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Lophyrus spinosus C. Duméril & A. Duméril, 1851, a case of mistaken identity

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Abstract

Lophyrus spinosus Duméril & Duméril, 1851 has been considered synonymous with *Bronchocela marmorata* Gray, 1845 since its original description. The name-bearing type of *Lophyrus spinosus* is the specimen collected by Hombron and Jacquinot (MNHN 6896) by original designation and the holotype by monotypy of *Bronchocela marmorata* is the specimen deposited under NHMUK 1946.8.11.16. Accordingly, these two scientific names do not share name-bearing types. Prior to the original descriptions of *Lophyrus spinosus* and *Bronchocela marmorata* Hombron & Jacquinot (1843) published a plate depicting *Lophyrus spinosus*, but only naming the species in French. The nomenclatural implications of this publication are discussed.

Our comparison of the holotypes reveals that these two species are not identical. Therefore we resurrect *Lophyrus spinosus* from its synonymy with *Bronchocela marmorata* and show that the specimen collected by Hombron and Jacquinot actually belongs to the genus *Hypsilurus*. Duméril and Duméril (1851) were the first to make the name *Lophyrus* (= *Hypsilurus*) *spinosus* available and the authorship has to be assigned to them. Based on evidence from original travel reports and biogeography we propose that the collection locality of *Lophyrus spinosus*, i.e. *Hypsilurus spinosus* Duméril & Duméril (1851), should be corrected to Triton Bay, Kaimana, West Papua, Indonesia.

Key Words

Lophyrus spinosus, *Bronchocela marmorata*, synomymy, taxon resurrection, *Hypsilurus spinosus* comb. nov.

Introduction

Duméril and Duméril (1851: 91–92) described a new lizard *Lophyrus spinosus* based on a single specimen that had been collected during the expedition of the corvettes L'Astrolabe and La Zélée to Oceania and the South Pole. The expedition had lasted from 7th September 1837 until 6th November 1840. All specimens collected during the Astrolabe expeditions were assigned to Hombron & Jacquinot in the introduction of a treatise of the reptiles and fishes by Jacquinot and Guichenot (1853). *Lophyrus spinosus* had been illustrated and named in French on Plate 3 in Hombron and Jacquinot (1842–1854), a collection of plates (atlas) depicting some of the animals encountered during their voyage. The plates were distributed in 28 parts (livraisons) over a period of 12 years and the plate depicting *Lophyrus spinosus* had been published in 1843 according to the wrappers of the livraisons held by the British Library (Clark and Crosnier 2000). Consequently in their description Duméril and Duméril (1851) did not use "nobis" behind the name (which would indicate the description is theirs) but wrote instead: "L. [Lophyre / *Lophyrus*] épineux *Spinosus* Hombron et Jacquinot (*Voy. au pôle sud et dans l'Océanie*

sur les corvettes l'Astrolabe et la Zélée, *Rept*., pl. 3, sans texte)". The next line quotes the description by Gray (1845) of "*Bronchocela marmorata* Gray, *Cat. of Liz*., p. 242". These lines appear before the description of the species and have several nomenclatural implications. Firstly, Hombron and Jacquinot were the collectors of the specimen and probably took notes collated into a manuscript during their journey because Duméril and Duméril (1851) as well as Jacquinot and Guichenot (1853) referred to these notes. As stated by Jacquinot and Guichenot (1853: 1), in their manuscript Hombron and Jacquinot already proposed ("imposé") names for the specimens collected. But the manuscript was never published and therefore no name was made available in accordance with the Code of the International Commission on Zoological Nomenclature (ICZN 1999, in the following text "the *Code*"). The only published document concerning *Lophyrus spinosus* was the plate "Sauriens pl. 3" within the atlas published by Hombron and Jacquinot (1842–1854), a figure using the French name "Lophyre épineux". No Latin scientific name was given and the French name is not available under the rules of the *Code*. The first valid publication, making the name *Lophyrus spinosus* available for nomenclatural purposes, was authored by Duméril and Duméril (1851: 91). Consequently the authorship for the taxon has to be assigned to Duméril and Duméril (1851). Secondly Duméril and Duméril (1851) appear to have considered *Lophyrus spinosus* conspecific with *Bronchocela marmorata* Gray, 1845. And in fact already Gray (1845: 242) cited Plate 3 of Hombron and Jacquinot (1843) when describing *Bronchocela marmorata.* However, Gray (1845) had doubts -indicated by a question mark- to allocate the specimen figured by Hombron and Jacquinot (1843) to his new species. Thus the single specimen of *Lophyrus spinosus* does not constitute a name-bearing type of *Bronchocela marmorata* according to Article 72.4.1 of the *Code* and we can assume that Gray's name was created based on a single specimen, namely the holotype (NHMUK 1946.8.11.16) by monotypy.

