

Remarks on the taxonomy and nomenclature of the genus *Hypsilurus* Peters, 1867 (Reptilia, Agamidae, Amphibolurinae)

Wolfgang Denzer¹, Ulrich Manthey²

¹ Society for Southeast Asian Herpetology, Calle Rio Segura 26, 30600 Archena, Murcia, Spain

² Society for Southeast Asian Herpetology, Kindelbergweg 15, 12249 Berlin, Germany

<http://zoobank.org/90C6EFC7-16E9-4FC8-AF34-C6B45DD1910D>

Corresponding author: Wolfgang Denzer (wolfdenoxford@yahoo.co.uk)

Abstract

Received 9 December 2015

Accepted 3 March 2016

Published 17 March 2016

Academic editor:

Johannes Penner

Specimens of *Hypsilurus* spp. corresponding to sequences deposited on GenBank were re-examined. The voucher specimens relating to GenBank sequences were tracked down and their species status confirmed. Sequences reported in earlier publication as *H. "bruijnii"* and *H. "nigrigularis"* turned out to be those of *H. magnus* and *H. schultzewestrumi* instead. Further confusion surrounded specimens of *H. modestus*, *H. dilophus* and *H. papuensis*. Based on these results a new phylogenetic tree was constructed and the genus name *Lophosaurus* Fitzinger, 1843 was resurrected.

Key Words

Hypsilurus

resurrection of *Lophosaurus*

Lophosaurus dilophus comb. n.

Lophosaurus boydii comb. n.

Lophosaurus spinipes comb. n.

Introduction

The Melanesian-Australian agamid genus *Hypsilurus* currently contains 20 species of which the majority (14 species) occurs on the main island of New Guinea (Manthey and Denzer 2006; Kraus and Myers 2012). Two species are endemic to Australia and several species inhabit the Bismarck Archipelago, Solomon Islands and d'Entrecasteaux Archipelago to the East, Aru Islands to the Southwest and Palau Islands to the North of New Guinea as well as most New Guinean offshore islands. The species with the widest distribution – and most probably the commonest species – is *H. modestus* which occurs on most of the before mentioned islands apart from the Solomons and Palau. *Hypsilurus dilophus* shows a similarly wide distribution and appears to be common in places where it occurs (Manthey and Denzer 2006).

The phylogeny of the genus *Hypsilurus* has been investigated within molecular studies concerned with agamid lizards in general by for example Macey et al. (2000a,

b), Schulte et al. (2003), Hugall et al. (2008) and Pyron et al. (2013). The phylogenetic studies of both Schulte et al. (2003) and Pyron et al. (2013) result in two clades for *Hypsilurus* rendering the genus paraphyletic. None of the studies compared the resulting phylogenetic trees to morphology-based taxonomy and consequently did not name individual clades for nomenclatural purposes.

Manthey and Denzer (2006) published a revision of the genus based on morphological characters. They proposed four species groups which can each be identified by a set of characters:

- 1) *godeffroyi* group: *Hypsilurus godeffroyi* Peters, 1867, *H. binotatus* Meyer, 1874, *H. bruijnii* Peters & Doria, 1878, *H. hikidanus* Manthey & Denzer, 2006, *H. longii* (Macleay, 1877), *H. macrolepis* Peters, 1872, *H. magnus* Manthey & Denzer, 2006, *H. ornatus* Manthey & Denzer, 2006, *H. papuensis* (Macleay, 1877), *H. schoedei* (Vogt, 1932), *H. schultzewestrumi* (Urban, 1999) and *H. tenuicephalus* Manthey &

- Denzer, 2006. This group also includes the recently described *H. capreolatus* Kraus & Myers, 2012.
- 2) *dilophus* group comprising *Hypsilurus dilophus* (Duméril & Bibron, 1837), *H. boydii* (Macleay, 1884) and *H. spinipes* (A. Duméril in Duméril & Duméril, 1851)
 - 3) *nigrigularis* group *Hypsilurus nigrigularis* Meyer, 1874, *H. geelvinkianus* (Peters & Doria, 1878), and *H. auritus* Meyer, 1874.
 - 4) *Hypsilurus modestus* Meyer, 1874 was considered as the sole representative of the *modestus* group.

Currently GenBank (gb, <http://www.ncbi.nlm.nih.gov/genbank/>) holds sequences for eight species. However, some specimen identifications and assignments of museum vouchers to their respective sequence have been questioned by Manthey and Denzer (2006) as several of the biomolecular studies preceded the revision of the genus and the material was prone to misidentification. Although our analysis does not include *Hypsilurus godeffroyi* – there are only two short 12S and 16S rRNA available – we note that the species identification of the specimen and corresponding sequence (gb AB031984; KUZ 45215, Kyoto University, Dept. of Zoology, collected in Irian Jaya, New Guinea) is most probably wrong as *H. godeffroyi* does not occur on New Guinea. Up to now the species is only known from two museum specimens of unreliable provenance and some bone fragments from Palau Island where the species may be extinct (Crombie and Pregill 1999, Bauer and Watkins-Colwell 2001, Manthey and Denzer 2006). With respect to the species investigated in this paper in particular the determination of *Hypsilurus nigrigularis* (gb AY133016 and HQ662413; TNHC 52009) and *Hypsilurus bruijnii* (gb AY133014; AMS R122474) were considered doubtful as both species are presumably only represented by very few specimens in museum collections and earlier descriptions were misleading (Boulenger 1914; de Rooij 1922). Currently *H. nigrigularis* is known only from its type locality (Rubi, Geelvink Bay) [nowadays Cenderawasih Bay or Teluk Sarera]. *H. bruijnii* specimens are only known from a few specimens near the type locality in the Arfak Mountains.

