

## Dragons in neglect: Taxonomic revision of the Sulawesi sailfin lizards of the genus *Hydrosaurus* Kaup, 1828 (Squamata, Agamidae)

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### Abstract

Currently three different species are recognized within the Southeast Asian agamid genus *Hydrosaurus*: *H. amboinensis* (Schlosser, 1768) from Ambon, Seram, Sulawesi and New Guinea, *H. pustulatus* (Eschscholtz, 1829) from the Philippines and *H. weberi* Barbour, 1911 from Halmahera and adjacent islands. Historically, two additional species were described from the island of Sulawesi, but were synonymized with *H. amboinensis* more than a century ago and have been treated as such in most subsequent publications. In order to revise the taxonomy and diversity of these enigmatic agamid lizards, we examined the corresponding type specimens and additional material originating from Sulawesi and compared them to photographs of live specimens from field trips. Due to differences in colour pattern and scalation characters, we resurrect the taxa *celebensis* Peters, 1872 and *microlophus* Bleeker, 1860 from the synonymy of *H. amboinensis*, which in turn is restricted to the central Moluccas and New Guinea. Hence, Sulawesi is currently the only known island within the genus' range to be inhabited by two different species of sailfin lizards. Our systematic investigation brings the number of recognized species within the genus *Hydrosaurus* to five.

**Key words:** Hydrosaurinae, Indonesia, type specimens, taxon resurrection, synonymy, distribution

### Introduction

Sailfin lizards of the genus *Hydrosaurus* Kaup, 1828 are the largest and belong to the most enigmatic agamid lizards reaching a total length of more than one meter. Their impressive dragon-like appearance is further enhanced by their characteristic high dorsal crest, particularly on the tail, which is supported by enlarged spinose processes of the caudal vertebrae. In addition, the digits possess broad scale fringes along the inner and outer sides thus enlarging their plantar surfaces considerably. Despite these morphological peculiarities research into diversity and taxonomy of sailfin lizards has been neglected for more than a century. While the genus name *Lophura* Gray, 1827 has generally been used for these iconic agamids in the 19<sup>th</sup> century (e.g. Boulenger 1885), this name is preoccupied by *Lophura* Fleming, 1822 (Aves: Galliformes: Phasianidae) as pointed out by Poche (1903). He replaced the genus name with *Hydrosaurus* Kaup, 1828 which was formerly applied to monitor lizards of the family Varanidae (e.g. Gray 1845, Günther 1872) but is still in use today for sailfin lizards. Molecular phylogenetic analyses showed that *Hydrosaurus* forms a separate and rather basal lineage within Agamidae, the subfamily Hydrosaurinae (Macey *et al.* 2000; Wiens *et al.* 2012; Pyron *et al.* 2013).

The first sailfin lizard species, *H. amboinensis*, was described by Schlosser (1768), a Dutch physician from Amsterdam, as *Lacerta amboinensis* from the Indonesian island of Ambon, formerly known as Amboina. He apparently based the description on a single specimen (indicated by the Dutch expression “dit dier”, which means “this animal”, singular). Accordingly he provided measurements and an illustration for this specimen (Figure 1)

which eventually found its way into the collection of the National Museum of Natural History in Stockholm (NRM 1047, Figure 2). Koch (2012) recently detailed how the holotype came from the Netherlands to Sweden. Next, Eschscholtz (1829) named a new species of sailfin lizard from the Philippines as *H. pustulatus* (types lost, see below for further information) and Barbour (1911) separated the population of Halmahera from the distribution range of the widespread *H. amboinensis*. He dedicated this new species, *H. weberi* (MCZ 7505 & 7506, holo- and paratype, respectively) to Max Weber (1852–1937), a famous German zoologist, who organised expeditions to present-day Indonesia, where he also collected sailfin lizards on Sulawesi (Weber 1890: 167). In addition, a further two species were described from the island of Sulawesi (formerly Celebes) in the 19<sup>th</sup> century, namely *Istiurus microlophus* Bleeker, 1860 and *Lophura celebensis* Peters, 1872 (see also below for further potentially available names). The latter was synonymized with the name *amboinensis* by Günther (1873). Bleeker's (1860a) older name remained mostly unused and was likewise later considered synonymous with Schlosser's taxon (Boulenger 1885).



**FIGURE 1:** Illustration of the holotype accompanying the description of *Lacerta* (= *Hydrosaurus*) *amboinensis* by Schlosser (1768). The typical vermiculated colour pattern is still partly visible.



**FIGURE 2:** Adult holotype (NRM 1047) of *Lacerta* (= *Hydrosaurus*) *amboinensis* Schlosser, 1768. Note that the original colour pattern as still partly visible in Figure 1 has disappeared due to longterm preservation. Photo by André Koch.



Günther's (1873) decision to consider *Hydrosaurus amboinensis* and the species described from Sulawesi as conspecific was subsequently followed by authors such as Meyer (1887), Boulenger (1897), Sarasin & Sarasin (1901), Roux (1904), de Rooij (1915) and Wermuth (1967). Only a few publications discussed a possible subspecies status (see for example Weber 1890) or treated specimens from Sulawesi as a distinct species, such as Barbour (1911, 1912 as *Hydrosaurus microlophus*) or Iskandar & Tjan (1996 as *Hydrosaurus celebensis*). Koch (2012) referred to specimens from Sulawesi as *H. cf. amboinensis*. At the same time, this author noted the taxonomic relevance of the name *microlophus* Bleeker, 1860.

Currently, only three species of sailfin lizards are recognized: the widely distributed *Hydrosaurus amboinensis* (Schlosser, 1768) from Ambon, Seram, Sulawesi, Waigeo and New Guinea, *H. pustulatus* (Eschscholtz, 1829) from the Philippines and *H. weberi* Barbour, 1911 from Halmahera, Ternate, Tidore (own observations, AGT, and new island record) and Bacan in the northern Moluccas (Boettger 1903; Uetz *et al.* 2019).

Siler *et al.* (2014) recently published a phylogenetic analysis that was mainly concerned with specimens from the Philippines, but also included samples from other species within the genus' distribution range. Their results revealed six major clades in the Philippines alone. The species statuses of *H. amboinensis* (albeit from a trade specimen without locality data) and *H. weberi* were confirmed and the samples from Sulawesi turned out to represent a distinct fourth clade showing a comparatively high genetic diversity. Siler *et al.* (2014) treated this clade as *Hydrosaurus* sp. and suggested the name *Hydrosaurus celebensis* (Peters, 1872) as available for the populations from Sulawesi. They overlooked, however, the fact that Bleeker's (1860a) description of *H. microlophus* precedes that of *H. celebensis* by Peters (1872).

Koch (2012) previously pointed out that two species may exist on the island that would require further investigation. In addition, during recent excursions on Sulawesi one of us (AGT) took various pictures of two clearly different phenotypes of sailfin lizards (Figure 3). Further photographs from Ch'ien C. Lee (2019) under the name *H. amboinensis* and from David G. Knowles (2019) under the name *H. celebensis* are available on the internet. These two phenotypes differ considerably both in colouration and arrangement (i.e. the absence or presence) of groups of enlarged and strongly keeled scales on the dorsum. In examining the photos it appears that they both constitute two different phenotypes that differ from the three currently known sailfin lizard species, namely *H. amboinensis*, *H. pustulatus* and *H. weberi*. Given the fact that the geologically complex island of Sulawesi (Hall 2012) is inhabited by several closely related but parapatric populations (or species) of various organism groups which are confined to discrete areas or peninsulas of the island, as is the case in macaques, tarsiers, toads, monitor lizards and flying lizards (Evans *et al.* 2003; Koch 2010, 2012; Merker *et al.* 2010; McGuire *et al.* 2007), it follows that more than one taxon of *Hydrosaurus* could be involved.

## Material and methods

In order to evaluate the taxonomic status of the Sulawesi sailfin lizard populations we studied museum specimens including the respective type specimens and gathered photographic records from different locations on Sulawesi and other islands situated within the distribution range occupied by the genus *Hydrosaurus*.

In total, we examined 51 voucher specimens from across the entire genus' range in various museum collections (acronyms see below) including the type specimens of *Lacerta amboinensis* Schlosser, 1768, *Lophura celebensis* Peters, 1872, and *Istiurus microlophus* Bleeker, 1860. We have, however, refrained from comparing the Sulawesi specimens to those from the Philippine species group of *H. pustulatus* s.l. (Eschscholtz, 1829) for the following reasons:

1. The type specimen of *Istiurus pustulatus* Eschscholtz, 1829 appears to be lost. We consulted collection databases and approached museum curators with enquiries about historical specimens in several museums including the natural history museum in Tartu (formerly Dorpat), Estonia—the birth, habitation and working place of Johann Friedrich [von] Eschscholtz (1793-1831). Should the type specimen have been deposited there it would have been destroyed during World War II together with most of the other wet collection material (pers. comm. V. Soon, Tartu). The agamid type catalogue of the Russian Academy of Sciences, St. Petersburg (Milto & Barabanov 2012) does not list *H. pustulatus* and we were unable to trace the type in the collection of the Lomonossow University. A potential candidate as type specimen would have been ZMB



66245 since it was donated by Eschscholtz to the Berlin Natural History Museum (ZMB). However, it does not match the measurements given in the original description by Eschscholtz (1829); there is a difference of approximately 200 mm with respect to the total length.



**FIGURE 3.** Comparison of *Hydrosaurus amboinensis* with the two phenotypes observed on Sulawesi. A: *Hydrosaurus amboinensis*, male, Air besar (Passo), Ambon, B: *Hydrosaurus amboinensis*, female, Air besar (Passo), Ambon, C: *Hydrosaurus celebensis*, male, Pattunuang, Sulawesi, D: *Hydrosaurus celebensis*, female, Pattunuang, Sulawesi, E: *Hydrosaurus microlophus*, male, Rompegading, Sulawesi, F: *Hydrosaurus microlophus*, female, Ujung Lamuru, Sulawesi. Note the pronounced differences in colour pattern as well as number and arrangement of enlarged scales dorsolaterally. Photos by Andrea Glässer-Trobisch & Dietmar Trobisch.



2. The ZMB collection contains three historical voucher specimens from Luzon (ZMB 66245, ZMB 678 and ZMB 4181) that differ morphologically from each other to such an extent that they could represent distinct subspecies or even species (W. Denzer & U. Manthey, pers. obs.).
3. Siler *et al.* (2014) in their analysis showed that the Philippine populations are phylogenetically diverse and form several clades that are clearly different from the Sulawesi specimens.

Sulawesi material used in this study together with further voucher specimens examined for comparisons are listed in Appendix 1. In addition, numerous photographs of live specimens taken during field trips by AGT and Dietmar Trobisch to Sulawesi and the Moluccas (Halmahera, Ternate, Tidore and Ambon) were available for comparisons.

While the pictures are of sufficient quality allowing for a full description of both taxa, such an act would constitute photography-based taxonomy (for a discussion see Ceriaco *et al.* 2016 and Pape *et al.* 2016), a method that has been approved by the ICZN (2017) but that should be employed under exceptional circumstances only.

In following best practice in taxonomy (Kaiser *et al.* 2013), we decided that the examination of historical material along with photos from the natural habitat was crucial to our integrative study aimed at clarifying the taxonomic statuses of the two above-mentioned phenotypes of Sulawesi sailfin lizards. Over the last two centuries several specimens have been recorded with some being described as new species of *Hydrosaurus* based on material that actually has been, or potentially could have been collected on Sulawesi. They all have to be taken into account in order to fully evaluate whether or not one of these could serve as a name-bearing type specimen for the sailfin lizards occurring on Sulawesi. Throughout this publication we will employ the unified species concept proposed by de Queiroz (2007). Further details are given under the discussion below.

Meristic and morphometric data were recorded from type specimens and additional material. Measurements were taken using a sliding calliper with a precision of 0.1 mm or using a ruler with a precision of 1 mm. Abbreviations used are as follows: SVL: snout–vent length; TL: tail length; HL: head length; HW: head width.

