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A break up of the genus *Acrochordus* Hornstedt, 1787, into two tribes, three genera and the description of two new species (Serpentes: Acrochordidae).

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ABSTRACT

This paper presents a revised taxonomy for the living Acrochordidae.
The species *Acrochordus javanicus* Hornstedt, 1787 divided by McDowell in 1979 into two species is further divided, with two new species from south-east Asia formally named for the first time. The taxon *A. arafurae* McDowell, 1979 is placed in a separate genus, named for the first time.

A. granulatus Schneider, 1799 is placed in a separate genus, for which the name *Chersydrus* Schneider, 1801 is already available.

Keywords: Taxonomy; Australasia; Asia; *Acrochordus*; *Chersydrus*; new genus; *Funkiacrochordus*; new tribes; Acrochordidini; Funkiacrochordidini; new subgenus: *Vetusacrochordus*; new species; *malayensis*; *mahakamiensis*.

INTRODUCTION

This paper presents a revised taxonomy for the living Acrochordidae.

The genus *Acrochordus* Hornstedt, 1787 as recognized to date has been studied by myself since the early 1980's (see photo taken in the 1980's of an albino specimen from Alligator River, NT on the cover of this journal. This has included the examination of specimens and photos of all species recognized to date, including two formally named for the first time here.

The material and methods forming the basis of the taxonomic decisions within this paper has been a thorough review of my data as well as the relevant published literature, including the definitive papers of McDowell (1979), Sanders *et al.* (2010) and corroborative data in many other published findings.

Coupled with a review of the molecular data published to date, including Pyron *et al.* (2013), geological records, as outlined by Molengraaff 1921a, 1921b, Voris 2000, sources cited by these authors and many other similar published studies. I have made the following taxonomic and nomenclatural judgements based on the evidence before me.
The species *Acrochordus javanicus*, divided by McDowell in 1979 into two species is further divided, with two new species from south-east Asia formally named for the first time. The taxon *A. arafurae* McDowell, 1979 is placed in a genus, named for the first time, while *A. granulatus* Schneider, 1799 is placed in a separate genus, for which the name *Chersydrus* Schneider, 1801 is already available.

To make further sense of the generic arrangement created herein, two tribes are erected for each main grouping.

I note also the following: In 2006 an online petition sponsored by a group of animal-hating pseudoscientists including Wolfgang Wüster, Mark O'Shea, David John Williams, Bryan Fry and others posted at: http://www.aussiereptileclassifieds.com/phpPETITION (Hunter *et al.* 2006) called for my successful wildlife education business and all my other herpetological activity to be shut down by the government of Victoria, Australia. These men were successful in that after a ruthless five-year campaign, on 17 August 2011, 11 heavily armed police and wildlife officers conducted a highly illegal and violent raid on our family home and research facility. Myself, my wife and two young daughters were arrested at gunpoint and held hostage in the kitchen of the house for nine hours while the facility was ransacked and effectively destroyed. Besides the unspeakable acts of killing captive snakes and criminal damage to cages, household goods, the raiding officers illegally shut down our business and effectively placed myself under house arrest at gunpoint for some months after the raid.
An application by myself to the Supreme Court of Victoria led to the re-opening of our unlawfully shut down wildlife education business.

Of greater relevance here is that at the time of the raid, research files, and the like spanning more than 40 years were taken and never returned, including materials and records relevant to this paper.

Material taken included all the computers, disks, hard drives, backups, cameras, scientific literature and other forms of information storage at the facility. All were loaded into the back of a truck and a very large trailer and carted off.

Faced with the dilemma of deciding whether to spend another fourty years gathering data, by which time I may be dead from old age, being aged 52 as of 2014 (and with a family history of deaths from heart disease from the 40's onward), or publishing the relevant paper/s with minimal data, I have opted to publish. Underlying this motivation has been an increasing concern that a delay to formally identify and name undescribed biodiversity may lead to its extinction before another scientist gets around to the matter.

Engstrom *et al*. (2002) wrote: “The documentation of this diversity must be seen as an activity that is done not just for posterity but for immediate action and protection.”

A number of authors including Kaiser (2012a, 2012b, 2013 and 2014), Kaiser *et al.* (2013), Naish (2013) and Wüster *et al.* (2014), all part of the group of people effectively controlled by Wüster, have been highly critical of the fact that I have assigned names to unnamed clades of snakes. Their unscientific and childish attacks, continued incessantly on social media such as Facebook and Twitter are rejected herein as destabilizing the nomenclature and impeding the progress of science.

Their ridiculous comments and false and defamatory statements are systematically rebutted by Hoser (2013).

I also note that many taxa formally named by myself for the first time in earlier publications (e.g. Hoser 2000a, 2000b) are in fact threatened species.

Therefore I note the sensible remarks of Engstrom *et al.* (2002) as a perfectly reasonable explanation for the publishing of taxon descriptions for such unnamed groups. This remains the case even if a sizeable amount of my original research, files, photos and data have been stolen and therefore cannot be relied upon and incorporated into these contemporary publications.

ACROCHORDUS HORNSTEDT, 1787

The taxonomic treatment of the genus *Acrochordus* Hornstedt, 1787 has been relatively stable. For most of the past two centuries, two well-defined species have been widely recognized. These are the Large Wart Snake *Acrochordus javanicus* Hornstedt, 1787 and the lesser wart snake *A. granulatus* (Schneider, 1799).

More recently *Acrochordus arafurae* McDowell, 1979 from northern Australia and southern New Guinea was described. This taxon was previously being regarded as *Acrochordus javanicus* Hornstedt, 1787.