In this paper we present the results of our investigation into the correct determination of the museum material and assignment of the corresponding GenBank sequences, followed by a phylogenetic analysis of the identified species and a comparison with our earlier morphological study. Finally, we will briefly discuss nomenclatural consequences of the results.

Material and methods

For specimen identification we compared photographs of preserved specimens with material, figures and descriptions given in Manthey and Denzer (2006). Additionally, curators and collection managers were asked to verify the identification of specimens housed in their museum.

Abbreviations for museum collections are as follows: ABTC – Australian Biological Tissue Collection, AMS – Australian Museum Herpetological Collection; ANWC – Australian National Wildlife Collection; BPBM – Bernice Pauahi Bishop Museum, QM – Queensland Museum; SAM – South Australian Museum and TNHC – Texas Natural History Collections. Localities and geographical data for *Hypsilurus* species were sourced online from OZCAM (Online Zoological Collections of Australian Museums, <http://ozcam.ala.org.au>) and VertNet (<http://vertnet.org>).

Gene sequences that have been used in the earlier studies by Pyron et al. (2013), Macey et al. (2000a, b) and Schulte et al. (2003) were retrieved from the Nucleotide database (GenBank) of the National Centre for Biotechnology Information (www.ncbi.nlm.nih.gov/nucleotide). GenBank accession numbers are listed in Appendix 1. Museum voucher specimens of *Hypsilurus* spp. corresponding to GenBank sequences are specified in Table 1. The sequence lengths were typically about 1700 bases (shortest sequence 1696, longest 1720 bases) and comprised the mitochondrial genes ND1 (partial CDS), tRNA-Gln, tRNA-Ile, and tRNA-Met (complete sequence), ND2 (complete CDS) tRNA-Trp, tRNA-Ala, tRNA-Asx, tRNA-Cys, and tRNA-Tyr (complete sequence) as well as COI (partial CDS) (see Macey et al. 2000a for further information). In our phylogenetic analysis of 19 amphibolurine species the sequence alignment there were 1292 complete sites, of which 753 were variable and 583 were phylogenetically informative (45.1% of complete sites). We employed SeaView 4.5.4 (Gouy et al. 2010) to evaluate the phylogenetic relationships between Australian amphibolurine lizards and species of the genus *Hypsilurus*. This program package uses Clustal Omega (Sievers et al. 2011) for the alignment procedure as well as PHYLIP 3.696 / dnapsars (Felsenstein 1989) and PhyML 3.1 (Guindon et al. 2010) to calculate most parsimonious (MP) and maximum likelihood (ML) phylogenetic trees, respectively. For non parametric bootstrap analysis of the best tree the number of bootstrap replicates was set to 1000. In PhyML the best tree was found by enabling both nearest neighbour interchange (NNI) and subtree pruning and regrafting (SPR).

Results

Initially material used in earlier studies (Macey et al. 2000a, b; Schulte et al. 2003; Hugall et al. 2008) and studied within this paper was re-determined in accordance with the key provided in Manthey and Denzer (2006). Two species turned out to have been misidentified. The corresponding voucher specimens are depicted in Figure 1. The specimen identified in earlier publications as *H. "bruijnii"* (gb AY133014; AMS R122474) could be determined as *H. magnus* (see also Kraus and Myers 2012). The voucher specimen clearly shows characters distinguishing it from *H. bruijnii*. There are 4 rows of small scales between the infralabialia and enlarged submandib-

