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# Nomenclatural and morphological notes on the rare agamid lizard *Pseudocophotis sumatrana* (Hubrecht, 1879) (Squamata: Agamidae: Draconinae)

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**Abstract.** The earless, nose-horned agamid lizard *Pseudocophotis sumatrana* is only represented by a few specimens in collections worldwide. We discovered a historical publication from 1855 by van der Hoeven where the species was described as *Calotes nasicornis* before the currently accepted original description by Hubrecht in 1879. In order to uphold nomenclatural stability, we provide proof that *Calotes nasicornis* is a nomen oblitum and that *Pseudocophotis sumatrana* is to be treated as a nomen protectum. Our investigations into historical records put the type locality on Sumatra in question and we conclude that *P. sumatrana* is most probably restricted to Java. Through examination of all known specimens, including the synonymised *Calotes aberrans*, we discuss taxonomic characters and add further details to the species diagnosis with respect to external and internal morphology. In particular by means of μ-computer-tomography we show that only the distal part of the tail is prehensile and for the first time we examine the cranial skeleton and dentition of *P. sumatrana*.

**Key words.** *Pseudocophotis*, *Calotes nasicornis*, *Calotes aberrans*, nomenclature, doubtful type locality, taxonomic characters, rostral appendage, prehensile tail, μ-CT

## INTRODUCTION

The earless, horned lizard *Pseudocophotis sumatrana* (Hubrecht, 1879) from Sumatra and Java is an extremely rare agamid lizard. Until now only six specimens were known to exist in museum collections, all of which were collected over a century ago. There are no reports of its natural habitat and not even its colouration in life is known. The holotype (RMNH. RENA 3782) came to Rijksmuseum in Leiden in 1848 with a shipment purportedly from Sumatra (but see below). It was labelled as *Calotes nasicornis* and stored away in a cabinet. The specimen was presumably labelled by Schlegel—at that time the curator of the collection—who used to assign preliminary names to what he considered undescribed species with the intention of a later description. Schlegel however, never published anything about this specimen, but his colleague Hubrecht (1879) provided the original description of it more than 30 years later under a different name. As Hubrecht observed a high degree of morphological similarity with the Ceylonese (Sri Lankan) agamid *Cophotis ceylanica* described by Peters (1861), he used this as justification to name the specimen *Cophotis sumatrana* to underline their similar morphology and highlight their disjunct distribution. In particular, both species agree in having the tympanum hidden (κωφός – kōphós – deaf, ὠτίς – otis – suffix for eared), having enlarged dorsal scales, the presence of nuchal, dorsal, and caudal crests, and a prehensile tail. The latter character, which is rare among Southeast Asian agamid lizards, was described by Hubrecht (1879) as "tail slightly prehensile". The main difference between the two species was the presence of a small horn-like rostral appendage in males of *Cophotis sumatrana* that was probably the reason for its earlier labelling by Schlegel as "*nasicornis*" which is Latin for "nose horn".

Interestingly, Rosén (1905) described a new agamid species from Java under the name *Calotes aberrans*. Despite several similarities with Hubrecht's description such as its general appearance and pholidosis, Rosén (1905) neither compared his specimen to *Cophotis sumatrana* or *C. ceylanica*, nor did he mention a prehensile tail or cite Hubrecht (1879) or Peters (1861). The specimen was a female and did not have a rostral appendage. Instead Rosén (1905) noted that the

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species "seems to be most allied to *C.*[*alotes*] *tympanistriga* (Gray), from which, however, it is quite distinct". *Calotes tympanistra* [sic!] Gray, 1831 is the type species of the genus *Pseudocalotes* (Fitzinger, 1843). *Pseudocalotes tympanistriga* certainly bears some similarities with *Calotes aberrans* but differs among other characters in having smaller dorsal scales and a longer tail. In the same year as Rosén's description of *Calotes aberrans*, it was synonymised with *Cophotis sumatrana* by Werner (1905) who stated that *C. aberrans* is most probably identical to *Cophotis sumatrana* ("... von denen ... *Calotes aberrans* von Java (?) [Taf. VIII, Fig. 3] wohl mit *Cophotis sumatrana* identisch ist ..."). However, it is important to note that Werner (1905) came to this conclusion only by comparison of the original descriptions of these species and not through personal examination of either the holotype of *Cophotis sumatrana* or the holotype of *Calotes aberrans*. Werner (1905) additionally appears to doubt the type locality Java reported by Rosèn (1905) but did not comment any further on the matter or provide a justification.

de Rooij (1915) claimed that the holotype of *Cophotis sumatrana* was the only known specimen of its kind. However, at that time the Leiden collection already contained a second specimen (see below) that was not seen by de Rooij (1915). Mertens (1921), apparently unaware of Rosèn's (1905) description and Werner's (1905) identification of *Calotes aberrans* as *Cophotis sumatrana*, reported a second specimen of *Cophotis sumatrana* and highlighted that it had been collected on Java for the first time. Mertens (1921) went so far to speculate that *C. sumatrana* possibly only constitutes a subspecies ["östliche Form" = eastern form] of *C. ceylanica*. The holotype of *Calotes aberrans* was sent for examination to London and in a letter dated 1928 to the Zoological Museum Lund from the British Natural History Museum its identification was clarified. The result was finally reported by Smith (1930), who had examined the holotype and corroborated Werner's earlier identification of *Calotes aberrans* as a female specimen of *Cophotis sumatrana*.

The taxonomic decision to consider *C. ceylanica* and *C. sumatrana* as congeneric was not questioned by subsequent authors and remained stable for many years. Only Moody (1980) in his unpublished PhD thesis and later in a publication (Moody, 1984) suggested that *Cophotis sumatrana* is not congeneric with *Cophotis ceylanica* and should be placed in a new genus. However, a paper on this matter was never published and no defining characters can be found in his thesis apart from the form of the caudal vertebrae (Moody, 1980: 75) and the presence of greatly elongated scales on the internasal region (Moody, 1980: 90). Manthey in Manthey & Grossmann (1997) eventually erected the new genus *Pseudocophotis* to accommodate the species. The main diagnostic characters differentiating *Pseudocophotis* from *Cophotis* were stated as granulated (*ceylanica*) vs. keeled, rhomboid, imbricate overlapping (*sumatrana*) scales on the sole of the feet, viviparous (*ceylanica*) vs. oviparous (*sumatrana*), and the presence of a rostral appendage in males (*sumatrana*) vs. absence (*ceylanica*). This was further corroborated by molecular phylogenetic studies where the cloud forest agamids of Southeast Asia were found to form a clade unrelated to *Cophotis* and other Sri Lankan agamid lizards (Macey et al., 2000; Schulte et al., 2002, 2004; Grismer et al., 2016).

Hallermann & Böhme (2000) questioned the placement of *Cophotis sumatrana* in the newly erected genus *Pseudocophotis* Manthey, 1997, and referred to an additional female housed at ZFMK (see also Böhme, 2014). They argued that viviparity vs. oviparity and a hidden vs. visible tympanum constitute adaptive characters and placed *sumatrana* in the genus *Pseudocalotes*. Ananjeva et al. (2007) discovered an agamid lizard in Vietnam that shared main characters (pholidosis, tympanum hidden, prehensile tail) with *Pseudocophotis sumatrana*. They further stated that the assignment of *sumatrana* to *Pseudocalotes* by Hallermann & Böhme (2000) was premature and that the genus name *Pseudocophotis* should remain valid. Based on synapomorphies with *P. sumatrana* they consequently named their new species *Pseudocophotis kontumensis*.