Collection acronyms are as follows: MCZ—Museum of Comparative Zoology, Harvard, USA; MNHN—Muséum National d’Histoire Naturelle, Paris, France; MVZ—Museum of Vertebrate Zoology, Berkeley, USA; MZB—Museum Zoologicum Bogoriense, Cibinong, Indonesia; NHMUK—Natural History Museum, London, formerly BMNH—British Museum (Natural History); NRM—Naturhistoriska Riksmuseet Stockholm, Sweden; RCSOM—Royal College of Surgeons Odontological Museum, London; RMNH—Rijksmuseum van Natuurlijke Historie, now Naturalis, National Museum of Natural History, Leiden, the Netherlands; SMF—Senckenbergmuseum Frankfurt, now Naturmuseum Senckenberg, Frankfurt a.M., Germany; ZFMK—Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; ZMA—Zoological Museum Amsterdam (collections now at Naturalis), the Netherlands; ZMB—Zoologisches Museum Berlin, now Museum für Naturkunde, Berlin, Germany; and ZMH—Zoologisches Museum Hamburg, Germany.

## Results

### Taxonomic and nomenclatural history of Sulawesi sailfin lizards

The earliest record of a sailfin lizard from Celebes can be found in Schlegel (1858), however, exploration of the (herpeto)fauna of Sulawesi started in the 1820s with the establishment of the “Natuurkundige Commissie voor Nederlandsch-Indië”, the Natural History Commission for the Netherlands Indies (Koch 2012, 2018). In Schlegel’s (1858) chapter about basilisks (which includes the genera now recognized as *Basiliscus*, *Hydrosaurus*, *Physignathus* and *Intellagama*) he described *Basiliscus* (= *Hydrosaurus*) *amboinensis* in detail. At the end of the description on page 19 he writes: “De Basilisken van Celebes en de Philippynsche zijn weinig, maar standvastig van de voorgaande afwijkende” [= the basilisks from Celebes and the Philippines are little, but consistently different from the previous (i.e. *H. amboinensis*)]. On page 544 he refers to figure 31 on plate II as “De basilisk van Celebes (*Basiliscus celebensis*)”. While this new taxon name would typically be considered a nomen nudum because Schlegel (1858) provided neither a description nor a diagnosis within the text, the illustration could be considered as designation of a (icono)type according to the ICZN (1999: Articles 72.5.6 and 73.1.4). Although Schlegel’s (1858) illustrations are in general fairly precise, the one depicting an apparently adult male sailfin lizard does not allow for an assignment to any of the two Sulawesi forms of *Hydrosaurus* described in later years. While the light coloured areas



on the neck and belly would point towards *H. microlophus* (Bleeker, 1860) other diagnostic features of Schlegel's illustration such as the absence of groups of enlarged scales on the dorsum point towards *H. celebensis* (Peters, 1872). The RMNH and ZMA collections at Naturalis do not include a specimen under the name *celebensis* neither do they appear to list any early records of specimens originating from Sulawesi. Two dried historical specimens (RMNH.RENA.25937 and RMNH.RENA.25938) lack precise locality data. They are recorded simply as originating from "Indonesia" and could potentially have been collected on Sulawesi but both voucher specimens show no resemblance to the figure given by Schlegel (1858) and therefore has to be excluded as potential types of Schlegel's (1858) new name.

Günther (1873) also reported a specimen of *Basiliscus celebensis* in the NHMUK collection received from the Leyden (= Leiden) Museum "many years ago". The author clearly stated that this specimen is an adult female. Günther (1873) considered this and all other specimens in the collection of the British Museum as conspecific with *Lophura* (= *Hydrosaurus*) *amboinensis*. He "hesitate(d) to adopt [...] the *Lophura celebensis* recently described by Peters". In the *amboinensis* account of his catalogue, Boulenger (1885) only reported one specimen originating from Celebes that had been received from the Leyden Museum ("b, Hgr." = specimen b, half-grown) but did not refer to it as *Basiliscus celebensis*. However, Günther's (1873) specimen is still present in the NHMUK collection. It is still in its original jar with the original labels attached to the outside. The uppermost label says "*Basiliscus celebensis*, Celebes 49.3.2.36 (1849.3.2.36), Mr Frank's coll" (note that Mr. Frank is not mentioned by Boulenger 1885). The second label underneath (commonly added to display the most recent redetermination) says "*Lophura amboinensis*" following the logic stated in Günther's (1873) text and accepted by Boulenger (1885). The half-grown ("Hgr") specimen was received by the British Museum in 1849 as confirmed by the register for this year (which again mentions Mr. Frank). Mr. Frank was an Amsterdam based dealer in natural history items who sold many specimens to the British Museum (see for instance Ingle 1991).

Given the details outlined above, we are convinced that this voucher specimen corresponds to specimen "b Hgr" in Boulenger's (1885) catalogue. There is obviously a discrepancy between Günther (1873) and Boulenger (1885) as to the sex and age of the specimen, but it is now nearly impossible to decide which of these two authors was correct since the specimen has been dissected and all the soft tissue elements including its organs removed. There is no record providing details of who performed the dissection or when it was done. Additionally, adult females and subadult males of *Hydrosaurus* lizards do not differ much in the development of their sailfin and are thus prone to be confused. In general appearance and colouration NHMUK 1849.3.2.36 agrees with *H. celebensis* (Peters, 1872) and we consider it to belong to this taxon. Since the specimen does not agree with Schlegel's (1858) illustration (which shows an adult male with a high sailfin along the tail base), it cannot have served as the name-bearing type of *Basiliscus celebensis* Schlegel, 1858.

With regard to nomenclature this situation could be considered a dilemma. On the one hand Schlegel (1858) provides a figure that could serve as iconotype predating the descriptions by Bleeker (1860a) and Peters (1872), and would therefore have nomenclatorial priority; on the other hand it is not clear to which biological species (or phenotype) Schlegel's figure refers because it lacks important diagnostic characters. If it were either *H. microlophus* (Bleeker, 1860) or *H. celebensis* (Peters, 1872) the respective name would become a junior synonym of *H. celebensis* (Schlegel, 1858). In the case that Schlegel's figure actually represented *H. microlophus* this species would become *H. celebensis* and a new name would have to be assigned to Peters' *H. celebensis*. For the purpose of stability in nomenclature we therefore propose to consider Schlegel's (1858) *Basiliscus celebensis* a nomen nudum and a nomen dubium since (1) no description or diagnosis was provided, and (2) the figure holding the name cannot be assigned unambiguously to a recognized species or available type specimen. If in the future a specimen matching Schlegel's figure is rediscovered, a case will have to be submitted to the ICZN in order to conserve *celebensis* Peters, 1872 and *microlophus* Bleeker, 1860 as available names and, despite an apparent priority, to disregard Schlegel's (1858) *celebensis* for reasons of nomenclatural stability.

Beside the nomenclatural issues outlined above, there are three further species names for sailfin lizards whose descriptions predate those of *H. microlophus* and *H. celebensis*, namely *Lacerta javanica* Hornstedt, 1785 (= *Hydrosaurus javanensis*, for validation of the species epithet see Bonnaterre (1789) and comments below), *Lacerta lophura* Shaw, 1802 and *Lophura shawii* Gray, 1845. Despite all not having reliable locality data, it is possible that the voucher specimens on which these names were defined may have originated from Sulawesi. Hence, they are also discussed below.

Hornstedt (1785) described a sailfin lizard from Java in Swedish and Latin but he did not use Linnean binominal



nomenclature in his description. Instead, the Latin expression he used was “*Lacerta cauda compressa, longa, basi pinna radiate, dorso dentato*” (= lizard with a long compressed tail, radiating spines, denticulated dorsally), at the time this included a broad range of lizards to which *Lacerta* was widely applied being the Latin word for lizard. At the end of his publication he provided figures of a male and a female sailfin lizard specimen, the latter merely as a contour drawing. While the body and tail of the male are shown in much detail and with correct proportions, the head and neck lack details and do not exhibit the typical proportions of any currently recognized *Hydrosaurus* species. In particular, the scales of the gular region and those at the onset of the limbs are much larger than expected. In addition, the head is pointed and does not resemble the shape typical of a *Hydrosaurus*. However, the NRM collection still holds two *Hydrosaurus* specimens (NRM 6845, formerly NRM 1048, and NRM 1049) collected by C. F. Hornstedt before 1802 (he visited Java between July 1783 and July 1784 according to Rookmaaker 1988), with their origin given as “probably Jakarta area”. The correctness of the locality given by Hornstedt (“Java”) is highly doubtful if not erroneous (de Rooij 1915). The Javanese herpetofauna is represented in museum collections by thousands of specimens. In the early 19<sup>th</sup> century Johan Coenraad van Hasselt (1797-1823) and Heinrich Kuhl (1797-1821) collected extensively on Java, mainly in the Bogor area. Their collection was sent to the Rijksmuseum in Leiden, the Netherlands, and formed the basis for the unpublished “*Erpetologie de Java*” by Heinrich Boie (1794-1827), who later also travelled to Java where he continued to collect reptiles and amphibians. Further collections were made by Caspar Georg Carl Reinwardt (1773-1854) and Heinrich Christian Macklot (1799-1832) for the Rijksmuseum in Leiden and by Robert Mertens (1894-1975) for the Senckenberg Museum in Frankfurt (Mertens 1957). Despite all their efforts not a single additional specimen of *Hydrosaurus* was ever found on the island. Nevertheless, Boulenger (1885) mentioned Java as part of the general distribution of the genus. He may have been led to this assumption based on Günther (1873) who wrote: “There are fifteen examples of all sizes in the British Museum; the localities where they have been obtained are Java, Amboina, Celebes, and the Philippine Islands.” In his catalogue Boulenger (1885) did not list a specimen from Java and we were unable to locate such a specimen in the current NHMUK collection or catalogue. The NRM specimens were most likely collected in the Moluccas, transferred to Java, where they were acquired by Hornstedt and finally shipped from Jakarta (Batavia in former times) to Europe leading to the false claim that they were allegedly collected on that island.

Although Hornstedt’s figure of a male depicting the pronounced enlarged scalation in the nuchal and chest regions possibly represents *H. microlophus* (or perhaps *H. weberi*) the specimens deposited by him in the NRM are clearly not identical with either of these two species. Instead, both specimens closely match the description and the type specimen of *H. amboinensis* and, therefore, most probably originated from Seram (formerly Ceram) or Ambon in the Moluccas, the latter island of which was a major colonial port in the past. Because the NRM specimens were neither catalogued as types, nor do they agree with measurements given by Hornstedt (1785) we conclude that they do not represent type specimens.

Wermuth (1967) listed “*Lacerta javanica* Hornstedt in Gray, 1845 [nomen nudum fide Gray 1845]” as a synonym of *H. amboinensis* apparently unaware of Hornstedt’s (1785) original publication and later publications using binominal nomenclature which cited Hornstedt. Hornstedt (1785) did not use a Latin binomen for his species description and therefore did not provide an available name under nomenclatural rules (ICZN 1999, Articles 11.4 & 11.5). To our knowledge Bonnaterre (1789: 41) was the first reviser of Hornstedt’s publication. He gave a short description in French and was the first to apply a binomen to the species for which the name *L.[acerta] javanensis* was given. Bonnaterre (1789) therefore has to be seen as the first taxonomist to have made this binominal name available. Suckow (1798: 109) referred to Hornstedt’s description and introduced the name *Lacerta jauanica* (sic!), albeit as a synonym of *Lacerta amboinensis*. Later, Gray (1845) used *Lac. (Lacerta) javanica* and synonymized this name with his *Lophura shawii*. The nomenclatural efforts of Suckow (1798) and Gray (1845) can be seen as providing a nomen substitutum pro *javanensis* although this name was not mentioned by either of the authors. By citing Hornstedt (1785) but not Bonnaterre (1789) and by not using “*Lac. javanica*” as a valid taxon name, this name did not become available (ICZN Article 11.5). The first author to make the name *Lacerta iavanica* (sic!) available was Wiegmann (1834) who considered the species status as incertae sedis. However, according to the rules of nomenclature (ICZN Art. 23, Principle of Priority) the name has to be considered a junior synonym of *javanensis* Bonnaterre, 1789. The species name *javanensis* in conjunction with any synonymous genus name of *Hydrosaurus* has to our knowledge not been used since Bonnaterre (1789). We consider it therefore a nomen oblitum that should not be applied to any species of the genus *Hydrosaurus*. As the species name *javanica* constitutes a nomen substitutum pro *javanensis* it is therefore also not available for nomenclatural purposes with respect to the genus *Hydrosaurus*.



