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Snakes of a Continental Island

History and Patterns of Discovery of the Snake Fauna of Borneo to the Start of the Anthropocene

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C1S1

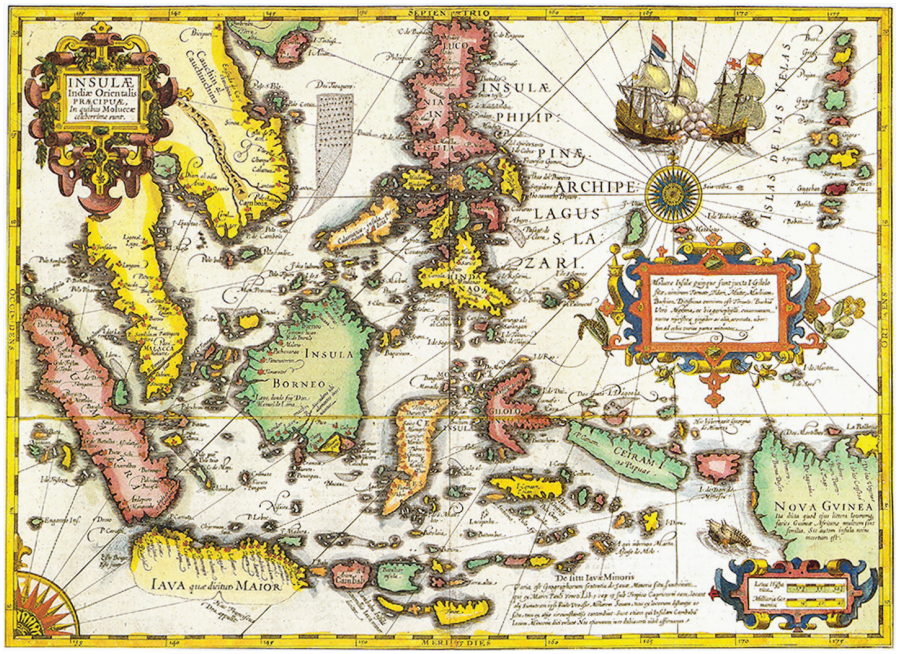
Introduction

C1P1 Its biological diversity "hidden in plain sight" (Poe 1844), the gigantic tropical island of Borneo (Figure 1.1) was known to ancient seafarers as "Land Below the Wind" (Keith 1940), yet not worthy of conquest or exploration (this was before the realization of the value of timber or petroleum). The English traveler Earl (1837) wrote that the north coast was "scarcely known even to the native trader," and it is thus unremarkable that scientific research and explorations of the island were to commence much later compared to the adjacent and smaller islands of Sumatra and Java.

C1P2 Croizat (1958) described Borneo as a geological composite. As a part of Sundaland, the island is situated on the eastern rim of the Sunda Shelf, a Laurasian continental plate. Pleistocene glaciations saw sea levels drop 120–200 m below current levels (Wang and Wang 1990), both connecting it to the Asian mainland and joining the other islands of the Sundas (Morley and Flenley 1987). Reconstructions of the region's archipelago systems during the period are in Heaney (1991) and Voris (2000). Stretching between 04°S and 07°N and from 109° to 119°E, Borneo is the second largest tropical island in the world (after New Guinea), and it covers a land area of approximately 743,380 km^2. A major part of the island falls in the Indonesian portion referred to as Kalimantan (area: 539,460 km^2), most of the balance within the east Malaysian states of Sarawak (124,450 km^2) and Sabah (73,710 km^2). Nearly enclosed by Sarawak State is the Sultanate of Negara Brunei Darussalam (5,760 km^2). Based on the hosted biota, Ali (2018) classified it as a shelf island, also being geologically contiguous with the Asian mainland, and with a shallow intervening seabed.

C1P3 This chapter describes four phases in the history of description of the snakes of Borneo, classified according to a temporal timeline that correlated with regional and international sociopolitical events and highlighting notable personalities, species, and localities.

Islands and Snakes. Harvey B. Lillywhite and Marcio Martins, Oxford University Press. © Oxford University Press 2023.
DOI: 10.1093/oso/9780197641521.003.0001



C1F1 **Figure 1.1** An early 17th-century map of Borneo and adjacent regions of southeast Asia by Jodocus Hondius (1563–1612), as reproduced in Gerard Mercator's (1816) atlas.

C1S2 Phase One: The Age of Linnaeus and Cabinets of Curiosities

C1P4 > Plants and animals from the extra-European world became what the science studies scholar Bruno Latour has referred to as "Immutable and combinable mobiles," objects that became portable and stable could be compared and combined, allowing for simultaneous study on a global scale.

C1P5 **—Parsons and Murphy (2012)**

C1P6 The first snakes known from Borneo do not bear precise localities (*e.g.*, *Coluber pelias*, equivalent to *Chrysopelea pelias* and *Coluber buccatus*, equivalent to *Homalopsis buccatus*, both mentioned as from "*in* Indiis," referring to either the East or West Indian Archipelagos), and are contained in Linnaeus's (1758) *Systema Naturae* (10th edition). The former (holotype of *C. pelias*) originate from Museum De Geer, the private collection of the Dutch industrialist and amateur entomologist, Baron Charles de Geer (1720–1779). The latter (holotype of *C. buccatus*) was donated to Uppsala University by the Councilor of Commerce, Jonas Alstromer, and was formerly in the Museum Adolphi Fredrici, the personal collection of Adolf Fredrik (1710–1771),

King of Sweden (Das 2012). The provenance of the collection remains unclear, and at least some of the ichthyological types were thought to have been obtained during the voyages of ships of the Swedish East India Company along the India–China route, according to Ng and Kottelat (2008).