We recently discovered a further specimen of *Pseudocophotis sumatrana* from Java in the Naturalis collection. We also became aware of an overlooked publication by van der Hoeven (1855) describing *Calotes nasicornis* and found archived documents that raise doubts about the Sumatran type locality of *P. sumatrana* as reported by Hubrecht (1879). In the following we will discuss nomenclatural implications, the origin of a hitherto unreported second Sumatran specimen that has been present in the Naturalis collection for many years, as well as the origin of Hubrecht's holotype. We will further provide additional information regarding taxonomically relevant characters, skeletal anatomy, and dentition based on our examination of all currently known specimens of *Pseudocophotis sumatrana* and will briefly discuss the inclusion of *Pseudocophotis kontumensis* in this genus.

## MATERIAL AND METHODS

Meristic and morphometric data were recorded from type specimens of *Cophotis sumatrana* and *Calotes aberrans* as well as all known *Pseudocophotis sumatrana* specimens. Additional agamid species were examined for comparisons. Measurements were taken using a sliding calliper with a precision of 0.1 mm or using a ruler with a precision of 1 mm (SVL: snout–vent length; TL: tail length; RAL: rostral appendage length; InfraLab: number of infralabial scales; SupLab: number of supralabial scales; AG: scales between axilla and groin; MBS: number of scales around midbody; SDL: number of subdigital lamellae underneath 4$^{th}$ finger (F4S) and 4$^{th}$ toe (T4S)).

For obtaining information on skeletal anatomy, specimens of *Pseudocophotis sumatrana* (ZFMK 20790) and *Cophotis ceylanica* (ZFMK 52524) were scanned with a Skyscan 1173 µ-computer-tomographer (µ-CT) (Bruker, Billerica/USA) at Museum Koenig in Bonn, Germany. The scans were performed with the following parameters: 65 kV, 123 µA, and 500 ms exposure time for *P. sumatrana* and 40

kV, 160 µA, and 500 ms exposure time for *C. ceylanica*, 0.25° rotation steps over 360° for *P. sumatrana* and 0.27° over 360° for *C. ceylanica*, frame averaging of 5 for *P. sumatrana* and 8 for *C. ceylanica*, random movement of 15 and image pixel size 19.65 µm for both. The scans were reconstructed with the software NRecon (Bruker, Billerica/USA). Segmentation of the resulting scans was performed with Amira 5.3 (Thermofisher, Waltham/USA). Subsequent volume rendering was done using VG Studio 3.3.4 (Volume Graphics, Heidelberg/Germany). Final images and plates were edited using Adobe Illustrator CS6 (Adobe, San Jose/USA).

Museum abbreviations are as follows: Zoological Collection in the Biological Museum in Lund, Sweden (MZLU), Naturalis Biodiversity Center, Leiden, The Netherlands (RENA), Senckenberg Forschungsinstitut und Naturmuseum Frankfurt/M., Germany (SMF), Zoologisches Forschungsmuseum Alexander Koenig – Leibniz-Institut für Biodiversität der Tiere, Bonn, Germany (ZFMK), Muséum national d'Histoire naturelle, Paris, France (MNHN) and Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russian Federation (ZISP). The former collections of the Rijksmuseum voor Natuurlijke Historie (RMNH) and the Zoölogisch Museum Amsterdam (ZMA) are now included in the Naturalis collection.

Specimens studied:
***Pseudocophotis sumatrana*** Hubrecht, 1879, 7 ex.: RMNH. RENA 3872, holotype of *Calotes nasicornis* and *Cophotis sumatrana*, male, Sumatra, 1848; MZLU L897/3430, holotype of *Calotes aberrans*, female (three eggs), Tjibodas, coll. Hj. Möller, 1897; RMNH.RENA 4933, male, Sumatra(?), coll. / don. W. J. E. Hekmeijer; RMNH.RENA 8384, male, Gedeh, Tjibodas [= Cibodas], Java, coll. F. Kopstein, 1935; SMF 9741 (old SMF 4276a), male, Gunung [Mount] Pengalengan, West Java, coll. H. Fruhstorfer, purchased in 1895; ZMA. RENA 15190, male, Pengalengan, Preangar, Java, coll. P. A. Ouwens, 1906; ZFMK 20790, female, Buitenzorg (= Bogor), Jawa Barat, Westjava, coll. / don. H. M. C. L. Graf Solms zu Laubach, 1884.
***Cophotis ceylanica*** Peters, 1861, 2 ex.: ZFMK 14306, male, Sri Lanka; ZFMK 52524, male, Horton Plains, Sri Lanka.
***Harpesaurus tricinctus*** Dumeríl & Dumeríl, 1851, 1 ex.: MNHN-RA 0623, Java (only photographic records).

## RESULTS

**Nomenclature.** During Hermann Schlegel's time as the curator of the Rijksmuseums' herpetological collection in the 1850s, his later arch-rival for the directorship of that museum, Jan van der Hoeven, was preparing a second edition of his Handboek der Dierkunde. Over the course of this work, van der Hoeven examined specimens present in the Leiden collection and prepared short descriptions for his handbook. One of the specimens that he examined was that of *Calotes nasicornis*. In a footnote on pp. 533–534, van der Hoeven (1855) clearly described and named it as a new species: "In het Museum van Leiden bevindt zich een voorwerp onder den voorloopingen naam van *Calotes nasicornis*, dat in kleur en in plaatsing der schubben met de afbeelding van *Arpephorus* [*tricinctus*] overeenkomt, doch slechts een klein, puntig een week aanhangsel op den snuit heeft. Ook zijn de schubben, die vrij groot en bijkans vierkantig zijn, duidelijk gekield, waarvan Duméril niets vermeldt. Een uitwendig trommelvlies kan ik niet waarnemen." [English edition from 1858, Vol. II, footnote on p. 308: "In the Museum at Leiden there is a specimen with the provisional name of *Calotes nasicornis*, that in colour and in position of the scales corresponds with the figure of *Arpephorus*, but has only a small pointed and soft appendage on the snout. The scales also, which are very large and almost quadrangular, are conspicuously keeled, of which Duméril gave no notice. I cannot perceive an external tympanum"]. The question of whether this description of a new species was intended or unintentional cannot be answered a posteriori, although the wording "provisional" (or alternatively "preliminary", our translation) appears to imply that a description was not intended at that stage. Formally, however, the description complies with the ICZN code for zoological nomenclature (in the subsequent text called the Code) as it contains morphological characters to define a species (rostral appendage, pholidosis) and further diagnostic characters (keeled scales, tympanum covered) that differentiate it from a similar species, in this case *Arpephorus* [= *Harpesaurus*] *tricinctus* A. H. A. Duméril in Duméril & Duméril, 1851.

In the herpetological literature, the original authorship of the taxon is unambiguously assigned to Hubrecht (1879) with only *Cophotis sumatrana* as an available name, presumably because van der Hoeven's description had been overlooked. The rules of the Code do not automatically invalidate descriptions made in secondary literature such as zoological handbooks or biology textbooks. As van der Hoeven's (1855) description precedes that of Hubrecht (1879), the original authorship would have to be assigned to the first author. Consequently, the species should be called *Pseudocophotis nasicornis* (van der Hoeven, 1855) and the name *Cophotis sumatrana* Hubrecht, 1879 would become a junior synonym. However, van der Hoeven's name was neither used in any subsequent publication other than the different language editions (Dutch, English, and German) of van der Hoeven's Handbook of Zoology, nor was it applied by any subsequent author. In contrast Hubrecht's original name *Cophotis sumatrana* was widely applied as a taxon name for over a century (e.g., Werner, 1905; de Rooij, 1915; Smith, 1935; Wermuth, 1967; Moody, 1984). In later years, the species epithet *sumatrana* was used in combination with the generic names *Pseudocophotis* and *Pseudocalotes* (e.g., Manthey & Grossmann, 1997; Hallermann & Böhme, 2000). We therefore make use of Article 23.9.1 of the Code and reject the name *Calotes nasicornis* van der Hoeven, 1855 as a nomen oblitum in favour of its junior synonym *Cophotis sumatrana* Hubrecht, 1879 as a nomen protectum. A list of publications in support of the species epithet *sumatrana* Hubrecht, 1879 as a nomen protectum is provided in the Appendix. Consequently, the taxon name *Calotes nasicornis* van der Hoeven, 1855 (nomen oblitum) is no longer available for nomenclatural purposes. The long-standing usages of the species epithet *sumatrana* in conjunction with

*Cophotis*, *Pseudocalotes*, or *Pseudocophotis* can prevail. Under currently accepted taxonomy the species is called *Pseudocophotis sumatrana* (Hubrecht, 1879).