Gray (1845) treated specimens from Ambon (= *H. amboinensis*) and those from the Philippines (= *H. pustulatus*) as conspecific and combined them under *Lophura amboinensis*. Based on the absence of a crested nose, the presence of which he considered characteristic for his combined *H. amboinensis* group including *H. pustulatus*, Gray (1845) described *Lophura shawii* as a new species based on a single specimen lacking locality data. He further regarded *L. shawii* not only conspecific with Hornstedt's *Lacerta javanica* but interestingly also with *Lophura amboinensis* Wiegmann [sic!], a species which he also mentioned as a synonym of *H. amboinensis*. Wiegmann (1834) described a specimen from the Philippines (ZMB 678, Manila, Luzon, collected by Meyen) in detail and added “mihi” to the description, indicating that he should be considered the original author. Although this is clearly wrong, Gray (1845) apparently accepted this point of view. Wiegmann's specimen is now considered to represent a member of the *H. pustulatus* group. On page 214 of his Latin diagnoses Wiegmann (1834) distinguished *L. [=Lophura] amboinensis* by the absence of a nasal crest and homogeneous dorsal scalation (“mesorhinio plano non cristato, squamis laterum parvis, aequalibus”) from *L. pustulata* (“mesorhinio cristato, squamis laterum inaequalibus” = nasal crest, dorsolateral scales unequal). This statement most probably led Gray (1845) to assume that *L. shawii* was a valid species as his specimen did not have a nasal crest but enlarged scales across the back. However, with respect to the latter character it is perhaps questionable why he referred to Wiegmann's *L. amboinensis* in his synonymy since Wiegmann (1834) clearly stated that the dorsolateral scales are small and equal.

Gray's (1845) short description of *Lophura shawii* is based on “Dr. Shaw's specimen”, which he described as “Green, vermiculated with black; scales unequal, with cross ridges of larger scales; [scales] of head small, keeled, all equal; nose not crested in front.” The specimen is referenced as “*Lac. [=Lacerta] Lophura* Shaw, Zool. iv. t. 62”. Unfortunately, this assignment contains a number of mistakes. First, volume four of Shaw's (1802) General Zoology deals with fishes and not with reptiles, these are dealt with in Volume three. Secondly, Shaw (1802) does not provide an illustration of *Lacerta lophura*. Plate 62 in Shaw (1802) instead shows the “Amboina Guana”. This illustration is a near identical black-and-white reproduction of the colour plate 403 in Shaw & Nodder (1799), which in itself is nearly identical to Schlosser's (1768) illustration of *Lacerta amboinensis* apart from certain differences in colouration. In both, Shaw & Nodder (1799) and Shaw (1802), *Lacerta amboinensis* is used as the taxon name and is also referred to Schlosser's (1768) description. In the older publication of 1799 this name is, however, only given in the Latin section of the description and not in the English section. In the latter section he used the common name “Amboina Lizard” or “The variegated Amboyna Lizard”.

Wermuth (1967) following Gray (1845) listed “*Lacerta lophura* Shaw, 1802 (Gen. Zool. 3 1: 218)” in his synonymy for *Hydrosaurus amboinensis* (Schlosser, 1768). However, despite having described *H. amboinensis* in length (pp. 203-206) and illustrating it on plate 62, and again on page 218 in the same volume Shaw (1802) described *Lacerta lophura* as a new species “at first view much resembling the Teguxin (...)”. This name was at that time typically used for *Tupinambis teguixin* (Linnaeus, 1758), a teiid species inhabiting South America and parts of Middle America, which bears no resemblance to *Hydrosaurus*. Shaw (1802: 235) himself described this species as Variegated Lizard (*Lacerta teguixin*) in the same volume. Additionally, Shaw (1802) described the “back and tail” as “serrated throughout” (characters not present in *T. teguixin*) for *Lacerta lophura* but that of *L. amboinensis* as “furnished above with a very broad, rising crest (...) internally strengthened by several bony radii resembling those in the fin of a fish”. If *Lacerta lophura* Shaw, 1802 constituted a *Hydrosaurus* species he would have certainly compared it to *H. amboinensis* instead of *Tupinambis teguixin*. At the end of his description Shaw (1802) mentions that specimens were available “in the British Museum and that of Dr. William Hunter”. We could, however, neither locate a specimen under that name in the NHMUK collection nor in The Hunterian Museum in Glasgow (for website see References), where the zoological specimens of William Hunter were deposited. The handwritten catalogue page for *Hydrosaurus* specimens in the NHMUK collection has xxiii 36a, 1946.8.11.61 as the type for *L. shawii* as well as for *L. lophura*. However, the type assignment to both species is written in red ballpoint pen ink and was therefore added a long time after Shaw, Gray or Boulenger. As Shaw (1802) did not provide a figure of this specimen and his description appears to refer to a completely different and unidentifiable species, the name *Lacerta lophura* Shaw, 1802 should be considered a nomen dubium and be removed from the synonymy of *Hydrosaurus*.

Gray's (1845) assignment of “Dr. Shaw's specimen” and a later assignment of this specimen as the type of *L. shawii* by Boulenger (1885) are somewhat confusing. This specimen cannot be identical with *Lacerta lophura* (Shaw, 1802), but most likely should match the one described in Shaw & Nodder (1799) and Shaw (1802) as *Lac. amboinensis*. Notably, Boulenger's (1885) assignment of the type *Lophura shawii* refers to a female (specimen “v”, current catalogue number NHMUK 1946.8.11.61, formerly NHMUK xxiii.36a) and subsequent catalogues are



consistent with this at the NHM(UK). The specimen is still in its original jar and is labelled “*Lophura amboinensis* (*L. shawii*—type)”.

In both Shaw & Nodder (1799) and Shaw (1802) only a single specimen of *Lacerta amboinensis* is mentioned, held in the collection of the “Museum of the late Mr. John Hunter”, now the Hunterian Museum of the Royal College of Surgeons (RCS) in London. With no. 568 the catalogue of holdings (Gray 1859) mentions a specimen of “The crested or Amboyna Lizard” as *Istiurus amboinensis*. A search using the online catalogue (available at <http://surgicat.rcseng.ac.uk>), however, yielded no such result. The only specimen of *Hydrosaurus* in their catalogue at present is a skull (RCSOM/A 407.1, *H. amboinensis*). In the preface to the 1859 RCS museum catalogue it is mentioned that “many of specimens described by Dr. Shaw were duplicates; and in the year 1843 upwards of 400 of these were (...) transferred to the British Museum”. As Gray’s earlier publication dates 1845 he may therefore have had the original specimen described by Shaw to hand and the catalogue record of the Royal College of Surgeons may be in error. The initial catalogue of Hunter’s collection was compiled shortly after his death by Shaw, who finished the manuscript in 1806 as mentioned in the preface to the catalogue (Gray 1859). If this manuscript served as the basis for the 1859 catalogue and was not updated after 1806, it is conceivable that the specimen would have been considered as still present in the Hunterian collection in 1859. If the specimen was, however, among those that were transferred to the then British Museum, Gray would have had Shaw’s specimen to hand and Boulenger’s (1885) assignment as a type would thus be correct.

The origin of the specimen selected as type for *H. shawii* by Boulenger (1885) is unknown. The specimen does not agree with the type of *H. microlophus* as it differs in the arrangement of the groups of enlarged scales and also has oval shaped nostrils. Similarly, it does not agree with the type specimen of *H. celebensis* in colour and arrangement of the enlarged scales on the dorsum (*celebensis* has only a few grossly enlarged scales next to each other, the *shawii* type has a number of slightly enlarged scales on the dorsum). From *H. weberi* the type of *H. shawii* differs in the absence of the grossly enlarged and keeled scales in the chest region near the onset of the forelimbs. Because of its resemblance with the type of *H. amboinensis* we preliminary refer to the type of *H. shawii* as *H. cf. amboinensis*. However, there is still a chance that one of the Philippine populations of *H. pustulatus* s.l. could match the type of *H. shawii*. Should it turn out that the Philippines are inhabited by more than one sailfin lizard (sub)species, as indicated by the study of Siler *et al.* (2014), and one of these taxa was morphologically identical with NHMUK 1946.8.11.61, then the name *Hydrosaurus shawii* would need to be taken into account for nomenclatural purpose.

Overall, we conclude that neither of the two earlier described names (i.e. *javanensis* / *javanica* and *shawii*) refers to specimens from Sulawesi. Furthermore, we consider the names *javanensis* and *javanica* as nomina dubia and not available for nomenclatural purposes with respect to species of the genus *Hydrosaurus*. There exists no type material for either of the two taxon names just an ambiguous illustration including a Latin description which was published by Hornstedt (1768) without the use of Linnean binominal nomenclature. Equally, the name *Lacerta lophura* Shaw, 1802 constitutes a nomen dubium since no type material is available for comparisons and the original description does not even appear to relate to the genus *Hydrosaurus*. Consequently, the name should be removed from the synonymy of *Hydrosaurus* species. We currently identify *Lophura shawii* Gray, 1845 as *H. cf. amboinensis*, however, because the type of *H. pustulatus* is unknown the specimen could equally be a member of the Philippine *Hydrosaurus pustulatus* complex group.

Additionally, we have demonstrated that the name *celebensis* as defined and used by Schlegel (1858) for voucher specimens in the Leyden Museum is also not available for nomenclatural purposes. Also Günther’s (1873) later description of a specimen held in the collection of the British Museum and received from the Leyden Museum (NHMUK 1849.3.2.36) does not validate *Basiliscus celebensis* Schlegel, 1858 as it does not agree with Schlegel’s illustration but rather constitutes a junior synonym of *Lophura celebensis* Peters, 1872 because it agrees well with Peters’ type. Hence, only *microlophus* Bleeker, 1860 and *celebensis* Peters, 1872 have to be considered as available names for Sulawesi’s sailfin lizards and are further discussed below.

### **The type specimen of *Istiurus* (= *Hydrosaurus*) *microlophus* Bleeker, 1860**

Bleeker (1860a) described *Istiurus microlophus* from “Makassar (formerly Ujung Pandang, Figure 8), Celebes (= Sulawesi)” based on a juvenile voucher specimen. Because the nuchal and tail crests were only slightly developed he called the new species *microlophus* (derived from *micro* / μικρός Greek meaning small and *lophos* / λόφος Greek meaning crest). According to Bleeker (1860a) the nuchal crest is only slightly jagged and not serrated and extends onto the back. The tail crest is not very well developed and extends only as far as the front section of the tail

consisting of small tooth-shaped scales. *Istiurus microlophus* is further characterized by Bleeker (1860a) as having four enlarged scales on either side of the neck, as well as three transverse rows of enlarged scales on the dorsum between the fore and hindlimbs. The general colouration is given by Bleeker (1860a) as brownish both dorsally and laterally and white ventrally. Yellow bands are present dorsolaterally and the tail is marked with numerous yellow, narrow transverse bands. The specimen has a total length of 275 mm and part of the tail is missing. Despite this, the remnant tail is more than twice the snout-vent length.

Boulenger (1906: 529) reported that a large series of reptiles from the Malay Archipelago, including the types of many species described by Pieter Bleeker (1819–1878), was purchased by the British Museum in 1863 (see also Norman & Whitehead 1984).

Under the name *Lophura amboinensis*, there is one specimen originating from Celebes mentioned in Boulenger's (1885) Catalogue of Lizards in the British Museum. However, this specimen was not marked as the type of *Istiurus microlophus*. Nevertheless, a re-examination of the respective voucher specimen revealed a near complete match of NHMUK 1863.12.4.35 (Figure 4A) with Bleeker's (1860a) description, and combined with its measurements we are convinced of its type status. The specimen measures 257 mm instead of 275 mm. This difference is probably due to an erroneous transposition of digits by Bleeker (1860a). The ventral colouration is currently more cream than white; the colour change may be an artefact due to preservation in alcohol. Bleeker (1860a) described the dentition as follows: "Upper jaw on each side with 8 or 9, three-pointed compressed and 2 or 3 short-conical teeth, the lower jaw with 8 or 9, three-pointed compressed and 2 or 3 shorter cone-shaped teeth." In our examination we counted seven tricuspid teeth on each side plus four to five short conical teeth on each side in the upper jaw and three to four shorter cone-shaped teeth in the lower jaw instead.