While the plate depicting *L. spinosus* was already published in 1843, the publication of the text volume was delayed for another ten years, and finally Jacquinot and Guichenot (1853) stated the following in their account: "mais dont plusieurs d'entre elles [species] cependant étaient entièrement nouvelles pour la science, à l'époque ou elles ont été déposées dans les collections du Muséum de Paris (fevrier 1841)" [but several of them, however, were entirely new to science, at the time when they were deposited in the collections of the Paris Museum (February 1841)]. As the plate of *Lophyrus spinosus* had been published in 1843 and the specimen as well as the notes of Hombron and Jacquinot were most certainly available already in 1841, Duméril and Duméril (1851) gave nomenclatural priority to Hombron and Jacquinot (1843) and treated *Bronchocela marmorata* Gray, 1845 as a junior subjective synonym. This nomenclatural action has been wrongly considered as a nomen substitutum pro *Bronchocela marmorata* by subsequent herpetologists (see for example Wermuth 1967; Hallermann 2005).

The name-bearing type of *Lophyrus spinosus* is the specimen collected by Hombron and Jacquinot, MNHN 6896, by original designation as "type" and the holotype of *Bronchocela marmorata* must be considered a paratype as Duméril and Duméril (1851) refer to this specimen when creating the name. Thus these two scientific names do not share name-bearing types. However, by considering the two holotypes as belonging to the same species (Duméril and Duméril 1851), in this case *Lophyrus spinosus* Duméril & Duméril, 1851 effectively becomes a junior subjective synonym of *Bronchocela marmorata* Gray, 1845 on grounds of priority as Gray's description was published first. This view has been the opinion of generations of herpetologists for over 150 years. The main reason for this is probably that the type specimen of *Lophyrus spinosus* was purportedly from Zamboanga, Mindanao, Philippines where *Bronchocela marmorata* was thought to occur. Already Taylor (1922) questioned whether *Bronchocela marmorata* actually inhabits Mindanao and he did not include *L. spinosus* in his synonymy of *Bronchocela marmorata*. No herpetologist appears to have looked at the actual specimen or the illustration on which the description of *L. spinosus* was based.

Only Hallermann (2005) in his review of the genus *Bronchocela* Kaup, 1827 doubted that *Lophyrus spinosus* Duméril & Duméril, 1851 is conspecific with *Bronchocela marmorata* Gray, 1845 and stated that *Lophyrus spinosus* "is in fact a *Gonocephalus sophiae* (Gray, 1845)". Unfortunately Hallermann (2005) did not communicate how he arrived at his conclusion or provided evidence that would corroborate his identification of the *spinosus* holotype as *Gonocephalus sophiae*. His main reasons for the identification were actually based on an examination of the holotype of *L. spinosus*. The specimen was clearly not a member of the genus *Bronchocela* but had the general appearance of an anglehead lizard of the genus *Gonocephalus* Kaup, 1825. Additionally he was misled by the assumption that the type locality of *L. spinosus* was on Mindanao, Philippines. This combined only left one conclusion, namely to consider the specimen as *Gonocephalus sophiae*.

