), devil's ivy (*Epipremnum aureum*, Araceae), peace lilies (*Spathiphyllum* sp., Araceae), prayer plants (*Marantha leuconeura*, Marantaceae), and small ferns.

The terrarium of this sciaphilic species that is sensitive to heat jams is illuminated during the warmer months of the year with a low-heat 25-W spotlight, mounted inside the terrarium. A warming, 60-W light bulb is operated outside the terrarium in winter. Neither of these light sources provides bright light, ensuring optimal lighting conditions for the species. UV irradiation is provided by a Lucky Reptile Bright Sun UV Jungle® (Waldkirch, Germany; luckyreptile.com) through the terrarium's mesh lid, for three hours every other day, even though nocturnal lizards probably require no UV-B light (Adkins et al. 2003).

The ambient room temperature, in conjunction with the spotlight, creates a temperature range of 22–29°C inside the terrarium; the basking spot right below the light bulb is warmed to temperatures of 29–34°C. This temperature regime is concordant with daytime temperatures in the natural habitat. We also recommend reducing the temperature by 2–4°C at night. *Eremiascincus* are "cryophilic" lizards (Bennett & John-Alder 1986, John-Alder & Bennett 1987) prone to heat stroke and should therefore never be exposed to excessive temperatures. The vegetation and substrate are sprayed with moderate amounts of water once or twice daily, maintaining a relative humidity of approximately 70%. Although relative humidity in the natural environment might be higher (> 80%), substrate moisture would appear to be of greater importance for emulating natural conditions.

These skinks are only infrequently observed basking and usually only if the basking spot is not exposed to view (e.g., concealed by overhanging vegetation). Usually only the anterior part of the body protrudes from a hiding place (see also Rankin 1978), and the animals will quickly disappear into the substrate when they notice movements in their surroundings. In our experience, night skinks rarely bite, even when handled, but will readily autotomise their tails (see Brown 2012).

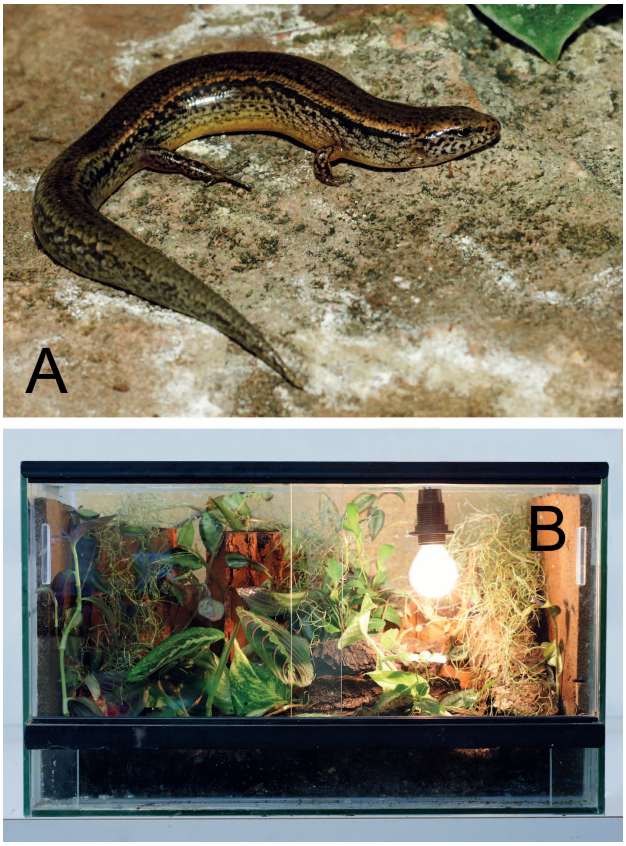

Figure 2. A) A captive specimen of *Eremiascincus* "Ermera" in a terrarium at the Philipps-Universität Marburg, Germany; B) The terrarium of the first author in which three adult specimens of *Eremiascincus* "Ermera" are kept. Photos by Thomas Beitz.

The *Eremiascincus* "Ermera" specimens in our care are fed with insects (e.g., fruit flies, stick insects, small crickets, locusts, and mealworms). During the summer months, the skinks are also fed a wide variety of non-protected, field-collected arthropods and caterpillars. Live feeder animals are regularly dusted with supplementary mineral aggregate mixtures, such as Korvimin® (WDT, Garbsen, Germany; wdt.de) and Sera® Reptil (Sera, Heinsberg, Germany; sera.de). The size of food items does not appear to play a significant role in the nutrition of these skinks. Small insects (offered in large quantities) are consumed equally readily as medium-sized crickets or mealworms. We never observed the skinks drinking. Interestingly, the captive *Eremiascincus* individuals defecate only in one particular spot of the terrarium, a habit that has also been recorded from the skink genera *Egernia* and *Liopholis* (D. Brown in litt.).

Captive breeding and raising of juveniles. The reproduction of the night skinks in our care in late 2012 came as a surprise, and happened under circumstances similar to those described by Rankin (1978) for the Queensland endemic *E. pardalis* (Macleay, 1877). During routine maintenance on 15 October 2012 (a date corresponding to the late dry season in Timor-Leste), a neonate skink of ca 40 mm in total length was found on a vertically arranged piece of bark in the upper part of the terrarium. A thorough search was performed immediately, and three additional juveniles with reddish flanks were captured (one juvenile is depicted in Fig. 3A, B). The small skinks were found hiding under items of decoration or in the bottom substrate, where they would be reasonably safe from potential cannibalism by the adults. Subsequently, the terrarium was cleaned out (the rear wall at that time was covered with corkboard only) and the bottom substrate removed; the latter was thoroughly searched for eggshells, but none were found.

On 9 December 2012 (a date corresponding to the early wet season in Timor-Leste) three more juveniles were captured in the terrarium, and once again a search yielded no eggshells (see Reproductive mode of *Eremiascincus* "Ermera"). No courtship behaviour or copulation events were ever observed by us, likely due to the secretive lifestyle of these skinks.

The juveniles were separated from the adults, and housed and raised in small plastic terraria (18 × 11.5, height 11.5 cm; one terrarium for one or two young), as a precaution against potential cannibalism by the adults. They were fed the same types of small invertebrates as the adults; the first feeding session took place the day after the juveniles were found and food was provided at least every other day. All their food was supplemented with Korvimin® and hatchlings were exposed to UV irradiation twice weekly. Unfortunately, three hatchlings died in early January 2013 when the heating system for the room housing the terraria and the terrarium lighting failed on a cool winter weekend.

Based on our overall experience, we advise against trying to raise juvenile tropical *Eremiascincus* in small terraria like those described above. Although these seem to be more easily managed (e.g., individuals can be captured quickly), an adequately naturalistic microclimate is difficult to emulate, and shortfalls in this regard (e.g., deficient substrate moisture) may quickly result in moulting problems or overheating. The remaining juveniles were transferred to larger, densely planted tanks, measuring at least 30 × 20 cm. The young skinks became used to the presence of a caretaker quickly and even began taking food from tweezers.

These two instances of captive breeding are the first ones documented for a Lesser Sundan *Eremiascincus*, and only the second published for a tropical taxon of this genus. Given the exploratory nature of keeping these skinks, we intentionally did not measure all hatchlings in an effort to minimise stress. We therefore measured the SVL and tail length (TailL) of only a single representative individual from the first litter (captured on 15 October 2012) in order to establish a baseline and expecting that growth in all individuals would follow a similar pattern. One month after having been found, this individual had a total length of 51 mm (SVL = 24 mm; TailL = 27 mm), indicating that TailL approximately equals SVL during the first phase of ontogeny (SVL/TailL = 0.89). At seven months of age, on 14 May 2013, the same individual had a total length of 101 mm (SVL = 40 mm, TailL = 61 mm). This individual had nearly doubled in length (+ 49.5%) during the intervening 6-month period (mid-November 2012 to mid-May 2013). The increase in SVL was less (+ 40.0%) than in TailL (+ 55.7%) and the SVL/TailL ratio decreased from 0.89 to 0.66. By comparison, the largest adult specimen with an original tail measured 148 mm with an SVL/TailL ratio of 0.68. Thus, after approximately half a year, individuals may reach body proportions that match those of adults. When the second set of measurements were taken, the characteristic yellow ventral coloration was also noticed for the first time. Maximum body size appears to be reached approximately one year after hatching. At that point in their development, two specimens from the second litter had SVLs of 52 and 53 mm with TailLs of 77 and 80 mm, respectively, arriving at SVL/TailL ratios of 0.68 and 0.66.

We were not able to verify whether the skinks reproduced in 2013 and 2014. Because the first author was conducting fieldwork overseas during the months that included the period of deposition in 2012, it is possible that the skinks reproduced but that resultant juveniles were overlooked by stand-in caretakers and fell victim to cannibalistic adults. There is also the possibility that the females of this species may not reproduce annually.

Reproduction in *Eremiascincus*

Reproductive mode of *Eremiascincus* "Ermera". – Owing to the fact that authors use the terms "ovoviviparity" and "ovoviviparous" to distinguish between quite different reproductive patterns, we herein use "viviparity" and "viviparous" (= live-bearing) sensu Blackburn (1994: 65) to describe "species in which the female retains eggs to term in her reproductive tract and bears fully-developed, autonomous offspring." Species with offspring that are still surrounded by an egg membrane at birth, but hatch immediately are also considered viviparous. The terms "oviparity" and "oviparous" are used in their literal sense, i.e., in reference to taxa that deposit unhatched eggs that continue to develop extracorporeal. For a discussion of these terms see Blackburn (1994).

The subject population of *Eremiascincus* from the Timor-Leste highlands (altitude ca 1,200 m) is apparently viviparous, as no remains of eggshells could be traced after either instance of our unexpectedly-found juveniles. Whereas Rankin (1978) concluded on the basis of a similar observation that *E. pardalis* was a live-bearer (or at least certain populations of this species), he offered as an alternative explanation that adults could have consumed any eggshell remnants. Although this scenario is theoretically

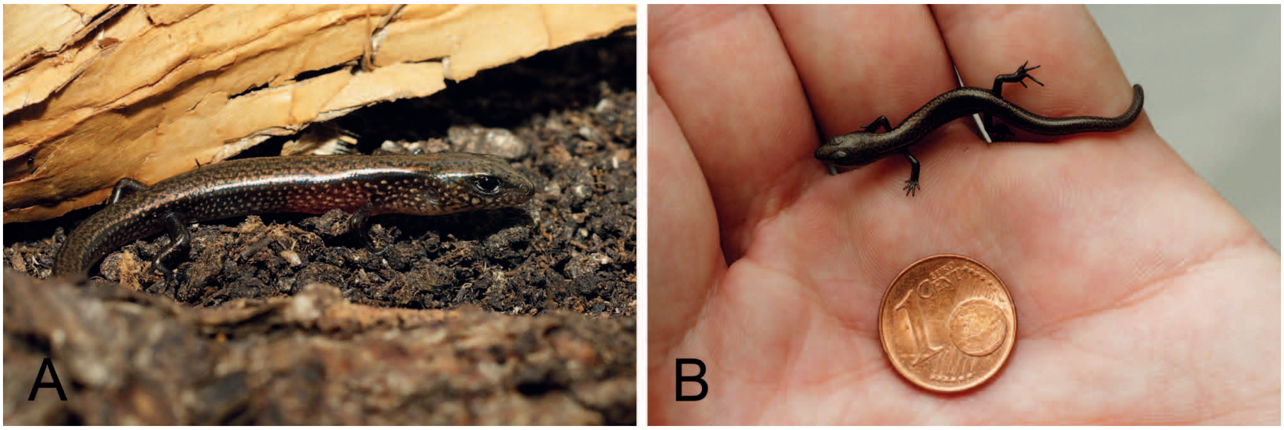

Figure 3. A + B) A juvenile specimen of *Eremiascincus* "Ermera". Note the differences between the juvenile and adult colour pattern (cf. Fig. 2A). The specimen was approximately two days old when it was photographed. Photos by Thomas Beitz.

Table 1. Reproductive data for night skink species (genus *Eremiascincus*). Sample size [n] is given in square brackets, mean values in parentheses. Abbreviations: (?) – reproductive mode unknown; O – oviparous; V – viviparous; NSW – New South Wales; NT – Northern Territory; SA – South Australia; QLD – Queensland; WA – Western Australia; SVL – snout–vent length; TailL – tail length; TL – total length. See also James & Losos (1991) whose data we did not use for this table due to the problems summarized in the "Results and discussion" section (Reproduction in *Eremiascincus*). No data on the reproductive biology of *E. brongersmai* and *E. timorensis* are available.

Species	Country	SVL of gravid females (mm)	Brood size	Reproductively active^{1}/ oviductal eggs or oviposition/ birthing period^{2}	Egg size (mm)	Size of juveniles after hatching or birth (mm)	References
E. antoniorum (?)	Indonesia (Timor)	64 [1]	–	^{1} from late August on (mid-dry season)	–	–	Greer (1990)
E. butlerorum (?)	Indonesia (Sumba Island)	–	–	^{1} late dry to early wet season	–	–	Aplin et al. (1993)
E. douglasi (O)	Australia (NT, northern wet/dry tropics)	70 [1]	5 [1]	^{1} November to January (mid-wet season) (James 1983 quoted in Greer 1989)	–	–	Greer (1989)
E. emigrans (O)	Indonesia (widely distributed in Lesser Sundas)	–	–	^{1} specimens collected in November (late dry season) on Komodo with follicular development	–	–	Auffenberg (1980)
E. fasciolatus (O; V – reports questionable)	Australia (eastern QLD)	123 [1]	8 [1]	^{2} early December (early wet season)	–	–	Mecke et al. (2013) (cf. Waite 1929, Worrell 1963, Greer 1979, 1989)
E. intermedius (O)	Australia (arid NT, northeastern WA)	74–82 (78.3) [3]	4–5 (4.5) [2]	^{2} early November to mid-March (wet season)	–	–	S. Mecke pers. obs.
E. isolepis (O) species complex, the Mitchell Plateau form reproduces at a smaller size and tends to have smaller clutches*	Australia (WA, NT, QLD, northern wet/ dry tropics)	–	4 [1]	^{1} September to February (mid-wet season) (James 1983 quoted in Greer 1989); specimens examined by S. Mecke had oviductal eggs from mid-October to end of January. A single specimen in WAM (R132597) collected in May contained large oviductal eggs.	–	–	Loveridge (1949)
		51–64 (58.8) [4]	3–8 (4.8) [4]		–	–	Greer (1989)
		51–72 (59.6) [17]	1–9 (5.2) [14]		4.0–9.2 × 2.8–5.9 (6.8 × 4.7) [9]	–	S. Mecke pers. obs.
E. musivus (O)	Australia (WA, Pilbara)	57 [1]	3 [1]	^{2} mid-February (mid-wet season)	11.4 × 5.7–6.2 (11.4 × 6.0) [3]	–	S. Mecke pers. obs.
E. pallidus (O)	Australia (arid WA, western NT, northwestern SA)	65–69 (67) [2]	1 [1]	^{2} mid-October to January (early to mid-wet season)	7.4 × 5.1 [1]	–	S. Mecke pers. obs.
E. pardalis (O, V)	Australia (QLD, Cape York)	–	4 [1]	^{2} end of January (mid-wet season)	–	SVL=25–26 TailL=34–35	Rankin (1978) (reported as V)
		67–68 (67.5) [2]	3–6 (4.5) [2]	–	–	–	Greer (1989; reported as O; see Greer & Parker 1974)

Species	Country	SVL of gravid females (mm)	Brood size	Reproductively active[1]/ oviductal eggs or oviposition/ birthing period[2]	Egg size (mm)	Size of juveniles after hatching or birth (mm)	References
E. phantasmus (O)	Australia (inner Lake Eyre basin)	–	2–7 [?]	–	16–17× 10–12 [?]	SVL=32–36 TailL=72–75	Brown (2012); Mecke et al. (2013)
		84–93 (87.2) [5]	3–4 (3.3) [3]	[2] early to mid-November	–	–	S. Mecke pers. obs.
E. richardsonii (O) species complex; the Nullarbor Plain form reproduces at a smaller size (61–71) (66) [2]	Australia (arid WA, SA, NT, QLD, NSW)	79–116 (94.6) [5]	3–7 (4.6) [5]	–	–	–	Greer (1989)
		–	2–8 [?]	–	16.5–19.5× 9.9–10.1 [?]	SVL=31–34 TailL=77–80	Brown (2012)
		89–113 (94) [5]	5–6 (5.5) [5]	[2] mid-October to mid-February	–	–	S. Mecke pers. obs.
E. “Ermera” (V)	Timor-Leste	~55	3–4 (3.5) [2]	[2] October to December (late dry to early wet season)	–	TL=~40	S. Mecke pers. obs.