A number of recent authors have placed the species *granulatus* within Schneider’s monotypic 1801 genus *Chersydrus*, including most recently Sharma (2004). While people have argued about the morphological significance of the characters differentiating Schneider’s species from the *javanicus* group, molecular evidence arguing for division of all three currently recognized species into three (separate) genera, remaining within the family Acrochordidae is clear and undeniable (Sanders *et al*. 2010, Pyron *et al*. 2013).

Sanders *et al.* (2010), found divergence times of 16 and 20 million years for each divergent group, which in the normal course of events would result in the relevant species being placed in separate genera and without argument.

However the relevant authors did not even go so far as to place each within subgenera. Noting that all remain within the all-encompassing family Acrochordidae, there is no instability in nomenclature caused by such division of the genus *Acrochordus* as presently understood.

Hence I have corrected the nomenclature of the group based on known phylogeny, while maintaining stability of the nomenclature in a broad sense as per the rules of the ICZN (Ride *et al.* 1999) including all the optional recommendations of the code.

Resurrecting *Chersydrus* leaves just one unnamed group to be named which I do so herein.

In answer to the repeated criticisms by Wüster *et al.* that I have named too many species of reptiles, thereby depriving them or other as yet unborn herpetologists of their alleged “right” to name species, I again refer to Engstrom *et al.* (2002).

Therefore I have no hesitation whatsoever in naming the clade first properly identified by Sanders *et al.* in 2010. In my view that clade should have been named by them at the time and I have no hesitation whatsoever in doing what is in effect inevitable.

That clade is described herein as *Funkiacrochordus gen. nov.*.

Noting that Sanders *et al*. (2010), found divergence times of 16 and 20 million years for each divergent group, the lower time period being that where *Chersydrus* and the *arafurae* group (herein defined as *Funkiacrochordus gen. nov.*.) split, it is entirely appropriate that the two main groups be given recognition as tribes, even though such designations are currently rarely used in herpetology.

Therefore each new tribe Acrochordidini *tribe nov*. and Funkiacrochordidini *tribe nov*. are both formally defined herein.

The genus *Acrochordus* (*sensu lato*), including the species *A. javanicus* as recognized to date was subject to audit by myself since before I published images of specimens of different specimens of *A. arafurae* in Hoser (1989).

It has been apparent for some time that specimens from mainland south-east Asia, including Peninsula Malaysia and nearby Thailand are different morphologically from those of Indonesian islands Java and Borneo. However Sumatran specimens appeared to fit both forms and due to the apparent absence of major geographical barriers it was initially thought that the differences observed were both relatively insignificant in a phylogenetic sense and/or likely to have intermediates that I had not observed or seen.

Notwithstanding this issue, my own inspections of specimens and photos from Sumatra, found that specimens from the Batanghari River and south corresponded to the nominate form, while those from the Kampar River drainage and north corresponded with the specimens from the Malay Peninsula.

Further investigations by myself seeking evidence of a biogeographical barrier revealed that each group did in fact correspond with the two main drainages of the composite Molengraaff River systems (Molengraaff 1921a, 1921b, Voris 2000). These being present during peaks of recent ice-age maxima, when sea levels were at their lowest (see maps within Voris 2000)
The two basins corresponding to the species distributions were one drainage basin flowing north and the other flowing north-east, (Sepentrional running north and Molengraaff running north-east). It is has also become clear that each form remains separated from one another in the present interglacial period and so each warrant species recognition.

With no available name for the Peninsula Malaysian species (Sepentrional basin), it is formally named as *Acrochordus malayensis sp. nov.* herein.

A similar situation existed in terms of specimens from Eastern Borneo (Kalimantan).

By observation of the consistent differences in patterning alone, these snakes are consistently more divergent from the South Sumatran and Javanese form than those from Peninsula Malaysia. Even in times of recent glacial maxima, this population was clearly cut off from the others and so must by simple logic be a different species. With no available name for the east Borneo population, they are formally described herein as *Acrochordus mahakamiensis sp. nov.*.

The literature reports that all these snakes (Acrochordidids) have considerable marine tolerance, (e.g. Cogger 1975, p. 362), who for *A. arafurae* in Australia, then identified as *A. javanicus* wrote: “Largely restricted to fresh-water streams and lagoons, wherever monsoonal floods permit them to enter permanent waters; however, they freely enter estuarine waters and the sea”.

As Cogger’s works remain definitive authorities, the same sorts of comments have been repeated widely.

However my own studies show that regular movements in salt water only seem to be the case for the widely distributed taxon *Chersydrus granulatus* (Schneider, 1801), this being a common species distributed continuously in marine environments from Australasia to southern Asia. My own observations of the other two genera as defined herein show that they are not able to colonise areas separated by sea boundaries and while not able to cross seas very well are able to cross limited flat land barriers with some ease; especially at times of flooding.

While this is in part corroborated by the non-intermingling of the two Sumatran populations, this is further corroborated by the modern distribution of the relevant species. None are known from Sulawesi, which according to Voris (2000), Fig. 1, has never been joined by land to the physically nearby Borneo, or alternatively the apparent absence of any *Funkiacrochordus* in the north of island New Guinea.

While the absence of relevant species (excluding *Chersydrus*) from smaller islands is noted and perhaps due to a lack of potentially available habitat, my belief is that a better explanation is the relative inability of the species to be able to cross sea barriers.

Sanders *et al.* (2010) also noted that this hypothesis is "corroborated by the occurrence of all fossil *Acrochordus* in inland fluvial deposits (Hoffstetter, 1964; Head, 2005; Head *et al.* 2007; Rage and Ginsburg, 1997).

What hasn't yet been speculated is reasons why all Acrochordidae do not readily cross seawater barriers except for the single species *granulatus* in light of a distribution across two continental plates.