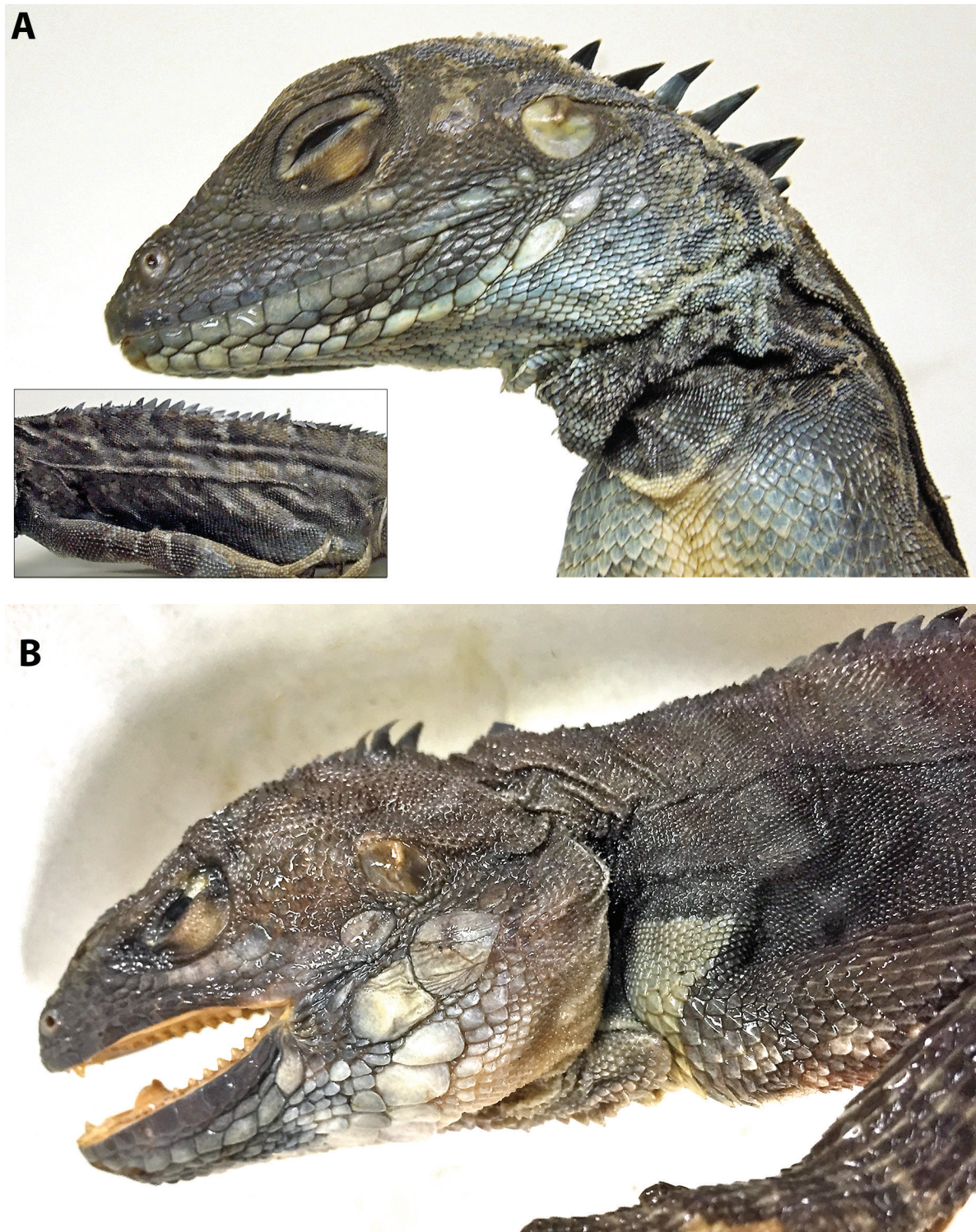


Figure 1. Photographs of re-determined specimens. **A:** *Hypsilurus magnus* (AMS R122474, previously identified as *H. bruijnii*). Please note the number of small scale rows ($n=4$) between infralabialia and enlarged submandibular scales. Insert: Lateral view of the dorsum showing crossbands. Photos: Cecilie Beatson. **B:** *Hypsilurus schultzei* (TNHC 52009, previously identified as *H. nigrigularis*). Please note the large gular plates that characterize this species. Photo: Travis LaDuc

ular scales (3 rows in *H. bruijnii*) plus it possesses several dorsal crossbands (no crossbands in *H. bruijnii*). The *H. "nigrigularis"* specimen (gb AY133016; TNHC 52009) could be identified as *Hypsilurus schultzei*. The gular region and the sides of the head of the voucher spec-

imens are covered with large plates as it is typical for *H. schultzei* (gular scales small in *H. nigrigularis*).

Some of the confusion surrounding the identification (or rather misidentification) of *Hypsilurus nigrigularis* specimens in museum collections most probably result-

Table 1. Museum and GenBank collection / accession numbers and collection data of *Hypsilurus* species used in this study. Where the currently accepted nomenclature differs from the species name provided on GenBank this is indicated below the gb accession number.

Species	Catalog No.	Genbank No.	Locality	Coordinates
<i>Hypsilurus boydii</i>	QM J60630	AY133013	Mt. Boolbun, South Queensland, Australia	15°55'S, 145°9'E
<i>Hypsilurus dilophus</i>	AMS R122449	AF128466	Namosado, Southern Highlands, Papua New Guinea	6°15'S, 142°47'E
<i>Hypsilurus magnus</i>	AMS R122474	AY133014 <i>H. bruijnii</i>	Fogamayu [=Fogomaiu on Google Maps], Southern Highlands, Papua New Guinea	6°31'S, 143°05'E
<i>Hypsilurus modestus</i>	AMS R115478	AY133015	Yuro, Chimbu District, Papua New Guinea	6°32'S, 144°51'E
<i>Hypsilurus papuensis</i>	BPBM 24102	AY133017	Wau, Morobe Province, Papua New Guinea	7°20'S, 146°43'E
<i>Hypsilurus schultzei</i>	TNHC 52009	AY133016 <i>H. nigrigularis</i>	Kaironk Village, ~10 km NW Simbai, Papua New Guinea	5°16'S, 144°32'E
<i>Hypsilurus spinipes</i>	ANWC R05324	AY133018	Nana Creek Area, N(orth) of Coffs Harbour, New South Wales, Australia	30°12'S, 152°57'E

ed from two earlier published figures, both of which did not depict “*Gonyocephalus nigrigularis*” [= *H. nigrigularis*] as written in the figure captions. In fact Boulenger (1914: pl.XXVIII, fig. 4) shows *H. magnus* and AMNH (1972:92) shows a photograph of *H. schultzei* instead. To our knowledge the only published figure of a true *H. nigrigularis* is the photograph of the type specimen in Manthey and Denzer (2006: 9, fig. 6).