Further evidence for this voucher specimen having type status is the fact that it is one of four specimens that were received from the Leiden Museum or Bleeker, respectively (specimens a, b, n & o in Boulenger 1885). Despite only being marked as originating from the "Leyden Museum" in Boulenger's (1885) catalogue (specimen "b, Hgr.") the label on the jar has Bleeker's handwriting on it, which is just visible with the naked eye. This specimen was later assigned the catalogue number NHMUK 1863.12.4.35. We therefore consider this specimen as the original holotype of *Istiurus microlophus*.

#### **The type specimen of *Lophura* (= *Hydrosaurus*) *celebensis* Peters, 1872**

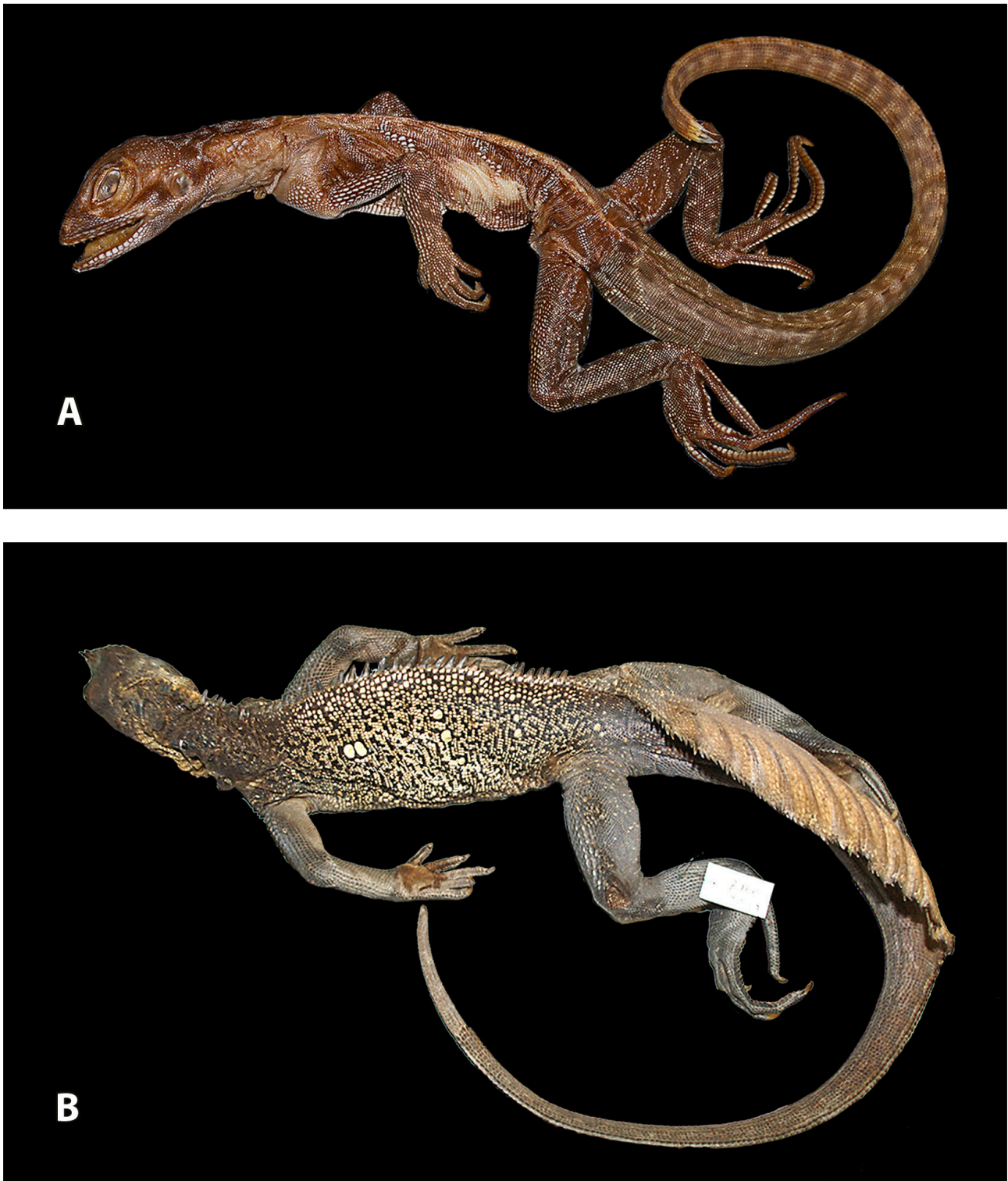
In 1872 Peters reported a new species of sailfin lizard from Celebes that he called *Lophura celebensis*. The holotype ZMB 7393 is shown in Figure 4B. He provided a very short description stating that the colour of the body is yellow with numerous black dots sometimes forming larger spots and that large scales (of the same size as the tympanum) are interspersed in the dorsal scales. Note, in the type specimen there are three grossly enlarged scales on the dorsum, the largest of which is approximately three fourths the size of the tympanum. As Boulenger (1897) pointed out with regard to a specimen from Paloppo (= Palopo, northern part of South Sulawesi), Peters' (1872) statement is slightly exaggerated. Boulenger (1897) found the tympanum to have an actual diameter of 9 mm and the largest scale a diameter of 5 mm only. Peters (1872) further stated that the ventral scales are longer than wide and that this specimen has 12 femoral pores on either side. The total length is given as 945 mm with the tail measuring 600 mm (TL/SVL = 1.74). It should be noted that the posteriormost part of the tail appears to be regenerated. Although ZMB 7393 is without doubt the type specimen of *L. celebensis* our examination revealed a few differences as compared to Peters' (1872) description. With respect to the measurements we found SVL to be 360 mm and TL 580 mm (TL/SVL = 1.61). The number of femoral pores we determined to be 6 and 8 (left/right), respectively.

#### **The type specimen of *Lacerta* (= *Hydrosaurus*) *amboinensis* Schlosser, 1768**

Schlosser's (1768) type specimen (NRM 1047, Figure 2) is an adult male with a SVL of 282 mm, the tail measures 570 mm (TL/SVL = 2.0). The tail tip is missing and not regenerated. The tympanum has a diameter of 8 mm. A crest on the nose is missing. The nuchal and dorsal crests are continuous consisting of pointed scales measuring up to 6 mm. The crest on the tail has a maximum height of 60 mm. On the ventral surface, the specimen exhibits a total of 14 femoral pores. It has 10/10 supralabials and 10/10 infralabials. Under the fourth toe, which exhibits a lateral row of 32 enlarged scales, there are 44 slightly keeled subdigital scales. The lateral body scales are mostly keeled and non-homogenous in size with single enlarged scales being interspersed along the back not forming distinct groups. Along the side of the neck there are two slightly enlarged scales. Due to long-term preservation, the specimen shows a plain dark brown body colouration lacking the typical vermiculated colour pattern of male sailfin lizards of the



Ambon population in the wild (Figure 3A&B). One diagnostic character that has been considered as differentiating from the remaining species of the genus is the presence of an oval nostril. While this is true for the type and some specimens we examined (MCB 1533a-c), it appears to be a variable character. We have photographic records of live *H. amboinensis* specimens from Ambon and Seram that clearly show round nostrils.



**FIGURE 4.** A: The juvenile holotype (NHMUK 1863.12.4.35) of *Istiurus* (= *Hydrosaurus*) *microlophus* Bleeker, 1860 from Makassar, Southwest Sulawesi. Note the groups of enlarged scales on the dorsum. Photo by Patrick D. Campbell. B: The adult male holotype (ZMB 7393) of *Lophura* (= *Hydrosaurus*) *celebensis* Peters, 1872 from the Poso River, Central Sulawesi. Note the very few light enlarged scales on the dorsum. Photo by André Koch.

### Further morphological differences between the relevant type specimens

Apart from the differences stated in the original descriptions (Bleeker 1860, Peters 1872), the type specimens of *I. microlophus* and *L. celebensis* can be distinguished by several other morphological characters. *I. microlophus* has 13 infralabials and 11/12 supralabials (l,r), while *L. celebensis* has 10 infralabials and 9 supralabials. The number of femoral pores is higher in the type of *I. microlophus* (16/15 vs. 6/8, possibly 12 in *L. celebensis* if Peters' count was correct and this character state deteriorated over time). In *I. microlophus* the ventrals are equal to or larger than the dorsals while the ventrals in *L. celebensis* are smaller than the dorsals. In *I. microlophus* the ventral scale row count between the onsets of the extremities (axilla to groin) is 88 (vs. 70 in *L. celebensis*). In addition, they differ in their scalation underneath the fourth and fifth toes. While *I. microlophus* has several rows of flat or singly keeled scales (approx. 40 subdigitals under the fourth toe and 10 under the fifth toe) before the onset of wide, doubly keeled scales, broad, doubly or multiple keeled scales are already present near the base of the toes in *L. celebensis*.

In the literature (see above) both species have so far been considered as conspecific with *H. amboinensis*. However, the molecular phylogenetic study by Siler *et al.* (2014) demonstrated that specimens from Sulawesi are distinct from *H. amboinensis*. We thus compared the type specimens of *L. celebensis* and *I. microlophus* with the holotype of *amboinensis* (NRM 1047, Figure 2).

*H. microlophus* differs from *H. amboinensis* in the following characters: 1. in having groups of strongly enlarged, keeled and sharply pointed scales on the dorsum vs. few enlarged scales on the dorsum in *H. amboinensis*; 2. the dorsum in adult males is dirty yellow with enlarged scales a much darker colour, in adult females dark with enlarged scales whitish vs. greenish, black vermiculated dorsal colouration in *H. amboinensis* (according to original description and observations in live specimens); 3. in the possession of a nasal crest in adult males vs. absence of a nasal crest in *H. amboinensis*; and 4. in having round vs. oval nostrils in the *H. amboinensis* type.

*H. celebensis* differs from *H. amboinensis* in the following characters: 1. in having their ventral scales mostly smaller in size than dorsal scales vs. ventrals much larger than dorsals in *amboinensis*; 2. in the possession of a nasal crest in adult males vs. the absence of a nasal crest in *amboinensis* 3. in their dorsal colouration which in adults is yellow/black spotted vs. greenish, black vermiculated in *amboinensis* and 4. nostrils round vs. oval in the *amboinensis* type.

Main diagnostic morphological differences between *H. microlophus*, *H. celebensis* and *H. amboinensis* (preserved and alive) are listed in Table 1. Based on these morphological differences between the relevant type specimens outlined above we resurrect the taxon names *microlophus* Bleeker, 1860 and *celebensis* Peters, 1872 from the synonymy of *H. amboinensis* (Schlosser, 1768). In accordance with ICZN rules their names are *Hydrosaurus microlophus* (Bleeker, 1860) and *Hydrosaurus celebensis* (Peters, 1872).