My belief is that upon the genus *Chersydrus* developing good sea water tolerance, it was able to spread widely across the range of other Acrochordids. With each species competing with one another, a degree of character displacement took place, in effect pushing *Chersydrus* to the more marine environments and while keeping the other species more firmly in freshwater habitats and at the same time reducing potential tolerance to salt water that they may have once had.

This also explains the phylogenies produced on the basis of the molecular evidence.

Finally I note the comments of McDowell in 1979 who wrote: "The three living species of *Acrochordus*, *A . javanicus*, *A . arafurae*, and *A. granulatus*, differ from one another anatomically as much as do genera of Boidae and Colubridae, but it seems pointless to recognise three genera, each monotypic."

That was clearly the case in 1979 and in line with prevailing herpetological consensus at the time. In the period post-dating the publications of Wells and Wellington (1983, 1984), there has been an increased desire for groups to be split along phylogenetic lines and utilizing all levels of classification available.

Added to that is the clear recognition of at least two more species of *Acrochordus* (this paper), in addition to fossil material, meaning that the genus *Acrochordus*, even when split from the Australasian species is no longer monotypic.

In light of this situation the argument in favour of splitting *Acrochordus* as recognized to date is now compelling and I have no doubt that in spite of the non-stop unscientific conduct of Wüster *et al.* as detailed by Hoser (2013), herpetologists will eventually use the classification and taxonomy proposed within this paper.

Brief diagnoses of both *Acrochordus* and *Chersydrus* as defined in this paper are given below. For further diagnostic information in terms of these two genera and *Funkiacrochordus gen. nov.* refer to McDowell (1979). The family Acrochordidae is also defined at length by McDowell (1979).

GENUS *ACROCHORDUS* HORNSTEDT, 1787

Type species: *Acrochordus javanicus* Hornstedt, 1787.

Diagnosis: Scales of lower sides with three posterior cusps, the middle cusp only slightly longer than the flanking dorsal and ventral cusps; sides with isolated dark spots that usually fuse into a longitudinal stripe on the side of the neck; compound bone of lower jaw with coronoid process immediately posterior to rear of dentary; nasal bones (unfused) with broadly rounded and transverse anterior border; ectopterygoid with posterior end abruptly flexed mediad, its shaft with a flange-like expansion; maxillary teeth 20 or more; dentary teeth 21 or more, the last 4 short and mitre-shaped; hemipenis forked for more than half its length (the branches with spines or papillae).

Distribution: South-east Asia. Fossil material from southern Asia (see below).

Content (Living species): *Acrochordus javanicus* Hornstedt, 1787; *A. malayensis sp. nov.* (this paper); *mahakamiensis sp. nov.* (this paper).

CHERSYDRUS SCHNEIDER, 1801.

Type species: *Acrochordus granulatus* Schneider, 1799.

Diagnosis: Scales of lower sides with middle cusp much longer than flanking dorsal and ventral cusps, the latter sometimes so short that scale may be one-cusped; dark markings on sides either forming vertical bars being either with dark cross-bands or nearly uniform dark coloration; compound bone of lower jaw without coronoid process; nasal bones tapered anteriorly, together forming a median anterior point; ectopterygoid smoothly arched, without flange on shaft; maxillary teeth 19 or fewer; dentary teeth 17 or fewer, the most posterior similar in form to the other teeth; pterygoid teeth 5-7; nostrils directed strongly upward; nasal-eye scales 5-7; eye-lip scales 5-7; nasal bones completely separated by suture; hemipenis forked for about one-third its length and always less than half its length, the branches with spines or papillae.

Distribution: Southern Asia, across to Australasia, including northern Australia, New Guinea and the Solomon Islands.

Content: *Chersydrus granulatus* (Schneider, 1799).

FUNKIACROCHORDUS GEN. NOV.

Type species: *Acrochordus arafurae* McDowell, 1979.

Diagnosis: *Funkiacrochordus gen. nov.* is monotypic for the species *F. arafurae* (McDowell, 1979). As a result, the diagnosis for the species by McDowell in 1979 applies herein.

Funkiacrochordus gen. nov. are most easily separated from other living *Acrochordids* with which they have been confused, by the following suite of characters: 11-14 scales between the nasal and the eye, 9-11 scales between the lip and the eye (as opposed to 5-7 in both for *Chersydrus granulatus*), 11-16 pterygoid teeth (as opposed to 5-7 in *Chersydrus granulatus*); a fused nasal bone (unfused in both *Chersydrus* and *Acrochordus*); forward facing nostrils (upward facing in *Chersydrus*) and their distinctive colour pattern. This consists of being grey to dark brown above with broad darker brown to black reticulations extending from a broad vertebral band to form either vague cross-bands or a series of circular or oblong blotches within the reticulated pattern along the upper surface of the body; whitish below, the dark reticulations of the dorsal surface extend to the belly. Even in old and faded specimens, this pattern can be detected. The skin is very loose and flabby.

By contrast the three *Acrochordus* species (*A. javanicus*, *A. malayensis sp. nov.* and *mahakamiensis sp. nov.* described below) lack this colour pattern. Their patterning is described below.

Until now the taxon *Acrochordus malayensis sp. nov.* has been defined as a variant *of A. javanicus.* Besides being readily separated on the basis of distribution as defined below, the taxon *Acrochordus malayensis sp. nov.* is readily separated from *A. javanicus* (including the taxon described as *Acrochordus mahakamiensis sp. nov.* herein) on the basis of colouration.