Recently, one of us (WD) came across the original plate (Figure 1) that served as the template for the colour description of *Lophyrus spinosus*. We re-evaluated the original description by Duméril and Duméril (1851) and compared it to the image it was referring to and conclude that the specimen described by Duméril and Duméril (1851) is neither *Bronchocela marmorata* nor *Gonocephalus sophiae*, but has rather the appearance of a New Guinean anglehead lizard, namely *Hypsilurus auritus* (Meyer, 1874).

In order to evaluate the taxonomic status of *Lophyrus spinosus* Duméril & Duméril, 1851 we studied museum specimens including the type specimens of *Gonocephalus sophiae* and *Hypsilurus auritus* and compared the respective data to those of the holotype of *Lophyrus spinosus*.

Figure 1. The original plate depicting *Lophyrus spinosus* as published in 1843.

Material and methods

Meristic and morphometric data were recorded from type specimens and additional material mentioned in the text. 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, d_{tymp}: diameter of the tympanum, d_{eye}: diameter of the eye.

Collection acronyms are as follows: **MNHN** – Muséum National d'Histoire Naturelle, Paris, France; **MTKD** – Museum für Tierkunde Dresden, now Senckenberg Naturhistorische Sammlungen Dresden (**SNSD**); **NHMUK** – Natural History Museum, London, formerly **BMNH** – British Museum (Natural History); **ZMB** – Zoologisches Museum Berlin, now Museum für Naturkunde – Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany; and **ZSM** – Zoologische Staatssammlung München, Germany.

Results

In his review of the genus *Bronchocela* Hallermann (2005) stated that *Lophyrus spinosus* Duméril & Duméril, 1851 does not represent *Bronchocela marmorata* Gray, 1845, but that it is conspecific with *Gonocephalus sophiae* (Gray, 1845). However, a comparison of the morphometric data reported by Boulenger (1885) for the syntypes of *Gonocephalus sophiae* (NHMUK 1946.8.27.10–15, incl. *sophiae* and syntypes of its synonym *petersi*) and the holotype of *Lophyrus spinosus* (MNHN 6896, data from Brygoo (1988) and our measurements) already rules out this identification. *G. sophiae* hardly ever grows larger than a total length of 350 mm. Boulenger (1885) gives measurements for the largest specimen as follows: total length 326 mm, head 33 mm, body 78 mm and tail 215 mm. Not only is *G. sophiae* clearly smaller and differing from the measurements of the holotype of *L. spinosus* (total length 565 mm, head 35 mm, body 105 mm and tail 425 mm [our measurements]; Brygoo (1988) reports 575 mm total length and 420 as the tail length), the species also differ greatly in the ratio of tail length to snout-vent length, i.e. *G. sophiae* TL/SVL = 1.94 (largest male specimen of the syntype series) and *L. spinosus* TL/SVL = 3.04 (male holotype).

In their original description of *Lophyrus spinosus* Duméril and Duméril (1851) stated the following (our translation) "On the temple, before the enlarged scales situated behind the eye, there exists an elliptical plane, ... of which the anterior part is [surrounds] the tympanum. It [the ellipse] is bordered by a double row of scales that are considerably larger [than the surrounding scales] and approximately the same size as the postocular scales... The general colour is grey on the underside and reddish on the back and the flanks; the sides of the head and neck are near brick-red, as well as the broad rings on the tail, in alternation with irregular grey rings; the fingers and the edge of the throat fan are green-yellowish". The colour description clearly refers to Plate 3 in Hombron and Jacquinot (1843) [see Figure 1].