* Here we refrain from drawing inferences on species delimitation. In most contexts it is better to use a conservative approach than to potentially falsely delimit entities that do not represent actual evolutionary lineages. Hence, the data here presented for *E. isolepis* are data combined from different populations.

possible, we consider such behaviour unlikely. Species of *Eremiascincus* do not show any type of nest-, clutch-, or egg-guarding behaviour that could provide an opportunity for concomitant post-eclosion oophagy (e.g., to prevent potential predators from discovering newly hatched skinks). Furthermore, while there may be a nutritional reason to consume eggshells, which are an excellent source of dietary calcium, adults would have had to find such shells serendipitously and independently after the two described events, and also after the one described by Rankin (1978). We have also been unable to locate documented case examples of post-eclosion oophagy in lacertilian taxa; studies only report the well-known phenomenon of pre-eclosion oophagy, in which eggs are consumed whole as part of the diet (e.g., Angelici et al. 1997, Martínez-Torres 1999, Schwenk 2000). Reproductive data for *Eremiascincus* “Ermera” and other members of the genus (e.g., on brood size, reproductive and birthing period, and egg size), including some observations by the first author, are summarized in Table 1.

Notes on the reproductive biology of other *Eremiascincus* and related taxa. Information on the reproductive biology of the genus *Eremiascincus*, both in the wild and captivity, is quite limited and only available for selected species (e.g., Rankin 1978, Greer 1989, 1990, James & Losos 1991, Mecke et al. 2009, 2013, Brown 2012), most of which are oviparous. Table 1 shows that little data are available for egg and hatchling sizes. Data on the reproductive biology of Lesser Sundan *Eremiascincus* are practically non-existent, whereas species from Australia, especially arid-zone taxa, have been better, even if still not adequately, studied.

Although James & Losos (1991) published a comprehensive study on the reproductive biology of what they considered to be *E. richardsonii* (Gray, 1845) and *E. fasciolatus* (Günther, 1867), some of their data should be used with caution. It now appears that the desert-dwelling, broad-banded *E. richardsonii* actually represents a species complex (S. Mecke unpubl. data), and the narrow-banded *E. fasciolatus* (*E. fasciolatus* sensu lato) that was formerly thought of as widespread has recently been restricted to eastern Queensland (*E. fasciolatus* sensu stricto). This species is often confused with *E. richardsonii* in museum collections because of similar body proportions and its robust build (Mecke et al. 2013). The species diversity within the banded *Eremiascincus* is still significantly underestimated. Thus, James & Losos (1991) may inadvertently have combined data from specimens representing different taxa, and in the absence of a list of voucher specimens in their publication, it is not possible to reconcile which data came from which form. In general, their data show that females with oviductal eggs were collected, or are known to deposit clutches, between mid-October and mid-February. These data are consistent with those summarized for other members of the genus in Table 1. Brood size averaged 4–5 (James & Losos 1991; see also Table 1).

Viviparity has been reported for two taxa (*E. fasciolatus* sensu lato and *E. pardalis*), but some of these reports have been considered doubtful. Greer (1979) summarized and critically evaluated information on the occurrence of viviparity in *E. fasciolatus* sensu lato. Mecke et al. (2013) examined 22 specimens of the Queensland-endemic *E. fasciolatus* sensu stricto, and found that one female (QM J39996; SVL = 123 mm) collected in early December (early wet season) contained eight shelled oviductal eggs. James & Losos (1991) also reported that *E. fasciolatus* laid shelled oviductal eggs, and the data summarized in Table 1 likewise indicate that all narrow-banded *Eremiascincus* species formerly lumped in "*E. fasciolatus*", including *E. fasciolatus* sensu stricto, *E. intermedius* (Sternfeld, 1919), *E. pallidus* (Günther, 1875), and *E. phantasmus* Mecke et al., 2013, are oviparous. Evidence for the viviparity of *E. pardalis* was presented by Rankin (1978), who discovered four hatchlings in a terrarium housing an adult pair. Despite a thorough search, Rankin failed to locate eggshells in the tank, which contained a bottom substrate that was too dry to facilitate subterraneous egg incubation. He therefore concluded that *E. pardalis* must be a live-bearer, in contrast to Greer & Parker (1974), who reported the species as oviparous. On the basis of our observations and the description by Rankin (1978), we surmise that *Eremiascincus* "Ermera" also gives birth to live young (see above).

The incubation period in *Eremiascincus* can be very short, shorter than for most other lacertilian taxa for which data are available (based on a table of selected clutch and incubation parameters provided by Köhler 2003: Appendix III). Brown (2012 and in litt.) noticed that at least some *Eremiascincus* species seem to possess the ability to retain eggs and incubate them "in utero" (oviparous egg retention sensu Blackburn 1994), a reproductive mode that has been considered a step towards the evolution of viviparity (e.g., Shine 1983, 1985, 2004; Guillette 1993, Blackburn 2006; Parker & Andrews 2006). Brown (2012 and in litt.) was able to record extracorporeal incubation periods as short as 21 days for "*E. richardsonii*" and New South Wales *E. phantasmus* (listed as *E. fasciolatus*), and it seems likely that intrauterine embryonic development is found in more than these two *Eremiascincus* species, including mesic forms.

Short extracorporeal incubation periods (< 20 days) are rarely documented in lizards (see Köhler 2003, Appendix III), with the phrynosomatid *Sceloporus aeneus* Wiegmann, 1828 being one such example (12–14 days; Köhler 2003). This species is also known to retain eggs and incubate them "in utero" (Guillette & Lara 1986, García-Collazo et al. 2012), a mechanism known from other members of the Iguania (Pianka & Vitt 2003). Among the Lacertidae, viviparous populations of *Zootoca vivipara* (Lichtenstein, 1823) and *Iberolacerta monticola* (Boulenger, 1905) are able to retain eggs and show an advanced intrauterine embryogenesis (e.g., Brana et al. 1991, Rodríguez-Díaz & Brana 2011). The same applies to some populations of *Lacerta agilis* (Linnaeus, 1758) and *Dinarolacerta mosorensis* (Kolombatovic, 1886), the latter of which has been reported to have incubation periods as short as 17–19 days (Brana et al. 1991, Köhler 2003, Ljubisavljevic et al. 2007). Within the family Scincidae, egg retention and intrauterine embryogenesis is known from *Lerista bougainvillii* (Gray, 1839) and *Saiphos equalis* (Gray, 1825) (Qualls 1996, Linville et al. 2010, Stewart et al. 2010).

A small number of species within the Scincomorpha (and only taxa within this group) are well known to be reproductively bimodal: *Zootoca vivipara*, *Trachylepis capensis* (Gray, 1831), and *Lerista bougainvillii* (see Qualls et al. 1995; these authors listed more reproductively bimodal species, some of which were later identified as comprising several distinct taxa, all of which showed an unimodal reproductive lifestyle). However, the number of species that include both oviparous and viviparous populations might be much greater, considering that so little is known about the ecology and reproductive biology of taxa within the Scincidae in particular.

A comparative study on the reproductive biology of *Eremiascincus* under laboratory conditions would help to improve our knowledge concerning oviparous egg retention and the possible occurrence of egg retention at extreme levels (i.e., viviparity) in the genus and constitute an opportunity to shed light on the selective forces driving these modes on ontogenetic and phylogenetic levels.

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Appendix

Material examined

Eremiascincus intermedius. Northern Territory: NTM 15110, 12 km southwest Sangsters Bore, 20°52’0” S, 130°16’0” E. NTM 23342, 12 mile Stock Yards, Elsey National Park, 14°57’8” S, 133°13’8” E. NTM 33007, Alice Springs, 23°46’0” S, 133°52’60” E. NTM 32992, Tanami, 20°13’0” S, 131°46’0” E.

Eremiascincus isolepis. Northern Territory: AMS 60089, 60092, Burrells Creek., 29 km south Adelaide River on Stuart Highway, 13°21’0” S, 131°11’0” E. AMS 106815, West Island, Sir Edward Pellew Islands. Western Australia: AMS 123863, 123873, Mitchell Plateau, upstream from Mitchell Falls, 14°50’0” S, 125°41’0” E. WAM 20330, Derby, 17°18’0” S, 123°37’0” E. WAM 22361, Kimberley Research Station., Ord River, 15°39’ 0” S, 128°42’0” E. WAM 61566, Myaree Pool, Maitland River, 20°53’0” S, 116°37’0” E. WAM 77677, Mitchell Plateau, 14°35’0” S, 125°45’0” E. WAM 79027, Barred Creek Bore, Waterbank Station, 17°39’0” S, 122°12’0” E. WAM 83364, 16 km south southwest Mount Elizabeth Homestead., 16°27’0” S, 126°13’0” E. WAM 83550, 37 km north Broome, 17°38’0” S, 122°11’0” E. WAM 132597, Burrup Peninsula, 20°31’54” S, 116°47’41” E. WAM 135279, 7.5 km east Mount Hodgson, 20°48’36” S, 121º 13’54” E. WAM 139066, Mandora, 19°47’52” S, 121°26’52” E. WAM 139079, Mandora; WAM 139090, Mandora, 19°45’16” S, 121°26’59” E.

Eremiascincus musivus. Western Australia: WAM 135896, 10 km south southwest Mandora Homestead., 19°49’0” S, 120°48’0” E.

Eremiascincus pallidus. Western Australia: AMS 111617, Yule River, approx. 20 km south Port Hedland, 20°29’0” S, 118°10’0” E. WAM 161696, 43 km north northwest Goldsworthy, 19°59’54” S, 119°21’31” E.

Eremiascincus phantasmus. New South Wales: AMS 14449, Top Hut Road., 4.6 km east of Pooncarie – Wentworth Rd., 33°41’0” S, 142°28’0” E. AMS 155262, Sturt National Park, 13 km (by road) west of Binerah Downs Homestead on Middle Road, 29°01’30” S, 141°25’17” E. AMS 155285, 155405, Sturt National Park, 5.7 km west (by road) along Whitecatch Gate Road., 29°07’52” S, 141°08’57” E. South Australia: SAMA 63811, Cordillo, southwest Bloodwood Bore, 26°55’30” S, 140°54’41” E.

Eremiascincus richardsonii. South Australia: SAMA 44965, St. Mary Pool, 29°34’36” S, 139°24’52” E. SAMA 48982, 2.6 km east southeast of Lake Dam, South Gap Station., 31°47’4” S, 137°39’1” E. SAMA 58189, site BBB 00601, 17.3 km west northwest of Pile Hill, 28°45’06” S, 134 31’53” E. SAMA 61208, Whyalla, 8.5 km south southwest Moonbie Hills, 33°19’42” S, 137°12’53” E. South Australia (Nullarbor Plain): SAMA 9403, Ooldea, 30°27’ S, 131°50’ E. SAMA 62305 Noonina, 184 km south southwest of Wartaru, 28°30’31” S, 129°14’30” E. Queensland: AMS 60003, 13 miles north Blackall on Landsborough Highway, 24°16’0” S, 145°21’0” E.

6.7 Conclusions

In this chapter, I presented the first ecological study (food spectrum analysis) of a population of *Duttaphrynus melanostictus* introduced to a region where it does not naturally occur. The Asian toad presumably arrived in West Timor, Indonesia, around 1999–2000, entered Timor-Leste shortly afterwards (Trainor 2009) and was recorded in Timor-Leste's easternmost district (Lautém) for the first time in August 2014 (pers. obs; specimen from Com vouchered as MCZ A-149329 and housed in the collection of the Museum of Comparative Zoology at Harvard University). The range of this alien species now encompasses all but one of the districts that comprise Timor-Leste. Current capture patterns (paper 1, chapter 4) indicate that the habitat preference of *D. melanostictus* on Timor is open landscapes bordered by human habitations. The results summarized in paper 7 (this chapter) suggest that the Asian toad does not regularly consume vertebrates, although it was reported to prey on the blindsnake *Indotyphlops braminus* (paper 9, this chapter). The results from the gut content analysis are applicable to other introduced populations of *D. melanostictus* (e.g., on Madagascar), demonstrating that proposing similarities of this species with the invasive cane toad lacks a scientific basis. While direct predation on vertebrates, such as frogs or small reptiles, appears to be a negligible threat on part of the Asian toad, niche overlap between this species (and/or its life stages) and naïve regional fauna may have a much greater impact that is in urgent need of investigation. Furthermore, the presence of this species could have a negative impact on potential predators. On islands in the Lesser Sundas not yet invaded by *D. melanostictus*, this toad – once it arrives – could be consumed by larger vertebrates, such as the Komodo dragon (*Varanus komodoensis*) of Komodo, Flores, Gili Motang, Padar, and Rinca Islands (Ujvari *et al*. 2014), potentially imperiling the survival of this iconic giant lizard. Hence, safety precautions that prevent importation should be considered. Once *D. melanostictus* has established populations, eradication is difficult or even impossible, as stated in paper 8 (this chapter) and McClelland *et al*. (2015).

Food spectrum analyses carried out on museum vouchers necessitate methods to open the body cavity. Surprisingly, best practices for this procedure have never been reported and/or critically assessed with a view to their general or specific suitability. Museum vouchers can be used for answering diverse biological questions (see chapter 7) and hence, any method applied to them should be as minimally invasive and/or minimally destructive as possible. Several types of investigation, however, require incisions (e.g., taking samples for histological and genetic analyses, food spectrum analyses) and, for this reason, are often discouraged, particularly by museum curators (as indicated by an unpubl. poll by Mecke & Döring). The approach proposed in this chapter calls for a U-shaped incision that, although invasive, is less destructive than other methods applied, and thus considered optimal in preserved anurans. The location and shape of the proposed incision provides easy and adequate access to the relevant organs and does not damage structures that would be affected when using other methods. This new method may encourage other researchers to use preserved anurans for the purpose of food spectrum analyses and curators to make specimens available for this kind of research. It has already been adopted in lab manuals (Kaiser, pers. comm.)

In chapters 4 and 5 it became evident that – as for amphibians – many Southeast Asian reptile taxa are still undescribed and/or only poorly known, with limited information about their ecology available. Hence, for any research conducted on local Southeast Asian herpetofaunas, a multi-taxon-approach is advisable, to gather as many data from different groups (i.e. amphibians and reptiles) and fields (e.g., taxonomy, ecology) as possible. The superficial heterogeneity of the research presented in this chapter that includes ecological studies on toads (see above) and skinks (see below) is based on the fundamental drive to learn more about the herpetofauna of Southeast Asia, and to assemble missing pieces in a complex puzzle.

The reproductive ecology of an animal is – like its feeding ecology – a fundamental biological element, and may even provide additional information to resolve its taxonomy (see introduction in chapter 6 and paper 12, this chapter). The observation that *Eremiascincus* 'Ermera' is potentially viviparous would not have been possible in the field (chapter 4), as the taxon is secretive, semi-fossorial, and crepuscular to nocturnal. In the meantime, viviparity as a reproductive mode was confirmed by the observation of a birthing process on 13. June 2016, (pers. obs.), highlighting the importance of captive husbandry in herpetofaunal species to gather data on their biology (e.g., Rösler *et al.* 2017). Elucidating reproductive characters is essential for understanding a reptile's life cycle, but captive husbandry might not always be possible. The large collections of reptiles in museums worldwide, however, are a potential source of valuable information on their reproductive biology. One drawback of a mass-dissection approach is (again) the destructive nature of this method. Optimal incision methods, like the one for anurans discussed in this chapter, could provide a viable solution.

7 The Value of Natural History Collections for Biodiversity Research

The type specimen of the skink *Anomalopus leuckartii*, as depicted in Figure 1 in Mecke *et al*. (2016): Tracking a Syntype of the Australian Skink *Anomalopus leuckartii* (Weinland, 1862): "Lost" Treasures in the Senckenberg Natural History Collections Dresden Highlight the Importance of Reassessing and Safeguarding Natural History Collections. *Vertebrate Zoology*, **66**(2): 169–177 (paper 1, this chapter).

7.1 Introduction

Natural history collections have two important functions, education and research (e.g., Murariu 1997; Cook *et al*. 2014; Powers *et al*. 2014). For the purposes of education and teaching, permanent or temporary museum exhibits are indispensable, but to facilitate meaningful and long-term research, large collections of specimens must also exist behind the closed doors of museums and universities (e.g., Murariu 1997). Research collections are invariably much larger and much more diverse than the collections on exhibit. Collected over a long period of time by generations of scientists, they house unique specimens that are indispensable material for answering diverse questions in biodiversity research, including studies on the evolution, ecology, biogeography and taxonomy of organisms (e.g., Cracraft 1997; Mehrhoff 1997; Nudds & Pettitt 1997; Ward 2012; Webster 2017). These repositories of biological diversity should be understood as large libraries of information that allow reconstructing the past, understanding current patterns and processes, and even predicting the future of the biosphere (Nudds & Pettitt 1997; Shaffer *et al*. 1998; Lister & Climate Change Research Group 2011; Kemp 2015). The nowadays often neglected natural history collections were perhaps never in human history as important as today, at a time when species' extinction rates increase and biodiversity decreases at an alarming speed (Pettitt 1997; Krishtalka 2009; Ceballos *et al.* 2015).