The specimen of *H. dilophus* (gb AF128466; AMS R122449) is currently catalogued as *H. magnus* (OZCAM). This specimen is also erroneously (pers. comm. F. Kraus) listed in Kraus (2010) as AMS R12249 (sic! =R122449) and identified as *H. magnus* but citing a differing locality, namely Fogamayu instead of Namosado (Southern Highlands District) as given on OZCAM, GenBank and in earlier publications (Hugall et al. 2008, ABTC 46027; Schulte et al. 2003; Macey et al. 2000a). A re-examination of the specimen corroborated its original identification as *H. dilophus* and the collection locality as Namosado.

Additionally there were inconsistencies with respect to the GenBank sequence of *Hypsilurus papuensis* (gb AY133017) and its corresponding voucher specimen. In an earlier publication (Schulte et al. 2003; Appendix) the source is given a SAMA tissue sample 12965 (South Australian Museum) referring to a voucher specimen CCA 12965 (s. GenBank record). The abbreviation CCA typically refers to collection numbers by C. Austin (Louisiana State University) according to whom this number is too high for collections he made on New Guinea (pers. comm. C. Austin). Enquiries with the Australian Biological Tissue Collection (ABTC) revealed that the number should actually read AA12965 and that this represents a collection number by A. Allison (BPBM). The most recent and correct number for the tissue sample is ABTC 49747 and the corresponding voucher specimen is deposited under BPBM 24102.

Finally there also exists some confusion around *Hypsilurus modestus* on the OZCAM online database. Schulte et al. (2003) and we used the sequence gb AY133015 (voucher specimen AMS R115478). This specimen is still registered under its old name „*Gonyocephalus modestus*“. A different sequence (gb AF128464; AMS R122434)

was used by Hugall et al. (l.c.) and correctly identified as *H. modestus*. The online database (OZCAM) however, erroneously (pers. comm. G. Shea) assigns this number to a specimen of *H. magnus*.

Based on these findings we conducted a phylogenetic analysis the results of which are depicted in Figure 2. Both cladograms (MP and ML) are nearly identical and recover previously published phylogenetic relationships. Our analysis corroborates the rejection of the monotypic genus *Caimanops* and classification of *Caimanops amphiboluroides* (Lucas & Frost, 1902) as *Diporiphora* (Hugall et al. 2008) as well as the classification of *Rankinia adelaidensis* (Gray, 1841) as *Ctenophorus* (Melville et al. 2001, Hugall et al. 2008).

With respect to species of the genus *Hypsilurus* both trees clearly support different clades. Our maximum likelihood analysis yields a clade containing the two Australian species *Hypsilurus spinipes* and *H. boydii* as well as the wide ranging *H. dilophus* as a sister group to the other studied Australian Amphibolurinae. The remaining four Melanesian species are well supported in an apparently monophyletic clade but still with well supported branches differentiating between *H. modestus* and *H. magnus*, *H. papuensis*, *H. schultzei*. In our parsimony analysis a clade containing *Hypsilurus spinipes*, *H. boydii* and *H. dilophus* is formed that also contains the closely related species *Moloch horridus* and *Chelosania brunnea* as a sister group. This clade is nested between the Melanesian species of *Hypsilurus* and the remaining Australian amphibolurine lizards. The branch supports in our maximum likelihood and parsimony analyses for the *Moloch / Chelosania* clade are comparatively weak. None of the resulting topologies is sufficiently supported to present a clear case for either phylogenetic position of these two genera. Again, our parsimony analysis produces a node separating the branch containing only *H. modestus* (100% bootstrap support) from the branch comprising the other Melanesian species of *Hypsilurus*. In summary the two resulting *Hypsilurus* clades are well supported by molecular genetics and well-defined by morphology (see Manthey and Denzer 2006) such that their separation into two genera is justified.