More importantly there is one specific character given in the description of Duméril and Duméril (1851) that does neither fit *Bronchocela marmorata* nor *Gonocephalus sophiae*, i. e. the elliptical ring surrounding the tympanic area. As far as we are aware there is only one species of agamid lizard that shows this character, namely *Hypsilurus auritus* (Meyer, 1874). Meyer (1874) described *Gonyocephalus* (*Hypsilurus*) *auritus* based on five syntypes, that were deposited in the collection of the Dresden Museum (MTKD 398, 400–402) and in Berlin (ZMB 8782). Three of the original specimens (MTKD 398, 401–2) were destroyed during World War II. One specimen (MTKD 400) had been exchanged with a museum that could not be identified as the handwriting on the note was illegible and the specimen was therefore presumed lost by Manthey and Denzer (2006). Consequently these authors considered the only remaining specimen (ZMB 8782) as the holotype. However, this is not a valid nomenclatural act according to the *Code* as the name was based on a series of syntypes and this fact cannot be changed after the original publication unless a lectotype is designated. The label of the specimen (ZMB 8782) stated that it had been collected on Jobi [Yapen Island, West Papua, Indonesia] which was accordingly cited as the type locality by Manthey and Denzer (2006). Later Franzen and Glaw (2007) discovered a specimen (ZSM 187/1913) in the Munich collection that had been collected by Meyer in "Doré, westl. Neuguinea" [Manokwari, Indonesia] and was still bearing the original MTKD number "400". A re-inspection of the handwritten catalogue of the MTKD revealed that the note reads: "abgegeben an Zool. Mus. des bay. Staates im Tausch" (exchanged with Zool. Mus. of the Bavarian State), nowadays Zoologische Staatssammlung München. Under these circumstances the potential "holotype" status of the Berlin specimen cannot be held up and ZMB 8782 as well as ZSM 187/1913 have to be considered as syntypes. Additionally to the type locality "Yapen Island" given by Manthey and Denzer (2006) must be added the origin of the Munich specimen collected on mainland New Guinea. Both Yapen Island and Manokwari lie within the Geelvink Bay (Cenderawasih Bay) area and consequently constitute the type localities (symprotonymotope) for *Hypsilurus auritus*. The type locality encompasses both places, Yapen Island and Manokwari in Cenderawasih Bay as long as no lectotype is designated (see Frétey et al. 2018 for different categories of type localities, their precision and restriction).

Meyer's (1874) original description was rather short and read as follows (our translation):

"Related to the preceding species [*Gonyocephalus* (*Hypsilurus*) *binotatus*], but much smaller. Crest hardly interrupted, low. A black mark on the sides of the head that encircles the ear. No large plates below the tympanum. Gular pouch large, covered with small keeled scales." The reference to *Hypsilurus binotatus* was presumably made because of the dark coloured mark on ei-

ther side of the neck. Otherwise the similarity between these two species is rather low.

Further and more detailed descriptions of *Hypsilurus auritus* can be found in Peters and Doria (1878, in Italian, as *Gonyocephalus* [*Arua*] *auritus*) and in Manthey and Denzer (2006, 2016). Manthey and Denzer (2006) described the elliptical ring around the tympanum as consisting of slightly enlarged scales and used this character to differentiate between *Hypsilurus auritus* and all other species of the genus. The aforementioned descriptions by Peters and Doria (1878) and Manthey and Denzer (2006, 2016) agree well with the description of *Lophyrus spinosus* given by Duméril and Duméril (1851) and could be referred equally to both *Lophyrus spinosus* and *Gonyocephalus* (*Arua*) *auritus*.

Consequently, we compared the description and illustration as well as the holotype of *Lophyrus spinosus* (MNHN 6896, male) (Figure 2) to the syntypes of *H. auritus* (ZMB 8782, male; ZSM 187/1913, sex undetermined) (Figure 3) in order to clarify the taxonomic status of *Lophyrus spinosus*. Although all three specimens are similar in their general appearance and in having an ellipsoid of enlarged scales around the tympanum we found differences with respect to several characters (see Table 1).