In this chapter, I aim – with a single publication – to demonstrate the importance of natural history collections for the discovery of important specimens using the example of a 'lost' type specimen in the Senckenberg Natural History Collections Dresden and, at the same time, call attention to the important role of collections in biodiversity research. With this, I refer back to other studies presented herein, most notably the taxonomic research in chapter 5. None of the studies presented in this thesis, however, would have been possible without conducting work in natural history collections: The field work presented in chapter 4 – in the absence of field guides for the region – made it necessary to identify and diagnose the field-collected specimens by comparing them to museum vouchers in a preliminary study (not part of the publications). There is no doubt about the considerable use of museum vouchers for the studies presented in chapter 5, for which specimens from 13 national and international collections were examined, including material of species from locations where re-collection is no longer possible. The food spectrum analysis presented in chapter 6 would likewise not have been possible without the examination of preserved specimens. Therefore, the natural conclusion is to complete the cumulative part of this thesis with a chapter covering aspects that constitute an overall theme running through the entire work presented.

6.6 Paper 13

Mecke, S., Mader, F., Kieckbusch, M., Kaiser, H., Böhme, W. & Ernst, R. (2016): Tracking a Syntype of the Australian Skink *Anomalopus leuckartii* (Weinland, 1862): ‘Lost’ Treasures in the Senckenberg Natural History Collections Dresden Highlight the Importance of Reassessing and Safeguarding Natural History Collections. *Vertebrate Zoology*, **66**(2): 169–177.

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Tracking a syntype of the Australian skink *Anomalopus leuckartii* (Weinland, 1862): 'lost' treasures in the Senckenberg Natural History Collections Dresden highlight the importance of reassessing and safeguarding natural history collections

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Abstract

We here report the rediscovery of a type specimen of the Australian skink *Anomalopus leuckartii* (Weinland, 1862) in the Museum of Zoology (Museum für Tierkunde), Senckenberg Natural History Collections Dresden (accession number MTKD 10205), heretofore presumed lost during World War II. Eidonomic data for the specimen conform to the original species description, and combined with the specimen's history, we are able to unequivocally identify it as part of the original syntype series. Weinland's description was based on two specimens, one of which does indeed appear to be lost. Consequently, MTKD 10205 is designated as lectotype of *A. leuckartii*. This find invalidates the subsequent designation of AM R 44677 (Australian Museum, Sydney) as neotype for the species. The rediscovery highlights the importance of maintaining natural history collections, not merely as static archives but rather as dynamic and lively databases. This in combination with optimal taxonomic expertise as bedrock guarantees an environment, in which new discoveries are not impeded but actively promoted, thereby inevitably advancing modern biodiversity research.

Kurzfassung

Wir berichten über die Wiederentdeckung eines Typusexemplars des australischen Skinks *Anomalopus leuckartii* (Weinland, 1862) im Museum für Tierkunde, Senckenberg Naturhistorische Sammlungen Dresden (Sammlungs-Nr. MTKD 10205), das bisher als im Zweiten Weltkrieg verloren galt. Eidonomische Daten für das Exemplar entsprechen denen in der Originalbeschreibung. Anhand dieser Daten und der Geschichte des Exemplars ist es uns möglich, es unzweifelhaft als einen Teil der originalen Syntypen-Serie zu identifizieren. Weinlands Artbeschreibung basierte auf zwei Exemplaren, von denen eines tatsächlich als verschollen betrachtet werden muss. Daraus folgend designieren wir MTKD 10205 als Lektotypus für *A. leuckartii*. Der Fund macht den inzwischen festgelegten Neotypus für diese Art (Australian Museum, Sydney, Sammlungs-Nr. R 44677) ungültig. Die Wiederentdeckung unterstreicht die Wichtigkeit der Instandhaltung naturgeschichtlicher Sammlungen, die als dynamische Datenbanken und nicht als statische Archive fungieren sollten. Dies, kombiniert mit einer soliden taxonomischen Expertise als Fundament, schafft ein Umfeld, in dem neue Entdeckungen gefördert anstatt erschwert werden und trägt somit zur Weiterentwicklung einer modernen Biodiversitätsforschung bei.

Key words

Scincidae, Lygosominae, *Anomalopus leuckartii*, Australia, taxonomy, syntype, lectotype, morphology, natural history collections, museums.

Introduction

The holdings of the Museum of Zoology (Museum für Tierkunde) now housed in the just recently (2009) formed Senckenberg Natural History Collections Dresden, Germany (formerly the Staatliche Naturhistorische Sammlungen Dresden), are an excellent and poignant example of a collection that has seen dramatic changes and periods of turmoil (reviewed by Fritz, 2002): Dating back to the 16th century, and therefore one of the oldest natural history collections in the world, the institution was struck by disaster several times throughout its history. Consequently, it suffered from dramatic losses of valuable material. During the 1849 May Uprising in Dresden (struggles towards the end of the revolutionary upheaval that began in 1848, also known as the Spring of Nations), the collection fell victim to a fire, in which the majority of the zoological specimens was destroyed. After a period of growth and the addition of unique and valuable specimens, the collection was again almost entirely destroyed near the end of World War II, during the allied bombing of Dresden in the night from 13 – 14 February 1945. The alcohol-preserved collections, including the herpetological holdings, were severely hit, and the latter was reduced from 6,704 to only 98 specimens. In an effort to re-establish the collection in subsequent years, the museum received material from various sources, including former university collections. Among the specimens received, those from the collection of the former Zoological Museum at the University of Leipzig (herein abbreviated MUL) were probably one of the most diverse additions. This addition contained holdings collected and catalogued by Eduard Friedrich Poeppig (*1798 †1868), and was later revised by Willi Hennig (*1913 †1976), with a detailed treatment (Obst, 1977a, b) received from the former director of the Staatliche Naturhistorische Sammlungen Dresden, Fritz Jürgen Obst (*1939). Other, nonetheless interesting and significant parts of the collection have received less attention, partially because the provenance of these appeared much less traceable. As a consequence, some valuable specimens remained unrecognized in the drawers and on collection shelves for decades.

One such specimen is a syntype of the Australian lygosomine skink *Anomalopus leuckartii* (Weinland, 1862) that was assumed to have been lost (see Greer & Cogger, 1985). It was recently rediscovered in the herpetological section of the Senckenberg Natural History Collections Dresden. We here present an account of how this rediscovery was made and provide eidonomical data for the type, which we compare with those given in the original species description.

The rediscovery serves as an important example of a valuable, ‘lost or forgotten treasure’ hiding in a museum archive. Although as taxonomists we are well aware of the fact that discoveries of historical material, including new species, continue to be made in collections, we feel that the importance of natural history collections is not generally understood by the public and at present only insufficiently acknowledged by administrators. Hence, we discuss their value and call for safeguarding collections with highly elevated conscientiousness and under consideration of optimal expertise in taxonomy and natural history. Only then can natural history collections survive into the future as the powerful tool they have traditionally been for research in the life-sciences.

Material and Methods

The specimen in question is housed in the Museum of Zoology (Museum für Tierkunde), Senckenberg Natural History Collections Dresden (now MTD, formerly MTKD) under accession number MTKD 10205. The following measurements (in mm) and counts were made to allow both a comparison with the original description of the type material by Weinland (1862 – 63) as well as the data presented by Greer & Cogger (1985) for the species: snout-vent length (SVL), measured from tip of snout to vent; tail length (TailL), from vent to tip of tail; arm length (ArmL), from axilla to longest finger; leg length (LegL), from groin to tip of styliform appendix; head length (HeadL), measured from tip of snout to retroarticular process of lower jar; number of supralabials (SupraLab); number of infralabials (InfraLab); number of supraciliaries (SupraCil); number of supraocular scales (SupraOc); number of paravertebral scales, beginning with the scale bordering the parietal posteriorly to (1) level of cloaca (PVS1) and (2) to posterior edge of thigh (PVS2); number of scale rows around midbody (MBSR); number of supracaudals (SupraC), including all scales from cloaca to tail tip. Measurements and counts of characters occurring bilaterally were taken on the left side of the specimen. Note that in his count for paravertebral scales, Weinland included a parietal scale, which conforms to our PVS1 + one additional scale. Supracaudals are not normally counted in modern squamate taxonomy but this count allows further comparison with Weinland’s data. We do not provide a full description of the type specimen, since as, the only member of *Anomalopus* Duméril & Duméril, 1851 with didactyl forelimbs, the species is easily diagnosed. We also present a photograph of the rediscovered type to readily allow comparison with Weinland’s illustration.

Results

During a practical part of the ‘Senckenberg Course in Taxonomy’(www.senckenberg.de/taxonomy_school), the first author discovered in the herpetological collection of the MTD several valuable scincid specimens. The most important finding was the discovery of an Australian ly-

Fig. 1. *Anomalopus leuckartii*. (**A**) Photograph of MTKD 10205 in its current condition. (**B**) Illustration of MTKD 10205 as figured in the original description by Weinland (1862–63). Scale bar = 2 cm.

gosomine skink (MTKD 10205; Fig. 1 A) in a jar containing a label with the inscription "*Rhodona*" . *Rhodona* Gray, 1839 is a junior synonym of *Lerista* Bell, 1833 (see Greer 1967)[1], a diverse (> 90 species) Australian skink genus containing various morphotypes, ranging from short-bodied forms with well-developed limbs bearing five digits, to elongate and limbless forms (Wilson & Swan, 2013). In species of *Lerista* with reduced limbs, hindlimbs are always longer than forelimbs, and the opposite morphology (i.e., forelimbs longer than hindlimbs) is a rare trend in Australian lizards, known to occur in a single scincid genus only: *Anomalopus* (Wilson, 2012). Since the forelimbs of the MTD "*Rhodona*" specimen are longer than the styliform hindlimbs, we were able to identify the specimen as a member of the genus *Anomalopus*. Using the identification key for the genus in Cogger (2014) we diagnosed the specimen as *A. leuckartii* (Weinland, 1862).

Beyond the issue of misidentification, closer inspection of the label inside the jar focused our attention on the donor of the specimen, Karl Georg Friedrich Rudolf Leuckart (*1822 †1898), in whose honor David Friedrich Weinland (*1829 †1915) named *A. leuckartii*. The original species description appeared under the genus name *Brachymeles* Duméril & Bibron, 1839 and was based on specimens originating in "Neuholland" (= Australia). Weinland (1862–63) clearly indicated that only two specimens of his new taxon were available, and both formed the basis for the description; they must therefore be considered syntypes. The specimens were housed in the Giessen Zoological Museum (herein abbreviated GZM), Giessen, Germany, at the time of Weinland's description. The Zoological Institute Giessen, which included the collections, burned and was destroyed completely during World War II (Ankel, 1957). Hence, the two specimens of *A. leuckartii* were believed to have been lost in the disaster (Greer & Cogger, 1985).

Leuckart was professor for zoology in Giessen from 1850–69, and subsequently became chair of zoology and zootomy at the University of Leipzig as well as director of the MUL (Wunderlich, 1978; Daintith *et al.*, 1994). On the first page of the historical accession catalogue of the MUL (Accessions Catalog 1869), which is now kept at the MTD, some reptile specimens donated by Leuckart are listed, including a single "*Brachymeles Leuckarti*" from "Neuholland" (acquisition number 19). There is little doubt that this specimen, along with many others, was originally part of the GZM or of Leuckart's private collection (see Discussion). In 1933, Willi Hennig, then a student at Leipzig University, revised the herpetological collection. In one of his hand-written catalogues for the squamate reptiles (Hennig, 1933; part Sauria), a specimen of "*Lygosoma verreauxii*" (= *Anomalopus verreauxii* Duméril & Duméril, 1851) is listed with a direct reference to the original designation and catalogue entry as follows: "*Brachymeles Leuckartii* Weinl., Nova Hollandia, Leuckart d.dt. [= dono dedit], Acc. Cat. [= Accession Catalogue] 1869/70: Nr. 19." Hennig (1933) gave the specimen the catalogue/collection number RVa316. The MUL was dissolved in 1968 and partly acquired by the MTD in 1970/71. Based on a handwritten entry on the first page of Hennig's catalogue by Obst in 1974, 248 jars with lizards were received and the specimens integrated into the herpetological collection of MTD. In a more recent collection catalogue (Nr. 2) of the herpetological section of MTD (1972–79) the new number MTKD 10205 was assigned to RVa316. Curiously, the name "*Rhodona*" was used in the catalogue to refer to this particular specimen. The recent catalogue entry

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[1] Smith (1937) also treated *Glaphyromorphus pumilus* (Boulenger, 1887) and the three species of the genus *Isopachys* Lönnberg, 1916 known at that time as members of the genus *Rhodona*.

Table 1. Metric data (in mm), body proportions, and scale counts of MTKD 10205 (*Anomalopus leuckartii*), along with data from, or calculated from, the original description (Weinland 1862–63) and data presented by Greer & Cogger (1985). *n* = sample size.

Character	MTKD 10205	Weinland (1862–63)	Greer & Cogger (1985)
SVL	113	110	39–137 (*n* = 120)
TailL	121	124	—
HeadL	9.0	9.0	—
ArmL	3.6	4.0	—
LegL	1.5	1.5	—
TailL/SVL	0.93	1.13	0.69–1.24 (*n* = 43)
ArmL/SVL	0.03	0.04	0.03–0.04 (*n* = 18)
LegL/SVL	0.01	0.01	≤ 0.01 (*n* = 2)
SupraLab	6	6	6
InfraLab	6	6	6
SupraCil	6	—	5–7 (*n* = 96)
SupraOc	3	—	2–4 (*n* = 62)
PVS1	126	127[a]	—
PVS2	122	—	108–128 (*n* =19)
MBSR	20	20	18–22 (*n* = 56)
SupraC	139	139[b]	—

[a] Weinland (1862–63) counted paravertebral scales from the interparietal to a point above the cloaca, and hence his count (127) is higher than the value obtained by application of the commonly used counting method, beginning with the first scale bordering the parietal posteriorly.

[b] In addition to providing paravertebral scales (from interparietal to cloaca), Weinland (1862–63) stated that he counted scales from the cloaca to the tip of the snout ("… und von da [Kloake] bis zur Schnauzenspitze 139" [and from there (cloaca) to the tip of the snout] Weinland, 1862–63: 142). However, this would imply that Weinland counted dorsal scales back and forth, and included head scales in one of his counts. While this appears odd, the number of head scales does also does not equal 12 (the difference between 127 and 139 dorsals). It is more likely that the German term for snout tip [Schnauzenspitze] was confused with the one for tail tip [Schwanzspitze]. Both words look fairly similar if written in old-German handwriting, and it was common practice during Weinland's time to submit handwritten manuscripts to a journal. Hence, we assume that "Schnauzenspitze" is a transfer error for "Schwanzspitze" that occurred during type-setting. Moreover our count for SupraC yielded 139 scales, conforming to the number of scales Weinland obtained.

and species label in the collection jar alone provide little evidence and no unambiguous clues that would allow for the identification of a presumably lost type specimen.

Data of the relevant *Anomalopus leuckartii* specimen (MTKD 10205; Fig. 1A) are presented in Table 1, along with measurements, selected proportions, and scale counts given for the species by Weinland (1862–63) in the original species description and by Greer & Cogger (1985). Our eidonomical data (e.g., PVS1, MBSR) for MTKD 10205 agree very well with those reported by Weinland (1862–63), and since some of these characters are known to be quite variable interspecifically, this concordance in eidonomy supports the concept that Weinland described the taxon based on the individual now registered as MTKD 10205. Weinland (1862–63: Plate 4, Fig. 3) also illustrated a specimen that is identical to MTKD 10205 (see Discussion), based on the presence of an original tail (curled downwards under the body), and we present this figure herein for comparison (cf. Fig. 1A & B). Eidonomic data and the history of the specimen therefore corroborate that MTKD 10205 is indeed one of the syntypes that had been presumed lost. In the absence of the second syntype, we herein designate MTKD 10205 as lectotype of *A. leuckartii*. The neotype designation of Australian Museum specimen AM R 44677 by Greer & Cogger (1985) is thus invalid, since it is superseded by the original type rediscovered (see ICZN, 1999: article 75.8). MTKD 10205 thus becomes the oldest known herpetological type specimen in the MTD collection.

Discussion

Weinland's description of *Anomalopus leuckartii*. For his description of *Anomalopus leuckartii* (original name: *Brachymeles Leuckartii*), Weinland (1862–63) had two specimens available. However, his measurements are evidently based on a single specimen with an intact tail (see "Proportionen und Dimensionen des vollständig erhaltenen Exemplars" [proportions and dimensions of the complete specimen]; Weinland, 1862–63: 142), whereas the second specimen had a mutilated, partly regenerated tail ("… es liegen deren [= *A. leuckartii*] zwei zur Beschreibung vor, wovon Eines mit verstümmeltem aber theilweise wieder ersetztem Schwanz…" [there are two specimens available for the description, of which one has a mutilated but partly regenerated tail]; Weinland, 1862–63: 142) and was probably only used to describe coloration (see below). A second line of evidence showing that Weinland used only one of the available specimens comes from the listing of scale characters (PVS, MBSR, SupraC), which he obtained from a single specimen only. This can be inferred from the lack of mention of any variation in the descriptive data. Since both metric and meristic data in WEINLAND's description are essentially identical to those of MTKD 10205, we assume that scale counts were based only on the 'intact specimen' as well. Minor discrepancies in measurements or counts may be attributed to different ways of recording data, or perhaps on slight errors. The specimen with original tail was also the one illustrated in WEINLAND (1862–63: Plate 4, Fig. 3; Fig. 1B herein) and is considered to be identical with MTKD 10205.