**Synonymy list and chresonomy (nomenclaturally relevant literature only):**

*Calotes nasicornis* van der Hoeven, 1855 [rejected as *nomen oblitum*]
*Cophotis sumatrana* Hubrecht, 1879
*Calotes aberrans* Rosén, 1905
*Calotes aberrans* – Werner (1905); Smith (1930) [synonym of *Cophotis sumatrana*]
*Pseudocalotes sumatrana* – Hallermann & Böhme (2000) [comb. nov.]
*Pseudocophotis sumatrana* – Manthey & Grossmann (1997); Ananjeva et al. (2007) [comb. nov.]

**Origin of the holotype of *Cophotis sumatrana*.** There remain questions surrounding the type specimen of *Pseudocophotis sumatrana*, in particular its origin and type locality. According to Hubrecht (1879) the specimen had "been forwarded to [the] Museum from Sumatra" in 1848 but "the exact locality in the island of Sumatra ... was not noted". Hubrecht (1879) assumed "that it came from the environs of Padang" but did not give any indication how he arrived at this conclusion. In the minutes of the annual report 1847–1850 for incoming collections, the museum director Coenraad Jacob Temminck complained that the Natuurkundige Commissie for the Dutch East Indies had not sent any shipments for four years (letters in the Naturalis archives (Veth, 1879)). The only person apparently considered to be regularly sending specimens was Pierre-Médard Diard who was working on Java at that time. In a letter to Diard dated December 1848, Temminck complained that he was dissatisfied with the work of Carl Schwaner and Franz W. Junghuhn, both responsible for collecting and sending the museum natural history collections from the Dutch East Indies. If there was no shipment from Sumatra as described by Temminck the specimen may have come through other channels such as from Diard on Java unless it was donated by an unidentified source. The director's statement certainly puts the acquisition date of the holotype given by Hubrecht (1879) into question and therefore also its origin.

A second Sumatran specimen of *P. sumatrana* (RMNH. RENA 4933) is a male and presumed to have been collected by W. J. E. Hekmeijer. Hekmeijer had served on Java (Surabaya, March 1859 to March 1871) and subsequently returned to the Netherlands for two years at which time he sold part of his collection. From January 1873 to March 1875, he was again stationed in Surabaya (Java) before being sent to Aceh on Sumatra until 1876 (van der Lande & Holthuis, 1986). There are no records of him having visited the Padang area—Hubrecht's (1879) assumed type locality of *P. sumatrana*—which is not in the Aceh area and is situated several hundred kilometres southwest on the coast of Sumatra. Consequently, Hekmeijer's specimen would have had to have originated in North Sumatra. The remaining years (January 1876 to February 1885) of his placement in Indonesia he lived in Weltevreden, Batavia (all dates according to van der Lande & Holthuis, 1986). The Naturalis collection holds several more reptile specimens collected by Hekmeijer, such as *Boiga cynodon* (3881, labelled Java East Cost, 1872), *Hypsirhina enhydris* (RMNH. RENA 1181 = *Enhydris enhydris*), *Aplopeltura boa* (RMNH. RENA 1146) and *Calamaria linnaei* (RMNH.RENA 17487, labelled probably Java) found in the stomach of one of three *Calliophis* (= *Maticora*) *intestinalis* (RMNH.RENA 8695), all presumed to have originated from Java. The Javanese specimens as well as some reptiles from Borneo were among a lot of natural history items—mostly insects—that were purchased from Hekmeijer in 1872 as seen from the accession year in the catalogues. Unfortunately, the accession of the "*Cophotis sumatrana*" specimens has not been recorded and could not be established retrospectively, but before Hekmeijer left the Netherlands for Switzerland, his remaining collection was donated to the Leiden Museum in 1891. As Hubrecht (1879) did not mention a second specimen it can be assumed that the accession date of the second specimen was after his description, most probably in 1891. No further details are available, and the collection locality is only given as "Sumatra (?)" presumably because the type locality of *Cophotis sumatrana* was given by Hubrecht as Padang area, Sumatra. van der Lande & Holthuis (1986) detailed a case of erroneous type locality regarding *Eoperipatus sumatranus* (collected [presented?] by Hekmeijer) where they concluded that it was in fact most probably collected on Mount Arjuno, Java and not in East Sumatra as indicated by Hekmeijer.

Therefore, it can be assumed that neither the locality given by Hubrecht (1879) nor the provenance of the Hekmeijer specimen unambiguously corroborate a Sumatran origin of these two specimens. Although a non-occurrence of a species is impossible to prove and our retrospective analysis of the provenance may be inconclusive, it should be noted that the type locality may be in error and the species epithet "*sumatrana*" may be misleading.

**The Javanese specimens of *Pseudocophotis sumatrana*.** There are currently four Javanese specimens (two males and two females) present in herpetological collections that have been reported in previous publications (Hubrecht, 1879; Rosén, 1905; Mertens, 1921; Hallermann & Böhme, 2000; Harvey et al., 2018). All specimens appear to be adults or at least semi-adults. The female holotype of *Calotes aberrans* contains three oval-shaped eggs between 15–16 mm in length and approximately 8 mm in width. Werner's apparent doubt regarding the origin of the holotype of *Calotes aberrans* lacks any foundation. The specimen in question was collected by Hjalmar August Möller, a Swedish scientist, who travelled to Java (and Burma) in 1879 where he was mainly concerned with botanical collections. While Rosén (1905) only mentioned Java as the origin of the specimen, the catalogue entry of the Lund Museum collection restricted the collection locality to Tjibodas [= Cibodas]. The remaining non-typical Javanese specimens agree well with the male holotype of *Cophotis sumatrana* by Hubrecht (1879) (Fig. 1A) and the female holotype of *Calotes aberrans* by Rosén (1905) (Fig. 1B). In particular, the male specimens (SMF 9741, ZMA.RENA 15190) possess a rostral appendage as