The morphometric data of *L. spinosus* also differ from those that have been reported for *H. auritus* specimens. Urban (1977, unpubl. PhD thesis) examined 45 *auritus* specimens (27 males, 18 females) and recorded a maximum SVL of 130 mm (vs. 140 mm in *spinosus*) and a maximum TL of 390 mm (vs. 425 mm in *spinosus*). The tympanum / eye ratio in *auritus* was given as 1 (vs. smaller than 1 [0.6–0.76] in *spinosus*: right side d_{tymp} 5.0 mm, d_{eye} 6.6 mm / ratio ~ 0.76, left side d_{tymp} 4.5 mm, d_{eye} 7.5 mm / ratio = 0.6). With respect to *auritus* Urban (1977) characterized the shape of nuchal crest scales as triangular and equal in size to that of the diameter of the eye (vs. lanceolate and larger than the diameter of the eye in *spinosus*).

Furthermore the colouration of the *L. spinosus* holotype is different from that of the two known type specimens of *H. auritus* (see Figures 2, 3). This may be partly a result of preservation, but – if considered in conjunction with the colour description by Duméril and Duméril (1851) and the accompanying illustration by Hombron and Jacquinot (1843) – the type specimens of *H. auritus* will probably not have displayed a colouration similar to that of *L. spinosus*. All live specimens of *H. auritus* known so far have been described as "dorsally predominantly green with a brown or turquoise shadings" (see Manthey and Denzer 2016). This shadings or mottling can still be seen in both syntypes of *H. auritus* (Figure 3) but is not observed in

Figure 2. Holotype of *Lophyrus spinosus* Duméril & Duméril, 1851, valid as *Hypsilurus spinosus* comb. nov. (MNHN 6896).

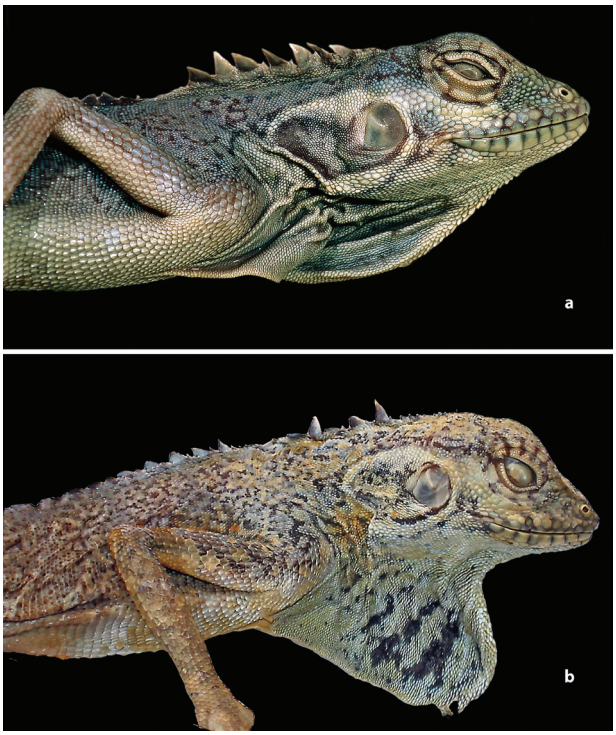

Figure 3. a Syntype 1 of *Hypsilurus auritus* (ZMB 8782) **b** Syntype 2 of *Hypsilurus auritus* (ZSM 187/1913).

Table 1. Scale characters differentiating the holotype of *Lophyrus spinosus* from the syntypes of *Hypsilurus auritus*.

Character	*Lophyrus spinosus*	*Hypsilurus auritus*
Number of scales between nasal and first supralabial	Three	Single
Size of enlarged scales adjacent to the infralabials	Equal in size until approx. $6^{th}/7^{th}$ infralabial scale	Decreasing in size, largest adjacent to the 1^{st} infralabial scale
Shape of scale of nuchal	Lanceolate, longer than the diameter of the tympanum	Triangular, smaller than the diameter of the tympanum
Size of first dorsal crest scales	Nearly equal in size to the ones of the nuchal crest	Smaller than largest nuchal crest scale
Shape of scales of dorsal crest	Lanceolate and backward curved; initially larger or as large as the diameter of the tympanum	Triangular, much smaller than the diameter of the tympanum

the holotype of *L. spinosus* nor shown on the original illustration of Hombron and Jacquinot (1843).