In *Acrochordus malayensis sp. nov.* the dorsal colouration invariably consists of the following pattern, this being a thick dorsal line bound by thick lighter lines for the entire length of the body, the upper mid-flanks consisting of either a thick dark line or large ovoid blotches (usually in the configuration of lines anterior and blotches throughout the mid-body). By contrast *A. javanicus* has a dorsal colouration that invariably does not include a preponderance of large ovoid blotches on the lower flanks. While in both taxa there are markings within the dark thick dorsal mid-line, this is indistinct in A. *malayensis sp. nov*., whereas these markings are well defined in *A. javanicus* and the region is also punctuated by small patches of light pigment.

For the third species *A. mahakamiensis sp. nov*. currently only reported from East Borneo, the pattern is a distinctive one including numerous small dark jagged edged markings on the lower flanks within lighter pigment, being a configuration not seen in the other two species.

All three *Acrochordus* species are most easily separated from *Funkiacrochordus gen. nov.* by the distinctive colour pattern of the latter genus. This consists of being grey to dark brown above with broad darker brown to black reticulations extending from a broad vertebral band to form either vague cross-bands or a series of circular or oblong blotches within the reticulated pattern along the upper surface of the body encircling the lighter areas; whitish below, the dark reticulations of the dorsal surface extend to the belly. Even in old and faded specimens, this pattern can be detected.

By contrast the three *Acrochordus* species (*A. javanicus*, *A. malayensis sp. nov*. and *A. mahakamiensis sp. nov*. described above) lack this colour pattern.

The skin is very loose and flabby.

Funkiacrochordus and *Chersydrus* differ from all living and extinct *Acrochordus* by the absence of a parazygosphenal foramina (Sanders *et al.* 2010).

Acrochordus and *Funkiacrochordus* species are separated from *Chersydrus granulatus* (in most texts identified as *Acrochordus granulatus*) by not having 5-7 scales between the nasal and the eye, and 5-7 scales between the lip and the eye.

Species within all three living genera of Acrochordids (as defined herein) can be readily separated by hemipenal morphology as detailed by McDowell (1979).

In *Funkiacrochordus* the hemipenis is forked only at its extreme tip, with the sulcus forking at the furcation of the hemipenis; there are no spines or papillae, nor are there any calyces or flounces, but each distal lobe of the organ bears a thickened pallet containing the distal extremity of the sulcus spermaticus.

In *Chersydrus* the hemipenis is forked for one-third its length, with the sulcus forked much more proximally, at the midpoint of the organ; the branches of the organ, except for the lips of the sulcus, are covered with proximally directed pointed papillae or spines (presumably depending on age) and a

few spines (or papillae) extend just proximal to furcation of the organ, but not to the level of furcation of the sulcus.

In *Acrochordus* (as defined within this paper) the hemipenis is forked for more than half its length,

with the sulcus forked at the furcation of the organ; each branch of the organ (except at the extreme tip) is covered with spines or spine-like papillae (presumably depending on age), which occur on the lips of the sulcus but are longest opposite the sulcus; a few short spines extend proximally onto the unforked part of the organ, flanking the sulcus; the tip of each lobe is smooth, with a pallet-like expansion of the lips of the sulcus.

Distribution: Drainages running into the Arafura Sea from northern Australia and southern New Guinea, west of Cape York and the equivalent point in New Guinea. There are unconfirmed records east of this point. The genus does not occur west of Wallace's Line. There it is replaced by *Acrochordus. Chersydrus* occurs throughout south-east Asia to northern Australia, New Guinea and nearby islands including the Solomon Islands.

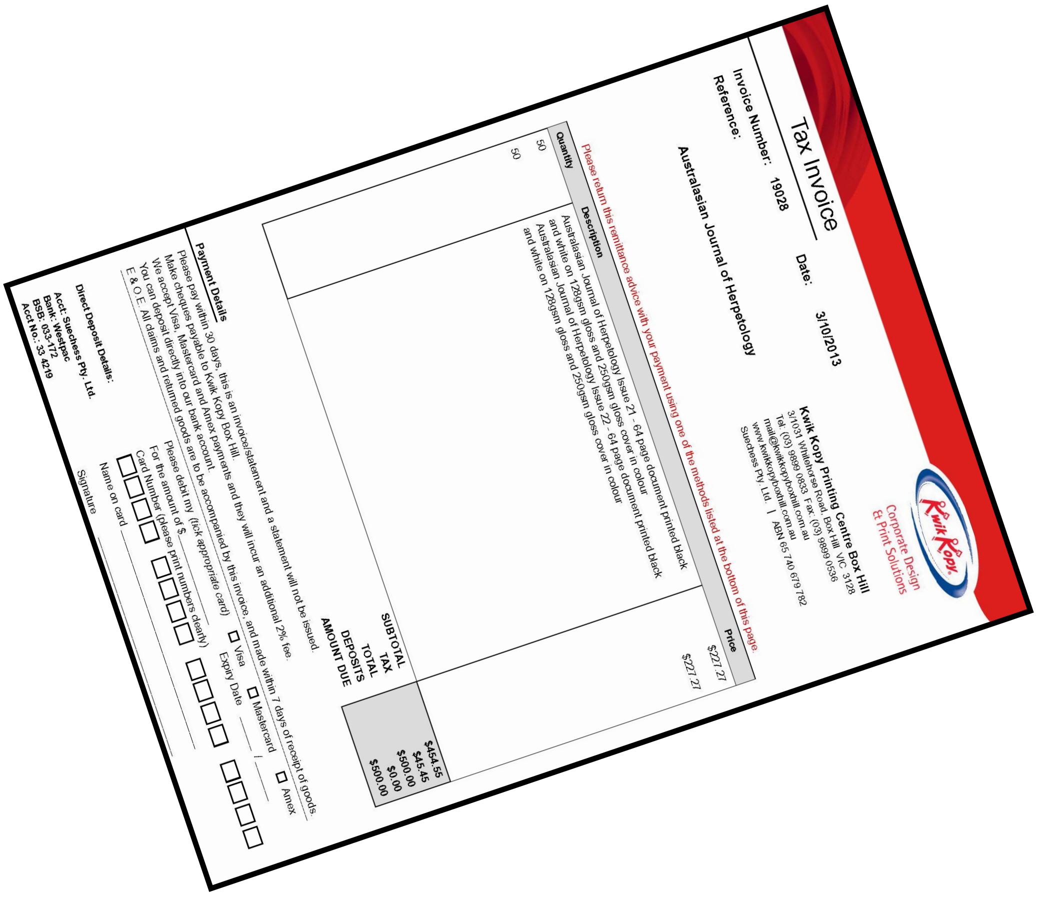
Etymology: Named in honour of Mesa, Arizona, USA-based herpetologist, Dr. Richard Funk.