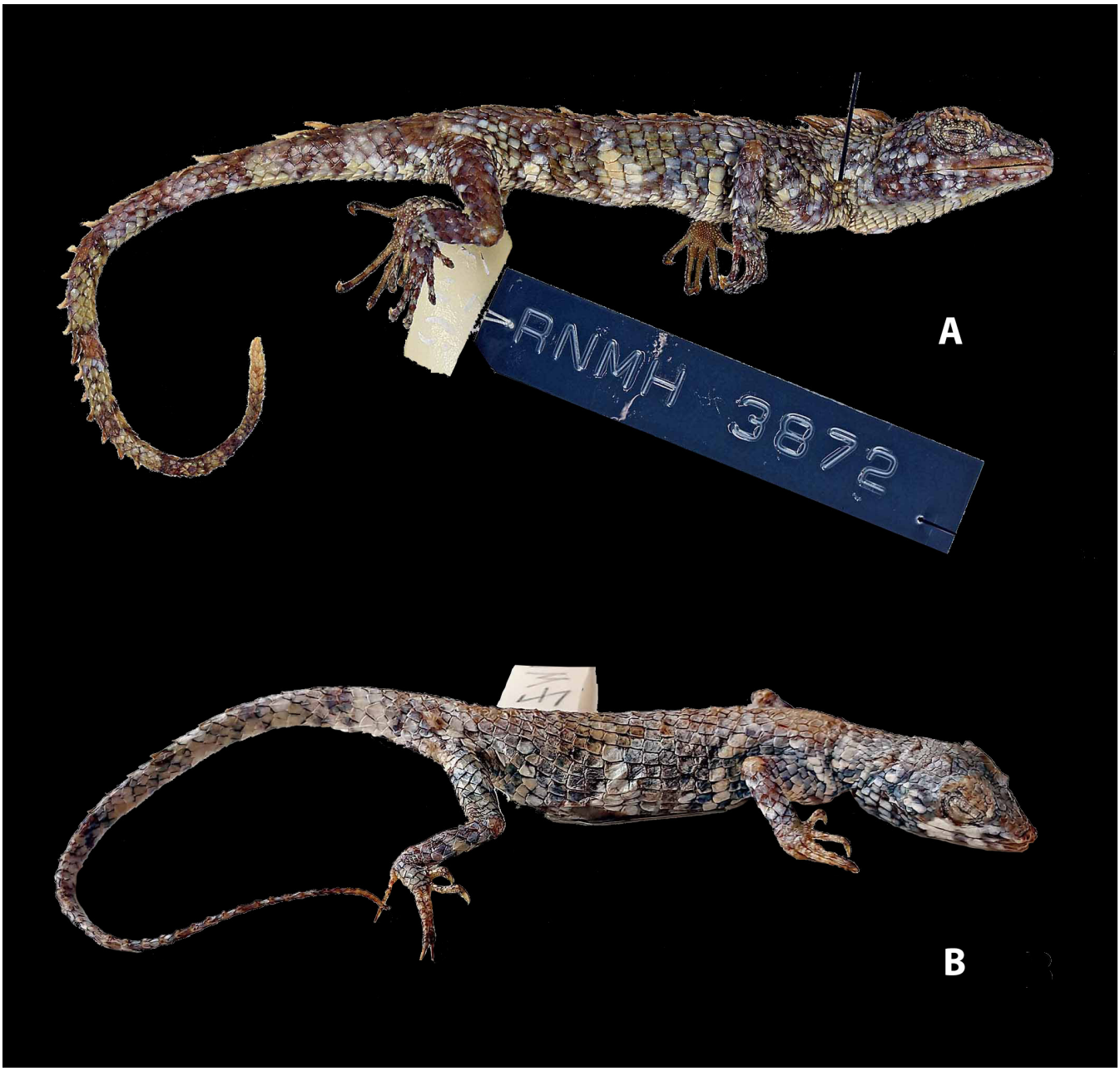


Fig. 1. A, male holotype of *Calotes nasicornis* and *Cophotis sumatrana* (RMNH.RENA 3872); B, female holotype of *Calotes aberrans* (MZLU L897/3430); not to scale.

well as a corona of triangular scales above the eye, a unique character combination not found in any other agamid lizard from Southeast Asia. The female specimen (ZFMK 20790) shows the same, rather regularly arranged, dorsal scalation as the holotype of *Calotes aberrans*.

We recently discovered a fifth Javanese specimen of *P. sumatrana* in the Naturalis collection that had been labelled as "*Harpesaurus tricinctus*" (RMNH.RENA 8384, Gedeh, Tjibodas, Java, coll. F. Kopstein, 1935) (Fig. 2). Kopstein's identification is most probably based on colouration and the form of the rostral appendage. Although not as pronounced as in the holotype of *H. tricinctus* (MNHN-RA 0623), the specimen shows three dark bands across the body, one behind the forelimbs, a second on the midbody, and a third before the hindlimbs. Between these bands are areas with lighter sometimes yellowish transverse scale rows. Furthermore, the specimen possesses a smooth, slightly compressed and possibly backward curving rostral appendage. However, the specimen has clearly triangular supraciliary scales (a character not reported for *H. tricinctus*), less scale rows between axilla and groin (AG = 30 in RMNH.RENA 8384, 25–30 in *P. sumatrana*, more than 40 in *H. tricinctus*) and a lower number of scales around midbody (MBS = 28 in RMNH. RENA 8384, 28–36 in *P. sumatrana*, 41 in *H. tricinctus*). Owing to these character differences, we consider RMNH. RENA 8384 as *P. sumatrana*.

All Javanese specimens came with precise locality records as opposed to the two Sumatran specimens (see map, Fig. 3). The female holotype of *Calotes aberrans* was collected near Tjibodas (Cibodas, West Java) as was the specimen

Fig. 2. Specimen of *Pseudocophotis sumatrana* initially identified as "*Harpesaurus tricinctus*" (RMNH.RENA 8384 from Gedeh, Tjibodas, Java).


Fig. 3. Distribution map of *Pseudocophotis sumatrana*. The type locality is indicated by a star and Sumatran records indicated by a question mark.

collected by Kopstein (RMNH.RENA 8384); the female in the collection of the ZFMK was collected near Buitenzorg (Bogor, West Java) and the additional males present in the Senckenberg (SMF 9741) and the Naturalis collections (ZMA. RENA 15190) originated from the Gunung (= mountain) Pengalengan area in West Java. All three localities lie within 100 km air-line distance of each other and Cibodas as well as Pengalengan are located at altitudes between 1,400 m and 1,650 m asl. The collector of ZFMK 2790, Graf Solms, was the director of the botanical garden in Göttingen who travelled to Java in 1884, mainly to visit the botanical garden at Buitenzorg (Bogor). He originally deposited the specimen in the collection of the zoological museum in Göttingen; this collection was taken over by the ZFMK in 1977. Bogor is situated at a much lower altitude (around 300 m asl) but close to mountain ranges such as Gunung Pangrango and Gunung Gede. Whether the ZFMK specimen had been collected in the grounds of the botanical garden or rather in the mountainous vicinity of Bogor cannot be established. Based on their Javanese records we therefore speculate that *Pseudocophotis sumatrana* inhabits the submontane and montane forests of the mid to high altitude areas of West Java.

**Previous accounts of *Pseudocophotis sumatrana*.** A detailed description of the holotype and a good illustration of *Cophotis sumatrana* can be found in de Rooij (1915). Mertens (1921) compared SMF 9741, formerly SMF 4276a, to this illustration along with the data provided by Hubrecht (1879). Hallermann & Böhme (2000) provided photographs of SMF 9741 and ZFMK 20790 in comparison to a specimen of *Cophotis ceylanica* (ZFMK 14306) and several *Pseudocalotes* species. They also listed morphometric and meristic data on these two specimens, some of which differed from the measurements given in Mertens (1921) who reported SVL = 75 mm and TL = 115 mm for SMF 9741. Repeated measurements of the SMF specimen corroborated the values (SVL = 68.4 mm, TL = 106.1 mm) published in Hallermann & Böhme (2000). Manthey in Manthey & Grossmann (1997) only provided a short diagnosis for the erection of *Pseudocophotis*, a summary of which reads as follows: "Comparatively small agamid lizards with prehensile tail as well as nuchal and dorsal crests; variably broad, rhomboid dorsal and lateral scales arranged in irregular rows; tympanum hidden; scales on the soles of the feet rhomboid, strongly keeled and overlapping; a horn-like rostral appendage; females oviparous" [our translation]. Further characters are mentioned in the species description of *P. sumatrana* and as such they cannot be counted as characters defining the genus. It should be noted that this diagnosis was derived from the scarce data available for three specimens known at that time when only the description of the holotypes (Hubrecht, 1879; Rosèn, 1905) and the comparison by Mertens (1921) had been published. The genus diagnosis and species description in Manthey & Grossmann (1997) was accompanied by the figure published in de Rooij (1915). Based on our examination of the type specimen and further material, we are able to evaluate some of the diagnostic characters given in earlier publications and to add further details that allow us to compile a revised and extended description.