Although the illustration of *L. spinosus* is pretty detailed and clearly depicting the actual type there is one character that could not be verified and may be down to the artist's impression; the illustrated specimen has nuchal and dorsal crest continuous, however the type does not. We examined the type for a possible loss of crest scales on the neck and concluded that no scales are missing and therefore nuchal and dorsal crest have to be considered as interrupted.

As a result of our research we remove *Lophyrus spinosus* Duméril & Duméril, 1851 from its synonymy with *Bronchocela marmorata* Gray, 1845. Furthermore we resurrect *L. spinosus* to full species status to which the name *Hypsilurus spinosus* (Duméril & Duméril, 1851) should be applied. Based on our comparisons with respect to the type material we conclude that *Hypsilurus spinosus* and *Hypsilurus auritus* (Meyer, 1874) are not conspecific and should be considered as distinct species

Given the "nomenclatural rollercoaster" *Lophyrus spinosus* went through, we present a short list of synonyms and chresonyms as follows:

Hypsilurus spinosus (Duméril & Duméril, 1851), new combination

Lophyre épineux – Hombron and Jacquinot 1843: table 3.

Bronchocela marmorata – Gray, 1845: 242. Comment: when describing *Bronchocela marmorata*, the specimen figured by Hombron and Jacquinot is cited by Gray (1845) with a question mark expressing the doubt of the author; hence it should not be considered to be a syntype (see Article 72.4. of the Code).

Lophyrus spinosus – Duméril & Duméril, 1851: 91. Name-bearing type: MNHN 6896, holotype by original designation as "type". Type-locality: "Zamboanga, Mindanao, Philippines"; apparently in error considering the distribution of *Hypsilurus*; probably "Triton Bay, New Guinea".

Calotes marmoratus – Boulenger, 1885: 318 (partim). Comment: Boulenger (1885) following Gray (1845) cites Plate 3 of Hombron and Jacquinot and *Lophyrus spinosus* in the synonymy of *Calotes marmoratus*, preceded by a question mark.

Calotes marmoratus marmoratus – Brygoo 1988: 45.

Gonocephalus sophiae – Hallermann 2005: 173.

Discussion

Hypsilurus spinosus belongs to the *H. nigrigularis* species group of as defined by Manthey and Denzer (2006). All members of this group (*H. nigrigularis* [Meyer, 1874], *H. geelvinkianus* [Peters & Doria, 1878], *H. auritus* and *H. spinosus*) are only known to be distributed in the western part of New Guinea as well as adjacent islands (and some questionable localities on the eastern part of New Guinea; see below). The type locality of *Lophyrus* (now *Hypsilurus*) *spinosus* (Zamboanga, Mindanao, Philippines) reported by Duméril and Duméril (1851) is clearly erroneous as the genus *Hypsilurus* is not distributed further west than some offshore islands of New Guinea and Waigeo. The type specimen of *H. spinosus* therefore must have been collected on New Guinea or an adjacent island.

The L'Astrolabe and La Zélée expedition sailed along the New Guinean coast three times. The first approach was from Ambon Island towards the southwestern coast of New Guinea but they did not land and proceeded to the north-western coast of Australia. Their second approach coming from Australia past Aru Island was in April 1839 as detailed in Dumont d'Urville (1844: 108–145). The expedition visited Dobo on Aru during 12th–21th April 1839, subsequently proceeding to the southwestern coast of New Guinea. From 24th April until 30th April 1839 they anchored in Dubus Harbour (Havre Dubus à la baie de Triton). Nowadays this area is called Kaimana, West Papua.