C1P7 Two other snakes known from Borneo and with Linnaean names exist: *Coluber laticaudatus* Linnaeus 1758 (currently *Laticauda laticaudata*) and *Anguis platura* Linnaeus 1766 (currently *Hydrophis platurus*); the provenance of the first is given as "*in* Indiis," that of the latter is unspecified in this subsequent work which formed the 12th edition. The first mentioned originate from the Museum Adolphi Federici, the latter from "Mus. Fr. Ziervogel Pharmac," the private collection of Friedrich Ziervogel (1727–1782), Apothecary Royal and in charge of packing the royal collections, who accompanied Linnaeus on his travels (Sandermann Olsen 1997).

C1P8 For the 23 names of Asian taxa dealt with by Linnaeus, which represent 21 biological species, Das (2012) showed that three localities could have served as the combined geographical source. Apart from the extralimital nature of the first (Sri Lanka), the Malay Peninsula, the island of Java, and their surrounding seas are suspected to have been the source of all four species of snakes now known from Borneo.

C1P9 A major source of material early descriptions were private collections of rich aristocrats and merchants, sometimes referred to as "cabinets of curiosities," the most famous ones being those accumulated by the Dutch apothecary Albertus Seba (1665–1736). His two-volume (1734–1735) *Locupletissimi Rerum Naturalium Thesauri Accurata et Descriptio, et Iconibus Artificiosissimus Expressio, per Universam Physices Historiam*, published by Janssonio-Waesbergios, J. Wetstenium, and Gul. Smith in Amsterdam, was indeed a source of several Linnean (and other early) names.

C1P10 The late 18th century thus marked the first period of discovery for Borneo (as for the rest of the world) and resulted in the naming of specimens in private collections using poorly associated geographical data.

C1S3 Phase Two: More Cabinets and the Rise of European Museums

C1P11

> [Private natural history collections or cabinets of curiosities were] the centre of literary gatherings, where a fresh and continuous dialogue was established between the expert and the simply curious. This dialogue took place between experts and the wealthy aristocratic owner of the collections.

C1P12 —Valdecasas *et al.* (2006)

C1P13 The next phase coincides with the work of early zoologists on cabinets of the rich and famous as well as the efforts of museum curators based in Europe, primarily

the German philologist and zoologist Johann Gottlob Theaenus Schneider (1750–1822) and, secondarily, English botanist and zoologist George (sometimes written as "Georgius") Kearsley Shaw (1751–1813) between the end of the 18th and the first decade of the 19th centuries. Global in scope (see Bauer and Lavilla 2022), their work described numerous species, and, relevant for Borneo were the several familiar ones, in the case of Schneider.

C1P14 His two-volume work, *Historiae Amphibiorum naturalis et literariae*, contained the description of five (three in volume one, 1799; two in volume two, 1801) snake species that occur on Borneo. These were based on Schneider's study of material in private holdings as well as literature.

C1P15 Species on Borneo in the said works and their type localities are listed below, although there is no evidence that any were actually collected from the island. The original orthography is retained here.

C1P16 1. *Hydrus Colubrinus* Schneider 1799; currently *Laticauda colubrina* (Hydrophiidae). The type locality of this nominal species was not specified in the original description, although the data associated with the holotype (ZMB 9078) indicate that it is from "ostindisches Meer" east Indian seas), according to Bauer (1998). It was originally examined at the Lampe collection (see below).

C1P17 2. *Hydrus Granulatus* Schneider 1799; currently *Acrochordus granulatus* (Acrochordidae). The holotype was originally in the Lampe Collection and is at present untraced and presumably lost (*fide* McDowell 1979). The type locality was given as "Indici" (from India) and was restricted by David and Vogel (1996: 44) to "Madras, India" (Chennai, in southeastern India). However, the presumed area of activity of its collector, Christoph Samuel John (1747–1813), a Danish missionary based at the Protestant mission who sent material to a fellow member of the Gesselschaft für Naturforschender Freunde zu Berlin, Marcus (Markus) Elieser (Elisar) Bloch (1723–1799), was Tranquebar (currently, Tharangambadi, a town in Mayiladuthurai District, Tamil Nadu State, more than 250 km south of Chennai), on the Coromandel coast (see Das 2004a).

C1P18 3. *Hydrus Enhydris* Schneider 1799, currently *Enhydris enhydris* (Homalopsidae). This was based on the description and color plates in Russell (1796: 35; Pl. XXX) of a specimen from "Ankapilly Lake" (Anakapalle, East Godavari District, Andhra Pradesh, southeastern India). The type locality is mentioned as "Indiae orientalis" in the original description. Patrick Russell (1726–1805), surgeon and polymath-naturalist (Das 2015), collected snakes and prepared two folio volumes on the fauna of the southeast coast of India, employing vernacular names to refer to species.