**Prehensile tail.** One character that needs verification is the presence of a prehensile tail. While Hubrecht (1879) noted "tail slightly prehensile", neither Rosén (1905) nor van der Hoeven (1855) reported this character. We assume that Hubrecht's statement is probably based on the fact that a prehensile tail was known from *C. ceylanica* and he considered homology likely because he regarded *sumatrana* as congeneric. He could not have arrived at this conclusion by just looking at the tail of a preserved specimen; only observations of live specimens would have allowed such a statement (at that time), but such observations for *Pseudocophotis sumatrana* have, to our knowledge, never been reported. Mertens (1921) assumed that only the final 20 mm of the tail, where no more caudal crest scales are present, constitute the actual prehensile part. Smith (1930) after having examined the holotype of *Calotes aberrans* stated: "the tail, though now much shrivelled, was evidently prehensile". Moody (1980: 75) described the caudal vertebrae as "short, blunt" and also considered the tail prehensile. To evaluate the presence or absence of this character we obtained µ-CT scans of the tails of *C. ceylanica* and *P. sumatrana* in order to allow for comparisons. As can be seen in Fig. 4, not only the number of caudal vertebrae relative to the actual tail length differs between the two species, but also their shape. A detailed view of the caudal vertebrae is given in Fig. 5. While the caudal vertebrae in *C. ceylanica* are short and numerous, they are elongated and more than double the size in *P. sumatrana*, becoming shorter only in the distal section of the tail. This can also be seen in the holotype of *Calotes aberrans* (Fig. 1B), and most probably led to the statement given by Smith (1930). Although shorter vertebrae allow for a more rounded curl of the tail, a supporting muscle structure is necessary to facilitate movement. A size reduction of caudal processes associated with the curling of a prehensile tail has already been recorded in other prehensile tail-bearing lizard species, such as skinks (*Corucia*), chameleons (*Furcifer*), or eublepharid geckos (*Aeluroscalabotes*) (Zippel et al., 1999; Koppetsch et al., 2020). While the caudal vertebrae of *C. ceylanica* possess less developed apophyses (ventral osseous processes also referred to as hemal arches, that might be associated with attachment points of extrinsic tail muscles (Ritzman et al., 2012)), this character is more prominent in *P. sumatrana*, but reduced in the most distal part of the tail. We therefore conclude that the tail of *P. sumatrana* is not prehensile in its entirety and possibly only—as suggested by Mertens (1921)—in its distal part.

**Rostral appendage.** The male specimens that have been described so far all have a rostral appendage that appears to be a single pointed scale. We assume that the appendages of the males described in earlier publications as pointed, horn-like scale (de Rooij, 1915; Mertens, 1921) are either an artefact owing to preservation or constitute an ontogenetic character in the beginning of development. In particular, the male specimen RMNH.RENA 4933 clearly possesses a well-developed, smooth and rounded appendage of approximately 4.5 mm length. Its size (SVL: 74.9 mm; TL: 112.3 mm) compares to that of the holotype and the specimen in the SMF collection. But in contrast to these specimens the horn is more developed in RMNH.RENA 4933. The

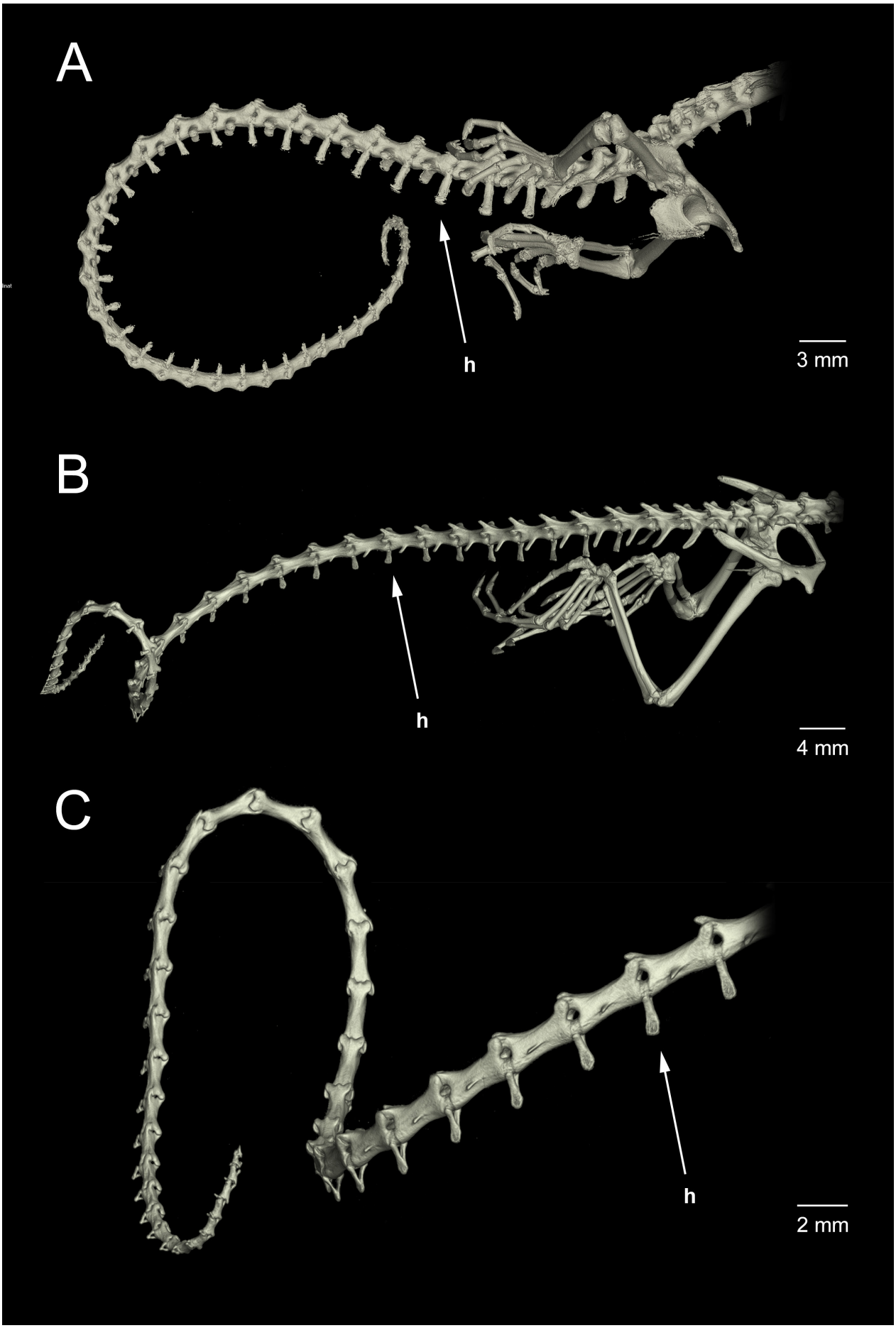


Fig. 4. µ-CT of the tails of *Cophotis ceylanica* (A, ZFMK 52524) and *P. sumatrana* (B, C, ZFMK 20790) in lateral view. Please note the presence of hemal arches (h) in *C. ceylanica* along the entire length of the tail.