The "acrochordus" part of the etymology refers to the warty nature of the snake's epidermis.

ACROCHORDUS MALAYENSIS SP. NOV.

Holotype: A juvenile specimen at the US National Museum (USNM), Washington DC, USA, specimen number 142402 from Kuala Lumpur, Prince's Road, under bridge, near T.P.C.A., Selangor Province, Peninsula, Malaysia. The US National Museum, Washington DC, USA, is a facility that allows scientists access to specimens.

Paratype: A juvenile specimen at the US National Museum (USNM), Washington DC, USA, specimen number 142403 from Kuala Lumpur, Prince's Road, under bridge, near T.P.C.A., Selangor Province, Peninsula, Malaysia. The US National



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Museum, Washington DC, USA, is a facility that allows scientists access to specimens.

Diagnosis: Until now the taxon *Acrochordus malayensis sp. nov*. has been defined as a variant *of A. javanicus*. Besides being readily separated on the basis of distribution as defined below, the taxon *Acrochordus malayensis sp. nov.* is readily separated from *A. javanicus* (including the taxon described as *Acrochordus mahakamiensis sp. nov*. herein) on the basis of colouration.

In *Acrochordus malayensis sp. nov*. the dorsal colouration invariably consists of the following pattern, this being a thick dorsal line bound by thick lighter lines for the entire length of the body, the upper mid-flanks consisting of either a thick dark line or large ovoid blotches (usually in the configuration of lines anterior and blotches throughout the mid-body). By contrast *A. javanicus* has a dorsal colouration that invariably does not include a preponderance of large ovoid blotches on the lower flanks. While in both taxa there are markings within the dark thick dorsal line, this is indistinct in A. *malayensis sp. nov*., whereas these markings are well defined in *A. javanicus* and the region is also punctuated by small patches of light pigment. For *A. mahakamiensis sp. nov*. the pattern is a distinctive one including numerous small dark jagged edged markings on a lighter background on the lower flanks, this configuration not seen in the other two species.

All three *Acrochordus* species are most easily separated from *Funkiacrochordus gen. nov.* by the distinctive colour pattern of the latter genus. This consists of being grey to dark brown above with broad darker brown to black reticulations extending from a broad vertebral band to form either vague cross-bands or a series of circular or oblong blotches within the reticulated pattern along the upper surface of the body; whitish below, the dark reticulations of the dorsal surface extend to the belly. Even in old and faded specimens, this pattern can be detected.

By contrast the three *Acrochordus* species (*A. javanicus*, *A. malayensis sp. nov*. and *A. mahakamiensis sp. nov*. described above) lack this colour pattern.

The skin is very loose and flabby.

Acrochordus species are separated from *Chersydrus granulatus* (in most texts identified as *Acrochordus granulatus*) by not having 5-7 scales between the nasal and the eye, and 5-7 scales between the lip and the eye.

Distribution: Thailand, West and East Peninsula Malaysia, including Singapore, North Sumatra, south to the province of Riau, central Sumatra including the Kampar River drainage.

The species *A. javanicus* is herein confined from south-central Sumatra in the region of the province of Jambi, including the Batanghari River and further South in Sumatra and Java, this including the central part of the so-called Molengraaff River system as defined by (Molengraaff 1921a, 1921b and Voris 2000).

A. javanicus may also occur in south and west Borneo (Kalimantan), but this is not known.

A. mahakamiensis sp. nov. occurs in eastern Borneo (Kalimantan), known at this stage only from the region of the type locality the Mahakam River drainage system.

Etymology: Named in reflection of the centre of distribution of the taxon and in recognition of the fact that the other species in the genus are similarly named on the basis of locality of origin of the type specimens as seen in *A. mahakamiensis sp. nov.* and *Acrochordus javanicus* Hornstedt, 1787, or for that matter as seen in *Funkiacrochordus arafurae* (McDowell, 1979).

ACROCHORDUS MAHAKAMIENSIS SP. NOV.

Holotype: Specimen number 49964 at the US National Museum, (USNM), Washington DC, USA, collected from the Mahakam River, Kalimantan (Borneo). The US National Museum, Washington DC, USA, is a facility that allows access to its collection by scientists.

Paratype 1: Specimen number 49780 at the US National Museum, (USNM), Washington DC, USA, collected from the Mahakam River, Kalimantan (Borneo).

Further paratypes: A collection of embryo's (individual) numbers 49965-49974 at the US National Museum, (USNM), collected from the Mahakam River, Kalimantan (Borneo).

The US National Museum, Washington DC, USA, is a facility that allows access to its collection by scientists.