**TABLE 1.** Main diagnostic morphological differences between *H. microlophus*, *H. celebensis* and *H. amboinensis*.

	<i>H. amboinensis</i>	<i>H. microlophus</i>	<i>H. celebensis</i>
Nasal crest in males/females	absent/absent	more or less pronounced in both sexes	mostly present/ sometimes present
Enlarged lateral scales in males/female	few (if any), coloured/coloured, slightly keeled, scattered	many, dark/light, strongly keeled, distinct groups	few, light/light, keeled, indistinct groups
Dorsal colour pattern in males	dark and yellow-green vermiculated	dirty yellow, beige	yellowish and dark speckled
Eye colour in males	iris: dark red-brown with white margin, sclera: blue	iris: light grey-blue to dark brown, sclera: dark	iris: light blue, sclera: dark

### Species accounts

#### *Hydrosaurus microlophus* (Bleeker, 1860)

##### Chresonymy:

*Istiurus microlophus* (Bleeker 1860a: 80, 1860b: 85)



*Istiurus amboinensis* (part) (Bleeker 1860b: 85)  
*Lophura amboinensis* (part) (Boulenger 1885: 402; Casto de Elera 1895: 417; de Rooij 1915: 128)  
*Lophura amboinensis* var. *celebensis* (Weber 1890: 160, 167)  
*Hydrosaurus amboinensis* (part) (Wermuth, 1967: 64)

**Type:** Holotype NHMUK 1863.12.4.35, juvenile, collected by P. Bleeker, 1855.

**Type locality:** Makassar (= Ujung Pandang), Southwest Sulawesi, Indonesia (Figure 8).

**Description of holotype:** See above.

**Diagnosis:** Large species exceeding 1000 mm in total length; largest specimen, SMF 35996, SVL = 325mm, TL = 745mm (TL/SVL = 2.29), tip of the tail missing; complete specimen, MZB Lac 5870, SVL 131 mm, TL 315 mm (TL/SVL = 2.4) [Remark: The MVZ database gives 370 mm as tail length]. Head black; sometimes with yellowish colour around the eyes, the same on the lower half of the neck and in front of the shoulders as well as in the gular region; nuchal region black; a group of enlarged conical or pyramidal scales on either side of the neck; nuchal and dorsal crests continuous; in males, the sides of the body are dirty yellow with three groups of enlarged conical or pyramidal scales, often forming a triangular shape, between fore and hindlimbs that decrease in size ventrally to form transverse bands, the largest scales being black in colour; adult females are black with yellow enlarged scales; some females (presumably subadults or non-reproducing specimens) and juveniles typically grey with the groups of enlarged scales being whitish in colour; yellow ventrally, limbs on the upper side black and on the underside yellow (grey in subadults and juveniles); scales under fourth and fifth toes initially flat or singly keeled; tail black with some irregular yellow markings; sail dirty yellow to light brown with black stripes.

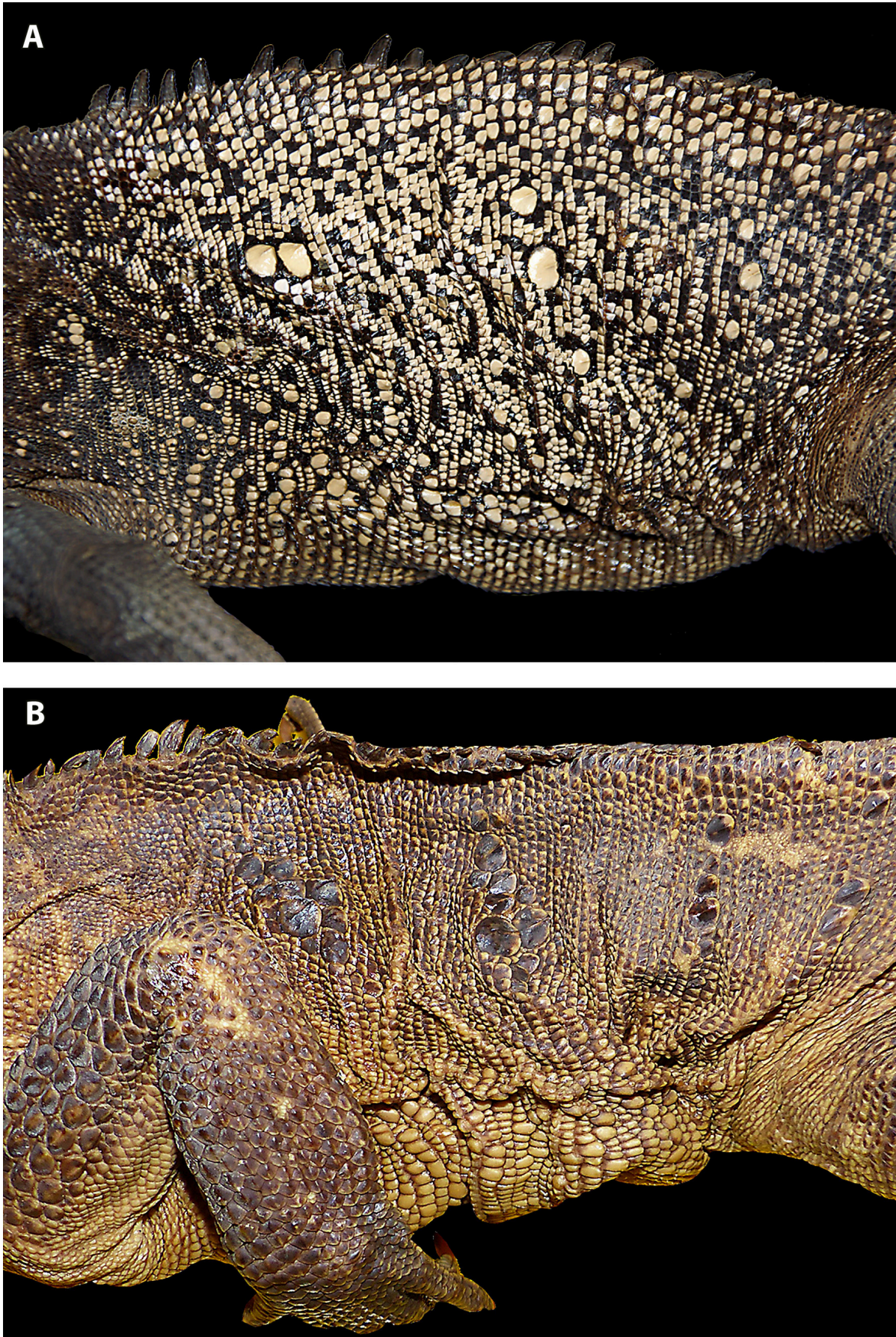
**Allocation of adult museum specimens to *Hydrosaurus microlophus*.** The preserved type material is only represented by a single specimen each. In the case of *H. celebensis* we located additional adult voucher specimens that match the holotype of this species (see Appendix 1). However, we were not able to locate any juvenile specimens that can be assigned unambiguously to *H. celebensis*.

However, in the case of *H. microlophus* the holotype is a juvenile and corresponding adult specimens present in museum collections had to be inferred as belonging to this species following morphological comparison. The main diagnostic characters for assignment of adult specimens to *H. microlophus* is the presence of groups of enlarged, strongly keeled scales dorsolaterally and the highly variable number of enlarged scales on the sides of the neck ( $\geq 3$  up to eleven) as well as their shape and arrangement.

The Senckenberg collection holds three specimens (SMF 35996-98) from Sulawesi without precise locality or collector details. These specimens were received in 1930 from the Zoological Society Frankfurt and determined under the curatorship of Robert Mertens as *H. amboinensis microlophus*. All three specimens agree well with the characters outlined as specific for the *H. microlophus* type (i.e., enlarged dorsal scales in groups, ventral scales equal or larger than dorsal scales, 10/11 supra- and infralabials, respectively). Therefore, we consider the Senckenberg material adult representatives of *H. microlophus* (see also below for a comparison of live specimens). Two of these specimens lack parts of their tails but one has a nearly complete tail (SVL = 325mm, TL = 745mm, with only the tip of the tail missing according to G. Köhler [SMF, pers. comm.], TL/SVL = 2.3). Currently the specimens, although kept in the same jar, are not individually numbered. For clarity we consider the nearly complete specimen as SMF 35996, the specimen measuring SVL = 295mm, TL = 90mm as SMF 35997 and the one measuring SVL = 333mm, TL = 220 mm as SMF 35998. Gaulke (1989) examined these specimens and concluded that they were conspecific with *H. (cf.) pustulatus* unaware that the Philippine populations of *Hydrosaurus* constituted a species complex (Siler *et al.* 2014). A comparison with the juvenile type shows that the enlarged dorsal scales have a much more pronounced keel in adults and that these may exhibit a conical or near pyramidal shape. In the juvenile holotype the enlarged dorsal scales are white while they appear to be brown (SMF 35997), dark brown or black (SMF 35996 and SMF 35998) in the preserved adults. This is in contrast to the black and yellow speckled dorsal colouration in *H. celebensis*. Additionally, the enlarged dorsal scales in *H. celebensis* are typically light coloured or even white. A comparison between the type specimen of *H. celebensis* and an adult *H. microlophus* specimen (SMF 35996) is shown in Figure 5.

Bleeker (1860b) reported specimens from “Boni” as *Istiurus* (= *Hydrosaurus*) *amboinensis*. There is a dried specimen at Naturalis (ZMA 12611) that was previously housed in the collection of the Tropeninstituut Amsterdam, and subsequently transferred to the ZMA collection (now at Naturalis). Boni (or Bone State) was a former sultanate on the east coast of the southwestern arm of Sulawesi near Danau (=Lake) Tempe. The specimen has enlarged conical, near pyramidal scales on either side of the neck and two groups of similar scales on the back. As its dorsal



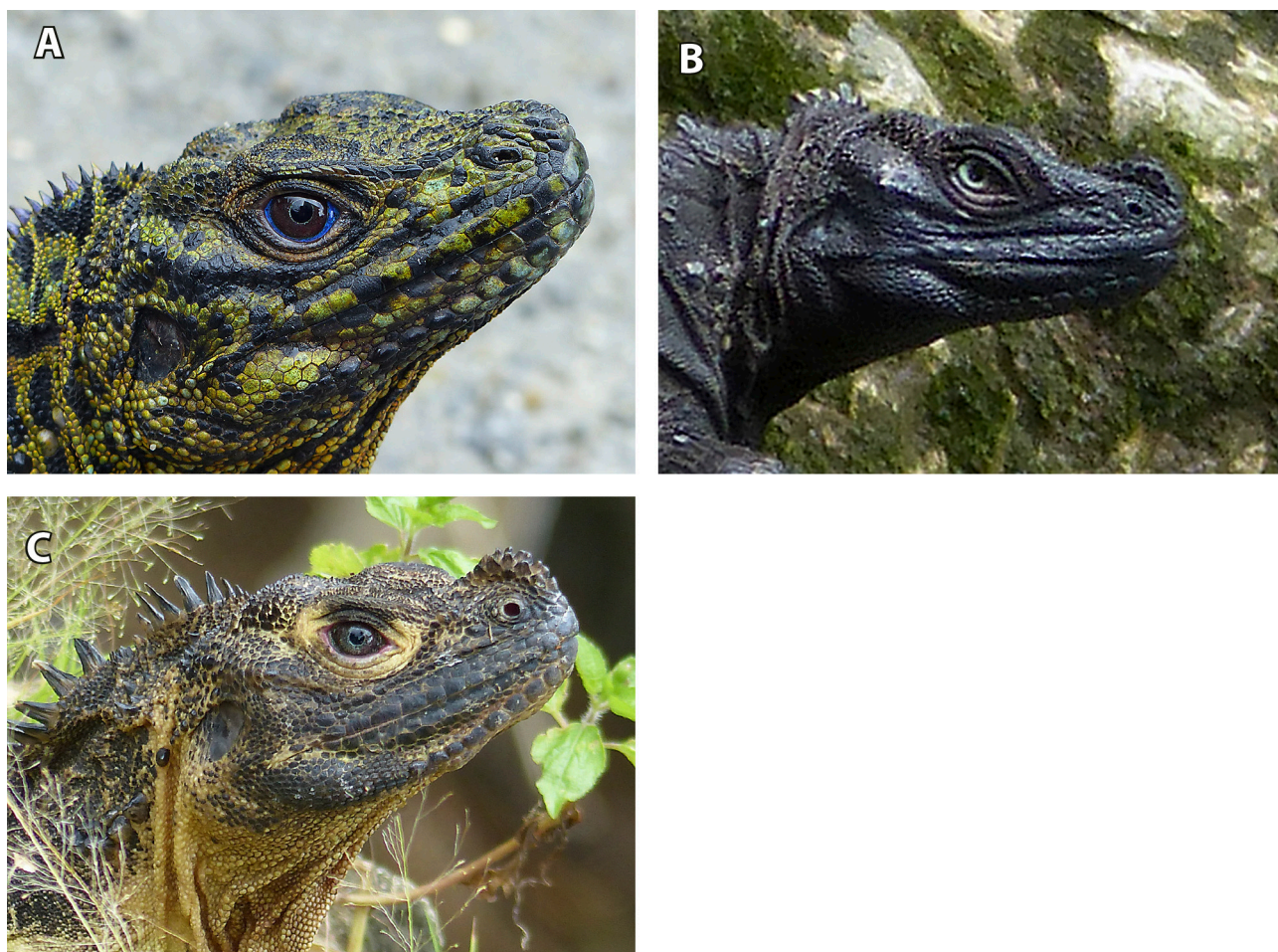


**FIGURE 5.** Comparison of dorsal scalation between the type specimen of *H. celebensis* (A, ZMB 7393) and an adult specimen of *H. microlophus* (B, SMF 35996).



scalation matches that of *H. microlophus* and the locality record falls within the range of this species it should be classified as such.