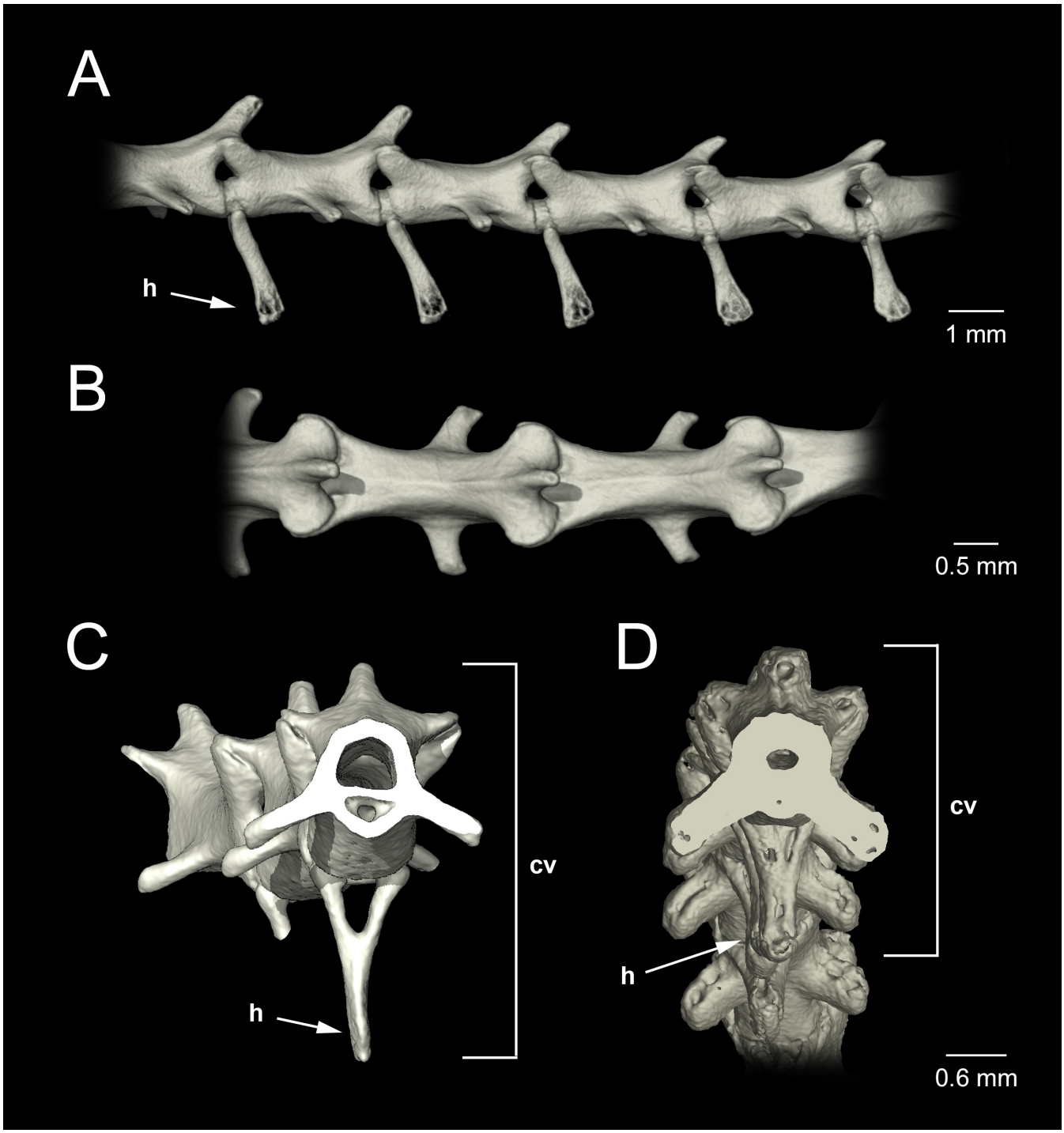


Fig. 5. Detailed μ-CT of the caudal vertebrae of *Pseudocophotis sumatrana* (ZFMK 20790) in lateral (A) and dorsal (B) view. Comparison of a transverse section of the caudal vertebrae (cv) of *P. sumatrana* (C) and *Cophotis ceylanica* (D, ZFMK 52524) (h, hemal arch).

rostral appendage of RMHN.RENA 3782 (holotype, Fig. 6A) appears to be slightly cylindrical compared to that of RMNH.RENA 8384 which is clearly laterally compressed (Fig. 6B) and approximately 6 mm long.

**Scales underneath feet and toes.** Manthey & Grossmann (1997) referred to the sole scalation as strongly keeled. Hallermann & Böhme (2000) as well as Manamendra-Arachchi et al. (2006) erroneously interpreted this character as being concerned with the subdigital scales and described the subdigital scales accordingly as (strongly) keeled. Our re-examination revealed that this is not the case. In particular the basal scales underneath the fingers are smooth and the basal scales underneath the toes are (only) slightly keeled. This was already observed by Harvey et al. (2018) who studied three specimens present in the Naturalis collection and concluded "that the condition of the hands is clearly intermediate between the near absence of keels in *Lophocalotes* and high keels of other Draconinae".

**Cranial and dental characters.** μ-CT scans of cranial skeleton and dentition are depicted in Fig. 7. The circumorbital bones are made up of jugal, lacrimal, prefrontal, frontal and postorbital (see Fig. 7A, B). Jugal and lacrimal are in contact

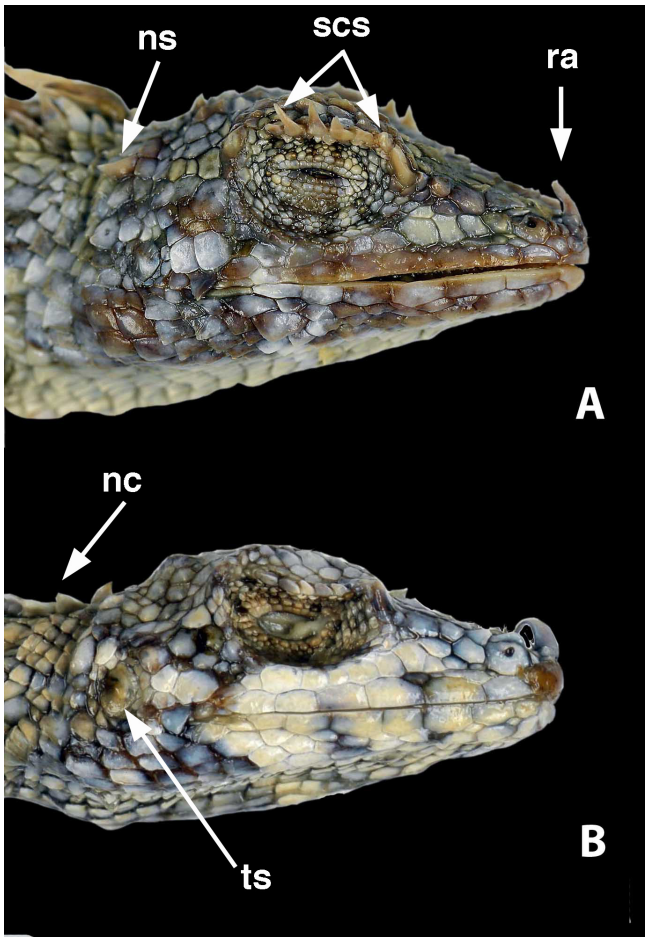


Fig. 6. Rostral appendages of *P. sumatrana* (A, RMNH.RENA 3782; B, RMNH.RENA 8384). Please note that the rostral appendage in RMNH.RENA 8384 is laterally compressed. (ns, nuchal spine; scs, corona of supraciliary scales; not to scale; ra, rostral appendage; nc, nuchal crest scales; ts, scaled tympanum)

such that the maxilla does not contribute to the orbital rim. In several other Southeast Asian agamid lizard genera such as *Phoxophrys* and *Pelturagonia*, the lacrimal bone is missing (see Harvey et al., 2020). Absence or presence can even be encountered within a single genus; for example, in the genus *Draco* there exists a clade that possesses a lacrimal bone while the majority of species are missing this feature (McGuire & Kiew, 2001). The postorbital bone has a rounded process, named the postciliary ornament by Harvey et al. (2020), that supports a large postciliary scale at the posterior dorsal edge of the orbit. Similarly, in the type of *C. aberrans* a large projecting scale is well developed at the anterior dorsal edge of the orbital rim. This is supported internally by a large lateral process of the prefrontal. Female specimens have a helmet-like elevation on the occiput that is rather concealed by the onset of the nuchal crest in males. This helmet is internally supported by an elevated parietal bone (Fig. 7B). The hyobranchial skeleton (hyoid apparatus) is well developed (Fig. 7C) and capable of supporting the expansion of the gular pouch (sac).