Diagnosis: *Acrochordus mahakamiensis sp. nov*. from eastern Borneo (Kalimantan) is readily identified and separated from all other *Acrochordus* by its colour pattern arrangement. The pattern is a distinctive one including numerous small dark jagged edged markings on a lighter background on the lower flanks, this configuration not seen in the other two species. It is also often reddish-brown in colour as opposed to a more-greyish brown in the other species of *Acrochordus.*

Until now the taxon *Acrochordus malayensis sp. nov.* has been defined as a variant *of A. javanicus*. Besides being readily separated on the basis of distribution as defined within this paper, the taxon *Acrochordus malayensis sp. nov.* is readily separated from *A. javanicus* (including the taxon described as *Acrochordus mahakamiensis sp. nov*. herein) on the basis of colouration.

In *Acrochordus malayensis sp. nov*. the dorsal colouration invariably consists of the following pattern, this being a thick dorsal line bound by thick lighter lines for the entire length of the body, the upper mid-flanks consisting of either a thick dark line or large ovoid blotches (usually in the configuration of lines anterior and blotches throughout the mid-body). By contrast *A. javanicus* has a dorsal colouration that invariably does not include a preponderance of large ovoid blotches on the lower flanks. While in both taxa there are markings within the dark thick dorsal line, this is indistinct in A. *malayensis sp. nov*., whereas these markings are well defined in *A. javanicus* and the region is also punctuated by small patches of light pigment. For *A. mahakamiensis sp. nov*. the pattern is a distinctive one including numerous small dark jagged edged markings on a lighter background on the lower flanks, this configuration not seen in the other two species.

All three *Acrochordus* species are most easily separated from *Funkiacrochordus gen. nov.* by the distinctive colour pattern of the latter genus. This consists of being grey to dark brown above with broad darker brown to black reticulations extending from a broad vertebral band to form either vague cross-bands or a series of circular or oblong blotches within the reticulated pattern along the upper surface of the body; whitish below, the dark reticulations of the dorsal surface extend to the belly. Even in old and faded specimens, this pattern can be detected.

By contrast the three *Acrochordus* species (*A. javanicus*, *A. malayensis sp. nov*. and *A. mahakamiensis sp. nov*. described above) lack this colour pattern.

The skin is very loose and flabby.

Acrochordus species are separated from *Chersydrus granulatus* (in most texts identified as *Acrochordus granulatus*) by not having 5-7 scales between the nasal and the eye, and 5-7 scales between the lip and the eye.

Distribution: *A. mahakamiensis sp. nov.* occurs in eastern Borneo (Kalimantan), known at this stage only from the region of the type locality the Mahakam River drainage system.

Acrochordus malayensis sp. nov. is found in Thailand, West and East Peninsula Malaysia, including Singapore, North Sumatra, south to the province of Riau central Sumatra including the Kampar River drainage.

The species *A. javanicus* is herein confined from south-central Sumatra in the region of the province of Jambi, including the Batanghari River and further South in Sumatra and Java, this including the central part of the so-called Molengraaff River system as defined by (Molengraaff 1921a, 1921b and Voris 2000).

A. javanicus may also occur in south and west Borneo (Kalimantan), but this is not known.

Etymology: Named in reflection of the centre of distribution of the taxon and in recognition of the fact that the other species in the genus is similarly named on the basis of locality of origin of the type specimen as was *Funkiacrochordus arafurae* (McDowell, 1979) and *Acrochordus javanicus* Hornstedt, 1787.

ACROCHORDININI *TRIBE NOV.*

(Terminal taxon: *Acrochordus javanicus* Hornstedt, 1787).

Diagnosis: All three living *Acrochordus* species (the entire living content of this tribe) are most easily separated from *Funkiacrochordus gen. nov.* (*tribe* Funkiacrochordidini *tribe nov.*) by the distinctive colour pattern of the latter genus. This consists of being grey to dark brown above with broad darker brown to black reticulations extending from a broad vertebral band to form either vague cross-bands or a series of circular or oblong blotches within the reticulated pattern along the upper surface of the body; whitish below, the dark reticulations of the dorsal surface extend to the belly. Even in old and faded specimens, this pattern can be detected.

By contrast the three *Acrochordus* species (*A. javanicus*, *A. malayensis sp. nov*. and *A. mahakamiensis sp. nov*. described above) lack this colour pattern.

The skin is very loose and flabby.

Acrochordus species are separated from *Chersydrus granulatus* (in most texts identified as *Acrochordus granulatus*) (also now placed in tribe Funkiacrochordidini *tribe nov.*) by not having 5-7 scales between the nasal and the eye, and 5-7 scales between the lip and the eye.

Acrochordus species have 11-14 scales between the nasal and the eye, 9-11 scales between the lip and the eye.

Other than *A. javanicus*, *A. malayensis sp. nov.* and *A. mahakamiensis sp. nov.*, there are no other living species within the tribe Acrochordidini.

The mainly Miocene fossil species *Acrochordus dehmi* Hoffstetter, 1964, with relevant material dated from 18 MYA and the most recent material dated to 6.35 MYA (Head 2005) is clearly within the genus *Acrochordus* as defined herein and therefore within the same tribe as well (Head 2005, Sanders *et al.* 2010).

However in the light of the following important facts:

1/ The taxon is readily separated from extant *Acrochordus* species by the following suite of characters; larger adult size, possession of lymphapophyseal foramen and tall neural spines with

straight dorsal margins; 2/ Its known distribution centering on India and Pakistan and not the extant range of living *Acrochordus* and 3/ the relative antiquity of the species, it is appropriate that it be placed within a separate subgenus. This is formally defined and named herein as *Vetusacrochordus subgen. nov.*.

Distribution: Living species are confined to South-east Asia and not east of Wallace's line. An extinct taxon, now placed in the subgenus *Vetusacrochordus subgen. nov.* is known from Pakistan, India, Nepal and Thailand.

Content: *Acrochordus* Hornstedt, 1787.