C1P19 4. *Boa Reticulata* Schneider 1801, currently *Malayopython reticulatus* (Pythonidae). The species was based on specimens in the Göttingen Museum (at present not extant). Thus, the species is not just based on color plates in Seba (1734: Pl. lxii; 1735: Pl. lxxix), as generally mentioned (*e.g.*, David and Vogel 1996: 41; McDiarmid *et al.* 1999: 179). The type locality is mentioned as "Orient"

(Seba 1734: Pl. 62), "mountains of Japan" (Seba 1735; Pl. 79; in error), and "Nova Hispania" (Seba 1735; Pl. 80; in error) and emended to "Java" (in the Greater Sundas, Indonesia) by Brongersma (1972).

C1P20

5. *Pseudoboa Fasciata* Schneider 1801, currently *Bungarus fasciatus* (Elapidae); ZMB 2771–72 (syntypes; fide Bauer 1998). The species is based on additional material in the collection of Linck (formerly at Leipzig; see A. M. Bauer and Wahlgren 2013) as well as on the description and color plates in Russell (1796), whose specimen was from "Mansoor Cottah, Bengal" (at present Gopalpur-on-Sea, c. 24 km south of Ganjam, Odisha State, southeastern India). The type locality is not specified in the original description, although the ZMB catalog indicates that the provenance of their syntypes is "Indien" (India): these were originally in Musei Blochiani.

C1P21

A few words on three of the most important private collections may be pertinent here. The first, Musei Blochiani, was the private collection of Marcus Elieser Bloch (1723–1799), a German medical doctor, zoologist, and publisher based in Berlin. Between 1782 and 1795, he published *Allgemeine Naturgeschichte der Fische*, a 12-volume work on fishes that is considered encyclopedic in scope (Hirschberg 1913). His natural history cabinet was enriched through donations from his correspondents in Asia. Of the famous Lampe Collection, rather little is known of Johann Bodo Lampe (1738–1802) except for his appointment as Leibchirurgus (personal surgeon of the monarch; see Goldmann *et al.* 2021) in Hannover. His collections included zoological (Bauer and Lavilla 2022) and human specimens that were presumably of relevance for anatomical studies particularly related to surgery (Goldmann *et al.* 2021). Finally, the Linck Collection was amassed by Heinrich Linck (1638–1717) and his grandson, Johann Heinrich Linck the Younger (1734–1807), the latter an acquaintance of Schneider (Bauer and Lavilla 2022); see Bauer and Wahlgren (2013) for a history of the collection.

C1P22

In contrast, all Bornean species named by George Shaw (1751–1813) in his 1802 work are members of the genus *Hydrophis* (Hydrophiidae) and based on vouchered specimens that are extant at the Natural History Museum, London. Those occurring on Borneo are enumerated below (although, as in Schneider's case, there is no evidence of a Bornean provenance). Shaw was a preeminent biologist of his time, served as Keeper of the Natural History Department of the British Museum for 22 long years, and co-founded the Linnean Society of London (Adler 1989). While Shaw was neither a collector nor traveler, the Museum at the time was the recipient of material from the numerous voyages, scientific as well as associated with administration of Britain's colonies worldwide. These provided much material for his *General Zoology or Systematic Natural History*, a series of 16 volumes, of which Shaw prepared the first eight.

C1P23

1. *Hydrus Gracilis* Shaw 1802, BMNH 1946.1.17.37 (ex-BMNH III.4.1.a; holotype; fide McCarthy 1993: 235), type locality not specified in the original description.

C1P24 2. *Hydrus Caerulescens* Shaw 1802, BMNH 1946.1.3.90 (ex-BMNH III.6.13.a; holotype; fide McCarthy 1993: 232), "an East-Indian species." Restricted to Vizagapatnam (Vishakhapatnam, Andhra Pradesh, southeastern India) by Cogger *et al.* (1983: 250).

C1P25 3. *Hydrus Curtus* Shaw 1802, BMNH 1946.1.17.59 (ex-BMNH III.2.1.a; holotype; fide McCarthy 1993: 244), reportedly "An East-Indian species."

C1P26 4. *Hydrus Spiralis* Shaw 1802, BMNH 1946.1.6.94 (ex-BMNH III.6.10.c; holotype; fide McCarthy 1993: 241), type locality "Indian Ocean" and unspecified in original description.

C1P27 This second phase of snake discoveries was doubtless important in the naming of species that are familiar today. Nonetheless, locality knowledge continued to remain poor, and specimens are suspected to have been brought in by commercial activities, such as via sale by sailors and apothecaries. The challenges of transporting specimens over water during voyages lasting months and perhaps years must have been formidable (see Parsons and Murphy 2012), and specimens preserved in brandy, wine, or rum were particularly vulnerable to consumption by sailors "unconcerned with the protein content" (Stearns 1952).

C1S4 Phase Three: The First Explorations

C1P28

> . . . a strong motive for the donors of specimens to the Society's Museum must have been that they were supporting the body which would publish the papers they submitted, or which would gain them an audience for their studies being read at a meeting. . . . Another category of presents of specimens which the Society would have had difficult in refusing when offered were those from distinguished patrons or men of science, and collections which were known to be important.