The dentition (see Fig. 7B) is as follows: premaxillae 1/1 pleurodont teeth, maxilla 2/2 pleurodont teeth (second largest) before acrodont dentition; dentary 2/2 pleurodont teeth (second largest) before acrodont dentition; maxillary 13/13 acrodont teeth (anterior 6 monocuspid, posterior 7 tricuspid), dentary 14/14 acrodont teeth (anterior 6 monocuspid, posterior 8 tricuspid with median cusp markedly elongated). The upper and lower acrodont teeth are alternating, i.e., maxillary teeth fit into a gap in the dentary and vice versa; the dentary is indented to accommodate the elongated median cusp of the acrodont maxillary teeth.

In addition to this, males have a peculiar small gular sac, the scales of which are surrounded by an inverted V-shaped fold (Fig. 8). This character can also be seen in the holotype of *sumatrana* and even in the female holotype of *aberrans* but to a lesser extent. The iuxtagular scales adjacent to the gular sac are convex and strongly enlarged. Furthermore, males possess two conical scales on the upper forehead as well as an erected, pointed scale dorsolaterally on each side of the neck that has been denoted as a nuchal spine by Hallermann & Böhme (2000).

**Revised and extended diagnosis of *Pseudocophotis sumatrana* (Hubrecht, 1879).** Medium-sized agamid lizard (SVL up to 81 mm, TL up to 119 mm, TL/SVL 1.34–1.57, based on seven specimens); tympanum covered by a large scale; males with a soft, small, cylindrical or laterally compressed rostral appendage; 6–7 supralabials, 5–7 infralabials; nasal in contact with first supralabial; corona of triangular superciliary scales, two conical scales on the upper forehead anterior to the eyes; a large pointed scale (smooth nuchal spine) behind the eyes. A bony ridge on the occipital region. A small gular sac (in males) with adjacent inverted V-shaped fold; gular fold present; gular scales smooth, rhomboid and partially overlapping laterally; iuxtagular scales large, convex. Nuchal crest composed of lanceolate spines, separated from the dorsal crest; a nuchal spine present in adult males. Scales of the neck and shoulder region strongly keeled, pointing backwards. Dorsal and lateral scales squarish to rhomboid, mostly smooth only some of them keeled, arranged in slightly irregular rows; 25–30 scales between axilla and groin; 28–36 scales around midbody; dorsals much larger than ventrals; ventral scales strongly keeled and sharply pointed; number of smooth subgular and keeled ventral scales (approximately 90–100 from the tip of the snout to the vent). Dorsal crest composed of triangular-shaped scales, continuous with caudal crest consisting of similar scales present on most of the tail length; limbs dorsally with strongly keeled scales; third and fourth toe nearly equally long; basal subdigital lamellae not or only little keeled (T4S 22–27, F4S 19–22 for four specimens). Tail probably only prehensile in the distal part. There exists a clear sexual dimorphism: females are lacking a rostral appendage and the corona of supraciliary scales is only weakly indicated; their dorsal and lateral scales are arranged in rather regular rows; females have only a low nuchal crest, dorsal and caudal crests are not developed, but are merely a denticulated ridge.

As is the case in several other draconine species, younger specimens have a rather female appearance. For example, ZMA.RENA 15190 (SVL 65.5 mm, TL 93.0 mm) is a

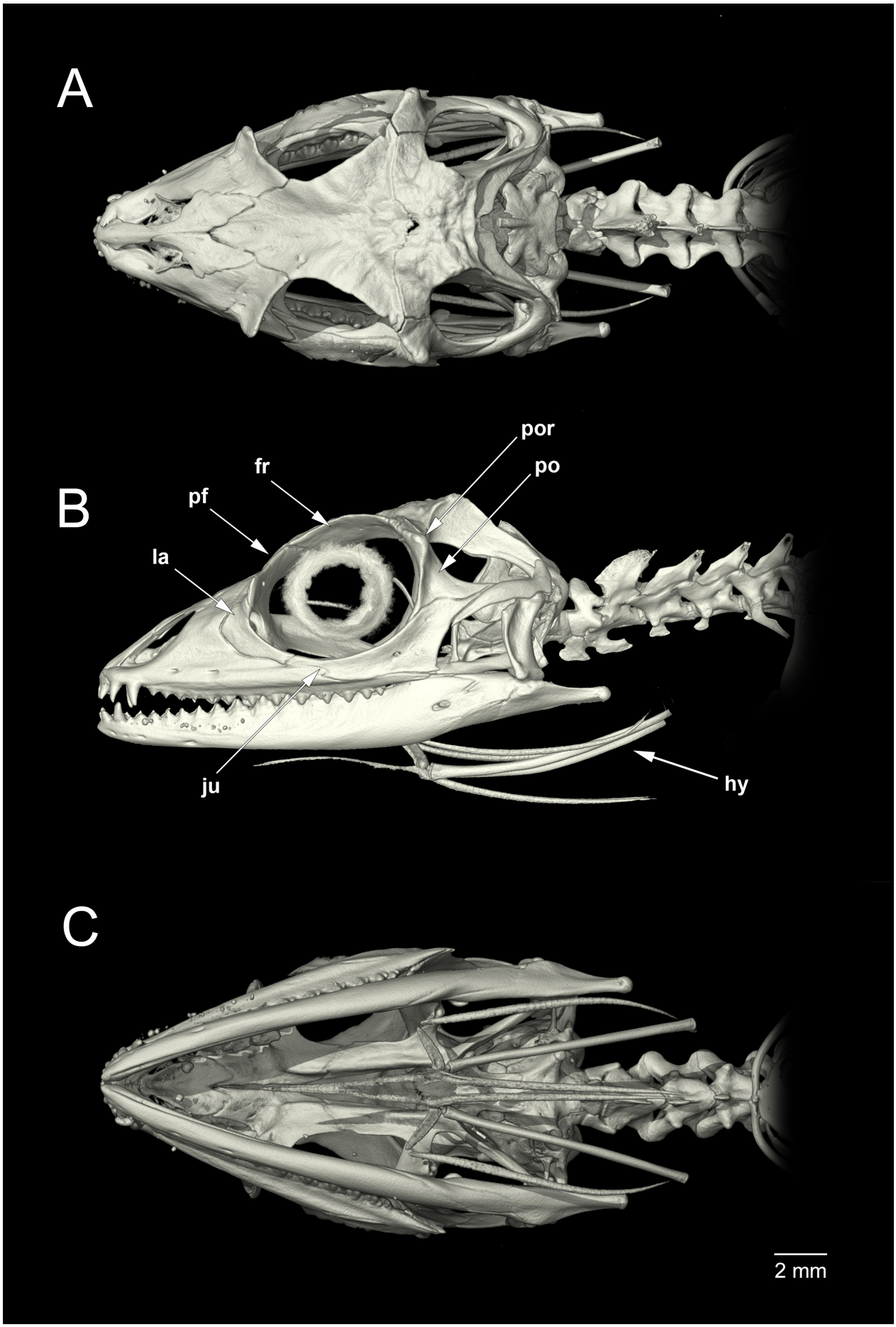


Fig. 7. µ-CT of the cranial skeleton of *P. sumatrana* (ZFMK 20790) in dorsal (A), lateral (B) and ventral (C) view (ju, jugal; hy, hyoid apparatus; la, lacrimal; fr, frontal; pf, prefrontal; po, postorbital; por, postciliary ornament).