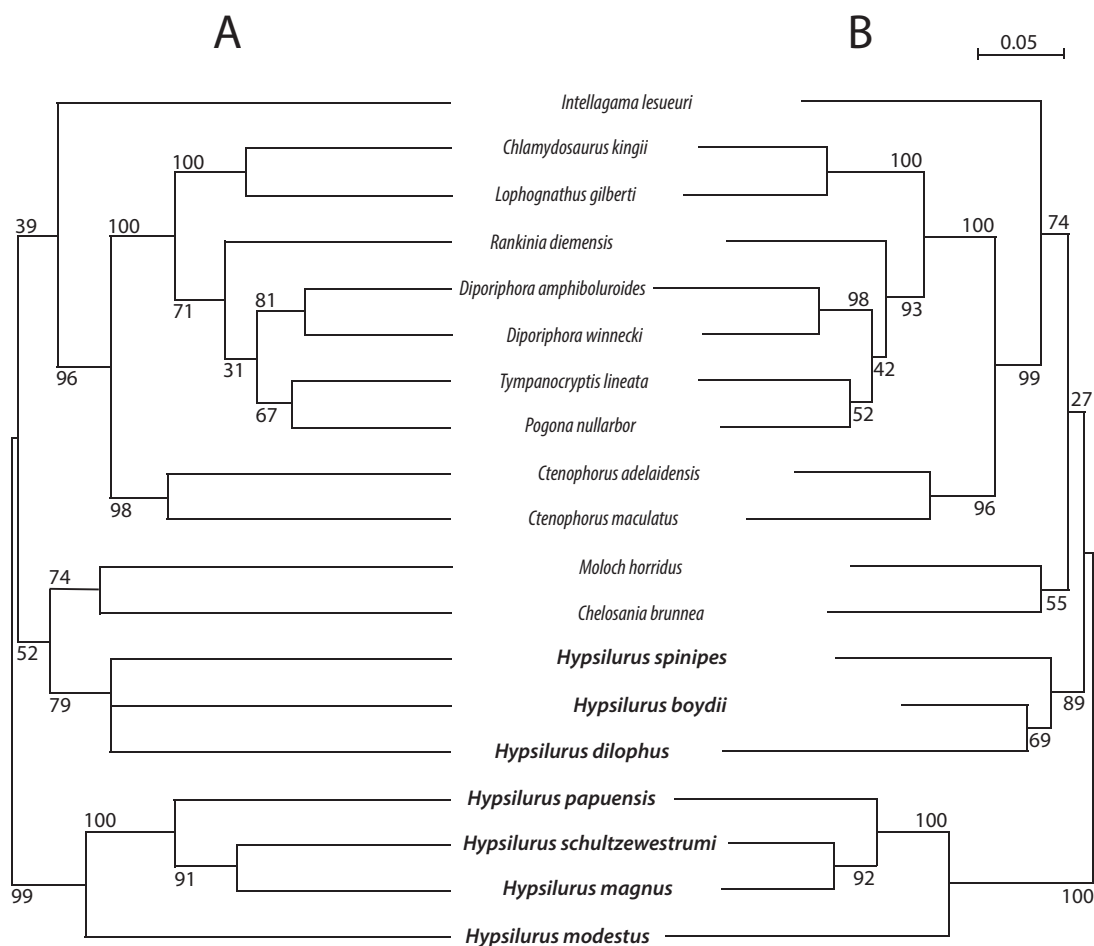


Figure 2. Phylogenetic analysis of *Hypsilurus* spp. and some Australian agamid lizards belonging to the subfamily Amphibolurinae. **A:** Most parsimonious tree (PHYMLP/Dnapars); **B:** Maximum likelihood tree (PhyML). Branch length scale represents number of substitutions/site. Branch support values are given above or next to the branch. Both trees clearly show that *Hypsilurus* is paraphyletic and forms two distinct clades.

Discussion

First, we would like to note that, if sequences are retrieved from databases or databases are consulted for identifying museum material, it may be necessary and appropriate to re-determine the voucher specimens. Great care has to be taken to ensure correct species identification or otherwise misleading phylogenies are published that do not reflect the true intra- and intergeneric relationships between species in accordance with their morphology based taxonomy. For an in-depth discussion on issues related to GenBank see Federhen (2014).

With respect to *Hypsilurus* species our analysis corroborates the results of earlier published phylogenetic studies by Schulte et al. 2003, Hugall et al. 2008 and Pymon et al. 2013, where the Australian species (*H. boydii* and *H. spinipes*) cluster with *H. dilophus*, while the Melanesian species *H. "bruijnii"* (= *magnus*, see results) and *H. "nigrigularis"* (= *schultzei*, see results) are closely related and form a second clade including *H. papuensis*; *H. modestus* is the basal taxon and a sister group to the remaining Melanesian *Hypsilurus* species. Macey

et al. (2000a, b) even considered *H. modestus* sufficiently genetically different from other *Hypsilurus* species that they used *Arua* Doria, 1874 as the genus name. The study by Hugall et al. (2008, included species: *H. modestus*, *H. "bruijnii"* (= *magnus*, see results), *H. spinipes*, *H. boydii*, *H. dilophus*) recovered a clade containing *Chelosania* and *Moloch* as well as *Hypsilurus* spp. that was considered to be the sister taxon to all remaining Australian amphibolurine taxa, Townsend et al. (2011, only *Hypsilurus boydii* included) found that *Chelosania* and *Moloch* constitute a sister taxon to a clade containing all Australian amphibolurine taxa and *Hypsilurus*. Hugall et al. (l.c.) report two clades with respect to *Hypsilurus* species; one comprising the *H. boydii*, *H. spinipes* and *H. dilophus*, the other clade contains *H. "bruijnii"* (= *magnus*, see results) and *H. modestus*. Morphologically they also found support for this split in the dentition of the species. While *H. boydii*, *H. spinipes* and *H. dilophus* possess "numerous (15–17) small marginal teeth and tiny anterior pleurodont teeth", *H. "bruijnii"* (= *magnus*, see results) and *H. modestus* possess "larger marginal teeth and enlarged 'caniniform' pleurodont teeth" (Hugall et al. 2008: 354).

Already in the original description of *Gonyocephalus (Arua) inornatus* [= *H. modestus* fide Boulenger 1885 and Manthey and Denzer 2006] Doria (1874) noted morphological differences between the subgenus *Hypsilurus* and the subgenus *Arua* proposed by him. Doria (l.c.) stated that *Arua* can easily be distinguished from *Hypsilurus*: “per la mancanza di grossi scudetti agli angoli della bocca, per un sacco golare poco ampio, per la cresta dorsale inconspicua...” [by missing large scales at the angle of the mouth, by a small gular sac, by an inconspicuous dorsal crest...]. The genus *Arua* was resurrected by Moody (1980) but unfortunately never published formally. Denzer et al. (1997: 323) treated *Arua* as a subgenus ad *Hypsilurus*. Macey et al. (2000) removed *H. modestus* from its synonymy with *Hypsilurus* species and placed the species in the genus *Arua*. It has to be noted that Peters and Doria (1878) and Moody (1980) also considered *Hypsilurus geelvinkianus* and *H. auritus* as members of *Arua*. While *H. geelvinkianus* is superficially similar to *H. modestus*, *H. auritus* is not. Both species have several morphological features in common with *H. nigrigularis* and were combined in a *nigrigularis* group by Manthey and Denzer (2006). For lack of material these species have not yet been investigated by molecular biological techniques and it may well turn out that species considered by us as belonging to *Hypsilurus* are more closely related to *Arua*, should the latter genus be resurrected in future.