The 'LEUCKART Collection': origin and whereabouts. The historical accession catalogue of the MUL (ACCESSIONS CATALOG 1869) at MTD clearly indicates that most specimens received during that period were donated by LEUCKART. About two thirds of the app. 1,200 specimens listed in the catalogue are marked as e.g., "Ex. don. Lt." [= specimen donated by Leuckart], and these include mainly parasitic and marine invertebrates; additional anatomical specimens are listed in a separate catalogue. However, it is not clear whether respective specimens were part of the GZM or LEUCKART's private collection, and specimens (especially duplicates) were likely exchanged informally and bidirectionally between the two collections when LEUCKART was professor at the University of Giessen. According to SPENGEL (1902) and SCHMIDT (1938), LEUCKART increased the collection of the GZM by adding specimens in spirits from all groups of the animal kingdom. There is evidence that LEUCKART donated to the GZM parts of his own collection (BISCHOFF, 1852: invertebrates), and that duplicates received were, at least in some cases, deposited in the GZM and LEUCKART's private cabinet (VON KÖLLIKER, 1872: *Kophobelemnon leuckartii*). WEINLAND (1862–63) noted that the only specimens of *Brachymeles Leuckartii* (the two syntypes) known to him were housed in the GZM. However, it is not unlikely that one of these specimens (MTKD 10205), as a duplicate, was already part of LEUCKART's private collection at the time of WEINLAND's description, which would indicate a possible error by WEINLAND (1862–63) or that the specimen came into LEUCKART's private cabinet later on.

While the exchange of specimens between the GZM and LEUCKART's private collection are difficult to trace in detail, it is evident that the MTD houses a large number of specimens donated by this famous zoologist, who was the founder of modern parasitology (e.g., KREIS, 1937; KRÄMER, 2006) and an advocate of comparative morphology (KRÄMER, 2006), corresponding with CHARLES DARWIN (*1809 †1882), and lecturing about Darwinian theories (WUNDERLICH, 1978; ELLIS & KIRCHBERGER, 2014). During his time in Giessen, LEUCKART had become one of zoology's leading scientists (WUNDERLICH, 1978), who was in contact with many renowned naturalists (e.g., CARL BERGMANN, ANTOINE RENÉ-EDOUARD CLAPARÈDE, HENRY JAMES CLARK, JUSTUS LIEBIG, KARL LINDEMANN, ILJA ILJITSCH METSCHNIKOW, JAPETUS STEENSTRUP, JEAN BAPTISTE VÉRANY, RUDOLF WAGNER, DAVID FRIEDRICH WEINLAND, and FRIEDRICH ALBERT VON ZENKER) and received specimens from a variety of sources (e.g., LEUCKART, 1863: parasites; LÜTKEN, 1892: a fish; GRIMPE, 1933: a cephalopod). He also made specimens from the GZM and/or his own collection available for examination by others (e.g., CLAUS in VON SIEBOLD & VON KÖLLIKER, 1860: siphonophores; CLAUS in VON SIEBOLD & VON KÖLLIKER, 1863: copepods; WEINLAND, 1862–63: skinks; VON KÖLLIKER, 1872: sea pens). According to WUNDERLICH (1978), LEUCKART also described almost 100 invertebrate species (many during his time in Giessen), and 27 taxa have been named in his honor (HESS, 1906).

LEUCKART's lively scientific exchange highlights the importance of the 'LEUCKART Collection' received by the MUL, now part of the MTD, which likely includes many type specimens. In a historical overview and annotated type list of the MTD's ichthyological collection, ZARSKE (2003) already reported the rediscovery of another type from the 'LEUCKART Collection': the holotype of the siluriform fish *Acanthopoma annectens* LÜTKEN, 1892, which LEUCKART received from the German botanist GUSTAV WALLIS (*1830 †1878), and which is also listed in the accession catalogue of the MUL (ACCESSIONS CATALOG 1869).

The importance of the 'LEUCKART Collection' is, however, only now becoming more fully appreciated, and the rediscovery of the *Anomalopus leuckartii* type specimen prompted a systematic search for LEUCKART material housed in various collections of different MTD sections.

A search for LEUCKART material in the collection for lower invertebrates yielded about 60 specimens that he had donated to the MUL, including many parasites (ANDREAS WECK-HEIMANN, pers. comm.). In the malacological collection (which includes additional invertebrate taxa) ANDRÉ REIMANN (pers. comm.) found a specimen of the pennatulacean (a group of Octocorallia) *Kophobelemnon leuckartii* from Nice, France, which is also listed in the accession catalogue (ACCESSIONS CATALOG 1869) and likely was used by VON KÖLLIKER (1872) to describe the taxon; this potentially represents another 'lost' type specimen.

The accession catalogue of the MUL (ACCESSIONS CATALOG 1869) is a powerful tool that can be used to trace more of LEUCKART's specimens. Entries in the catalogue referring to LEUCKART might vary, since they were likely being written by different employees and/or at different times. The collection locality data "Gießen," where LEUCKART was professor before he took up his position in Leipzig, as noted in the catalogue (in the column titled "Herkunftsland" [country of origin]) and on specimen labels, also provides evidence for a donation by LEUCKART, even if a direct reference to the donor is lacking. Scientific publications on particular taxa, providing information on LEUCKART specimens, including collection numbers of the Leipzig museum, are available as well. For example, GRIMPE (1933), in his overview on arctic cephalopods, notes under the name *Sepietta scandica* (STEENSTRUP, 1887) that LEUCKART received a giant, "original" (= type) specimen of that taxon from the describer (Steenstrup) and provided the MUL collection number "Nr. 69/71." Based on our preliminary observations, we are confident that a more detailed reconstruction of the 'Leuckart Collection' is feasible. This will likely yield additional types that have been presumed be lost.

The importance of reassessing and safeguarding natural history collections: a herpetological perspective. From their origin as private 'cabinets of curiosities' or 'cabinets of wonders' in the 16th and 17th centuries to the modern-day tools of scientific research and public education, natural history collections have undergone substantial changes in the course of history (Alexander & Alexander, 2007). Present day collections are more than just physical backups of the extinct and recent organismic diversity, but rather represent all-encompassing databases that contain a wealth of information that can be used to track the past, document the present, and even predict the future of the biosphere (Nudds & Pettitt, 1997; Shaffer *et al*., 1998; Lister, 2011; Kemp, 2015). Moreover, these 'repositories of knowledge' are the basis for higher and formal education programs and therefore rank as irreplaceable, high-value assets (Lane, 1996; Nudds & Pettitt, 1997; Bradley *et al*., 2014). Unfortunately, the importance of collections and their multiple functions is not always recognized and acknowledged. Collections throughout the world are currently more directly than ever before confronted with shortsighted development plans that emerge from a harsh climate of economic decision-making (see Dalton, 2003; Bradley *et al*., 2014). This situation is particularly lamentable given that we have entered a century that has been called the "Age of Biology" (Glover, 2012), in which the life sciences have already made unprecedented progress. This appears like an almost euphoric atmosphere for research, and both the scientific community and political representatives are sometimes heard to proclaim that the study of organismic biology must now be redefined to meet future challenges and develop a next-century road map that aims at serving both science and society. Natural history collections should certainly remain particularly important in this respect, thereby heightening the prospects for the road map.

The use and appreciation of natural history collections has, however, always been unsteady and fluctuating throughout the centuries. As a result, collections historically underwent dramatic changes. Holdings were variously destroyed, sold off, relocated and dispersed, dissolved (completely or in parts), or simply left unattended due to a lack of interest or a cut in the economic resources required to maintain such facilities.

This fluctuation for herpetological collections is perhaps best exemplified by the natural history cabinet of the Dutch-German natural history collector Albertus Seba (*1665 †1736), whose first collection was sold to Peter the Great (*1672 †1725) (Engel, 1937; Boeseman, 1970), with a second, rebuilt and even larger collection auctioned and dispersed following Seba's death (e.g., Engel, 1937; Boeseman, 1970; Juriev, 1981; Daszkiewicz & Bauer, 2006; Bauer & Günther, 2013). Fortunately, some dispersed specimens were subsequently rediscovered, such as in the Museum für Naturkunde, Berlin, Germany (ZMB) (Bauer & Günther, 2013). Other examples include the cabinet of the German naturalist and explorer Prince Maximilian zu Wied-Neuwied (*1782 †1867), whose collection was purchased for the American Museum of Natural History (AMNH) in 1869 and only recently received full attention, including the identification of many type specimens (Vanzolini & Myers, 2015). Some of Wied's specimens may also have survived in the Zoologische Sammlung der Universität Marburg, Germany (ZSUM; Mecke pers. obs.), a university collection dating back to 1818/19 that contains a large number of important (but largely neglected) specimens; the unsteady history of this collection was summarized by Bohle (2015). The private collection of Alexander Macleay (*1767 †1848), now at the University of Sydney and rich in type specimens, may serve as another example for a collection that went through many periods of neglect. In 1969, the type specimens that could be located were sent to the Australian Museum on permanent loan (Cogger, 1979). However, since then other types have been found in the collection (Glenn Shea, in litt.; for a list of herpetological types see Goldman *et al*., 1969; Cogger, 1979; Cogger *et al*., 1983; Shea & Sadlier, 1999).

The rediscovery of the type of *A. leuckartii*, together with other recent (re)discoveries of valuable herpetological specimens, including new species and presumably lost types (e.g., Nowak-Kemp & Fritz, 2010; Bauer & Wagner, 2012; Bucklitsch *et al*., 2012; Bauer & Günther, 2013; Borczyk, 2013; Böhme, 2014; Kathriner *et al*., 2014; Böhme *et al*., 2015; Hartmann *et al*., 2016; Kieckbusch & Mecke *et al*., 2016) in natural history collections, highlights their outstanding importance for clarifying many of the most fundamental questions in organismic biology. However, this requires that unique knowledge about the history of particular collections (including knowledge about the naturalists that were associated with them) is preserved. Moreover, sound taxonomic expertise, and an extensive organismic background are necessary to detect potentially interesting specimens in the first place. In the case reported herein, the rediscovery of a single specimen (the type of *Anomalopus leuckartii*) that was long presumed lost, led to the discovery of many other valuable specimens, yet to be reported on. These finds might be regarded as a case example of how discoveries, in combination with the relevant expertise, can change our knowledge about whole collections.

We also believe that collections house a vast number of undescribed amphibians and reptiles, a phenomenon well documented for other groups (Green, 1998: insects; Bebber *et al*., 2010: plants). Authors of this study, for example, have discovered many new reptile species based on museum material alone, with shelf lives (the gap between the collection and formal description date of a new species) of three recent discoveries, *Varanus nesterovi* Böhme *et al*., 2015, *Cyrtodactylus klakahensis* Hartmann *et al*., 2016, and *Cylindrophis subocularis* Kieckbusch *et al*., 2016 being 102, 87 and 79 years, respectively (see also Green, 1998; Fontaine, 2012).This highlights the need for describing an appreciable amount of already catalogued but still undescribed biodiversity. Natural history collections also house treasures that are important witnesses of past human influences on the biosphere (e.g., specimens of already extinct taxa, first or historic distribution records) and thus allow predicting future impacts of human activities on global biota.

Such discoveries, however, can only continue to be made, when the importance of natural history collections is more sufficiently acknowledged, and this is only possible by maintaining these facilities and by funding researchers, who are engaged in collection-based science. Without museum-based taxonomic research the proper identification of species is impossible, and this affects other disciplines, such as ecology and conservation (e.g., Wägele *et al*., 2011; Bradley *et al*., 2014). Many collections struggle for survival and the traditional taxonomist is already on the edge of extinction, due to limited support by funding agencies and universities that almost entirely focus on molecular rather than organismic disciplines (e.g., Kemp, 2015). Hence, some of the world's largest collections are maintained by the lowest possible number of staff only, which allows specimen conservation but does not allow collection-based research carried out by qualified museum employees. Collections thus run the risk of becoming static archives rather than active and lively databases essential for any meaningful scientific research. This is particularly unfortunate considering that we are in the midst of a biodiversity crisis (Ceballos *et al*., 2015), and a 'simple' quantification what is there and what is lost is of paramount importance. Yet about half of the specimens kept in collections may be labeled with wrong names (see Goodwin *et al*., 2015: tropical plants), thus hampering a sound assessment. Molecular methods applied to museum specimens and digitization of collections to make them more accessible are advantageous but are insufficient in the absence of specific expertise in taxonomy. We need to work toward overcoming the current 'taxonomic impediment,' because only then can collections survive, and remain valuable and powerful tools for research.

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7.3. Conclusions

Natural history or biodiversity collections are essential in the life sciences because their preserved specimens provide incredible resources for scientists, educators, and the general public (Allmo 1994; Nudds & Pettitt 1997; Melber & Abraham 2002; Bradley *et al*. 2014; Powers *et al*. 2014; Ballard *et al*. 2017; paper 13, this chapter). Natural history itself – organismic and comparative biology in its broadest sense – is the core discipline of the life sciences; it structures and integrates all biological knowledge (Arnold 2006). Hence, every collection-based discovery provides additional information to the diverse field of organismic biology, including the history of collections and science, taxonomy and systematics, biogeography, ecology, and even conservation. Specimens in natural history collections contain a wealth of information that is important not only to the pursuit of basic scientific knowledge, but to our everyday lives, ranging from environmental to human health issues (Miller 1985; Cotterill 1997; Bradley *et al*. 2014). The paper herein may serve as a case example that the identification of type specimens appears to be of particular importance, taking into consideration that they represent a permanent reference associated with biological entities, and hence, provide a fundamental basis for biological studies (e.g., Culley 2013).

Collections have also long been the backbone of basic and applied research in herpetology, depending on either specimens or the associated data. It is logical that these collections exist, and that they deserve support that goes beyond maintaining, preserving, and expanding these facilities. In fact, where would the life sciences and society be without natural history collections?

Within the scientific community, however, some people have called into question the value of and need for specimens and/or entire collections (Minteer *et al*. 2014, see also Sluys 2013; Kemp 2015; Astrin & Schubert 2017), and recent media coverage and popular literature (e.g., Jones 2017; Kemp 2017; Styles 2017; Zhorov 2017) has fueled public and political debate about this topic. This neglect of natural history collections and even the associated scientific fields, constitutes a global disaster. The value of natural history collections, however, goes even beyond scientific or educational merits: they are cultural assets, just like historical literature in libraries and pictures by great artists. Considerable public, institutional and governmental support, as well as mechanisms to help secure funding, are needed to ensure that natural history collections continue to be nurtured so that they can rise to fulfill their immense potential.

I have highlighted the need for continued maintenance and better funding of collections throughout this chapter, but we should not ignore the complementary need for increasing the number of eminently qualified professionals entering the field of natural history either (see e.g., Sluys 2013). Today's biology students will be responsible for our collections; training and support to encourage this 'next generation' is a necessity. With currently not a single professorship for systematics and taxonomy in Germany (Open letter of the 'Junge Systematiker' by Kaiser, S. *et al.* 2011; the situation remained unchanged since the letter has appeared), there is the need to bring solid natural history lectures and research back to universities. For example, biology students should participate in collecting trips, learn how to prepare voucher specimens and how to curate specimens, and gain experience with cataloguing and other database activities. It is imperative that the 'next generation' appreciates the value and importance of voucher specimens and collections, because only then can these goldmines of biological information survive.

8 General Conclusions

The studies presented herein are an important step towards a comprehensive understanding of the Sunda Island herpetofauna, and the results I present carry relevance for studies in adjacent regions. These publications cover field research and/or collection-based studies in biological fields or disciplines that I refer to as "segments" below: faunistics (chapter 4), taxonomy (chapter 5), and ecology (chapter 6). While such an assignment is necessarily simplistic, there exist many causal relationships and synergistic effects between these segments, which increases the value of the presented thesis as a whole. As the diagram in Fig. 3 shows, my research took place in the field and in collections (including libraries) to varying degrees. These basic reservoirs from which we obtain knowledge are critical scientific resources, the use of which varies with specific research questions. I find that nowadays there is a lot of justifiable emphasis on fieldwork but, unjustly, there is less than the necessary attention given to collections (the repository of already accumulated knowledge). I believe researchers should always use fieldwork and collection-based work in combination, shifting the emphasis one way or another as the project dictates, and as indicated by a slider symbol in Fig 3. In my own investigations, sometimes this slider moved left, towards the field, but at other times it shifted to the right when the use of collections was the critical aspect of the project.

In this context, fieldwork in Timor-Leste led me to faunistic investigations inevitably linked to taxonomic and ecological research. Moreover, in the web of my research interactions, bidirectional synergistic effects emerged between the faunistic, taxonomic, and ecological research, where a finding in one area led to a need of investigations in another. Taxonomic research was strongly associated with collections and libraries, with a direct positive feedback towards collections, since research in the institutions holding collections increases the collections' value, with the latter discussed in chapter 7. In the broader context, my research is based on an iterative process – that is, nearly every segment was subject to new research questions that subsequently also affected allied segments (and vice versa) and their resource requirements (field *vs* collections). The combination of different segments and resources to answer research questions led me to results (indicated by a grey arrow in Figure 3) that can be directly used by decision-makers in biodiversity and conservation management. These decision-makers may decide, for example, to protect a particular fauna or species, or to manage an introduced taxon. For species protection measures, additional data from the field may be required, and these can again provide results regarding a species' taxonomy and/or ecology.