Table 1. Morphological comparison of *Pseudocophotis sumatrana* specimens.

| Collection No. | MZLU L897/3430 | RMNH 3872 | RMNH 4933 | RMNH 8384 | SMF 9741 | ZMA 15190 | ZFMK 20790 | Range |
|---|---|---|---|---|---|---|---|---|
| sex | female | male | male | male | male | male | female | |
| SVL in mm | 81.3 | 70.3 | 74.9 | 64.1 | 68.4 | 65.5 | 80.0 | 64.1–81.3 |
| TL in mm | 119.2 | 110.1 | 112.3 | 87.2 | 106.1 | 93.0 | 110.7 | 87.2–119.2 |
| TL/SVL | 1.47 | 1.57 | 1.49 | 1.36 | 1.56 | 1.41 | 1.38 | 1.36–1.57 |
| RAL in mm | none | 2.9 | 4.5 | 6.0 | 1.5 | 1.4 | none | 0–6.0 |
| SupLab | 7 | 7 | 6 | 6 | 6 | 6 | 7 | 6–7 |
| InfraLab | 6 | 6 | 5 | 7 | 7 | 6 | 7 | 5–7 |
| AG | 25 | 25 | 26 | 30 | 30 | 26 | 27 | 25–30 |
| MBS | 36 | 30 | 34 | 28 | 32 | 30 | 34 | 28–36 |
| T4S | 25 | 22 | 27 | 26 | 25 | 26 | 27 | 22–27 |
| F4S | – | 19 | – | 22 | 20 | – | 21 | 19–22 |

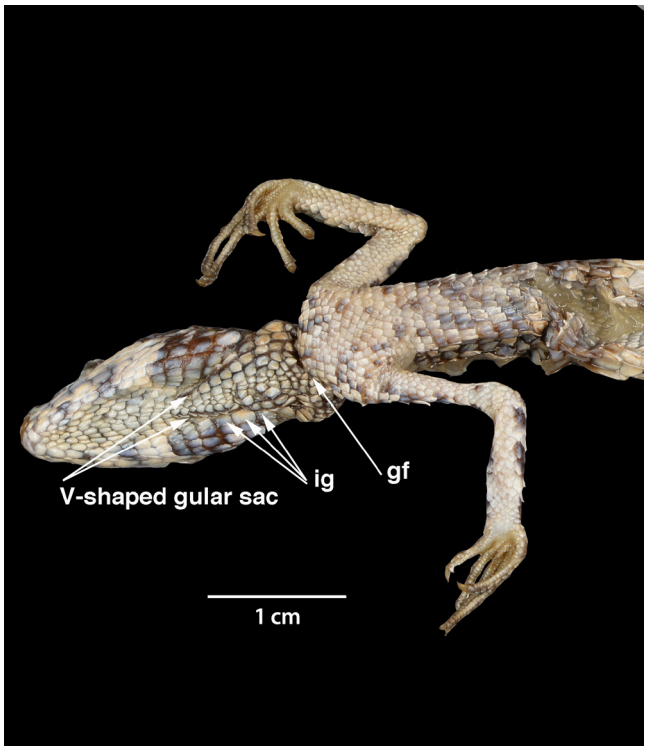


Fig. 8. Gular region of *P. sumatrana* (RMNH.RENA 8384). Please note the V-shaped limitation of the gular sac. (gf, gular fold; ig, enlarged iuxtagular scales).

(subadult) male with a small rostral appendage (RAL: 1.4 mm) and a low corona of triangular supraciliary scales. The dorsal scales are rather smooth, arranged in near regular rows, only some with a keel. Not only does the development of the rostral appendage appear to be ontogenetic but also the formation of strongly keeled scales in the nuchal region, ventrally and on dorsal surfaces of the limbs. The nuchal crest is composed of a single row of triangular scales in young males; in adult males the nuchal crest is composed of three to five scale rows, the longest scales lanceolate, curving backwards. Supraciliary scales, if at all present, are only weakly indicated in female specimens and constitute another ontogenetic character in males. Some morphometric and meristic data are summarised in Table 1.

The colouration in alcohol was given by Rosén (1905) as bluish which could mean that the specimen had a green (bluish) colouration in life. Nowadays the darker parts of the preserved specimen are made up from shades of brown. Mertens (1921) also noted that the colouration in life would probably be a light bluish green. He further stated the dorsal colour as "body with three very broad, irregular dark bands of brownish black colour, tail with 13 such bands", and that there are "dark radiating lines around the eyes" [our translation]. Most of the specimens show a white line underneath the eye including several white supralabial scales. The midgular region is mainly light coloured while the enlarged iuxtagular scales appear to be brownish. The underside is either dirty white without pattern or mottled with brown spots (including underside of extremities). The gular region of RMNH.RENA 8384 and the venter of ZFMK 20790 are mottled with spots of a rather bluish taint. The banded pattern of RMNH.RENA 8384 appears to be present ventrally such that it can be assumed that the dark bands surround the whole body. Like other draconine lizard species, *P. sumatrana* is probably capable of colour changes.

## DISCUSSION

Currently there are two species recognised within the genus *Pseudocophotis*, the Sundaic *P. sumatrana* and the Vietnamese endemic *P. kontumensis*. Hallermann & Böhme (2000) placed *Pseudocophotis sumatrana* in *Pseudocalotes*. However, their arguments are invalid if their own diagnosis of *Pseudocalotes* is taken into account. Apart from the fact that no other *Pseudocalotes* species has a rostral appendage, a corona of triangular supraciliary scales, a

hidden tympanum, and a (possibly) prehensile tail, most species of *Pseudocalotes* have a TL/SVL ratio of close to two or more (exceptions *floweri* 1.8 and *dringi* 1.6) while *Pseudocophotis* has a ratio of 1.36–1.57. The lowest number of midbody scales reported for any *Pseudocalotes* species was 38 for *Pseudocalotes flavigula* while *sumatrana* has 28–36 scales around the midbody (data for *Pseudocalotes* species from Hallermann & Böhme, 2000). It should also be noted that recent phylogenetic studies by Harvey et al. (2017a, b) revealed that *Pseudocalotes* is polyphyletic and that Javan and Sumatran species are more closely related to the Sumatran genera *Dendragama* and *Lophocalotes* than to mainland Thai-Malaysian and Indochinese species of *Pseudocalotes*. It also appears that *Pseudocophotis sumatrana* is morphologically more closely related to *Harpesaurus tricinctus*, except for the large sword-like horn of the latter, than to any *Pseudocalotes* species occurring on Java or Sumatra.

In light of our findings, the taxonomic placement of *kontumensis* needs to be re-assessed. The main synapomorphies that led Ananjeva et al. (2007) to include *kontumensis* in *Pseudocophotis* were a hidden tympanum, pholidosis, morphometric data, and a short, prehensile tail in accordance with Manthey & Grossmann's (1997) genus diagnosis. Given the short genus diagnosis (see above) provided by Manthey & Grossmann (1997), the inclusion of *kontumensis* in *Pseudocophotis* as argued by Ananjeva et al. (2007) is understandable. However, apart from significant morphological differences in species level such as the missing rostral appendage and the absence of a corona of supraciliary scales, there are also zoogeographical arguments against the inclusion of *kontumensis* in *Pseudocophotis*. To our knowledge there exists no agamid lizard genus that occurs in both the Indochinese and Sunda regions but lacks a representative on the Thai-Malaysian peninsula. It is our view that the inclusion of *kontumensis* in *Pseudocophotis* will not be upheld once genetic material of *sumatrana* and *kontumensis* becomes available for molecular phylogenetic studies.

The phylogenetic position of *Pseudocophotis* itself within the subfamily Draconinae is unclear. *Pseudocophotis sumatrana* shows several morphological characters that corroborate the earlier decision to consider the genus as monotypic. We will currently abstain from transferring *Pseudocophotis kontumensis* to the genus *Pseudocalotes*, although in most aspects there appears to be a larger affinity of *kontumensis* with mainland specimens of the latter genus than to *Pseudocophotis*. Similarly, *Pseudocophotis sumatrana* agrees in several characters with those described for *Harpesaurus tricinctus* such that the potential affinity of *Pseudocophotis* to *Harpesaurus* necessitates further investigations. In the case of *P. sumatrana*, observations of a live specimen are unavailable and the distribution as well as its ecology remain a mystery.

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## APPENDIX

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