The clade containing *H. magnus*, *H. papuensis* and *H. schultzei* is supported by morphological data and these species are members of the *godeffroyi* group as defined by Manthey and Denzer (2006). Common characters are enlarged scales or plates at the angle of the mouth or below the tympanum, a row of enlarged submandibular scales (called submaxillaries by Manthey and Denzer [2006]), a homogeneous dorsal scalation and anterior gular pouch scales larger than posterior gular pouch scales.

The clade containing the species *Hypsilurus spinipes*, *H. boydii* and *H. dilophus* was recognised as a species group by Manthey and Denzer (2006). The group can be characterised morphologically by a heterogeneous dorsal scalation and their short tail length (TL/SVL < 2.3 in most cases smaller than 2). In their original description *H. boydii* were placed in the genus *Tiaris* Duméril & Bibron, 1837 and *H. dilophus* in the genus *Lophyrus* Duméril, 1805. *Tiaris* is preoccupied and hence not available (*Tiaris* Swainson, 1827, Aves: Passeriformes); the same is true for *Lophyrus* which is preoccupied by *Lophyrus* Poli, 1791 (Mollusca). Manthey and Denzer (l.c.) showed that *Lophosaurus* Fitzinger, 1843 is a nomen oblitum preceding *Hypsilurus* Peters, 1867 and available if *H. dilophus* is removed from its synonymy with *Hypsilurus*. Therefore the only name available for nomenclatural purposes for this group of lizards is *Lophosaurus* Fitzinger, 1843 with *H. dilophus* as the type species.

Conclusion

We currently consider the clade containing *Hypsilurus modestus* and all Melanesian species of *Hypsilurus* (apart

from *H. dilophus*) as monophyletic. We suggest to leave these species in *Hypsilurus* sensu lato until additional material becomes available and further biomolecular studies can be conducted that include additional species of *Hypsilurus* s.l. Morphologically *Hypsilurus* s.l. can be divided into a *godeffroyi* species group, a *nigrigularis* species group and the monotypic *modestus* species group (s. Manthey and Denzer 2006 for definitions). All three groups may turn out to be genera in their own right, in particular further analysis may warrant the resurrection of the genus *Arua* Doria, 1874 for *Hypsilurus modestus*. We also consider the clade containing the Australian species *Hypsilurus boydii* and *H. spinipes* as well as the Melanesian *H. dilophus* as monophyletic and propose to resurrect the genus name *Lophosaurus* Fitzinger, 1843 for this group of agamid lizards. The name is masculine gender and therefore the species epithets remain the same.

Lophosaurus Fitzinger, 1843

Type species. *Lophyrus dilophus* Duméril & Bibron, 1837.

Nomenclature of the type species. On p. 419 Duméril and Bibron (1837) introduce the new species *Lophyrus dilophus*. A line further down they refer to a drawing of this species on plate 46 under the genus name of *Tiaris*. This discrepancy is explained on p. 421 where the authors state that it was originally intended to erect a new genus *Tiaris* for this species and that they decided against it at a later stage. We assume that the plates containing the name *Tiaris* had already been printed and subsequent changes would have been difficult to realize. On the same page the authors remark that the Leiden Museum holds specimens of this species under the name *Calotes megapogon*. This name has never been published in conjunction with a description and therefore constitutes a nomen nudum.

Diagnosis. Medium to large sized, arboreal amphibolurine lizard without femoral or precloacal pores (present in all Australian agamid lizards apart from *Chelosania* and *Moloch*); no spines on the body (present in *Moloch*), no frill around the neck (present in *Chlamydosaurus*); a transverse gular fold (absent in *Chelosania*), dorsal scales heterogeneous in size (homogeneous in all *Hypsilurus* s. l.); TL/HBL < 2.3, typically < 2; lacrimal bone present (absent in all Australian Amphibolurinae apart from *Intellagama* and *Chelosania*)

Content

Lophosaurus dilophus (Duméril & Bibron, 1837)

Distribution: New Guinea and adjacent islands

Lophosaurus boydii (Macleay, 1884)

Distribution: Australia (Northeastern Queensland)

Lophosaurus spinipes (Duméril & Bibron, 1851)

Distribution: Australia (Southeastern Queensland, north-eastern New South Wales)

Key to the species

- 1a Median line of gular pouch without lanceolate scales *L. spinipes*
 1b Median line of gular pouch with lanceolate scales 2
 2a Diameter of conical scales below tympanum > ½ diameter of the tympanum *L. boydii*
 2b Diameter of conical scales below tympanum << ½ diameter of the tympanum *L. dilophus*

Acknowledgements

We are grateful to Travis LaDuc and David Cannatella (both TNHC), Cecilie Beatson and Ross Sadlier (AMS) as well as Molly Hagemann (BPBM) for providing photographic records of specimens held in their collections. Leanne Wheaton (SAM) tracked down the tissue specimen for *H. papuensis* and provided vital information regarding the voucher specimen. Chris Austin (Louisiana State University) shared his view on the collection number of *H. papuensis*; Allen Allison and Molly Hagemann (both BPBM) confirmed the identity and collection data of the voucher specimen. Fred Kraus (University of Michigan) shared his knowledge on *H. magnus* specimens in the collection of the Australian Museum and confirmed their identification. Glenn Shea (University of Sydney) helped to identify the voucher specimen for *H. dilophus* and checked the identities of *H. modestus* specimens held in the Australian Museum. We very much appreciate their help in solving the “mysteries” surrounding some of the specimens used in this study.