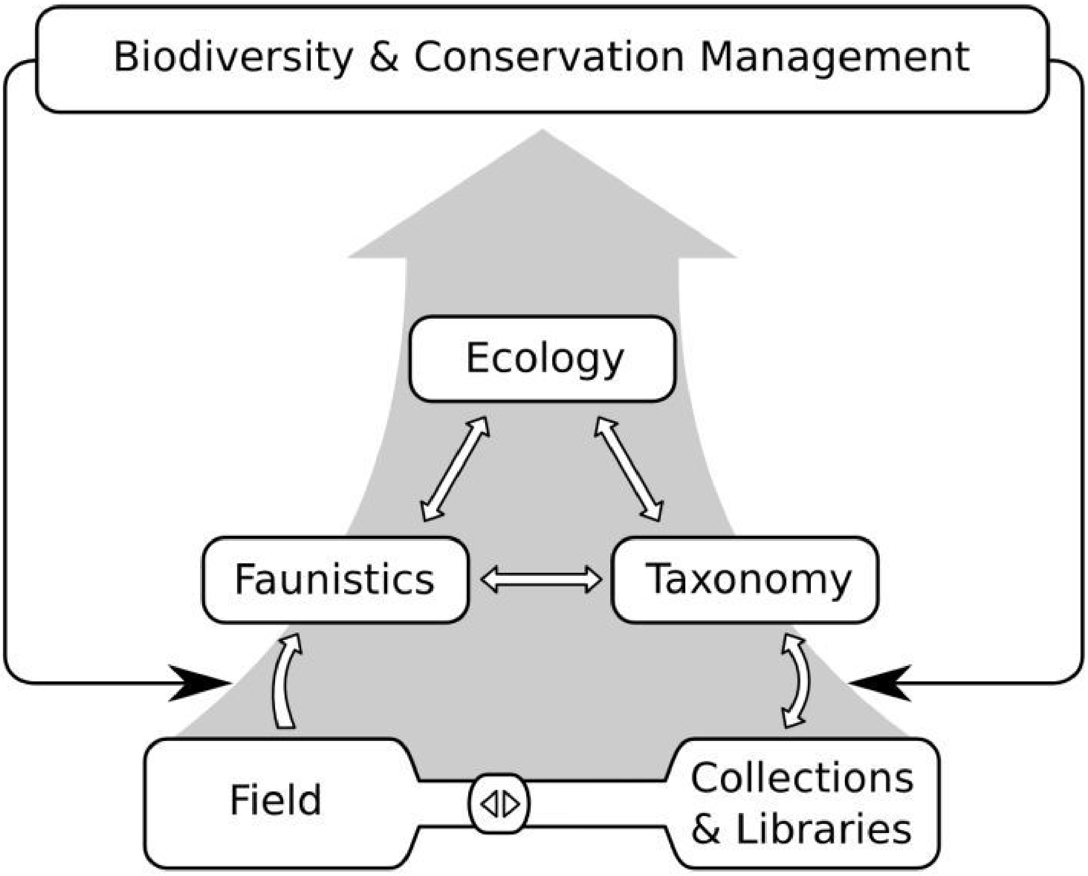

Fig. 3. Diagram showing the causal relationships and synergistic effects between fieldwork, collection-based work and different biological fields. The overall research is based on an iterative process. Figure prepared by Heike Worth.

For clarification, I believe Fig. 3 is best explained using an example: Faunistic fieldwork (symbol “Field”) in Timor-Leste led to the discovery of bent-toed geckos of the genus *Cyrtodactylus* previously not reported for Timor (chapter 4: papers 1 & 2). This discovery necessitated collection-based taxonomic work (arrow pointing from “Faunistics” to “Taxonomy”) on some widely distributed Sundanese taxa (*C. fumosus* and *C. marmoratus*) within this genus to resolve their identity and distribution, with the latter shown to be much more restricted than previously supposed (chapter 5: papers 4 & 5). This taxonomic research even led to the discovery of a new species (chapter 5: paper 3) and indicated that some taxa differ in their autecology (lowland *vs*. highland niches; arrow between “Taxonomy” and “Ecology” pointing both ways). These discoveries provided an excellent example for the value of particular collections and museums as a whole, which, I hope, may help these institutions to survive promoting research, including student projects (arrow between “Taxonomy” and “Collections & Libraries” pointing both ways; see also chapter 7: paper 13). The resolution of the taxonomy of *Cyrtodactylus* geckos beyond Timor provides positive feedback for the accomplished faunistic research, with the Timorese taxa identifiable as candidate species that are currently under description (see Outlook; arrow pointing from "Taxonomy" to "Faunistics"). Faunistic surveys in Timor-Leste also led to ecological research, including the food spectrum analysis of the Asian toad, *Duttaphrynus melanostictus* (arrow pointing from "Faunistics" to "Ecology"; chapter 6: paper 11), an introduced taxon that was considered a potential predator of small vertebrates such as lizards (chapter 6: paper 9). The occurrence of this toad on Timor posed a potential threat to some of the smaller *Cyrtodactylus* geckos as well, which, fortunately, does not appear to be the case (arrow pointing from "Faunistics" to "Ecology"). Results relevant for decision-makers (large, grey arrow) in biodiversity and conservation management include the following: (1) The examined bent-toed geckos (*Cyrtodactylus fumosus* and *C. marmoratus*) thought to be widely distributed in the Sunda Islands, are endemic to single islands or regions within an island, and the same applies for the newly described *C. klakahensis*; (2) Timor harbors an endemic *Cyrtodactylus* fauna as well, including several limited-range endemics; (3) the introduced Asian toad does not appear to pose a direct threat to Timor's lizard fauna through direct predation. Due to the ongoing habitat destruction on most of the Sunda Islands, protection measures for some of the limited-range endemics within *Cyrtodactylus* – both in Timor and on other islands need to be considered (black arrow pointing from "Biodiversity & Conservation Management towards "Filed" and "Faunistics"). A comprehensive level of taxonomic knowledge is needed to ensure success in preserving these species (black arrow pointing from "Biodiversity & Conservation Management towards "Collections & Libraries" and "Taxonomy").

By combining different but interrelated segments and reservoirs (field and collections), this thesis highlights the feasibility of a multidisciplinary and multitaxon approach in Southeast Asian herpetological research, not usually applied. Only by means of this approach was I able to – at the same time – provide comprehensive accounts for the herpetofauna of Timor-Leste, move towards resolving the taxonomy of some of the most complicated Southeast Asian reptile taxa, and to study the impact of the introduced Asian toad on the Timorese herpetofauna – constantly underlining the value of collections for the discoveries made. In the studied groups from the Sunda Islands, where collection permits are often hard to obtain, the validation of species identifications and detection of inaccuracies in already published accounts is essential and only possible by examining historic specimens, including the relevant types, and by thoroughly studying the related historic literature associated with these vouchers. The presented results (in the form of 13 publications) confirm that, in the age of DNA barcoding and photography-based taxonomy (see Appendix: Ceríaco *et al*. (2016)), classic zoological research still remains important and coherent. It also has an important role in species conservation.

No conservationist would doubt that e.g., taxonomy is an essential tool for understanding biodiversity. Poor taxonomy, however, has vast implications in conservation. Red Lists – legal instruments that guide decisions within the context of the conservation of threatened species – are only effective tools if the quality of taxonomic delimitation of these species is guaranteed. Hence taxonomic confusion over a species is counterproductive. To avoid mistakes in species conservation, I advocate that a comprehensive level of taxonomic (or natural history) knowledge is needed to ensure success in preserving species. This can be achieved by offering a targeted training to actors in biodiversity and conservation management and/or through their active participation in the research process. Complementarity of taxonomy (and other fields, such as ecology) and conservation guarantee stronger conservation actions. The widely distributed *Cyrtodactylus fumosus* sensu lato (species concept used before the papers in chapter 5 were published), would – under IUCN criteria – be most likely listed “Least Concern”, including a stable population trend. However, this category and trend may be inappropriate for the revised *C. fumosus* and the new species described that was masquerading under that name.

Despite the achievements made in this thesis, more research on the amphibians and reptiles of the Sunda Islands and adjacent regions is needed. For ongoing and new projects related to this research field, the reader is referred to the “Outlook section.”

9 Outlook

The following compilation contains projects that arose from the research presented in this dissertation. Because of the “taxonomic vandalism”[5] threat (see Aplin 1999; Wüster & Fry 2006; Kaiser *et al*. 2013a), I refrain from providing exact locality data and museum numbers of taxa under description or identified as candidate species.

As a result of the fieldwork conducted in Timor-Leste and collection-based comparative studies, the descriptions of new Timorese lizard species, identified by both morphological and molecular genetic analyses (targeted COI, 16s, and ND2 barcoding) are currently in preparation. These include several new species of *Cyrtodactylus* geckos and skinks of the genera *Eremiascincus* and *Sphenomorphus* (main collaborators: Hinrich Kaiser, Smithsonian Institution, USA & Mark O’Shea, University of Wolverhampton, UK). Several *Cyrtodactylus* species originally described from Indonesia are currently in the process of redescription and the descriptions of new species from islands of the Lesser Sundas (except Timor), the Moluccas, and Sulawesi are in preparation as well. Many of these yet undescribed species are only known from historic museum vouchers. New country and island records are to be reported on (own research projects). As indicated in paper 6, the diversity in the genus *Cylindrophis* is still significantly underestimated. A first molecular phylogenetic assessment of the snake genus *Cylindrophis* is in preparation, two new species are currently under description, and several candidate species were identified. For the phylogeny two mitochondrial genes (16s, ND2) and one nuclear gene (R35) were sequenced. Concatenation and species tree methodologies recovered identical and well-supported topologies, with highly divergent, yet undescribed, lineages (own research project; main collaborators: Justin Bernstein, Rutgers University, USA; Max Kieckbusch, Munich, Germany & Hinrich Kaiser, Smithsonian Institution, USA; Fig. 4). For the above projects a nearly complete morphological dataset was assembled during this PhD project, which is, in the case of the *Cylindrophis* project, extended by micro-CT scans. A preliminary unpublished analysis of micro-CT scans by Mecke & Kieckbusch revealed major differences in the skull morphology of several pipe snake lineages, highlighting the value of this non-invasive and non-destructive method for collection-based studies. The systematics, biogeography, and evolution of the groups mentioned, would make an ideal postdoctoral project, since the already existing data would greatly increase the chance of success.

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[5] Taxonomic vandals name new taxa without producing their own evidence, in effect usurping others’ work in progress, and presenting it to support these names. This issue has been particularly egregious for in the case of reptiles in the last decade.

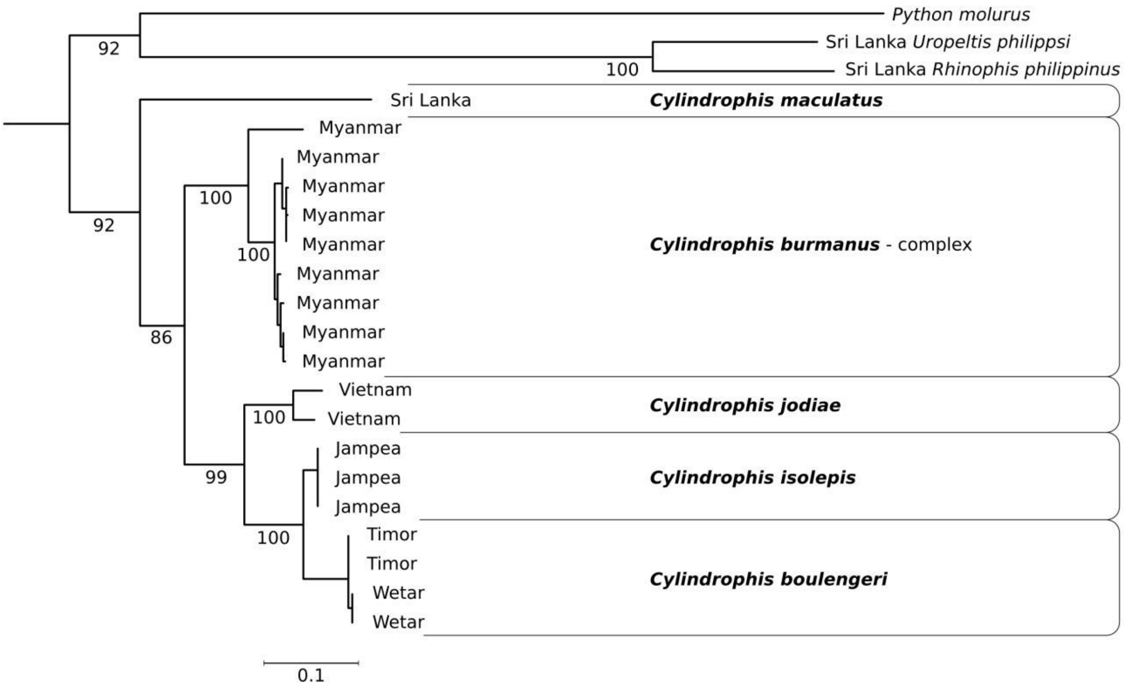

Fig. 4. Preliminary phylogenetic tree of snakes of the genus *Cylindrophis* from a maximum-likelihood analysis of DNA sequences of two mitochondrial genes (16s and ND2) and one nuclear gene (R35). A scale bar showing sequence change is indicated. The numbers at nodes are bootstrap support values. Low Support: 0–69, moderate: 70–94, high: 95–100.

Since the genus *Eremiascincus* is found in the Lesser Sundas and Australia, research on this group cannot be focused on the taxa occurring outside of Australia alone. The description of a new species of this genus from the iconic Pilbara region of Western Australia is currently in press (Mecke & Doughty). A first molecular phylogenetic assessment (CytB, nuclear dataset generated with RADSeq) of the *Eremiascincus richardsonii* group is in preparation, and this necessitates the resurrection and redescription of a taxon currently placed in synonymy. We also included Lesser Sunda taxa in this phylogeny to investigate their relations to Australian forms, and hence, this research contributes to the project outlined in the previous paragraph (collaborators: Mark Hutchinson, Steve Donnellan [both South Australian Museum, AU & Paul Doughty, Western Australian Museum, AU]).

As outlined in paper 13, specimens from the famous zoologist Rudolf Leuckart (1822–1898) in the collections at the MTD were recently identified. More were identified and digitized as part of a funded project in 2017. Several remarkable type specimens will be reported on and redescribed in the near future (collaborator: Raffael Ernst, Museum für Tierkunde Dresden, Germany).

A field guide to the reptiles of the Sunda Islands as a successor of De Rooij's *The Reptiles of the Indo-Australian Archipelago* is planned (together with Hinrich Kaiser, Smithsonian Institution, USA & Mark O'Shea, University of Wolverhampton, UK).

Forearmed with an immense knowledge of the morphology, taxonomy, and distribution of most Sundaic reptile groups, such a project would be feasible and mark a big step in my early career.

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11 Appendix – Other Publications

Figure 4 from Mecke (2017): Unterschätzte Artenvielfalt: Taxonomische Forschung führt zur Entdeckung unbekannter südostasiatischer Reptilien in herpetologischen Sammlungen. In: Materielle Kultur in universitären und außeruniversitären Sammlungen, Gesellschaft für Universitätssammlungen e.V. Berlin, Berlin 2017, 70–77. (book chapter, in Appendix). The figure shows a historical drawing of a *Cylindrophis* snake from a description in Wagler (1828–1833).

11.1 Paper 14

Ceríaco, L.M.P, Gutiérrez, E.E., Dubois, E. […] **Mecke, S.** […] & Zug, G. (493 authors, 2016): Photograph-based taxonomy is inadequate, unnecessary, and potentially harmful for biological sciences*.* *Zootaxa*, **4196**(3): 435– 445.

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Photography-based taxonomy is inadequate, unnecessary, and potentially harmful for biological sciences

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Note

The question whether taxonomic descriptions naming new animal species without type specimen(s) deposited in collections should be accepted for publication by scientific journals and allowed by the *Code* has already been discussed in *Zootaxa* (Dubois & Nemésio 2007; Donegan 2008, 2009; Nemésio 2009*a*–*b*; Dubois 2009; Gentile & Snell 2009; Minelli 2009; Cianferoni & Bartolozzi 2016; Amorim *et al.* 2016). This question was again raised in a letter supported by 35 signatories published in the journal *Nature* (Pape *et al.* 2016) on 15 September 2016. On 25 September 2016, the following rebuttal (strictly limited to 300 words as per the editorial rules of *Nature*) was submitted to *Nature*, which on 18 October 2016 refused to publish it. As we think this problem is a very important one for zoological taxonomy, this text is published here exactly as submitted to *Nature*, followed by the list of the 493 taxonomists and collection-based researchers who signed it in the short time span from 20 September to 6 October 2016.

