

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

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Abstract

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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-

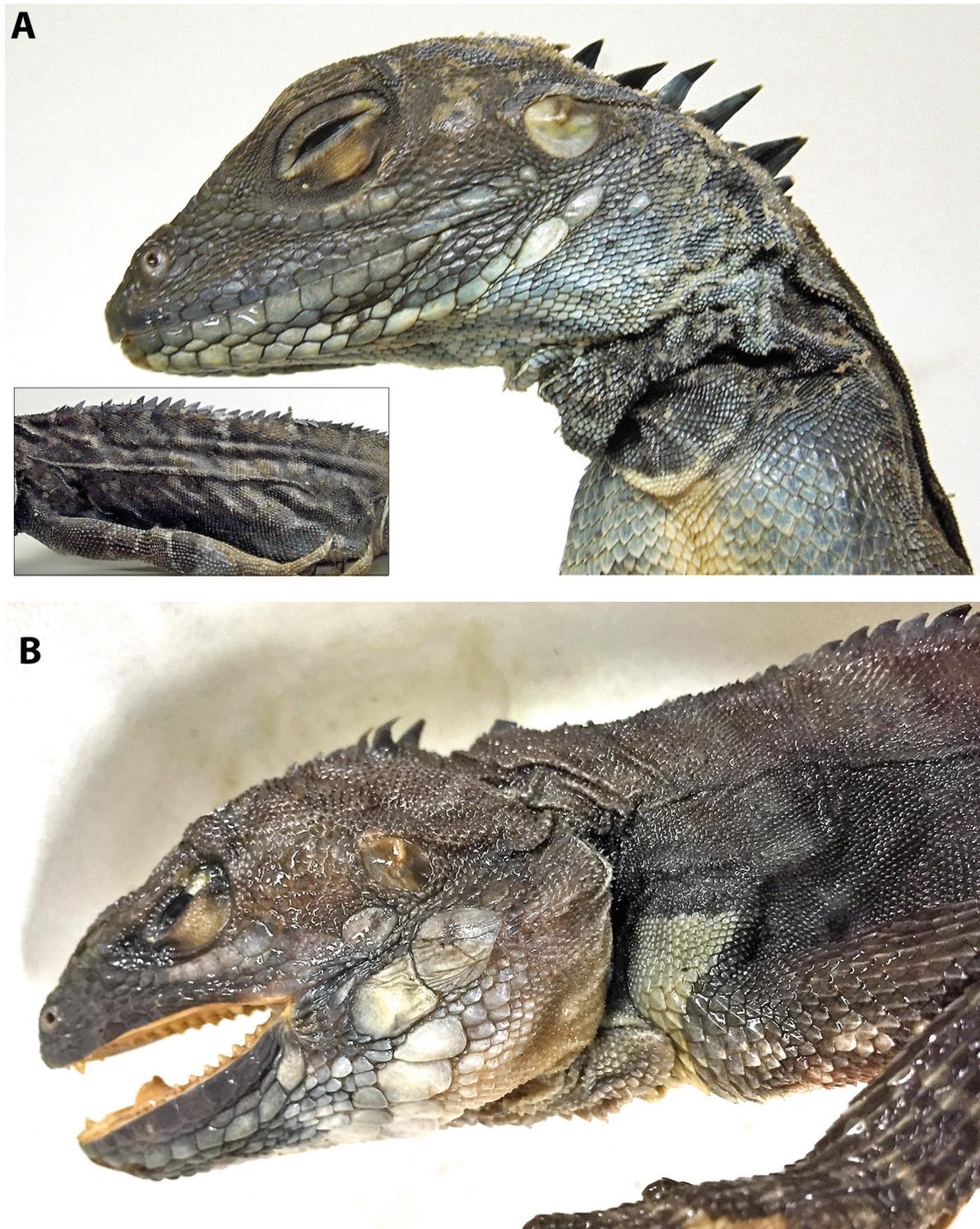


Figure 1. Photographs of re-determined specimens. **A:** *Hypsilurus magnus* (AMS R122474, previously identified as *H. bruijnii*). Please note the number of small scale rows ($n=4$) between infralabialia and enlarged submandibular scales. Insert: Lateral view of the dorsum showing crossbands. Photos: 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. nigricularis</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 nigricularis*" [= *H. nigricularis*] 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. nigricularis* 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.