C1P29 **—Wheeler (1995)**

C1P30 The third phase, and arguably the golden age of discovery of Borneo's snake fauna, can be seen from the 1820s to the end of that century. The period coincided with numerous sociopolitical events in Europe, from the dawn of the Victorian Era and progress in science and the Industrial Revolution, to the establishment of colonial rule over the region and entrenchment of bureaucracy, the realization of the intrinsic and scholarly value of knowledge, and, importantly, the travel of enlightened naturalists to those far-flung corners of the world. In the case of Borneo, it included, among many others, the traveling naturalists Alfred Russel Wallace (1823–1913), Marquis Giacomo Doria of Genoa (1840–1913), Odoardo Beccari (1843–1920), and John Whitehead (1860–1899), whose purpose were to provide botanical, zoological, and/or geological specimens for European museums. Another source of collections or

observations at the time can be attributed to civil servants of the administration, particularly that of Sarawak State, including Hugh Low (1824–1905), Alfred Hart Everett (1849–1898), Eric Mjöberg (1882–1938), Charles Hose (1863–1929), and Edward Bartlett (1836–1908). Specimens were more carefully acquired, particularly in the case of employees of the Sarawak Museum, and had at least the most basic locality information. Often, enough details of their work stations and travel itineraries remain in archives to permit a resolution of collection localities. Such materials (with some exceptions: Das and Leh 2005 mentioned colonial collections that were retained/returned to the Sarawak Museum) were sent to European collections (chiefly the British Museum of Natural History in London and, in some cases, as by Whitehead, to the Paris Museum). This often intense attention to the local biodiversity and accession of remote regions during the period (Gunung Kinabalu, for instance) resulted in several new species of snakes (including *Paraxenodermus borneensis*, initially allocated to *Stoliczkia*, an Indian genus of the Xenodermatidae). Figure 1.2 illustrates some of these "local" collectors and describers of species, their vitae sometimes

C1F2 **Figure 1.2** Portraits of significant Bornean collectors and authors of early snake descriptions. Top row, left, Odoardo Beccari (1843–1920); center, Hugh Low (1824–1905); right, Eric Mjöberg (1882–1938). Bottom row, left Robert Shelford (1872–1912); center, Alfred Russel Wallace (1823–1913); right, John Whitehead (1860–1899).

unknown outside of their "domiciled" or "adopted" countries (see Das 2004b). These greatly enriched European collections, particularly those in London and Paris, and also those in Berlin and Turin.

C1S5

Phase Four: Research in the Anthropocene

C1P31

> Species are going extinct rapidly, while taxonomic catalogues are still incomplete for even the best-known taxa. Intensive fieldwork is finding species so rare and threatened that some become extinct within years of discovery.

C1P32

—Lees and Pimm (2015)

C1P33 The two world wars had marked influence on species descriptions, with the relevant decades showing no accretion to the fauna. The next six decades, in fact, show little activity in terms of new species discoveries, which picked up only around the end of the 20th century. It would appear that the newly independent nations (in this case, Malaysia, Brunei, and Indonesia) had other priorities and/or less local expertise or visitations by foreign researchers with an interest in snakes. This final phase of snake species discovery is worthy of comment, with the description of a number of species that are endemic to the island. Nearly all of these are the result of either careful morphological analyses (possible through the accumulation of often rare rainforest species in numbers) or the utilization of quantitative methods and/or molecular (particularly DNA) techniques of recognition of cryptic species (or species morphologically similar but genetically unique; see Bickford *et al.* 2007).

C1P34 Table 1.1 presents the current checklist of the snake fauna of Borneo. Among the changes from the previously published list is the recognition of the family Pseudaspididae for members of the genus *Psammodynastes* (the so-called mock vipers) in southeast Asia and with other representatives in the Ethiopian region (Zaher *et al.* 2019). The lineage was formerly allocated to Lamprophiidae.

C1P35 Generic changes include recognition of a novel or revived names: *Paraxenodermus* to accommodate *Stoliczkia borneensis* Boulenger 1899; *Malayotyphlops* for *Typhlops koekkoeki* Brongersma 1934; *Malayopython* for *Python reticulatus* Schneider 1801; *Craspedocephalus* for *Trimeresurus borneensis* Peters 1872; *Miralia* for *Enhydris alternans* Reuss 1834; *Phytolopsis* for *Enhydris punctatus* Gray 1849; *Gonyosoma* for *Gonyophis margaritatum* Peters 1871; and *Hebius* for all Bornean species formerly allocated to *Amphiesma* of the Natricidae. Furthermore, *Macropisthodon* was synonymized under the medically important genus *Rhabdophis*, within the family Natricidae, including two species from Borneo, *flaviceps* (Duméril *et al.* 1854) and *rhodomelas* (Boie 1827).

C1P36 Faunal revisions have been associated with species accretions in general. For instance, the review of the genus *Calamaria* by Inger and Marx (1965) produced eight

C1T1 **Table 1.1** Checklist of the snakes of Borneo (current: November 20, 2022)

Acrochordidae—Wart snakes
Acrochordus granulatus (Schneider 1799)
Acrochordus javanicus Hornstedt 1787

Anomochilidae—Giant blind snakes
Anomochilus leonardi Smith 1940
**Anomochilus monticola* Das *et al.* 2008
Anomochilus weberi (van Lidth de Jeude 1890)

Cylindrophiidae—Pipe snakes
**Cylindrophis engkariensis* Stuebing 1994
**Cylindrophis lineatus* Blanford 1881
Cylindrophis ruffus (Laurenti 1768)

Pythonidae—Pythons
Malayopython reticulatus (Schneider 1801)
**Python breitensteini* Steindachner 1881