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In defense of a species description without preserved specimens, a few colleagues recently provided arguments that could lead to widespread use of photography-based taxonomy (PBT) (Pape *et al.* 2016). We 493 collection-based researchers refute these arguments.

The main purpose of the *Code*'s Article 73.1.4—which tolerates the naming of species described based on illustrations—is to allow the nomenclatural availability of species names established without reference specimens before the maturity of taxonomy. However, modern descriptions shouldn't be done without *material* evidence through at least one museum 'type' specimen, carrying many characters that cannot be seen on photographs and enabling objectivity, replicability and refutability.

Species delimitation is a matter of taxonomy, not of nomenclature, but taxonomic work requires such a specimen to make an *objective* link between a name and a natural population, without which the allocation of the name remains uncertain.

Alleged species known only from photographs can be referred to by non-scientific names until the collection of a specimen enables acceptable taxonomic descriptions.

Peer-review, which is not required by the *Code*, may indeed be useful for taxonomic works if carried out by competent referees, but it has repeatedly proved insufficient to prevent flawed descriptions. PBT will promote rapid dissemination of poorly reviewed descriptions based on unverifiable "evidence".

PBT is detrimental for fields of biology that depend on taxonomy: impeding approval of permits to collect—a strong nuisance for taxonomy; harming the credibility of and obstructing advances in taxonomy, as untrained/unscrupulous persons can easily flood life "catalogues" with dubious taxa; increasing instability and inaccuracy, as scrutiny is hindered by the lack of specimens.

The *Code* must be reformed to prevent that Articles designed to deal with contributions from the early ages of taxonomy are used to justify outdated practices that can harm science and biodiversity conservation.

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11.2 Book Chapter

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SVEN MECKE

ABSTRACT

Da die taxonomische Bearbeitung einiger Reptiliengruppen Südostasiens lückenhaft ist, wurden anhand von Sammlungsmaterial Studien ausgewählter Arten begonnen, um deren Identität und genaue Verbreitung zu klären. Zwei dieser Taxa, Cyrtodactylus fumosus *(Rauchiger Bogenfingergecko) und* Cylindrophis ruffus *(Rotschwanz-Walzenschlange), sind – begleitet von der Erforschung ihrer Taxonomie-Geschichte – neu definiert und ihr ursprünglich postuliertes Verbreitungsgebiet eingegrenzt worden. Mittels detaillierter morphologischer Untersuchungen und der Überprüfung relevanter Literaturquellen konnte gezeigt werden, dass sich noch unbeschriebene Taxa unter diesen Namen verbergen. Anhand historischen Materials wurden bereits zwei neue Arten wissenschaftlich beschrieben:* Cyrtodactylus klakahensis *(Klakah-Bogenfingergecko) und* Cylindrophis subocularis *(Südjava-Walzenschlange). Im vorliegenden Beitrag soll die methodische Vorgehensweise dieser Studien dargestellt werden, für die mehr als 700 Museumsexemplare im Detail untersucht und fotografisch dokumentiert wurden. Die Recherche nach entsprechenden Museumsexemplaren erfolgte unter anderem anhand der Schwerpunktsetzung einzelner Museen, der Lebensdaten von Sammlern und/oder der zur Verfügung stehenden Datenbanken. Für einige wichtige historische Belegexemplare fehlten schriftliche Informationen (z. B. genaue Herkunftsangaben) am Objekt. Die geleistete Forschungsarbeit hat jedoch gezeigt, dass relevante Informationen häufig sekundär vorhanden sind, jeder Fall aber eine eigene Recherche erfordert. Durch die genaue Identifikation und Einordnung der Exemplare, den Nachweis ihrer Herkunft und die Einbettung in den historischen Zusammenhang ergibt sich eine Fülle an Informationen, die als Basis auch für die Beschreibung bisher unbekannter Arten genutzt werden konnte und nun für künftige Forschungsarbeiten zur Verfügung steht.*

Einleitung und zentrale Forschungsfrage

Anstoß für die in diesem Beitrag dargestellten Forschungsarbeiten gab eine im Jahre 2009 initiierte und noch andauernde Bestandsaufnahme (Arteninventar) der Herpetofauna des südostasiatischen Inselstaates Timor-Leste (Ost-Timor), bei der die dort beheimateten Faunenelemente taxonomisch bearbeitet, also identifiziert und klassifiziert, werden. Die durchgeführte Freilandarbeit resultierte in zahlreichen Erstnachweisen und der Entdeckung von über 20 der Wissenschaft bisher unbekannt gebliebenen Amphibien- und Reptilienarten, die gegenwärtig auf ihre Beschreibung warten (z. B. O'Shea, Sanchez, Kathriner u. a. 2015; Kaiser, Sanchez, Heacox u. a. 2013). Die Gattung der Bogenfingergeckos (*Cyrtodactylus*) war vor Beginn dieses Forschungsprojektes von der Insel Timor gänzlich unbekannt, es konnten jedoch mittels morphologischer und molekulargenetischer Untersuchungen zehn Kandidaten-Arten[1] identifiziert werden. Der taxonomische Status der in Timor-Leste nachgewiesenen Walzenschlange ist bislang ungeklärt, und auch bei dieser Form könnte es sich um eine unbeschriebene Art handeln (Kaiser, Sanchez, Heacox u. a. 2013).

Die wissenschaftlichen Untersuchungen blieben zwangsläufig nicht auf Timor-Leste beschränkt. Die komplexe Taxonomie und postulierte großräumige Verbreitung vieler in der Region beheimateter Arten machten detaillierte Vergleichsuntersuchungen der potentiellen Neuentdeckungen mit ähnlichen Arten aus Südostasien nötig, deren Bearbeitung in der Vergangenheit lückenhaft geblieben war. Gründe für diese unzureichende Bearbeitung sind u. a. in vermeintlichen morphologischen Ähnlichkeiten zwischen verschiedenen Gattungsangehörigen und Fehlern in der relevanten

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[1] Kandidaten-Arten sind Arten, die der Wissenschaft mit hoher Wahrscheinlichkeit nicht bekannt sind und daher als Kandidaten für eine offizielle Benennung eingestuft werden können.

Literatur zu suchen. Diese haben dazu geführt, dass man einen einzigen, gültigen Namen für Populationen verwendet hat, die sich jedoch auf Artniveau unterscheiden (worauf im Material- und Methodenteil des Beitrages noch näher eingegangen wird).

Zwei dieser problematischen Arten sind der Rauchige Bogenfingergecko *Cyrtodactylus fumosus* (Müller, 1895) und die Rotschwanz-Walzenschlange *Cylindrophis ruffus* (Laurenti, 1768), deren genaue Identität und Verbreitung bisher unklar geblieben sind. Der Name *„Cyrtodactylus fumosus"* wurde in der Vergangenheit für Gecko-Populationen von Sumatra, Java, Bali, Sulawesi und Halmahera verwendet (z. B. De Rooij 1915; Mertens 1929, 1934; Manthey & Grossmann 1997; Endarwin 2006); das Verbreitungsgebiet von *„Cylindrophis ruffus"* (Typus-Lokalität: Java, vermutlich Nordwest-Java) erstreckt sich laut der einschlägigen Literatur über den gesamten Sundaland-Hotspot (Malaiische Halbinsel und Große Sundainseln; Kieckbusch, Mecke, Hartmann u. a. 2016). Für die taxonomischen Bearbeitungen ergibt sich daraus die zentrale Forschungsfrage: Handelt es sich bei *Cyrtodactylus fumosus* und *Cylindrophis ruffus* tatsächlich um weitverbreitete Arten, oder verbergen sich noch unbekannte Taxa (biologische Einheiten) unter den bekannten Namen?

Material und Methoden

Den hier besprochenen taxonomischen Bearbeitungen von *Cyrtodactylus fumosus* und *Cylindrophis ruffus*, inklusive deren Neudefinition und der Beschreibung neuer Arten, liegt vor allem das erstmals von Simpson (1951, 1961) formulierte und durch spätere Arbeiten vielfach abgewandelte Evolutionäre Artkonzept („lineage-based species concept") zugrunde.[2] Die neubeschriebenen Arten sind von anderen Linien geografisch isoliert (Allopatrie) und unterscheiden sich von diesen durch eine Reihe auffälliger, diagnostischer Merkmale der äußeren Morphologie, von denen einige apomorphieverdächtig sind. Neben phänetischen Unterschieden am Objekt selbst konnten anhand der angegebenen Fundorte auch Habitatunterschiede zwischen den Populationen rekonstruiert werden (im Falle der Bogenfingergeckos, die man unter dem Namen *„Cyrtodactylus fumosus"* zusammengefasst hat, sind einige Arten z. B. Bewohner des Tieflandes, während andere nur von Lokalitäten auf über 1.000 Meter ü.NN bekannt sind). Die neubeschriebenen Arten sind somit Linien, die getrennt von anderen Taxa evolvierten und ihre eigenen, einzigartigen evolutionären Rollen und Tendenzen haben (im Sinne von Simpson 1951, 1961).

Für die morphologischen Vergleichsuntersuchungen wurden verschiedene Längenmessungen mit digitalen Messschiebern durchgeführt und die Daten durch Indexbildung oder das Anwenden einer Allometrieformel von größenbedingten Unterschieden bereinigt (siehe z. B. Kieckbusch, Mecke, Hartmann u. a. 2016). Ebenso wurden meristische Daten erhoben, wie etwa die Anzahl bestimmter Schuppen oder, im Falle der Bogenfingergeckos, die Anzahl der Poren auf den Schenkeln. Alle Zählungen wurden unter einem Seziermikroskop vorgenommen. Für die Beschreibung der Färbung und Muster wurde das Werk von Köhler (2012) herangezogen. Zeichnungen wurden anhand von Fotografien angefertigt und in jeder Publikation bereitgestellt.[3] Auf molekulargenetische Untersuchungen musste aufgrund des Alters vieler Belegexemplare (einige wurden vor über 100 Jahren gesammelt) und dem Fehlen frischer Gewebeproben (vor allem aus Indonesien) bisher verzichtet werden (siehe jedoch den Ausblick des vorliegenden Beitrages).

Für die Studien wurde Material aus 13 Sammlungen untersucht. Dabei erwies sich das Material aus den folgenden Museen (Abkürzungen nach Sabaj Pérez 2014) für die Untersuchungen als besonders wichtig: *American Museum of Natural History*, New York (AMNH); *Natural History Museum*, London (BMNH); *Museum of Comparative Zoology*, *Harvard University*, Cambridge (MCZ); Museum für Tierkunde, Senckenberg Naturhistorische Sammlungen Dresden (MTD); Naturhistorisches Museum Basel (NMBA); Naturhistorisches Museum Wien (NMW); *Naturalis Biodiversity Center*, Leiden (RMNH & ZMA); und Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt (SMF).

Maßgeblich für die Studien war vor allem der Vergleich der neubeschriebenen Arten mit dem relevanten Typusmaterial[4] schon bekannter Arten. Für die Beschreibung eines neuen Bogenfingergeckos von Java, der bislang unter dem Namen *Cyrtodactylus fumosus* bekannt war, ist der Vergleich mit dem Holotypus von *C. fumosus* (NMBA 2662 aus Nord-Sulawesi) und weiteren topotypischen Exemplaren (d. h. das Material stammt aus derselben Gegend wie der Typus) unverzichtbar gewesen. Zudem wurde die neue Art mit der Typusserie der ebenfalls in Java beheimateten Art *Cyrtodactylus marmoratus* Gray, 1831 (RMNH. 2710.1–8, Paralectotypen; RMNH 2710a.1, Lectotypus; RMNH 2710 a.2–6, Paralectotypen) verglichen, die von Mecke, Kieckbusch, Hartmann & Kaiser (2016) erstmals im Detail beschrie-

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[2] Auf eine umfassende Behandlung der aktuell diskutierten Artkonzepte muss an dieser Stelle verzichtet werden.

[3] Für eine genaue Auflistung der relevanten Merkmale siehe Mecke, Hartmann, Mader u. a. (2016; *Cyrtodactylus*) und Kieckbusch, Mecke, Hartmann u. a. (2016; *Cylindrophis*).

[4] Ein Typus ist ein ausgewähltes Individuum, das die Grundlage zur Definition und Benennung eines Taxons bildet. Holotypus = einzelnes Exemplar, das als Basis für eine Erstbeschreibung fungierte; Lectotypus = nachträglich aus einer Typusserie als Namensträger bestimmtes Exemplar; Paralectotypen = die übrigen Exemplare der Serie, aus der ein Lectotypus festgelegt worden ist.

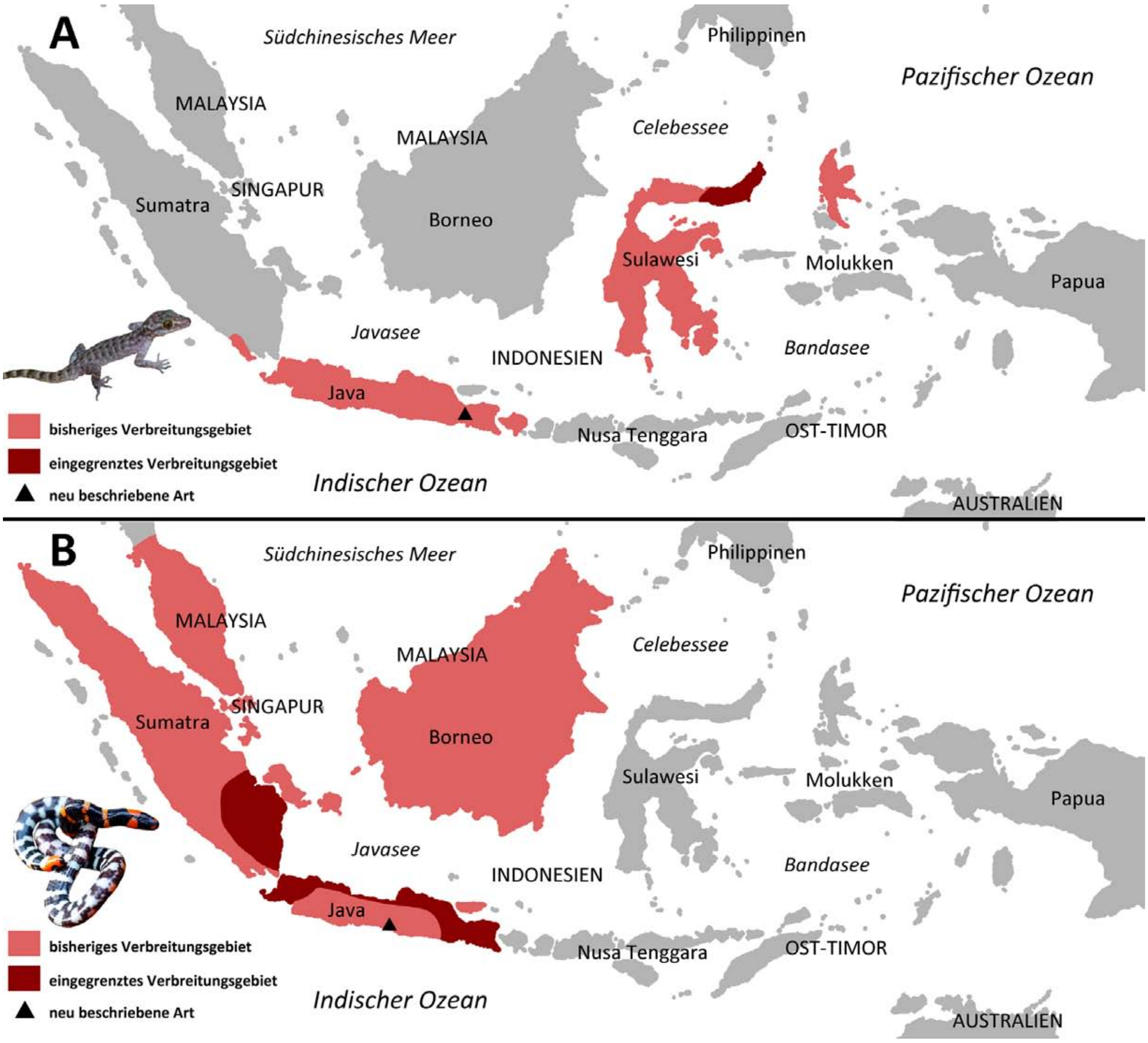

Abb. 1: Verbreitungsgebiete der untersuchten Arten in Südostasien vor (hellrot) und nach (dunkelrot) taxonomischen Bearbeitungen durch den Autor. (A) Verbreitung von *Cyrtodactylus fumosus. Cyrtodactylus fumosus* sensu stricto ist in seiner Verbreitung auf Nord-Sulawesi beschränkt. Die neuentdeckte Art *Cyrtodactylus klakahensis* (ehemals *Cyrtodactylus fumosus*) stammt aus Klakah, Lumajang, Jawa Timur Province, Java. (B) Verbreitung von *Cylindrophis ruffus. Cylindrophis ruffus* sensu stricto ist in ihrer Verbreitung auf das nördliche Java und südöstliche Sumatra beschränkt. Die neuentdeckte Art *Cylindrophis subocularis* (ehemals *Cylindrophis ruffus*) stammt aus Grabag, Purworejo, Jawa Tengah, Java. Karten: Max Kieckbusch

ben worden ist. Der Typus von *Cylindrophis ruffus* gilt als verschollen, und ein Neotypus wurde bislang noch nicht festgelegt (Mecke u. a., in Vorbereitung), sodass für die Beschreibung einer neuen Art aus diesem Komplex[5] vor allem ein Vergleich mit topotypischen Exemplaren von *Cylindrophis ruffus* unerlässlich gewesen ist.