The expedition's third and last approach was from the Louisiade Archipelago near the eastern most tip of New Guinea in late May / early June 1840 (see Dumont d'Urville 1846: 205–242). They intended to anchor at Orangerie Bay and Hood Point (both on New Guinea) but decided against it. On 31st May they visited Darnley (Erub, Arruob), an island in the Torres Street but did not collect natural history specimens. On 1st June 1840 L'Astrolabe and the accompanying La Zélée went aground near Tudu Island in the Torres Street. It took them 10 days to recover the ships. Visits were made to Tudu Island but the island is described as having no water, mostly sandy soil with grass and some scrubs as well as a small patch with trees and palms on the northern end of the island. The lack of water and the vegetation would most certainly not support an arboreal lizard population of a *Hypsilurus* species that is typically found in the rainforest. This chain of events renders it highly unlikely that the type was collected during their third approach.

Consequently, Hombron and Jacquinot could have collected the specimen only on New Guinea or perhaps on Aru Island. Aru (and Kei) have been well sampled by Beccari in 1873 (see Doria 1874; Peters and Doria 1878) and later in 1908 by Roux (1910) who reported *Hypsilurus binotatus* and *H. modestus* as well as *Lophosaurus dilophus*. Until now no *Hypsilurus* species similar to *spinosus* or *auritus* has been collected on Aru. From the narrative of the expedition it is further known that despite continuous rainfall during their stay in Triton Bay Hombron and Dumont d'Urville undertook daily excursions (Dumont d'Urville 1844; Wichmann 1910: 45). Therefore we consider Triton Bay on New Guinea the most probable location for the collection of the type specimen. Consequently we propose that the collection locality of *Lophyrus* (= *Hypsilurus*) *spinosus* should be corrected to Triton Bay, Kaimana, West Papua, Indonesia (coll. Hombron and Jacquinot, April 1839). However, the type locality cannot be restricted under the rules of the *Code* (ICZN

1999). Triton Bay is only approx. 75 km away from the Cenderawasih Bay (the combined type locality of the *auritus* syntypes) but on the southern coast of New Guinea.

The Naturalis collection holds two specimens (ZMA. RENA.18893) that were collected at Etna Bay, merely 25 km away from our assumed collection locality for *H. spinosus*. These specimens have three scales between the nasal and first supralabial, a character found in the holotype of *H. spinosus*. Else they rather agree with the characters described above for *H. auritus*, e. g. the development of the nuchal and dorsal crest. Without additional material it is impossible to determine whether the differences we found between the type specimens of *auritus* and *spinosus* are sufficient to define each taxon or whether they represent clinal variations of phenotypic characters within the same species as the Etna Bay specimens would indicate. Until further (topotypic) specimens of *spinosus* become available we propose to consider both *Hypsilurus spinosus* and *H. auritus* as species in their own right.

The distributional ranges of the two species cannot be defined currently. Meyer (1874) did not cite a type locality and only gave New Guinea as the general distribution of *H. auritus*. In a later paper Meyer (1886) cites Doré, Passim, and Rubi as localities where he collected *H. auritus*. The locality for the type specimen ZMB 8782 is given in the handwritten catalogue of as Jobi [Ansus on Yapen Island]. All these localities lie in north-western New Guinea along the Geelvink (Cenderawasih) Bay that therefore could serve as the type locality as detailed above. A further restriction is, however, impossible. Manthey and Denzer (2006, 2016) reported *Hypsilurus auritus* from Misol Island, West Papua (including Vogelkop [Birdshead] Peninsula) and Papua province, Indonesia. Records further east (in Papua New Guinea) were considered doubtful. Some of the specimens that have been reported in earlier publications as *H. auritus* may belong to *H. spinosus* instead. Therefore it will be necessary to examine collection specimens and compare them to the characters given above for each species.

Additionally, further fieldwork will help to clarify not only the distribution but also the taxonomic status of different populations. It may well be the case that there exist additional undescribed species that are morphologically similar to *H. auritus* and *H. spinosus*.

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