Xenopeltidae—Sunbeam snakes
Xenopeltis unicolor Reinwardt 1827

Colubridae—Typical snakes and reed snakes
Colubrinae– Typical snakes
Ahaetulla fasciolata (Fischer 1885)
Ahaetulla prasina (Boie 1827)
Boiga cynodon (Boie 1827)
Boiga drapiezii (Boie 1827)
Boiga jaspidea (Duméril *et al.* 1854)
Boiga melanota (Boulenger 1896)
Boiga nigriceps (Günther 1863)
Chrysopelea paradisi Boie 1827
Chrysopelea pelias (Linnaeus 1758)
Coelognathus erythrurus (Duméril *et al.* 1854)
Coelognathus flavolineatus (Schlegel 1837)
Coelognathus radiatus (Boie 1827)
Dendrelaphis caudolineatus (Gray 1834)
Dendrelaphis formosus (Boie 1827)
Dendrelaphis haasi van Rooijen and Vogel 2008
Dendrelaphis kopsteini Vogel and van Rooijen 2007
Dendrelaphis pictus (Gmelin 1789)
Dendrelaphis striatus (Cohn 1905)
Dryophiops rubescens (Gray 1835)

(*continued*)

Table 1.1 Continued

Elapoidis fusca Boie 1826
Gongylosoma baliodeirum Boie 1827
Gongylosoma longicauda (Peters 1871)
Gonyosoma margaritatum Peters 1871
Gonyosoma oxycephalum (Boie 1827)
Liopeltis tricolor (Schlegel 1837)
Lycodon albofuscus (Duméril *et al.* 1854)
Lycodon capucinus (Boie 1827)
Lycodon effraenis Cantor 1847
Lycodon subannulatus (Duméril *et al.* 1854)
Lycodon tristrigatus (Günther 1858)
Oligodon annulifer (Boulenger 1893)
**Oligodon everetti* Boulenger 1893
Oligodon octolineatus (Schneider 1801)
Oligodon purpurascens (Schlegel 1837)
Oligodon signatus (Günther 1864)
**Oligodon vertebralis* Günther 1865
Oreocalamus hanitschi Boulenger 1899
Orthriophis taeniurus (Cope 1861)
Ptyas carinata (Günther 1858)
Ptyas fusca (Günther 1858)
Ptyas korros (Schlegel 1837)
Sibynophis geminatus (Boie 1826)
Sibynophis melanocephalus (Gray 1834)
**Stegonotus borneensis* Inger 1967
**Stegonotus caligocephalus* Kaiser *et al.* 2020
Xenelaphis ellipsifer Boulenger 1900
Xenelaphis hexagonotus (Cantor 1847)
Calamariinae–Reed snakes
**Calamaria battersbyi* Inger and Marx 1965
Calamaria bicolor Duméril *et al.* 1854
**Calamaria borneensis* Bleeker 1860
**Calamaria everetti* Boulenger 1893
**Calamaria grabowskyi* Fischer 1885
**Calamaria gracillima* (Gunther 1872)
**Calamaria griswoldi* Loveridge 1938
**Calamaria hilleniusi* Inger and Marx 1965
**Calamaria lateralis* Mocquard 1890
Calamaria leucogaster Bleeker 1860
Calamaria lovii Boulenger 1887

Table 1.1 Continued

Calamaria lumbricoidea Boie 1827
**Calamaria lumholtzi* Andersson 1923
Calamaria melanota Jan 1862
Calamaria modesta Duméril *et al.* 1854
**Calamaria prakkei* van Lidth de Jeude 1893
**Calamaria rebentischi* Bleeker 1860
Calamaria schlegeli Duméril *et al.* 1854
**Calamaria schmidti* Marx and Inger 1955
Calamaria suluensis Taylor 1922
Calamaria virgulata Boie 1827
**Pseudorabdion albonuchalis* (Günther 1896)
**Pseudorabdion collaris* (Mocquard 1892)
Pseudorabdion longiceps (Cantor 1847)
**Pseudorabdion saravacense* (Shelford 1901)

Natricidae—Water snakes
**Hebius arquus* (David and Vogel 2010)
**Hebius flavifrons* (Boulenger 1887)
**Hebius frenatus* (Dunn 1923)
Hebius petersii (Boulenger 1893)
Hebius saravacensis (Günther 1872)
**Hydrablabes periops* (Günther 1872)
**Hydrablabes praefrontalis* (Mocquard 1890)
**Opisthotropis typica* (Mocquard 1890)
Rhabdophis chrysargos (Schlegel 1837)
Rhabdophis conspicillatus (Günther 1872)
Rhabdophis flaviceps (Duméril *et al.* 1854)
**Rhabdophis murudensis* (Smith 1925)
Rhabdophis rhodomelas (Boie 1827)
Xenochrophis maculatus (Edeling 1864)
Xenochrophis trianguligerus (Boie 1827)

Pseudaspididae—Mock vipers
Psammodynastes pictus Günther 1858
Psammodynastes pulverulentus (Boie 1827)

Pseudoxenodontidae—False cobras
**Pseudoxenodon baramensis* (Smith 1921)

Elapidae-Cobras and kraits, coral and sea snakes
Elapinae–Elapid snakes
Bungarus fasciatus (Schneider 1801)

(*continued*)