Zusammenfassung der zentralen Ergebnisse

Mittels einer maßgeblich auf historischem Sammlungsmaterial beruhenden, morphologischen Studie ist es gelungen, die genaue Identität von *Cyrtodactylus fumosus* zu klären. Das bekannte Material am NMBA und BMNH (NMBA 2662, Holotypus; NMBA 2663, BMNH 1895.2.27.7, 1896.12.9.3, topotypische Exemplare) stammt aus dem Hochland Nord-Sulawesis (Sulawesi Utara, Indonesien) und unterscheidet sich in seiner Morphologie fundamental von anderen Gattungsangehörigen. Die Verbreitung des Taxons wurde somit entsprechend beschränkt (Hartmann, Mecke, Kieckbusch u.a. 2016; Mecke, Hartmann, Mader u. a. 2016, Abb. 1 A und 2 A). Durch die Aufarbeitung ihrer komplexen

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[5] Unter einem (Art)Komplex versteht man eine Gruppe von Arten, die durch Gemeinsamkeiten als Gruppe ansprechbar sind. Die einzelnen Mitglieder dieser Gruppe sind dabei nicht unbedingt wissenschaftlich beschrieben.

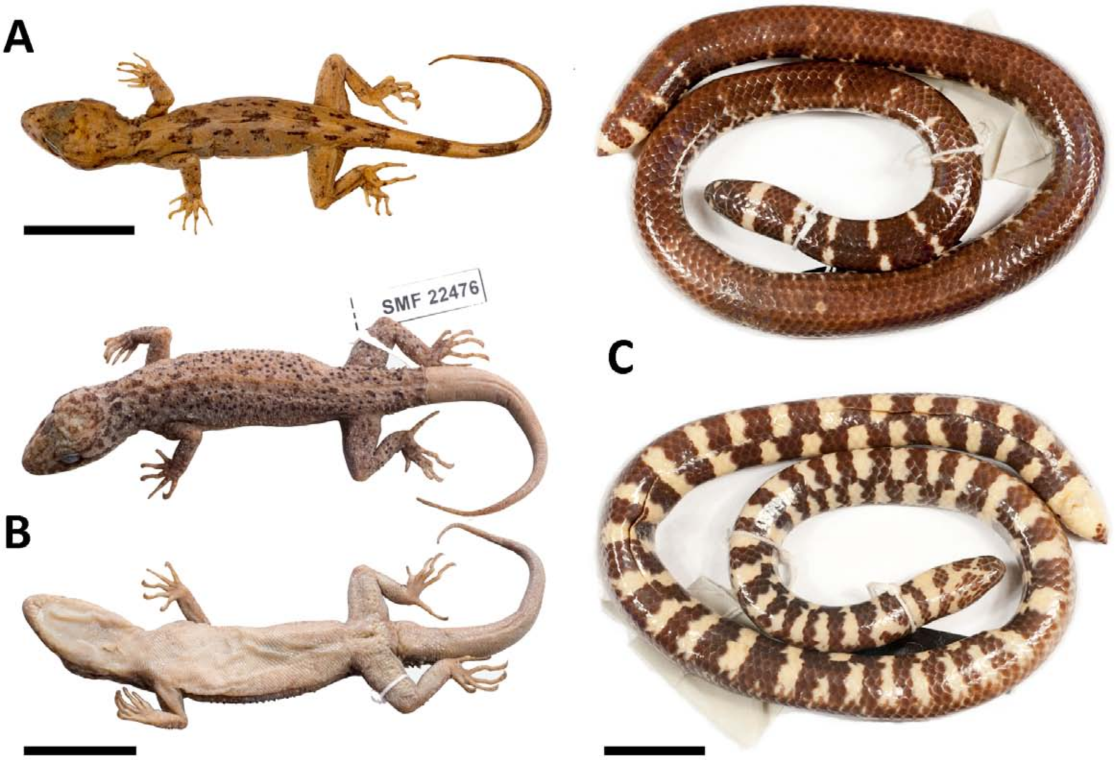

Abb. 2: Indonesische Bogenfinger-Geckos und Walzenschlangen. (A) *Cyrtodactylus fumosus*, ein nur selten gesammelter Gecko aus Nord-Sulawesi. (B) Adultes Männchen von *Cyrtodactylus klakahensis* in dorsaler und ventraler Ansicht. (C) Adultes Weibchen von *Cylindrophis subocularis* in dorsaler und ventraler Ansicht. Maßstäbe = 2 cm. Fotos: Sven Mecke

Taxonomie-Geschichte und anhand detaillierter morphologischer Vergleichsuntersuchungen konnte auch das Verbreitungsgebiet von *Cylindrophis ruffus* sensu stricto erheblich eingegrenzt und die Typuslokalität auf die Insel Java fixiert werden, wobei der Typus vermutlich in Nordwest-Java gesammelt worden ist (Kieckbusch, Mecke, Hartmann u. a. 2016; Mecke u. a., in Vorbereitung, Abb. 1 B).

Die Untersuchungen zeigten in beiden Fällen, dass sich außerdem unbeschriebene Taxa unter den bekannten Namen verbargen. Zwei neue Arten konnten bereits beschrieben werden, bemerkenswerterweise von der indonesischen Insel Java, deren Herpetofauna im Vergleich zu jener der anderen großen Sundainseln als besonders gut erforscht gilt (z. B. Teynié, David & Ohler 2010). Bei diesen beiden neuen Taxa handelt es sich um den Klakah-Bogenfingergecko *Cyrtodactylus klakahensis* Hartmann, Mecke, Kieckbusch, Mader & Kaiser, 2016 (Abb. 2 B) und die Südjava-Walzenschlange *Cylindrophis subocularis* Kieckbusch, Mecke, Hartmann, Ehrmantraut, O'Shea & Kaiser, 2016 (Abb. 2 C), die jeweils nur von wenigen Exemplaren bekannt sind, welche in der ersten Hälfte des 20. Jahrhunderts gesammelt worden sind. Die existierenden Museumsbelege waren als *Cyrtodactylus fumosus* bzw. *Cylindrophis ruffus* etikettiert. Die neu beschriebenen Arten lassen sich aber von diesen durch eine Reihe sehr auffälliger Merkmale (vor allem durch Unterschiede in der Beschuppung) unterscheiden.

Herangehensweise an Objekte und Sammlungen

Für die beiden durchgeführten Revisionen, inklusive der Beschreibung neuer Arten, wurden mehr als 700 überwiegend historische, in Konservierungsflüssigkeiten fixierte Museumsexemplare (mehr als 450 Walzenschlangen und mehr als 250 Bogenfingergeckos) aus 13 nationalen und internationalen Sammlungen im Detail untersucht, wobei jeweils über 50 äußere Merkmale, besonders der Beschuppung, verglichen worden sind. Derart umfangreiche Studien erlauben in der Regel eine geografisch flächendeckende Bearbeitung sowie eine eindeutige Merkmalsbewertung und damit taxonomische Zuordnung der Exemplare.

Nach Museumsexemplaren wurde auf unterschiedlichen Wegen recherchiert, was neben einer über die reine Taxonomie hinausgehenden Expertise (d.h. Sammlungen und Sammlungszusammenhänge betreffendes Wissen) auch eine Suchstrategie erforderte, um kompetent und zielführend durch die Datenflut zu navigieren. Die Suche orientierte sich deshalb in erster Linie an der bekannten (historischen und/oder geografischen) Schwerpunktsetzung einzelner Museen. Da die untersuchten Taxa in ihrer Verbreitung im Wesentlichen auf das Gebiet des heutigen Indonesiens beschränkt sind, das über einen sehr langen Zeitraum hinweg (1619–1949) bekanntlich eine niederländische Kolonie gewesen ist (Croissant 2015), bot sich im konkreten Fall ein Besuch der herpetologischen Sammlung des *Naturalis Biodiversity Centre* in Leiden (Niederlande) an. Dieses Museum beherbergt die Bestände des ehemaligen *Rijksmuseum van Natuurlijke Historie* (RMNH) und des *Zoölogisch Museum Amsterdam* (ZMA) und damit die umfangreichste Aufsammlung von Belegen aus dem heutigen Indonesien. Wenn keine direkte, institutionsbezogene Schwerpunktsetzung existiert, ermittelt man (z. B. durch ein entsprechendes Studium der vorhandenen Literatur) potentiell vorhandene Bestände über Expeditionen in die Region, bei denen das gesammelte Material an bestimmten Instituten hinterlegt worden ist. Beispielhaft soll hier die Novara-Expedition, die erste und einzige groß angelegte Weltumseglung der österreich-ungarischen Kriegsmarine in den Jahren 1857–1859 (Martiny 1973) genannt werden, bei der die gesammelten, wertvollen herpetologischen Objekte der Sammlung des Naturhistorischen Museums Wien (NMW) übereignet wurden. Die Suche nach Sammlungsbeständen kann sich aber unter Umständen auch an den Lebensdaten von Forschern orientieren. Beispielsweise war Robert Mertens (1894–1975), ein bedeutender deutscher Herpetologe (Amphibien- u. Reptilienkundler), im Jahre 1927 an einer Indonesien-Expedition, der Sunda-Expedition Rensch, beteiligt und hat den Großteil der während dieser Reise gesammelten herpetologischen Belege an seinem Heimatinstitut, dem Senckenbergmuseum in Frankfurt am Main, hinterlegt (Mertens 1930). Teilweise werden in der entsprechenden, älteren Primärliteratur aber auch Belegexemplare und ihr jeweiliger Standort direkt aufgelistet. Datenbanken, wie das durch die amerikanische *National Science Foundation* (NSF) und die *Global Biodiversity Information Facility* (GBIF) geförderte Vert-Net©, die Reptile Database, aber auch die elektronischen Verzeichnisse einzelner Museen, bieten eine digitale Infrastruktur, die Forschern den freien Zugang zu objektbezogenen Daten, wie dem Standort des Materials oder dessen Status (z. B. Typusmaterial), ermöglicht. Jedoch verfügen nicht alle Institute über entsprechende Datenportale. Es steht außer Frage, dass die verschiedenen Herangehensweisen nicht zwangsläufig unabhängig voneinander sind, sondern eine Kombination der mitunter ohnehin stark vernetzten Informationsquellen am besten zum Ziel führt. Die direkte Suche nach spezifischen Exemplaren in der relevanten Literatur oder in Datenbanken darf sich allerdings nicht alleine an den heute gültigen Bezeichnungen orientieren, sondern muss auch sämtliche Synonyme mit einbeziehen.

Obgleich es Forschern an wissenschaftlichen Institutionen in aller Regel möglich ist, eine kleine Anzahl von Exemplaren aus Sammlungen für Studienzwecke zu entleihen, erfordert die detaillierte und umfassende Untersuchung großer Bestände, wie für die hier dargestellten Studien, bei denen über 50 Merkmale pro Exemplar erfasst worden sind, einen Besuch vor Ort. Für diesen Zweck wurde ein zeitsparendes und effizientes sowie objektschonendes Verfahren der Datenaufnahme verwendet, das grundsätzlich zu empfehlen ist: Die umfangreichen Objektbestände werden in einer Forschergruppe von drei bis vier Personen bearbeitet, unter denen die notwendigen Arbeitsschritte aufgeteilt werden. Eine Person ist immer für einen Arbeitsschritt zuständig, wobei im Vorfeld alle beteiligten Personen jeden einzelnen Arbeitsschritt erlernen oder vertiefen, sodass auch etwa bei Ausfällen die Datenaufnahme reibungslos ablaufen kann. So könnte Person 1 für das Erfassen metrischer Daten (d. h. Längenmessungen wie Kopf- und Schwanzlänge) und Person 2 für die meristische Datenaufnahme (z. B. das Zählen von Schuppen) zuständig sein. Person 3 würde die Aufgabe zukommen, Farbe und Muster anhand objektiver Kriterien zu erfassen. Die Schwierigkeiten, die bei der Beschreibung bzw. Benennung der Farbtöne und Muster bestehen, werden dadurch umgangen, dass die Beurteilung anhand von Farbtafeln und objektiven Definitionen (in Köhler 2012) vorgenommen wird. Person 4 fertigt Detailaufnahmen jedes Exemplars an, die für spätere Vergleiche zur Verfügung stehen. Fotografien alleine sind für taxonomische Bearbeitungen nicht ausreichend, erlauben aber als zweiten Schritt (nach der originären Untersuchung physischer Objekte) die Suche und Bewertung von Merkmalen, was eine erneute Untersuchung von Exemplaren (z. B. bei Unklarheiten in den Datensätzen) in aller Regel überflüssig macht. Allein für die Walzenschlangen-Studie (Kieckbusch, Mecke, Hartmann u. a. 2016) wurden acht bis zehn Detailaufnahmen pro Individuum angefertigt. Dies resultierte in über 40.000 Fotografien, die in einer eigenen digitalen Datenbank hinterlegt worden sind und die den einzelnen Sammlungen nach Abschluss des Gesamtprojektes (siehe Ausblick) zur Verfügung gestellt werden.

Diese klassisch-morphologische Datenaufnahme ist keineswegs trivial, da Merkmale, einschließlich routinemäßig für Artbeschreibungen verwendeter Schlüsselmerkmale, in der einschlägigen Literatur oft ausgesprochen schlecht definiert sein können. Als Beispiel sei hier die Einfaltung auf dem Unterbauch mancher Bogenfingergeckos, die sogenannte Präkloakal-Vertiefung, genannt, die recht unterschiedlich ausgeprägt sein kann. Es handelt sich bei dieser Struktur um ein wichtiges Artunterscheidungsmerkmal, für das eine allgemeingültige und objektive Definition bisher fehlte. Mecke, Kieckbusch, Hartmann & Kaiser (2016) stellten daher im Zuge ihrer Forschungsarbeiten an indonesischen Bogenfingergeckos eine detaillierte Beschreibung und Terminologie für dieses Schlüsselmerkmal und seine Ausprägungen bereit, die eine klare Abgrenzung von Morphotypen (d. h. ähnlicher, aber morphologisch unterschiedlicher Arten) erlaubt (Abb. 3 A–F).

Neben zoologischen Sammlungen sind Bibliotheken mit einem historischen Buchbestand ein unverzichtbares Werkzeug für jede taxonomische Studie. Bei Revisionen ist z. B.