SUBGENUS *VETUSACROCHORDUS SUBGEN. NOV.*

(Terminal taxon: *Acrochordus dehmi* Hoffstetter, 1964).

Diagnosis: *Vetusacrochordus subgen. nov.* are known only from the fossil record (Head 2005).

While the snakes of this subgenus would normally key as *Acrochordus* (see above), they are readily separated from living *Acrochordus* by the following suite of characters: larger adult size (up to 2.5 metres total length as opposed to 2 metres), possession of lymphapophyseal foramen, and tall neural spines with straight dorsal margins.

Distribution: The fossil taxon is known from the lower and middle Siwalik Group of the Potwar Plateau, Pakistan, as well as middle Siwalik Group of Nepal and middle-upper Siwalik Group of Jammu, India and Thailand (Hoffstetter, 1964, Rage and Ginsburg, 1997, Head, 2005, Head *et al.*, 2007, West *et al.* 1991, Rage *et al.* 2001).

Content: *Acrochordus* (*Vetusacrochordus*) *dehmi* Hoffstetter, 1964.

FUNKIACROCHORDIDINI *TRIBE NOV.*

(Terminal taxon: *Acrochordus arafurae* McDowell, 1979).

The above terminal taxon is herein defined as *Funkiacrochordus arafurae* (McDowell, 1979).

Diagnosis: Species within the component genera *Funkiacrochordus* and *Chersydrus* differ from all living and (known) extinct *Acrochordus* (Acrochordidini) by the absence of a parazygosphenal foramina (Sanders *et al.* 2010).

Colour pattern differences between living members of this tribe and species within Acrochordidini are as follows:

All three living *Acrochordus* species (the entire living content of that tribe) are most easily separated from *Funkiacrochordus gen. nov.* (*tribe* Funkiacrochordidini *tribe nov.*) by the distinctive colour pattern of the latter genus. This consists of being grey to dark brown above with broad darker brown to black reticulations extending from a broad vertebral band to form either vague cross-bands or a series of circular or oblong blotches within the reticulated pattern along the upper surface of the body; whitish below, the dark reticulations of the dorsal surface extend to the belly. Even in old and faded specimens, this pattern can be detected.

By contrast the three *Acrochordus* species (*A. javanicus*, *A. malayensis sp. nov.* and *A. mahakamiensis sp. nov*. described above) lack this colour pattern.

The skin is very loose and flabby.

Acrochordus species are separated from *Chersydrus granulatus* (in most texts identified as *Acrochordus granulatus*) (also now placed in tribe Funkiacrochordidini *tribe nov.*) and the only other known taxon in this tribe by not having 5-7 scales between the nasal and the eye, and 5-7 scales between the lip and the eye.

Acrochordus species have 11-14 scales between the nasal and the eye, 9-11 scales between the lip and the eye.

Other than *A. javanicus*, *A. malayensis sp. nov.* and *A. mahakamiensis sp. nov.*, there are no other known living species within the tribe Acrochordidini.

Distribution: South Asia, south-east Asia across all of Indonesia and including northern Australasia, including New Guinea and the Solomon Islands.

Content: *Funkiacrochordus gen. nov.* (this paper); *Chersydrus* Schneider, 1801.

NOMENCLATURAL STATEMENT IN TERMS OF THE DESCRIPTIONS WITHIN THIS PAPER

Unless mandated by the zoological code, no names proposed within this paper should be amended in any way for the purposes of correction, gender change or the like. In terms of priority of names in the event of conflict, where more than one newly named taxon is deemed conspecific or within a single taxon group by a later author, the priority to be taken is by page priority, this meaning the first taxon described in full is the one to take precedent.

CONFLICT OF INTEREST

This author reports no conflict of interest in terms of any material within this paper.

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A logical new taxonomy for the Asian subfamily Draconinae based on obvious phylogenetic relationships and morphology of species (Squamata: Sauria: Agamidae: Draconinae).

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ABSTRACT

A number of recent molecular studies have highlighted divergences between south-east Asian agamid lizards within the Draconinae previously thought to be sufficiently close as to be placed in the same genera. Consolidating recently published studies and further investigations into relevant taxa, incorporating available molecular, morphological and geological evidence some genera as presently recognized are re-arranged to better reflect the relationships of species.

For some of these taxa, names are available and as a result of this review they are formally resurrected from synonymy. Where names for taxa don't exist, the species groups are formally named and defined herein according to the Zoological Code (Ride *et al.* 1999).

Well established genera that are in effect split up include the following:

Gonocephalus, Kaup, 1825 is divided into three genera. The nominate genus is also split into five subgenera, all named for the first time except for (*Dilophyrus* Gray, 1845) and the nominate subgenus.

Japalura Gray, 1853 is divided into three genera, one of which is named for the first time. Two genera are further divided into two subgenera.

Calotes Daudin, 1802 is divided into three genera, two also divided into subgenera.

The taxon originally described as "*Calotes andamanensis* Boulenger, 1891" is also placed in a new monotypic genus as it also clearly sits ouside the two genera in which it has been recently placed (*Calotes* and *Pseudocalotes* Kaup, 1827).

Ceratophora Gray, 1835, is divided in three, with the two most divergent taxa, *C. aspera* Günther, 1864 and *C. karu* Pethiyagoda and Manamendra-Arachchi, 1998 each placed in a new monotypic genus. The remaining *Ceratophora* are split into two obvious subgenera.

Bronchocela Kaup, 1827 is divided into two subgenera.

The taxon currently known as *Bronchocela cristatella* Kuhl, 1820 from the island of Halmahera, Indonesia is formally described as a new species. Other potential new species are identified.