Table 1.1 Continued

Bungarus flaviceps Reinhardt 1843
Calliophis bivirgatus (Boie 1827)
Calliophis intestinalis (Laurenti 1768)
Calliophis nigrotaeniatus (Peters 1863)
Naja sumatrana Müller 1890
Ophiophagus hannah (Cantor 1836)

Hydrophiinae–True sea snakes
Aipysurus eydouxii (Gray 1849)
Hydrophis annandalei (Laidlaw 1901)
Hydrophis anomalus (Schmidt 1852)
Hydrophis atriceps Günther 1864
Hydrophis brooki Günther 1872
Hydrophis caerulescens (Shaw 1802)
Hydrophis curtus (Shaw 1802)
Hydrophis cyanocinctus Daudin 1803
Hydrophis gracilis (Shaw 1802)
Hydrophis jerdonii (Gray 1849)
Hydrophis klossi Boulenger 1912
Hydrophis melanosoma Günther 1864
Hydrophis ornatus (Gray 1842)
Hydrophis platurus (Linnaeus 1766)
Hydrophis schistosus Daudin 1803
**Hydrophis sibauensis* Rasmussen *et al.* 2001
Hydrophis spiralis (Shaw 1802)
Hydrophis torquatus Günther 1864
Hydrophis viperinus (Schmidt 1852)

Laticaudinae–Sea kraits
Laticauda colubrina (Schneider 1799)
Laticauda laticaudata (Linnaeus 1758)

Homalopsidae—Puff-faced water snakes
Cerberus schneiderii (Schlegel 1837)
Enhydris enhydris (Schneider 1799)
Fordonia leucobalia (Schlegel 1837)
Gerarda prevostiana (Eydoux and Gervais 1822)
Homalopsis buccata (Linnaeus 1758)
**Homalophis doriae* Peters 1871
**Homalophis gyii* (Murphy *et al.* 2005)
Hypsiscopus plumbea (Boie 1827)

Table 1.1 Continued

Miralia alternans (Reuss 1834)
Phytolopsis punctata Gray 1849

Pareidae—Slug-eating snakes
Aplopeltura boa (Boie 1828)
**Asthenodipsas borneensis* Quah *et al.* 2020
**Asthenodipsas ingeri* Quah *et al.* 2021
Asthenodipsas laevis (Boie 1827)
**Asthenodipsas jamilinaisi* Quah *et al.* 2019
**Asthenodipsas stuebingi* Quah *et al.* 2019
Asthenodipsas vertebralis (Boulenger 1900)
Pareas carinatus Wagler 1830
**Pareas nuchalis* (Boulenger 1900)

Viperidae—Vipers and pitvipers
**Craspedocephalus borneensis* (Peters 1872)
**Garthius chaseni* (Smith 1931)
**Trimeresurus malcolmi* Loveridge 1938
Trimeresurus sumatranus (Raffles 1822)
Trimeresurus sabahi Regenass and Kramer 1981
Tropidolaemus subannulatus (Gray 1842)

Xenodermatidae—Strange-skinned snakes
**Paraxenodermus borneensis* (Boulenger 1899)
Xenodermus javanicus Reinhardt 1836

Xenophidiidae—Spine-jawed snakes
**Xenophidion acanthognathus* Günther and Manthey 1995

Typhlopidae—Blind snakes
Argyrophis muelleri (Schlegel 1839)
Indotyphlops braminus (Daudin 1803)
**Malayotyphlops koekkoeki* (Brongersma 1934)
Ramphotyphlops lineatus (Schlegel 1839)
**Ramphotyphlops lorenzi* (Werner 1909)
Ramphotyphlops olivaceus (Gray 1845)

Endemic and near-endemic species are marked with an asterisk; parentheses indicate species placement in a genus different from the original allocation (following Article 51.3 of the ICZN).

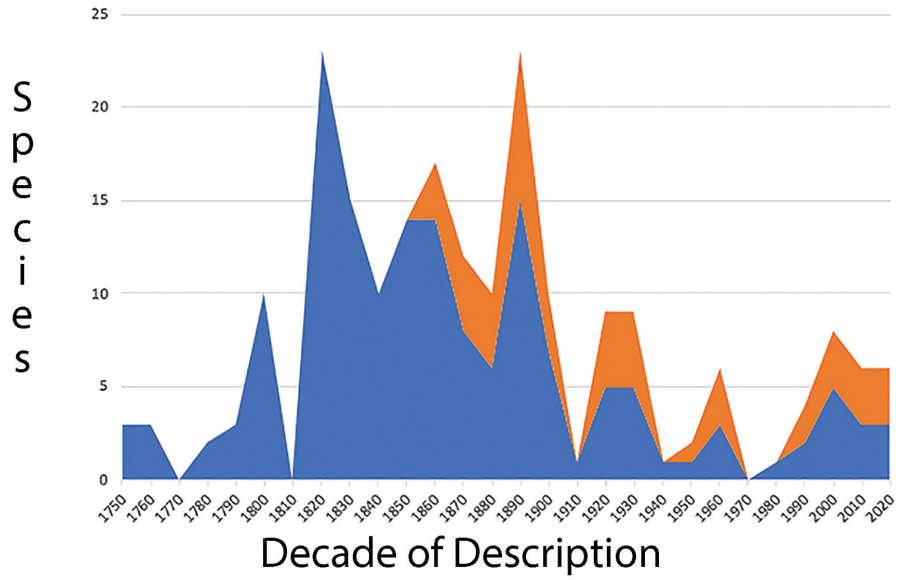
new species within its range, two of which are from Borneo. Similarly, work on another typically montane lineage, the Pareidae ("Slug-eating snakes") by Quah *et al.* (2019, 2020) has led to a doubling of the Bornean component of the fauna.