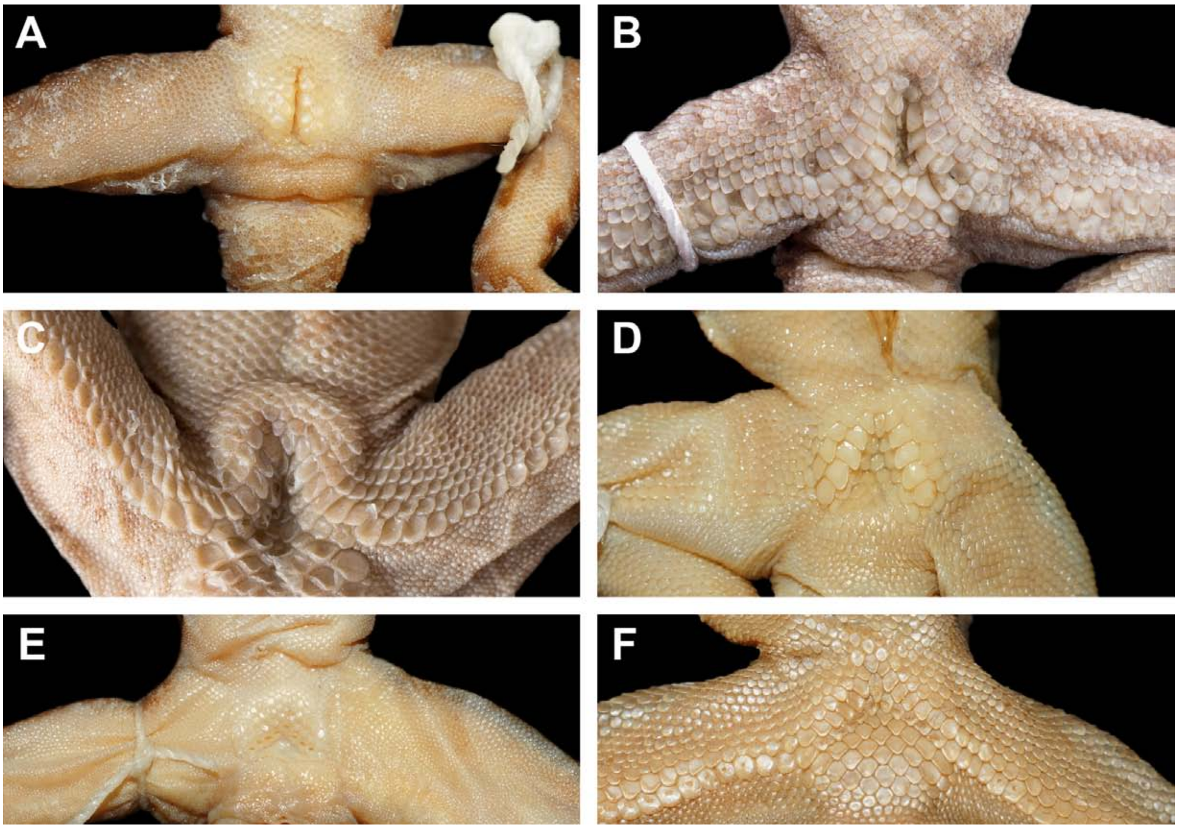

Abb. 3: Präkloakal-Vertiefungen verschiedener indonesischer Bogenfinger-Geckos (adulte Männchen). (A) *Cyrtodactylus pubisulcus* und (B) *C. klakahensis* besitzen eine schlitzförmige Präkloakal-Furche. (C) *Cyrtodactylus fumosus* besitzt eine Präkloakal-Furche, die nach unten geöffnet ist (umgekehrtes „Y"). (D) *Cyrtodactylus baluensis* weist eine Präkloakal-Grube in der Form eines umgekehrten „V" (spitzwinkliges Dreieck) auf. (E) *Cyrtodactylus consobrinus* besitzt eine Präkloakal-Grube in der Form eines stumpfwinkligen Dreiecks. (F) *Cyrtodactylus wetariensis* fehlt eine Präkloakal-Vertiefung. Einzelne Abbildungen nicht im gleichen Maßstab. Fotos: Sven Mecke

anhand aller relevanten Literaturquellen sorgfältig zu überprüfen, ob es für manche der potentiell unbeschriebenen Arten nicht schon einen offiziellen wissenschaftlichen Namen gibt, der nur übersehen worden ist. Lohnend ist die Untersuchung der Taxonomie-Geschichte, d. h. der Definition und Benennung einer Art im Laufe der Geschichte, in jedem Fall, weil sie ein Gewinn für die finale Präsentation jeder taxonomischen Studie ist (siehe z. B. die Abhandlung zur Taxonomie-Geschichte von *Cylindrophis ruffus* in Kieckbusch, Mecke, Hartmann u. a. 2016; Abb. 4). Eine Taxonomie-Geschichte aufzuarbeiten, ist eine detektivische und zeitintensive Arbeit – zeitintensiver als die Anfertigung einer Artbeschreibung. Für die bereits veröffentlichte Walzenschlangen-Studie (siehe auch Ausblick) wurden rund 100 Zeitschriftenaufsätze sowie Monographien studiert, wovon viele nicht digitalisiert, schwer zugänglich und auf Französisch oder Latein verfasst sind. Selbstverständlich umfasst das umfangreiche Literaturstudium im Zuge taxonomischer Arbeiten nicht alleine Fachliteratur, z. B. zur Herpetologie und Biogeografie, sondern auch Quellen zur Länder-Geschichte und zu einzelnen Sammlungen. Bei den sammlungs- und literaturbasierten Studien wurde das Einhalten der schriftlich fixierten ICZN-Regeln (Internationaler Code für Zoolgische Nomenklatur; Iczn 1999) berücksichtigt, die die Benennung und Klassifizierung aller tierischen Organismen normieren.

Sammlungsexemplare sind für die vorgestellten Studien generell nur dann von Nutzen, wenn einige grundlegende Informationen zu ihnen vorliegen. Von großer Bedeutung

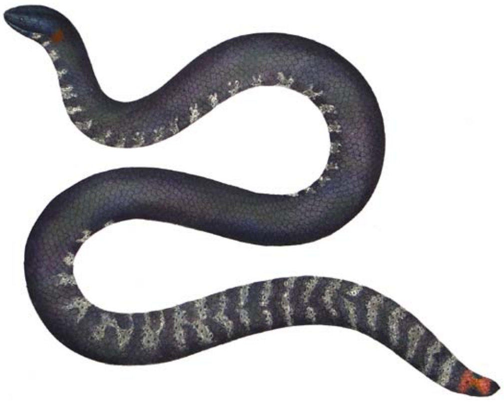

Abb. 4: Historische Walzenschlangendarstellung (*Cylindrophis resplendens*) aus einer Artbeschreibung von Wagler, 1828 – 1833. Bei *Cylindrophis resplendens* handelt es sich um keinen gültigen Namen, sondern um ein Synonym von *C. ruffus*.

ist hierbei die genaue Angabe der Herkunft, die Vergleichsuntersuchungen zwischen Populationen überhaupt erst möglich macht. Im Gegenzug bedeutet dies aber nicht, dass Museumsexemplare, für die genaue Herkunftsangaben am Objekt fehlen, wertlos sind. Die bislang geleistete Forschungsarbeit hat eindrücklich gezeigt, dass relevante Informationen häufig sekundär (z. B. in handschriftlichen Sammlungskatalogen) vorhanden oder aber rekonstruierbar sind (so kann der Fundort häufig über den Sammler ermittelt oder eingegrenzt werden). Bei der Beschreibung von *Cylindrophis subocularis* ergab sich z. B. das Problem, dass zwei Exemplare in der Sammlung des RMNH (RMNH 8785.80 & 81, nun RMNH 47931 & 32), die sich im selben Glas (8785) befanden wie ein Exemplar der neuen Art (RMNH 8785.51, nun RMNH 8785), nicht die Merkmale der Südjava-Walzenschlange zeigten, obwohl sie vom gleichen Fundort stammen sollten. Dies legte die Vermutung nahe, dass sie möglicherweise von einer anderen Lokalität gesammelt sein könnten. Dem Original-Sammlungskatalog der herpetologischen Sammlung des *Naturalis Biodiversity Center* in Leiden war folgende Anmerkung zu den betreffenden Exemplaren zu entnehmen (hier übersetzt aus dem Niederländischen):

„Das Glas (8785) beinhaltet nun drei Exemplare; diese wurden von E. M. J. Jaspars untersucht und erhielten die Nummern 51, 80, 81. Wahrscheinlich wurden die Nummern (Exemplare) 80 und 81 versehentlich von diesem Wissenschaftler im Glas untergebracht und sie stammen vermutlich aus Buitenzorg (Bogor), Java."

Die Informationen auf dem die Exemplare begleitenden Etikett wären in diesem Fall für eine sichere Zuordnung nicht ausreichend gewesen, wohingegen der Eintrag im Katalog einen direkten Hinweis auf den tatsächlichen Fundort der Exemplare RMNH 8785.80 & 81 lieferte.

Ausblick

Schon während der Vorarbeiten zu den hier dargestellten Studien zeigte sich, dass die Taxonomie der Gattungen *Cyrtodactylus* und *Cylindrophis* äußerst komplex ist. Besonders bei den Bogenfingergeckos der südostasiatischen Inselwelt stehen für viele der bereits beschriebenen Arten nur wenige Daten zu Morphologie und Verbreitung zur Verfügung, wobei sie sich in einigen Fällen auf die Angaben in den Originalbeschreibungen beschränken. Solide Neudefinitionen dieser Formen sind in Vorbereitung. Zudem konnten während der Arbeit in nationalen und internationalen Museumssammlungen über zehn unbeschriebene Bogenfingergeckos identifiziert werden, die gegenwärtig wissenschaftlich beschrieben werden. Obgleich die überwiegende Zahl dieser Neuentdeckungen in historischer Zeit in entlegenen Gebieten gesammelt worden ist, kommen einige, recht auffällige Kandidaten-Arten auf Inseln vor, die als besonders gut untersucht gelten, wie z. B. auf der Insel Bali.

Eine große Herausforderung stellt die Taxonomie der Rotschwanz-Walzenschlange dar, bei der es sich um einen Art-Komplex handelt. Hier wird die geleistete klassisch-morphologische Forschung in näherer Zukunft um andere Methoden zur Artidentifizierung und -abgrenzung erweitert werden (integrativer Ansatz), wobei weitere Walzenschlangen-Arten in die Untersuchungen einbezogen werden. Erste Micro-CT-Scans, die am Museum für Naturkunde in Berlin erstellt worden sind, weisen auf größere Unterschiede in der Schädelmorphologie der Walzenschlangen hin. An der Philipps-Universität Marburg sollen Raster-Elektronenmikroskopische Aufnahmen angefertigt werden, um die Mikroornamentation der Schuppen zu untersuchen. Ein Kooperationspartner aus den USA (*Villanova University*, Pennsylvania) arbeitet gegenwärtig an einer molekularen Phylogenie, um die Verwandtschaftsverhältnisse der Arten zu klären. Ein auf morphologischen Daten basierender, streng kladistisch rekonstruierter Stammbaum soll dieser Phylogenie gegenübergestellt und im Zuge weiterer Beiträge zur Walzenschlangen-Taxonomie präsentiert werden.

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Zum Autor

Sven Mecke studierte Allgemeine und Organismische Biologie in Marburg. Seit 2011 ist er wissenschaftlicher Mitarbeiter und Dozent am Fachbereich Biologie der Philipps-Universität Marburg. Er promoviert zum Thema „Taxonomy, natural history, and ecology of selected herpetofauna species from the Sunda Islands and adjacent regions – synergistic effects of fieldwork and museum collections for biodiversity research".

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13 Erklärung zum Eigenanteil an den Publikationen

Hiermit erkläre ich, dass der Eigenanteil an den folgenden Publikationen inhaltlich und prozentual wie folgt ist:

Chapter 4

O'Shea, M., Sanchez, C., Kathriner, A., **Mecke, S.**, Carvalho, V.L., Ribeiro, A.V., Soares, Z.A., De Araujo, L.L. & Kaiser, H. (2015): Herpetological Diversity of Timor-Leste: Updates and a Review of Species Distribution. *Asian Herpetological Research*, **6**(2): 73–131.

Eigenanteil (ca.15%) besteht in der Beschaffung von Material während dreier Expeditionen nach Timor-Leste, Beiträgen zu allen Kapiteln der Publikation und der eigenständigen Verschriftlichung der Beschreibungen zu den Gattungen *Cyrtodactylus*, *Eremiascincus*, *Sphenomorphus* und *Cylindrophis*.

Kaiser, H., Sanchez, C., Heacox, S., Kathriner, A., Ribeiro, A.V., Soares, Z.A., De Araujo, L.L., **Mecke, S.** & O'Shea, M. (2013): First Report on the Herpetofauna of Ataúro Island, Timor-Leste. *Check List*, **9**(4): 763–770.

Eigenanteil (ca.15%) besteht in der Beschaffung von Material während einer Expedition nach Ataúro, Timor-Leste, Beiträgen zu allen Kapiteln der Publikation und der eigenständigen Verschriftlichung der Beschreibungen zu den Gattungen *Cyrtodactylus* und *Eremiascincus*.

Chapter 5

Hartmann, L., **Mecke, S.** (joint first authors), Kieckbusch, M., Mader, F. & Kaiser, H. (2016): A New Species of Bent-toed Gecko, Genus *Cyrtodactylus* Gray, 1827 (Reptilia: Squamata: Gekkonidae) from Jawa Timur Province, Java, Indonesia, with Taxonomic Remarks on *C. fumosus* (Müller, 1895). *Zootaxa*, **4067**(5): 552–568.

Eigenanteil (ca. 50%) besteht in der Erhebung eines Teils der Daten und ihrer Bewertung sowie der Konzeption und dem Schreiben der Publikation.

Mecke, S., Kieckbusch, M., Hartmann, L. & Kaiser, H. (2016): Historical Considerations and Comments on the Type Series of *Cyrtodactylus marmoratus* Gray, 1831, with an Updated Comparative Table for the Bent-toed Geckos of the Sunda Islands and Sulawesi. *Zootaxa*, **4175**(4): 353–365.

Eigenanteil (ca. 95%) besteht in der Erhebung der Daten und ihrer Bewertung sowie der Konzeption und dem Schreiben der Publikation.

Mecke, S., Hartmann, L. (joint first authors), Mader, F., Kieckbusch, M. & Kaiser, H. (2016): Redescription of *Cyrtodactylus fumosus* (Müller, 1895) (Reptilia: Squamata: Gekkonidae), with a Revised Identification Key to the Bent-toed Geckos of Sulawesi. *Acta Herpetologica*, **11**(2): 151–160.

Eigenanteil (ca. 50%) besteht in der Erhebung eines Teils der Daten und ihrer Bewertung sowie der Konzeption und dem Schreiben der Publikation.

Kieckbusch, M., **Mecke, S.** (joint first authors), Hartmann, L., Ehrmantraut, L., O’Shea, M. & Kaiser, H. (2016): An Inconspicuous, Conspicuous New Species of Asian Pipesnake, Genus *Cylindrophis* (Reptilia: Squamata: Cylindrophiidae), from the South Coast of Jawa Tengah, Java, Indonesia, and an Overview of the Tangled Taxonomic History of *C. ruffus* (Laurenti, 1768). *Zootaxa*, **4093**(1): 1–25.

Eigenanteil (ca. 50%) besteht in der Erhebung eines Teils der Daten und ihrer Bewertung sowie der Konzeption und dem Schreiben der Publikation. Das Kapitel zur Taxonomie-Geschichte von *Cylindrophis ruffus* (S. 5–11) wurde eigenständig verfasst.

Mecke, S., Kieckbusch, M., O’Shea, M. & Kaiser, H. (2016): First Record of the Poorly Known Skink *Sphenomorphus oligolepis* (Boulenger, 1914) (Reptilia: Squamata: Scincidae) from Seram Island, Maluku Province, Indonesia. *Asian Herpetological Research*, **7**(1): 64–68.

Eigenanteil (ca. 95%) besteht in der Erhebung der Daten und ihrer Bewertung sowie der Konzeption und dem Schreiben der Publikation.

Chapter 6

Mecke, S. [and 11 co-signatories] (2014): Review Risks Before Eradicating Toads. *Nature* **511**: 534.

Eigenanteil 100%; im Gegensatz zu den übrigen peer-reviewed Publikationen eine Kurzmitteilung.

O’Shea, M., Kathriner, A., **Mecke, S.**, Sanchez, C. & Kaiser, H. (2013): ‘Fantastic Voyage’: A Live Blindsnake (*Ramphotyphlops braminus*) Journeys through the Gastrointestinal System of a Toad (*Duttaphrynus melanostictus*). *Herpetology Notes*, **6**: 467–470.

Eigenanteil (ca. 20%) besteht in der Beschaffung des Materials während einer Expedition nach Timor-Leste sowie Beiträgen zur Publikation.

Döring, B., **Mecke, S.** (joint first authors), Mader, F. & Kaiser, H. (2016): A Proposed Optimal Incision Method to Obtain Gut Contents from Preserved Anurans. *Amphibia-Reptilia*, **37**(4): 437–440.

Eigenanteil (ca. 50%) besteht in der Erprobung der Methode sowie der Konzeption und dem Schreiben der Publikation.

Döring, B., **Mecke, S.** (joint first authors), Kieckbusch, M., O’Shea, M. & Kaiser, H. (2017): Food Spectrum Analysis of the Asian Toad, *Duttaphrynus melanostictus* (Schneider, 1799) (Anura: Bufonidae), from Timor Island, Wallacea. *Journal of Natural History*, **51**(11–12): 607–623.

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Mecke, S., Kieckbusch, M., Graf, T., Beck, L.A., O’Shea, M. & Kaiser, H. (2016): First Captive Breeding of a Night Skink (Scincidae: *Eremiascincus*) from Timor-Leste, Lesser Sunda Islands, with Remarks on the Reproductive Biology of the Genus. *Salamandra*, **52**(2): 178–188.

Eigenanteil (ca. 95%) besteht in der Beschaffung von Lebend-Material während einer Expedition nach Timor-Leste, in der Erhebung der Daten und ihrer Bewertung sowie der Konzeption und dem Schreiben der Publikation.

Chapter 7

Mecke, S., Mader, F., Kieckbusch, M., Kaiser, H., Böhme, W. & Ernst, R. (2016): Tracking a Syntype of the Australian Skink *Anomalopus leuckartii* (Weinland, 1862): ‘Lost’ Treasures in the Senckenberg Natural History Collections Dresden Highlight the Importance of Reassessing and Safeguarding Natural History Collections. *Vertebrate Zoology*, **66**(2): 169–177.

Eigenanteil (ca. 95%) besteht in der Erhebung der Daten und ihrer Bewertung sowie der Konzeption und dem Schreiben der Publikation.

Eidesstattliche Erklärung

Hiermit versichere ich, dass ich meine Dissertation mit dem Titel

Taxonomy, Natural History, and Ecology of
Selected Herpetofaunal Species from the Sunda Islands and Adjacent Regions – Synergistic Effects of Fieldwork and Museum Collections for Biodiversity Research

selbstständig und ohne unerlaubte Hilfe angefertigt habe und mich keiner als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient habe. Diese Dissertation wurde in dieser oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinem sonstigen Prüfungszweck gedient.

S. Mecke

Marburg, 02.04.2018 Sven Mecke