References

- AMNH (1972) The American Museum of Natural History. An Introduction. The American Museum of Natural History, New York, 160 pp.
- Bauer AM, Watkins-Colwell GJ (2001) On the origin of the types of *Hypsilurus godeffroyi* (Reptilia: Squamata: Agamidae) and early German contributors to the herpetology of Palau. *Micronesica* 34(1): 73–84.
- Boulenger GA (1914) An annotated list of the batrachians and reptiles collected by the British Ornithologists' Union Expedition and the Wollaston Expedition in Dutch New Guinea. *Transactions of the Zoological Society of London*, Vol. XX: 247–275. doi: 10.1111/j.1469-7998.1912.tb07833.x
- Crombie RI, Pregill GK (1999) A checklist of the herpetofauna of the Palau Islands (Republic of Belau). *Oceania. Herpetological Monographs* 13: 29–80. doi: 10.2307/1467060
- Denzer W, Günther R, Manthey U (1997) Kommentierter Typenkatalog der Agamen (Reptilia: Squamata: Agamidae) des Museums für Naturkunde der Humboldt-Universität zu Berlin (ehemals Zoologisches Museum Berlin). *Mitteilungen des Zoologischen Museums Berlin* 73(2): 309–332. doi: 10.1002/mmnz.19970730209
- Doria G (1874) Enumerazione dei rettili raccolti da Dr. O. Beccari in Amboina, alle Isole Aru ed alle Isole Kei durante gli anni 1872–73. *Annali del Museo Civico di Storia Naturale di Genova*, ser. 1 vol. 6: 325–357.
- Duméril AMC (1805) *Zoologie analytique, ou méthode naturelle de classification des animaux, rendue plus facile à l'aide de tableaux synoptiques*. Allais, Paris, “1806”: i–xxxii + 1–344.
- Duméril AMC, Bibron G (1837) *Erpétologie générale ou Histoire Naturelle complète des Reptiles*. Librairie Encyclopedique de Roret, Paris, ii+572 pp.
- Duméril MC, Duméril MA (1851) *Catalogue méthodique de la collection des reptiles du Museum d'Histoire Naturelle de Paris*. Gide et Baudry, Paris, vi + 224 pp.
- Federhen S (2014) Type material in the NCBI taxonomy database. *Nucleic Acid Research* 43(Database issue): D1086–D1098.
- Felsenstein J (1989) PHYLIP – Phylogeny Inference Package (Version 3.2). *Cladistics* 5: 164–166.
- Fitzinger LJ (1843) *Systema Reptilium. Fasciculus Primus. Amblyglossae*. Braumüller & Seidel Bibliopolas, Wien, 106 pp.
- Gouy M, Guindon S, Gascuel O (2010) SeaView version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. *Molecular Biology and Evolution* 27(2): 221–224. doi: 10.1093/molbev/msp259
- Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. *Systematic Biology* 59(3): 307–321. doi: 10.1093/sysbio/syq010
- Hugall AF, Foster R, Hutchinson M, Lee MS (2008) Phylogeny of Australasian agamid lizards based on nuclear and mitochondrial genes: implications for morphological evolution and biogeography. *Biological Journal of the Linnean Society* 93: 343–358. doi: 10.1111/j.1095-8312.2007.00911.x
- Kraus F (2010) More range extensions for Papuan reptiles and amphibians. *Herpetological Review* 41(2): 246–248.
- Kraus F, Myers S (2012) New species of *Hypsilurus* (Agamidae) from Papua New Guinea. *Journal of Herpetology* 43(3): 396–401. doi: 10.1670/11-159
- Macey JR, Schulte II JA, Larson A, Ananjeva NB, Wang Y, Pethiyagoda R, Rastegar-Pouyani N, Papenfuss TJ (2000a) Evaluating Trans-Tethys migration: An example using acrodont lizard phylogenetics. *Systematic Biology* 49(2): 233–256. doi: 10.1093/sysbio/49.2.233
- Macey JR, Schulte II JA, Larson A (2000b) Evolution and phylogenetic information content of mitochondrial genomic structural features illustrated with acrodont lizards. *Systematic Biology* 49(2): 257–277. doi: 10.1093/sysbio/49.2.257
- Macleay W (1877) The lizards of the Chevert Expedition. *Proceedings of the Linnean Society New South Wales* 2: 97–104.
- Macleay W (1884) Notes on some reptiles from the Herbert River, Queensland. *Proceedings of the Linnean Society New South Wales* 8: 432–436. doi: 10.5962/bhl.part.28670
- Manthey U, Denzer W (2006) A revision of the Melanesian-Australian Angle Head lizards of the genus *Hypsilurus* (Sauria: Agamidae: Amphibolurinae), with description of four new species and one new subspecies. *Hamadryad* 30(1&2): 1–40.
- Melville J, Ritchie EG, Chapple SN, Glor RE, Schulte II JA (2011) Evolutionary origins and diversification of dragon lizards in Aus-