**Intraspecific Variation:** One variable character is the number of enlarged scales on either side of the neck. The enlarged scales along the neck are sometimes arranged in a single row and sometimes intermixed with slightly smaller ones forming a group (picture collection AGT). The number of enlarged scales varies from three to eleven. The lateral groups of enlarged body scales consist of 10 to 20 scales, with the anterior most group having the highest number of scales. Typically there are three groups of enlarged scales between the fore and hindlimbs. One specimen (picture collection AGT) contains a group of three enlarged scales between the midbody and the onset of the tail group.



**FIGURE 6.** Portraits of male sailfin lizards. A) *H. amboinensis* from Air besar, Ambon B) *H. celebensis* from Pattununang; C) *H. microlophus* from Bengo Bengo. Please note the oval nostril and absence of a nose crest in *H. amboinensis*. Photos by Andrea Glässer-Trobisch & Dietmar Trobisch.

**Sexual dimorphism:** Adult males of *H. microlophus* have a considerably higher dorsal sail and a typically more pronounced nasal crest than do females, although we also observed some females with a well-developed nasal crest. In addition, males and females show a clear sexual dimorphic colouration (dichromatism, see above). Thus, in female specimens the groups of enlarged scales are whitish/yellowish coloured on a dark grey to nearly black dorsal ground colour while male specimens typically show a dirty yellow dorsal colouration with the groups of enlarged scales being black or brown in colour.

**Comparisons:** *H. microlophus* differs from *H. amboinensis* by the possession of the following characters: grossly enlarged scales near the onset of the forelimbs; strongly enlarged conical or pyramidal scales in groups forming dorsolateral bands (all of these characters are either not or only slightly developed in *H. amboinensis*). Furthermore, *H. microlophus* differs from *H. amboinensis* in colouration (yellowish green in male *H. amboinensis* and green in females with black marbling in both sexes vs. dirty yellow dorsal colouration with the groups of enlarged

scales being dark coloured in male *H. microlophus*, plus dark dorsal colouration with the groups of enlarged scales being whitish/yellowish in female *H. microlophus* together with the top of the head and neck being black and the throat being yellow in colour in both sexes) they also possess a nasal crest (absent in *H. amboinensis*, see Figure 6a). Most noticeably, the males of *H. microlophus* differ in their pattern from the males of *H. celebensis* the latter having complete or near complete black heads, limbs and tails. *H. microlophus* differs from *H. weberi* in general colouration and pattern, the latter being grey green. *H. microlophus* differs from *H. celebensis* and *H. weberi* by having groups of enlarged (black in males, white or yellow in females) conical and pyramidal scales on the dorsum. In every case the number of scales in the major groups of enlarged scales is larger than that in *H. celebensis*. In *H. microlophus* the nuchal and dorsal crests are continuous, while they are separated by considerably smaller scales on the neck in *H. weberi*.

**Biology:** *H. microlophus* appears to prefer open freshwater habitats mostly surrounded by high trees. We observed this species mainly on stony or rocky ground. In Bantimurung specimens were seen in a river with large boulders and low vegetation on the banks. Remarkably, this site was near the entrance of the Bantimurung National Park that is highly frequented by many visitors. Some specimens even occurred near a busy building site.

Near Bengo-Bengo six specimens (one male and five females) were observed on a tree. It appeared as if this assemblage had a harem structure with the single male being the dominant individual. According to locals and own observations, individuals living close to human settlements are often seen in trees during the dry season to escape the hunting dogs. In contrast, during the rainy season a more terrestrial behaviour is observed. Individuals or groups of sailfin lizards of different ages are mainly seen on riverbanks and flee into the river when disturbed. We observed several specimens of all age groups living together within a relatively small range especially in the dry season. The semiaquatic habitat was shared with *Varanus togianus*, a potential predator of juvenile *Hydrosaurus*.

**Distribution:** *H. microlophus* is endemic to Sulawesi. It appears to be restricted to Southwest Sulawesi, the bordering southern part of Central Sulawesi and possibly also inhabits parts of West Sulawesi (Figure 8). See also the Discussion below.

### ***Hydrosaurus celebensis* (Peters, 1872)**

#### **Chresonymy:**

*Lophura amboinensis* (Günther 1873: 168)

*Lophura amboinensis* (part) (Boulenger 1885: 402; Meyer 1887: 6; Casto de Elera 1895: 417; de Rooij 1915: 128)

*Lophura amboinensis* var *celebensis* (Weber 1890: 160, 167)

*Hydrosaurus amboinensis* (part) (Wermuth 1967: 64)

*Hydrosaurus* cf. *amboinensis* (Koch 2012: 149)

*Hydrosaurus* sp. [Sulawesi] (Siler *et al.* 2014: 102)

*Hydrosaurus celebensis* (Siler *et al.* 2014: 104)

**Type:** Holotype ZMB 7393, adult male, collected by A. B. Meyer in 1870.

**Type locality:** “Ufer des Flusses von Posso in der Bai von Tomini” (= banks of the Poso river in the Bay of Tomini), Central Sulawesi, Indonesia (Figure 8).

**Description of holotype:** See above.

**Diagnosis:** Large species, exceeding 1000 mm in total length, possibly 1200 mm (assuming TL/SVL = 2.4, a complete tail of holotype amounts to 864 mm); largest specimen examined, holotype SVL 360 mm, TL 580 mm (TL/SVL = 1.61), part of the tail missing; complete specimen, MZB Lac271, SVL 233 mm, TL 563 mm (TL/SVL = 2.42). Head, neck, gular region and shoulder completely black; a row of enlarged flat, sometimes conical scales on either side of the neck; nuchal and dorsal crests continuous; a group of dirty white enlarged flat scales on the anterior part of the dorsum; few (<10) additional enlarged scales approximately at midbody and before the hindlimbs. Dorsal colouration typically yellowish, sometimes dark orange, interspersed with black spots; ventrally beige, limbs black with a few yellow spots; scales under fourth and fifth toes broad with several keels from near the base of the toe; tail black, sail black or dark violet with black stripes.

**Intraspecific Variation:** The number of enlarged scales along the neck varies from three to five. Equally, the number of enlarged scales on the dorsum varies in the anterior group from two to seven. At midbody and near the base of the tail there are typically only one or two enlarged scales. One male from Pattunung had the midbody group split into two groups of two scales giving the impression of a crossband. While the ventral scales in *H. ce-*



*lebensis* are typically smaller than the dorsal scales, a photograph (courtesy of J. McGuire) of the specimen (tissue sample JAM 6859) from Desa Jelaja, Southwest Sulawesi, used in the phylogenetic analysis conducted by Siler *et al.* (2014) shows that the size of the ventral scales appear to be larger than or equal to the size of the dorsal scale size.

**Sexual dimorphism:** Adult males of *H. celebensis* have a considerably higher dorsal sail and a more developed nasal crest than in females. In general, the colouration and pattern is more contrasted in males while females appear to be duller in colour. Typically males of *H. celebensis* are black and yellow (or light orange) spotted whereas in females the spotted pattern is less pronounced consisting of an olive-brown, greyish ground colour with black spots in the Pattunuang population and rather greenish with light spots in the Palopo population. The colour of the head and anterior part of the neck is black in males while it is dark brown or grey with white speckles in females.

**Comparisons:** *Hydrosaurus celebensis* differs from *H. amboinensis* by the possession of the following characters: a group of strongly enlarged, flat scales on the anterior part of the dorsum. The colour on the dorsum is yellowish (vs. yellowish green in male *H. amboinensis* and green in females). Head, limbs and tail of male *H. celebensis* are completely or nearly completely black whereas both sexes in *H. amboinensis* have an entirely black marbled body. Additionally, the gular scales of *H. amboinensis* are round and irregular in size, while those of *H. celebensis* are minute and decreasing in size from the mental towards the onset of the gular pouch. *H. celebensis* differs from *H. weberi* in its general colour and pattern on the dorsum which is yellowish with black dots (vs. grey green in *weberi*). *H. celebensis* differs from *H. weberi* and *H. microlophus* by less pronounced enlarged (i.e. armour-like) scales at the front of the forelimbs. In *H. celebensis* the nuchal and dorsal crests are continuous, while they are separated by considerably smaller scales on the neck in *H. weberi*.

**Biology:** *H. celebensis* was observed in a variety of habitats. In particular, the habitat of *H. celebensis* in the Pattunuang canyon differs from that in Bantimurung and near Palopo. The Pattunuang river is very stony and during the rainy season flows at a rapid pace. Its riverbank vegetation mainly consists of trees and only a few bushes. In Bantimurung specimens of *H. celebensis* were spotted in certain places where *H. microlophus* (see above) was not found. *H. celebensis* inhabited more inaccessible areas with dense vegetation on the banks and was often seen on branches above the water. Near Palopo *H. celebensis* inhabited an area near a slow flowing river without stones or rocks. Most of the individuals were found sitting in dense, low vegetation. Some of the subadults were spotted on thin branches above the water. In some places they were also spotted high up in trees where adults could be seen resting on branches. An adult female carrying eggs could also be observed in Pattunuang towards the end of March.

**Distribution:** *H. celebensis* is endemic to Sulawesi. It appears to inhabit the northern part of South Sulawesi, Central Sulawesi and South East Sulawesi (Figure 8). The populations in Pattunuang and Bantimurung (South Sulawesi) are possibly a result of recent introductions according to a local source (A. Siady Hamzah, Universitas Hasanuddin, Makassar, UNHAS, pers. comm.) and information on the website of the Bantimurung-Bulusaraung National Park by Taufik Ismail (2013). See also the Discussion below.

**Comparison between live specimens of *H. microlophus* and *H. celebensis*.** Based on available photographs of live specimens from Sulawesi both species can be further distinguished by pholidosis, colouration and pattern. While some of the pictured specimens (mostly males) can be directly assigned to *H. celebensis* (Peters, 1872) because they have a near identical appearance to that of the type specimen, others were quite difficult to identify and could only be assigned through inference to *H. microlophus*. In particular, juveniles within the presumed *H. microlophus* populations possess the same arrangements of groups of enlarged dorsal scales as the type specimen. All adults within the same populations also show these characteristic groups of enlarged lateral scales and we therefore consider these specimens as belonging to *H. microlophus*.

Specimens in various developmental stages of *H. microlophus*, were observed near Bantimurung, Bengo-Bengo / Camba and Rompegading on the southwestern peninsula of Sulawesi (Figure 8). Figure 7 depicts a juvenile specimen from Rompegading displaying the characters described by Bleeker (1860). In particular the arrangement, size and shape of the enlarged dorsal scales fit well with the type specimen. Since the adult specimens of the southwestern peninsula differ vastly from both the holotype and live specimens of *H. celebensis*, hence we conclude that they represent *H. microlophus*. Adult males (and most females) from these populations have a much more pronounced scalation on the dorsum. The enlarged scales on the dorsum of the adults are strongly keeled and have a tetrahedral appearance (vs. near flat and only slightly keeled in *H. celebensis*). In males these scales are black in colour and whitish to yellow in females. An additional feature seen in adult *H. microlophus* are the strongly enlarged scales on the anterior part of the forelimbs. This character very much resembles the description by Barbour (1911) for *H. weberi* who compared it to a piece of “armour”. The ground colour of



adult *H. microlophus* males is generally dirty yellow, with the upper parts of the head, extremities and enlarged dorsal scales blackish. The gular region is yellowish. Adult females show a very different colouration (Figure 3F); the general dorsal ground colour is grey to dark grey or nearly black, while the enlarged scales are light. We did not observe or find a preserved adult male specimen with such a colouration nor did we find a female specimen with dark enlarged scales as described above. The colouration of some subadult females is very similar to that observed in juvenile specimens of both sexes (i.e., grey with cream coloured enlarged scales). The change in colour and development of the shape of the scales from one that is less to one that is more pronounced appears to be in line with ontogenetic development since only adult specimens show sexual dichromatism.