C1P37 One does not fail to notice the paradox, though, of enhanced knowledge of global environmental issues, from climate change to rainforest loss and the loss of technical knowledge associated with species descriptions (*i.e.*, taxonomic procedures) and the relegation of associated disciplines (such as systematics and evolutionary biology) in general to second-class science. There seems to be no shortcut solutions to the issue (see Drew 2011).

C1S6 ## Conclusion

C1P38 Figure 1.3 shows the nature of snake discoveries on Borneo. The distinct temporal phases of research peaks are clearly visible, both in terms of overall species descriptions and those of species endemic to Borneo.

C1P39 Endemic lineages on Borneo are worthy of note. These may be classified into those strictly restricted to the island (true endemics) and a few others (near-endemics) that co-occur on adjacent land masses (all smaller offshore islands and considered part of the main island during certain glacial phases, such as Palawan in the Philippines (*Calamaria everetti*), Pulau Bunju (*Malayotyphlops koekkoeki*), Pulau Miang Besar



C1F3 **Figure 1.3** Descriptions of snake species known from Borneo, by decade (1760s to 2020s). Dark areas refer to all nominal species, pale areas refer to Bornean endemic and near-endemic species.

C1T2 **Table 1.2** Snake species of the major islands of the western Sundas and their land areas (in km^2)

C1P111

	Borneo	Sumatra	Java	Bali	Natuna	Palawan
Species	163	160	109	44	20	37
Land area	743,330	473,481	124,413	5,780	2,001	14,650
C1P112 Source	Table 1.1	David and Vogel 1996	de Lang 2017	Somaweera 2020	Iskandar and Colijn 2001	Griffin 1909

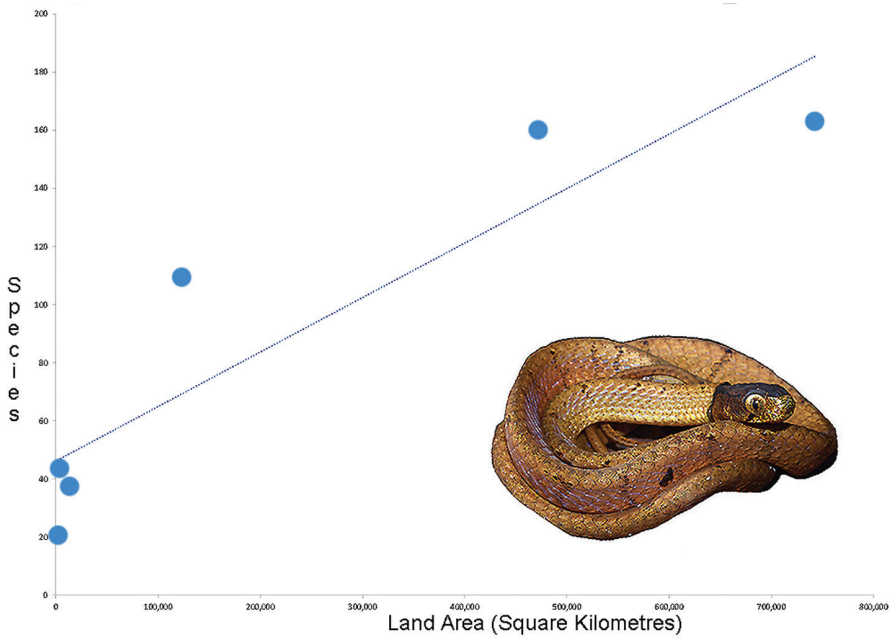
Source for the faunal richness indicated, updated where relevant from Uetz *et al.* (2022).

(*Ramphotyphlops lorenzi*), and the Natunas (*Lycodon tristrigatus*), the last three localities in Indonesia. Of the 163 currently recognized Bornean species, just 46 (or 28%) are restricted to the island system. Borneo's geologically recent (ca. 20,000 years before present, during the Last Glacial Maximum, or the last phase of the Pleistocene; Hanebuth *et al.* 2009) connection to the Asian mainland appears to be a factor influencing the low endemicity in its biota. Indeed, an examination of endemics demonstrate that a majority are restricted to mountain tops (such as all species of *Hydrablabes* and *Opisthotropis*, a majority of species of the genus *Calamaria* and of the Pareidae). Other endemic snake species are residents of special habitats, including inland waters (*Hydrophis sibauensis* and at least two species each of *Hebius* and *Homalopsis*), karst and limestone regions (*Cylindrophis lineatus*), beach forests (*Pseudorabdion sarawacense*), or small, remote islands (*Malayotyphlops koekkoeki*).

C1P40 As reflected in the title of this chapter, the island of Borneo's low endemicity and similarity to the Malay Peninsula and other islands of Sundaland is somewhat unsurprising in the light of discoveries in botanical research. Employing species distribution models, Raes *et al.* (2009) demonstrated richness and endemicity within specific regions within the island that are characterized by a relatively small range in annual temperature but with seasonality in temperatures within that range least affected by El Niño Southern Oscillation drought events and a number of other, local factors.