- tralia's tropical savannas. *Molecular Phylogenetics and Evolution* 58: 257–270. doi: 10.1016/j.ympev.2010.11.025
- Melville J, Schulte II JA, Larson A (2001) A molecular phylogenetic study of ecological diversification in the Australian lizard genus *Ctenophorus*. *Journal of Experimental Zoology: Molecular and Developmental Evolution* 291(4): 339–353. doi: 10.1002/jez.1133
- Meyer AB (1874) Eine Mitteilung von Hrn. Dr. Adolf Bernhard Meyer über die von ihm auf Neu-Guinea und den Inseln Jobi, Mysore und Mafoor im Jahre 1873 gesammelten Amphibien. *Monatsberichte der Königlichen Akademie der Wissenschaften zu Berlin*, 128–140.
- Moody SM (1980) Phylogenetic and historical biogeographical relationship of the genera in the family Agamidae (Reptilia: Lacertilia). Ph.D. Thesis, University of Michigan, 373 pp.
- Peters W (1867) Sitzung der physikalisch-mathematischen Klasse. Über Flederthiere (*Pteropus Gouldii*, *Rhinolopus Deckenii*, *Vespertilio lobipes*, *Vesperugo Temminckii*) und Amphibien (*Hypsilurus Godeffroyi*, *Lygosoma scutatum*, *Stenostoma narirostre*, *Onychocephalus unguirostris*, *Ahaetulla polylepis*, *Pseudechis scutellatus*, *Hoplobatrachus Reinhardtii*, *Hyla coriacea*). *Monatsberichte der Königlichen Akademie der Wissenschaften zu Berlin*, 703–724.
- Peters W (1872) Über neue oder weniger bekannte Saurier. *Monatsberichte der Königlichen Akademie der Wissenschaften zu Berlin*, 774–776.
- Peters W, Doria G (1878) *Catalogo dei rettili e dei Batraci raccolti da O. Beccari, L.M. D'Albertis e A.A. Bruijn nella sotto-regione Austro-Malese*. *Annali del Museo Civico di Storia Naturale di Genova*, Genova ser. 1(13): 323–450, Pls. 1–7.
- Pyron RA, Burbrink FT, Wiens JJ (2013) A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology* 13: 93. doi: 10.1186/1471-2148-13-93
- Rooij N de (1922) *Reptiles (Lacertilia, Chelonia and Emydosauria)*. Resultat de L'Expedition Scientifique Neerlandaise a la Nouvelle Guinee en 1912 et 1913 sous les auspices de A. Franssen Herderschee, Vol. XIII (Zoologie, Livr. I): 133–153.
- Schulte II JA, Melville J, Larson A (2003) Molecular phylogenetic evidence for ancient divergence of lizard taxa on either side of the Wallace's Line. *Proceedings of the Royal Society of London B* 270: 597–603. doi: 10.1098/rspb.2002.2272
- Sievers F, Wilm A, Dineen D, Gibson TJ, Karplus K, Li W, Lopez R, McWilliam H, Remmert M, Soeding J, Thompson JD, Higgins DG (2011) Fast, scalable generation of high-quality protein multiple sequence alignments using Clustal Omega. *Molecular Systems Biology* 7, 539. doi: 10.1038/msb.2011.75
- Townsend TM, Mulcahy DG, Noonan BP, Sites Jr JW, Kuczynski CA, Wiens JJ, Reeder TW (2011) Phylogeny of iguanian lizards inferred from 29 nuclear loci, and a comparison of concatenated and species-tree approaches for an ancient, rapid radiation. *Molecular Phylogenetics and Evolution* 61: 363–380. doi: 10.1016/j.ympev.2011.07.008
- Urban H (1999) Eine neue Agamenart der Gattung *Gonocephalus* aus Papua-Neu Guinea (Squamata: Sauria: Agamidae). *Herpetozoa* 11(3/4): 185–188.
- Vogt T (1932) Beitrag zur Reptilienfauna der ehemaligen Kolonie Deutsch-Neuguinea. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin* (5–7): 281–294.

Appendix 1

Genbank Accession Numbers and corresponding museum specimen data (for *Hypsilurus* specimens only): *Caimanops* (= *Diporiphora*) *amphiboluroides* (AF128472), *Chelosania brunnea* (AF128465), *Chlamydosaurus kingii* (EF090421), *Ctenophorus adelaidensis* (AF128471), *Ctenophorus maculatus* (AF375628), *Diporiphora winneckei* (AY133012), *Lophognathus gilberti* (AY133019), *Moloch horridus* (AF128467), *Physignathus* (= *Intellagama*) *lesueurii* (AF128463), *Pogona nullarbor* (AY133025), *Rankinia diemensis* (KF791202), *Tympa-nocryptis lineata* (AF128475).

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Zoosystematics and Evolution](#)

Jahr/Year: 2016

Band/Volume: [92](#)

Autor(en)/Author(s): Denzer Wolfgang, Manthey Ulrich

Artikel/Article: [Remarks on the taxonomy and nomenclature of the genus *Hypsilurus* Peters, 1867 \(Reptilia, Agamidae, Amphibolurinae\) 103-110](#)