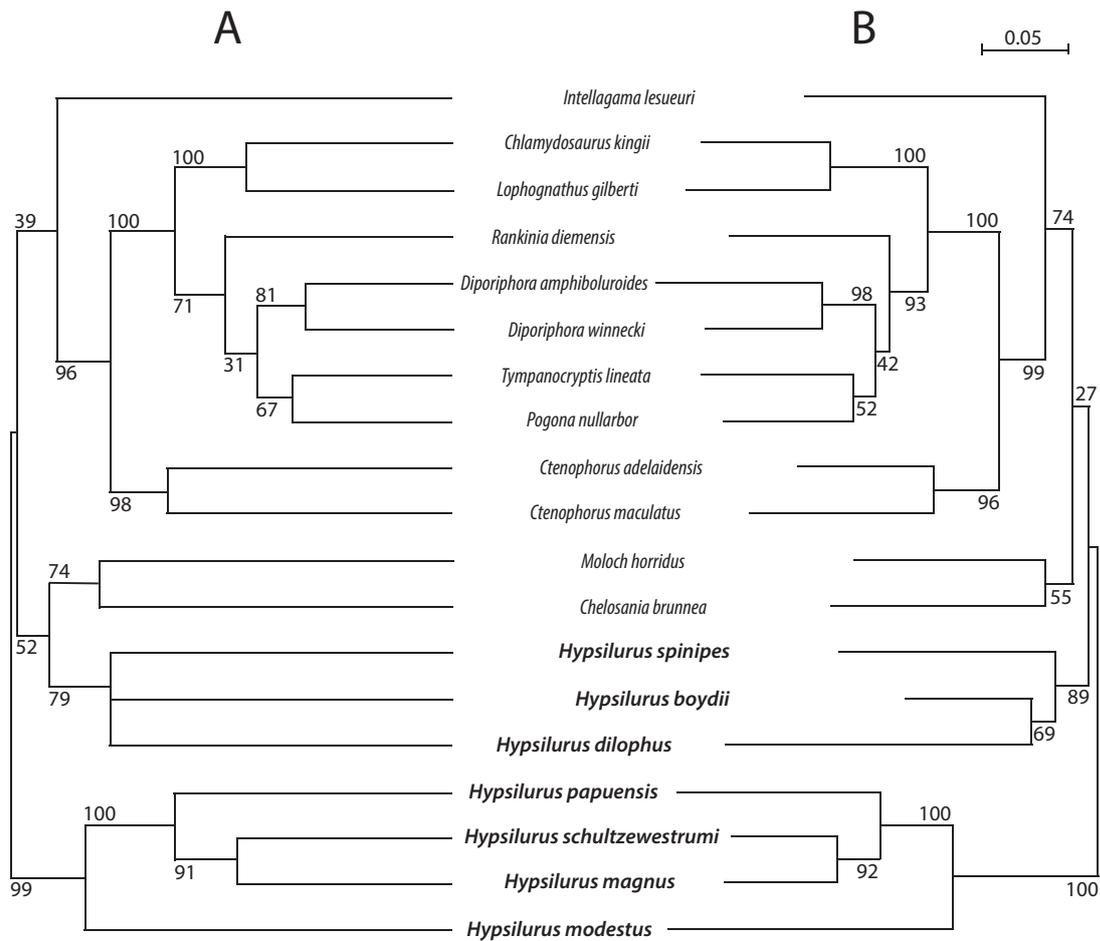


Figure 2. Phylogenetic analysis of *Hypsilurus* spp. and some Australian agamid lizards belonging to the subfamily Amphibolurinae. **A:** Most parsimonious tree (PHYMLP/Dnapars); **B:** Maximum likelihood tree (PhyML). Branch length scale represents number of substitutions/site. Branch support values 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. schultzewestrumi* 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*

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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).