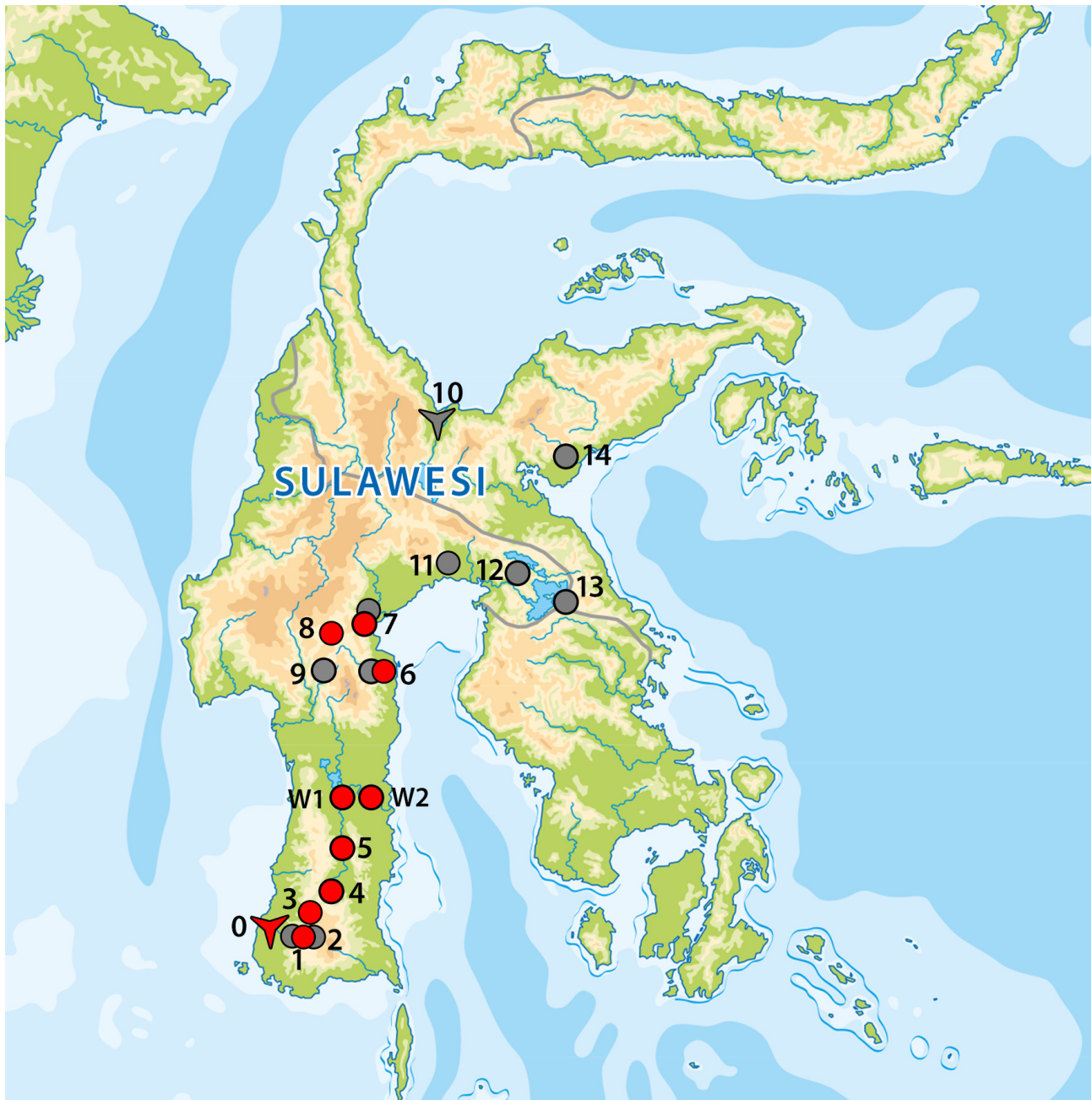


**FIGURE 7.** Juvenile specimen of *H. microlophus* from Rompegading displaying the characters described by Bleeker (1860). Photo by Andrea Glässer-Trobisch & Dietmar Trobisch.

A second distinct phenotype (Figures 3 C & D) was photographed in the south of South Sulawesi (in the valley of the Pattunuang river and in Bantimurung) in the vicinity of a *H. microlophus* population and in the north of the Southwestern peninsula near Palopo (Figure 8). Males of these populations agree completely with the holotype of *H. celebensis* (see Figure 4B). They only have a few enlarged scales interspersed on the dorsum and their dorsal colouration is a pattern which



is black and yellow spotted with white enlarged scales dorsolaterally. This particular colouration was observed during the dry season. During the wet season several males, but not all, displayed an even richer colouration, showing contrasts with the yellow coloured scales switching to a bright orange yellow colour. Head, gular region and extremities were completely black. Typically, females were slightly duller in colouration and less rich in contrast. Unfortunately, we were not able to find a juvenile within these populations that we could refer unambiguously to *H. celebensis*. In both Pattunuang and Palopo where populations of *H. celebensis* were found, almost all juveniles had more or less slightly marked crossbands of enlarged scales. In particular, we found that the juveniles of Pattunuang agreed with the general characteristics described for the type of *H. microlophus*. Both in Pattunuang and Palopo adult *microlophus* have not been observed but in Pattunuang it is probable that they are in contact with *celebensis* because the next localities of *microlophus* are only ca. 7 km (Bantimurung) resp. about 10 km (Bengo-Bengo) away.



**FIGURE 8.** Map of Sulawesi showing the distribution of *H. microlophus* (red) and *H. celebensis* (grey). Type localities are indicated by stars. . 0 Makassar; 1 Bantimurung; 2 Pattunuang; 3 Bengo-Bengo & Rompegading; 4 Camba; 5 Ujung Lamuru; 6 Belopa; 7 Palopo-Pompengan & Palopo-Siguntu; 8 Toraja; 9 Malele; 10 Poso River, Bay of Tomini; 11 Desa Jelaja; 12 Wasp-onda; 13 Desa Limbatu; 14 Morowali Nature Reserve; W1 Tempe („at the Minralang river near Tempe“ after Weber 1890: 167); W2 Pampanua („at Pampanua on the river Tjinrana“ after Weber 1890: 167)

## Discussion

### Species delimitation, sexual dimorphism and potential hybridisation in Sulawesi sailfin lizards

Above we have shown that Sulawesi sailfin lizards are represented by two morphologically different phenotypes. Despite the fact that most meristic values and morphometric ratios overlap, adult specimens are clearly distinguishable and readily identifiable with respect to their phenotypic characteristics. Based on the unified species concept proposed by de Queiroz (2007) we consider both phenotypes to represent distinct species. They constitute separately evolving metapopulation lineages, a notion common to all species concepts. De Queiroz (2007) argued that a range of different secondary properties (so called “lines of evidence”) can be relevant to species delimitation. In the present case the main properties (i.e. operational criteria) are phenetic distinguishability and diagnosability. Although we identified a population in Bantimurung where both phenotypes occur sympatrically (possibly due to human introduction), albeit that they did not share the same habitat and there appears to be a degree of geographical separation. The afore mentioned operational criteria provide evidence in accordance with previously defined species concepts, e.g. the phenetic similarity concept by Sokal and Crovello (1970) or the diagnosability concept by Nixon and Wheeler (1990), but these are not necessary prerequisites for species delimitation under the unified species concept.

Reproductive isolation, the basis of the biological species concept as proposed by Mayr (1942), does not constitute a necessity for species delimitation within the unified species concept (de Queiroz 2007). However, live specimens of *H. microlophus*, and to a certain degree, preserved voucher specimens, are clearly sexually dimorphic with respect to colouration (see above), a feature which is an obvious occurrence, although much less developed in *H. celebensis*. This sexual dichromatism may serve as a recognition mechanism based on visual (i.e. phenotypic) traits. Therefore, we hypothesize that it can potentially serve as a mating barrier between the two species. As such it constitutes an example of reproductive character displacement which supports prezygotic reproductive isolation (Brown & Wilson 1956, Pfennig & Pfennig 2009).

As far as we know, the two predominantly parapatric *Hydrosaurus* species with a presumed common ancestor share the same resources with respect to habitat and diet. They can even be observed sympatrically. In order to prevent hybridization and to preserve a permanently constant gene pool for each of the two partly sympatric species, their phenotypes diverged and a pronounced sexual dichromatism evolved in one of the species. Visual recognition serves as a mating preference discriminator between conspecific and heterospecific partners, with optically enhanced and enlarged scales serving as the visual stimulus. Furthermore, as both species possess femoral glands (pores), we hypothesize that species recognition may also be mediated chemically such that chemoreception serves as a discriminator against heterospecific mating partners.

Museum specimens of adult *Hydrosaurus* specimens from Sulawesi are relatively rare. Specific characters are easy to distinguish in most of the specimens we studied but some characters may prove less consistent as more material becomes available. For example the number and arrangement of enlarged scales along the neck appears to vary considerably between individuals and between populations. Additionally, the strongly keeled scales underneath the toes do not appear to be an invariable feature. We examined one museum specimen (MZB Lac 271) and also had one photo of a live specimen to hand (see below) where unambiguous assignment could be put down to potential character variability or interbreeding between the two species. In Bantimurung we found both species in sympatry. One particular specimen in the Museum Zoologicum Bogoriense collection (MZB Lac271) is an adult male (SVL 233 mm, TL 563 mm, TL/SVL= 2.42) collected in Malele at the northern part of South Sulawesi (Figure 8). At a first glance it matches *H. celebensis* in colouration, the dorsal pattern being brown and white speckled. Additionally, there is only one group of nine enlarged dorsal scales behind the shoulder as opposed to four groups present in adult *H. microlophus* (see e.g. SMF 35996, Figure 5). However, in MZB Lac271 the ventral scales are larger than (or equal to) the dorsal scales, the number of infralabials is 14, and scales underneath the toes and fingers are not strongly keeled. These characters point towards *H. microlophus*. Its collection locality appears to be at the northern distribution limit of *H. microlophus* and falls within the distribution range of *H. celebensis*.

In addition, we took photographs (picture collection AGT) of a male specimen from Pattunuang showing characters present in both species. The general colouration matches that of *H. celebensis*. However, the specimen has groups of enlarged scales on the dorsum that taper into lines dorsolaterally. While the latter character points towards *H. microlophus* it should be noted that the second and third group of enlarged scales are rather light coloured as with *H. celebensis* instead of black or dark brown as is typical for adult *H. microlophus*.



A possible reason for the presence of intermediate character states as observed in the aforementioned specimens could be hybridization between the two recognized species. From observations of captive animals it is known that interbreeding occurs between specimens of *Hydrosaurus* sp. from the Philippines (male) and Sulawesi (female) (S. Corning, website see References). The female exhibited conspicuous groups of enlarged dorsal scales and therefore most probably belonged to *H. microlophus*. Notably, the offspring of this interspecific crossing is fertile and currently the breeding group is in its third generation. Juveniles of the F<sub>3</sub> generation clearly show four groups of enlarged scales between the axilla and the groin and resemble the holotype of *H. microlophus*. In addition, a specimen from Samar Island, Philippines, was considered a possible hybrid between *H. amboinensis* and *H. pustulatus* (J. McGuire pers. comm. in Macey *et al.* 2000) although a recent study by Siler *et al.* (2014) places specimens from Samar into a clade with those from Leyte and Dinagat, which constitute a Pleistocene aggregate island complex (Siler *et al.* 2010). A notable result from the phylogenetic study by Siler *et al.* (2014) is the low genetic diversity within the genus *Hydrosaurus*. Their investigations revealed a low maximum pairwise sequence divergence of only 5.7% among the included specimens originating from the Philippines, Sulawesi and the Moluccas. With respect to specimens originating from Sulawesi it should be noted that the clade containing specimens from Sulawesi is more heterogeneous and shows lower sequence homogeneity than any of the six clades from Philippine populations or that of *H. weberi*.