C1P41 Borneo, the largest island of Sundaland, predictably has the greatest snake species richness (Table 1.2; Figure 1.4), as can be expected from the species-area power model (Conor and McCoy 2013). Nonetheless, Sumatra comes a close second, especially with the addition of the faunas of the adjacent Mentawai Islands which shows significant relictual elements in its vertebrate fauna (Wilting *et al.* 2012). In O'Shea and Maddock's (Chapter 2, this volume) comparison of the snake faunas of New Guinea, another large tropical island (785,753 km^2) and Borneo, the former has fewer families (nine) compared to Borneo (18, or 16 using the taxonomy followed in this work), although the total species counts of non-marine species are about the same (138 for New Guinea, 140 for Borneo).

C1P42 A few remarks on the ecological distribution of the snake fauna of Borneo may be relevant. Apart from the marine/coastal obligates, including members of the families



C1F4 **Figure 1.4** Species-area (in km^2) relationships of snake faunas of the major islands (and associated satellite archipelagos) of the western Sundas ($R^2 = 0.8259$).

Hydrophiidae (excluding *H. sibauensis* that reaches in central Borneo, hundreds of kilometers upriver) and representatives of the Acrochordidae (*Acrochordus javanicus*) and the Homalopsidae (*Cerberus schneiderii, Fordonia leucobalia* and *Gerarda prevostiana*), totaling 24 species, the Bornean snake fauna is largely linked to specific vegetational zones that correspond to elevations.

C1P43 The greatest diversity (105 species, or 80.2% of the non-marine/coastal fauna) of snakes are linked to lowland rainforests (at elevations up to 1,600 m asl), and a smaller subset (26 species, or 19.8%) are restricted to montane forests (>1,600 m asl). Included in these figures are species with limited ecological data, such as *Hebius arquus*, described in 2010, and *Hydrablabes praefrontalis*, described in 1890, both based on specimens collected over a century ago and assumed to be a lowland and highland species, respectively, based on respective collector itineraries.

C1P44 A few species defy the broad generalizations followed, such as the swamp-sluggish river–inhabiting *Acrochordus javanicus*, and, furthermore, a few species have wide distributions across elevations, ranging from lowland species to montane limits: *Calamaria schlegelii*, *Gongylosoma baliodeirum, Python breitensteini*, and *Rhabdophis chrysargos* (and were thus left out of the calculations). For a number of species pairs, a clear ecological replacement is evident: the familiar *Trimeresurus sumatranus* of the lowlands appears replaced at higher elevations by *T. malcolmi*; *Stegonotus borneensis*, also a lowland-dwelling taxon, is replaced by the newly

described *S. caligocephalus*; and, finally, the widespread lowland *Calliophis intestinalis* by the montane *C. nigrotaeniatus*. A majority of Bornean endemics are unsurprisingly restricted to mountain peaks and ridges, such as a number of species of *Calamaria, Anomochilus monticola, Rhabdophis murudensis, Pseudoxenodon baramensis*, and *Paraxenodermus borneensis.*

C1P45 Explorations of snake diversity in terms of species descriptions have had a long history in southeast Asia, particularly Sumatra and Java, and Borneo was initially given relatively less importance. The early collectors in Sarawak and Sabah were colonial administrators and European explorers who collected for museums in Europe, chiefly London and Paris. Far less important were Dutch collectors, although the activities of the latter were significant for both Java and Sumatra. The resulting body of knowledge was thus widely distributed in scholarly journals (and not always readily available).

C1P46 Haile (1958) presented the first comprehensive pan-Bornean snake checklist, in a paper remarkable for also including a key (albeit not dichotomous) to all recognized species. The next important attempts to synthesize the fauna were checklists of the snakes of the island by Stuebing (1991, 1994), resulting in a field guide by Stuebing and Inger (1999) that was revised a decade and half later (Stuebing *et al.* 2014). The volumes make available a remarkable fauna within reach of the general public in terms of appreciation and they form valuable tools for investigations into their research. Expectedly, the intervening eight years have seen active work on the snake fauna, including not only species descriptions but also changes in the generic (and even familial) allocation of species. Table 1.1 provides the most current checklist, updating species names (with particular emphasis of authority and dates of publication). As noted by Chan and Grismer (2021), systematics dominated the field of reptile research in terms of indexed publications for Malaysia as a whole over the past two decades, and one can foresee the future directions in the field, at least for the decade ahead. Such knowledge is surely the first step toward an integrative knowledge of the biodiversity of Borneo and will facilitate research in the field of conservation biology and promotion of biodiversity knowledge in its entirety.

C1P47 Acknowledgments

C1P48 Foremost, I am grateful to Harvey Lillywhite and Marcio Roberto Costa Martins for inviting me to contribute to this important volume and keeping their faith in its delivery, albeit beyond the initial deadline. I thank the Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, for support of my research, and the Niche Research Grant Scheme, Ministry of Higher Education, Government of Malaysia (IA010200-0708-0007) for field support. Kraig Adler, Aaron Bauer, Patrick David, David Gower, the late Robert F. Inger, Charles M. U. Leh, Alan Leviton, Colin McCarthy, and Robert B. Stuebing are thanked for publications, images, and information. Finally, I thank Genevieve V. A. Gee for reading a draft of the manuscript.

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