### Biogeography of Sulawesi Sailfin Lizards

It appears that Sulawesi sailfin lizards do not occur throughout the entire island. Instead both species have restricted distribution ranges. While *H. microlophus* mainly inhabits the southwestern peninsula, *H. celebensis* seems to be restricted to the central part of the island (see Figure 8). Meyer (1887, as *H. amboinensis*) and Supriatna & Hedberg (1998, as *Hydrosaurus* sp.) reported sailfin lizards from the Togian Islands in the Gulf of Tomini approximately 150 km northeast of the type locality for *H. celebensis*. Unfortunately, in both cases no voucher specimens are available for confirmation of these localities. Meyer's material was destroyed in World War II (R. Ernst and U. Fritz, pers. comm.). We consider a record of a *Hydrosaurus* from Manado, at the northern tip of Sulawesi, published by de Rooij (1915, as *H. amboinensis*) as highly questionable as we could not locate any voucher specimens collected from the northern peninsula. Therefore the Togian records currently represent the northern most occurrences of any of the two Sulawesi sailfin lizard species. Since all Sulawesi samples of *Hydrosaurus* sp. used in the study by Siler *et al.* (2014) originated from the central region and the northern part of the southeastern arm of the island they fall within the range of *H. celebensis*. At least one specimen (JAM 6859, see above) shows a high resemblance to *H. celebensis* as confirmed by photographs. Two juvenile specimens (JAM 6911 and 6955) used in the phylogenetic study lack the dorsolateral groups of enlarged scales (J. McGuire, pers. comm.) typical for *H. microlophus* and therefore probably represent juveniles of *H. celebensis*. Unfortunately, samples from the range of *H. microlophus* on the southwestern peninsula were not available for phylogenetic study.

Notably, Buton, the largest satellite island of Sulawesi located only a few kilometres off the shore of the southeastern peninsula seemed to lack any *Hydrosaurus* populations (Gillespie *et al.* 2005, 2015; B. Lardner, pers. comm., but see de Rooij 1915), whereas the Talaud Islands located in the very north of Sulawesi towards the Philippines are inhabited by sailfin lizards. De Jong (1928) reported *H. amboinensis* from Karakelong, the largest island of the group, while Koch *et al.* (2009) recently assigned a juvenile from neighbouring Salibabu Island (MZB Lac5081) to *Hydrosaurus* sp. due to the unresolved taxonomy of this lizard group. The latter authors mentioned that the specimen resembles a juvenile *H. pustulatus* from Panay Island in the central Philippines in colour pattern and scalation (Gaulke 2011). It also showed, however, a high similarity with *H. weberi* from Halmahera. Another photographic voucher (courtesy Nathanael Maury) shows a colourful adult male specimen from Salibabu, which exhibits a black head and a dorsal pattern rich in contrast, consisting of black and greenish-blue marbling turning orange towards the ventral side with single interspersed enlarged light blue scales laterally. In general, the herpetofauna of the Talaud Islands much more resembles that of Halmahera in the Northern Moluccas than either Sulawesi or the Philippines. Thus, several Australopapuan species (or species groups) of amphibians and reptiles, such as *Litoria infrafronata*, *Candoia paulsoni*, *Nactus pelagicus*, *Eugongylus rufescens*, and *Lipinia noctua* have their most north-western occurrences on that island group (Koch *et al.* 2009).

As the taxonomy of Philippine sailfin lizards is still unresolved, Sulawesi is currently the only island within the distribution range of sailfin lizards known to be inhabited by more than one species of these enigmatic agamid lizards. Though it seems unusual, several other vertebrate species from Sulawesi show similar species diversity and

distribution patterns as mentioned above. There are, for instance, seven different species of macaques occupying parapatric distribution ranges on mainland Sulawesi (Evans *et al.* 2003). Among Sulawesi reptiles, the flying lizards of the agamid genus *Draco* are represented by three parapatric species: *D. walkeri* inhabiting the southwestern peninsula and parts of central Sulawesi, *D. spilonotus* found on the northern peninsula reaching the west coast of the central part of the island, and *D. beccarii* which occupies the southeastern and eastern peninsulas, respectively (McGuire *et al.* 2007).

In general and when compared to the neighbouring Greater Sunda Islands, Sulawesi is relatively poor in species (Whitten *et al.* 2002) richness due to millions of years of long spatial isolation caused by deep ocean trenches surrounding the island (Hall 2012). Nonetheless, Sulawesi harbours a high percentage of endemic species including agamid lizards (Koch 2012). Only three agamid genera inhabit the island naturally (i.e., *Bronchocela*, *Draco*, and *Hydrosaurus*), a fourth (*Hypsilurus*) is known only from a photograph from the northern peninsula but its record can probably be considered an error (Manthey & Denzer, unpubl.) *Calotes versicolor* has been found in Palu in Central Sulawesi (A. Riyanto, pers. comm., MZB), but it has to be considered an introduced species. Thus, mainland Sulawesi is inhabited by only eight (perhaps nine) agamid species in total, six of which are endemics (i.e. 75 %).

## Conclusions and Outlook

Our study represents a good example of voucher specimen-based taxonomy in conjunction with photographic records of living specimens from their natural habitats in order to clarify the composite nature of an allegedly well-known species. Based on pictures of two different phenotypes of Sulawesi sailfin lizards, the direct comparison with historical type material revealed that they had already been recognized and described about 150 years ago. However, the subsequent synonymisation with *H. amboinensis* by two prominent scientists, namely Günther (1873) and Boulenger (1885), was uncritically adopted, thus obscuring the actual species diversity of these charismatic agamids for many decades.

While we are confident that the adults of *H. microlophus* as defined above are representatives of this species, it is still necessary to collect another juvenile specimen mirroring the type of *H. microlophus* as well as an adult from the same population, or at the very least possible to collect tissue samples from such individuals. This would allow for a comparison with the juvenile *H. microlophus* specimen from South Sulawesi (MZB Lac5870 [voucher specimen], MVZ 268131 [tissue sample]) and in addition, allow for a thorough molecular biological investigation in order to investigate their relationship to the material already available from the study of Siler *et al.* (2014). Furthermore, collecting a juvenile specimen from a population that clearly belongs to *H. celebensis* as defined in this paper, would prove highly worthwhile. Similarly, no sequences exist that can be unambiguously assigned to *H. amboinensis* from Ambon Island, the type locality.

Unfortunately, we were unable to unequivocally locate a type specimen of *Hydrosaurus pustulatus* (Eschscholtz, 1829). In order to conduct further taxonomic studies regarding the Philippine populations of *Hydrosaurus* and their phylogenetic relationships to non-Philippine sailfin lizards it will be necessary to designate a neotype from the type locality Luzon. Although historical material from Eschscholtz and Meyen is available in the ZMB collection we refrain from designating either of these specimens as a neotype, since modern phylogenetic analyses rely to a large degree on gene sequences. A more viable solution would be to designate a recently collected specimen from Luzon that shows characters identical to those given in the original description and for which tissue samples can be made available for molecular biological studies. Therefore, a neotype designation for *H. pustulatus* should also include the subsequent deposition of gene sequences in GenBank.

In conclusion, our systematic investigation brings the number of recognized species within the genus *Hydrosaurus* to five. At the same time, we underline the necessity for future taxonomic revisions of the sailfin lizard populations of the Philippines, the Moluccas, and New Guinea.

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## APPENDIX 1.

### Material examined:

#### *Hydrosaurus microlophus* (7 specimens):

NHMUK 1863.12.4.35 (Holotype), Makassar (= Ujung Pandang), Southwest Sulawesi, Indonesia, collected by P. Bleeker, 1855; MZB Lac5870 voucher specimen (field number JAM 5814, tissue sample MVZ 268131), Desa Pecinong, Sungai (= river) Kasingkang, near Danau (= lake) Tempe, Southwest Sulawesi, coll. J. McGuire, 26. Oct. 2006; ZMH R08618 (formerly ZMH 4207), “Celebes”, don. Hans Rosenberg, 1935; ZMA 12611, Boni, Southwest Sulawesi, coll. P. Bleeker; SMF 35996-98, Sulawesi without precise locality or collector details, Zoological Society Frankfurt, 1930.

#### *Hydrosaurus celebensis* (4 specimens):

ZMB 7393 (Holotype), near Poso river, Central Sulawesi (for details see above); MZB Lac271, “Malele”, Sulawesi, unknown collector; ZMH R08619 (formerly ZMH 1387), “Celebes”, don. Hans Rosenberg, Nov. 1934; NHMUK 1849.3.2.36, “Celebes”, purchased from Mr. Frank, London.

#### *Hydrosaurus amboinensis* (17 specimens):

NRM 1047 (Holotype), Ambon, Moluccas, prior to 1768, collector unknown; MZB Lac1533a-c, 3 specimens, Waai, Ambon, Moluccas, 1959, coll. A.M.R. Wegener; MNHN 2532, “Ambon”, collector unknown; MNHN 7373, Ambon, Moluccas, coll. Labillardière; MNHN 7374, Ambon, Moluccas, coll. Labillardière; ZMH R08620, Ambon, Moluccas, collector unknown; ZFMK 66305, Ceram, Moluccas, coll. H. Kotter; ZMB 4849, Ambon, Moluccas, coll. von Martens; ZMB 24855, Dutch New Guinea, coll. Moszkowski; ZMB 24856, Dutch New Guinea, coll. Moszkowski; ZMB 24871, Dutch New Guinea, coll. Moszkowski; ZMB 26452, Dutch New Guinea, coll. Moszkowski; ZMB 28415, Dutch New Guinea, coll. Moszkowski; NHMUK 1920.8.9.3, Ceram, Moluccas, coll. Pratt Brothers.; NHMUK xxiv.37a, Ambon, Moluccas, don. Leyden Museum.

#### *Hydrosaurus* sp. (7 specimens):

NRM 1049, “probably Jakarta area” doubtful, coll. C. F. Hornstedt, 1783-84; NRM 6845 (formerly NRM 1048), “probably Jakarta area” in error, coll. C. F. Hornstedt, 1783-84; MZB Lac5081 (field number AK049), Lirung, Salibabu Island, Talaud Islands, coll. A. Koch, 15.07.2005; NHMUK 1866.8.14.273, unknown locality, purchased from Mr. Damon; NHMUK 1946.8.11.61 (formerly NHMUK xxiv36a, holotype of *Lophura shawii* Gray, 1845), unknown locality and collector; RMNH RENA25937, “Indonesia”, unknown collector; RMNH RENA25938, “Indonesia”, unknown collector.

#### *Hydrosaurus weberi* (4 specimens):

ZMH R8621 (formerly ZMH 2707), Bacan, Moluccas, coll. Warburg; MZB field number BJE1135, Halmahera, coll. A. Hamidy, July 2006; MZB field number BJE1192, Halmahera, coll. A. Hamidy, July 2006; SMF 10385, Bacan, Moluccas, coll. W. Kükenenthal, Jan. 1895. Further specimens taken into account but not examined: MCZ holotype and paratype; RMNH. RENA 25939, RMNH.RENA 25941 from Bacan.

#### *Hydrosaurus pustulatus* s.l. (12 specimens):

ZSM 487/79, “Philippines”, collector unknown; ZSM 1021-2001, West Cebu, Kawasan Falls, Philippines, coll. M. Gaulke, 04.03.2001; NRM 3809, Cebu, Philippines, coll. D. Sjölander, 1923; MNHN 5866, Mindanao, Philippines, coll. Montano-Ray, 1881; MNHN 5811, “Philippines”, coll. Gerrard, 1878; ZMB 678, Manila, Luzon, Philippines, coll. Meyen; ZMB 4181, village Daraga, Luzon, Philippines, coll. F. Jagor; ZMB 66245, Luzon, Philippines, coll. J. F. Eschscholtz; NHMUK 1877.12.13.2, South Negros Island, Philippines, coll. A. Everett; NHMUK 1877.12.13.1, Placer, Mindanao Island, Philippines, coll. A. Everett; NHMUK 1872.8.20.24, Luzon, Philippines, coll. A. B. Meyer; NHMUK 1877.10.9.1, Dinagat Island, Philippines, coll. A. Everett.