Phoxophrys Hubrecht, 1881 is divided into three subgenera, one formally named for the first time.

Aphaniotis Peters, 1864 is subdivided into two subgenera as is *Ptyctolaemus* Peters, 1864.

Salea Gray, 1845 is divided into two subgenera for which a names are already available.

Draco Linnaeus, 1758 is herein conservatively divided nine ways into subgenera of which five are formally named for the first time. It is likely that other taxonomists may treat these divisions as full genera.

Furthermore, Draconinae taxonomy and nomenclature at the level between subfamily and genus is tidied up. The result is the formal erection of ten tribes and the addition six subtribes formally defined and named.

As a result of this scientific reorganisation of the subfamily, this paper presents a list of all recognized Draconinae species in correct tribes, subtribes, genera and subgenera.

Keywords: Taxonomy; nomenclature; genera; *Gonocephalus*; *Japalura*; *Cophotis*; *Calotes*; *Ceratophora*; *Diploderma; Aphaniotis*; *Phoxophrys*; *Bronchocela*; *Lophocalotes*; *Dendragama*; *Otocryptis*; *Ptyctolaemus*; *Mictopholis*; *Salea*; *Sitana*; *Otocryptis*; *Pseudocalotes*; *Paracalotes*; *Draco*; *Dilophyrus*; *Oriotiaris*; *Pelturagonia*; *Lyriocephalus*; *Coryphophylax*; *Ptyctolaemus*; *Mantheyus*; *Acanthosaura*; new genera; *Daraninagama*; *Doongagama*; *Maxhoseragama*; *Crottyagama*; *Skrijelus*; *Notacalotes*; *Pethiyagodaus*; *Manamendraarachchius*; subgenera; *Dracontoides*; *Rhacodracon*; *Pterosaurus*; new subgenera; *Honlamagama*; *Mantheysaurus*; *Denzeragama*; *Eksteinagama*; *Jamesschulteus; Rubercalotes*; *Ghatscalotes*; *Laccadivecalotes*; *Ceyloncalotes*; *Tamilnaducalotes*; *Freudcalotes*; *Khasicalotes*; *Amboncalotes*; *Ferebronchocela*; *Olorenshawagama*; *Proboscisagama*; *Mindatagama*; *Macguiredraco*; *Philippinedraco*; *Engannodraco*; *Somniadraco*; *Spottydraco*; new species; *Harradineus.* new tribes; Dracoiini; Maxhoseragamiini; Crottyagamiini; Daraninagamaiini; Pethiyagodaiini; Japaluraiini; Lophocalotesiini; Phoxophryiini; Mantheyiini; Dendragamaiini; new subtribes; Maxhoseragamiina; Sitanaiina; Acanthosauriina; Saleaiina; Pethiyagodaiina; Doongagamaiina.

INTRODUCTION

A number of recent molecular studies have highlighted deep divergences between relatively well-known south-east Asian agamid lizards. These lizards were thought to be sufficiently close until now as to be placed in the same genera. While general affinities have not been disputed, it has become clear that some species placed within given genera should be removed and placed elsewhere. This situation for some species is not just a case of being within the same genus group, but slightly divergent, but more often than not because the relevant species are not remotely related to the type species of the genus they have been placed in (e.g. *Gonocephalus* Kaup, 1825 as presently defined by most authors or *Japalura* Gray, 1853 as presently defined by most authors).

In a limited number of cases, genera with widely divergent species in need of a break up have also been identified (e.g. *Ceratophora* Gray 1835 or *Calotes* Daudin, 1802).

Following on from a number of molecular studies that have indicated splits of genera are warranted on a molecular basis, I audited all genera within the southern and south-east Asian agamid subfamily Draconinae to determine which needed to be divided.

The material and methods of the audit involved a thorough review of the published literature with a view to seeing if there were significant morphological differences between species as indicated by recently available molecular data. Added to this was direct inspection of several hundred live and dead specimens and photos of the relevant taxa with known and accurate locality data.

Genera, in the context of how they are recognized by most zoologists in 2013, as indicated by Pyron *et al.* (2013) found worthy of formal division included the following: *Gonocephalus*, Kaup, 1825; *Japalura* Gray, 1853; *Calotes* Daudin, 1802; *Ceratophora* Gray 1835; *Bronchocela* Kaup, 1827 and *Draco* Linnaeus, 1758.

For some of these taxa, and new genera to be defined, names are available and they are formally resurrected herein.

Where names for these taxa are not available, they are formally named herein according to the Zoological Code (Ride *et al.* 1999). Invariably these new genera, or at times herein more conservatively placed subgenera are readily defined using the significant and generally well-known morphological differences between relevant species-level taxa.

Well established genera that are in effect split up, include the following:

Gonocephalus, Kaup, 1825 with the erection of two new genera (hence a three-way split of the original genus), and the nominate genus divided five ways, all named for the first time except for (*Dilophyrus* Gray, 1845) and the nominate subgenus.

Japalura Gray, 1853 is divided into three genera, one of which is named for the first time. Two genera are further divided into two subgenera.

Calotes Daudin, 1802 is divided into three genera, two being further split into subgenera.

The taxon originally described as *Calotes andamanensis* Boulenger, 1891 is also placed in a new monotypic genus as it also clearly sits ouside the two genera in which it has been recently placed (*Calotes* and *Pseudocalotes* Kaup, 1827).

Mictopholis Smith, 1935 is tentatively recognized herein as a monotypic subgenus (for the species originally described as "*Salea austeniana* Annandale, 1908", now placed by most authors in the genus *Pseudocalotes* Fitzinger, 1843). However as the taxon can be readily placed with *Pseudocalotes* in terms of the various definitions and diagnoses used in this paper in terms of tribes and subtribes, it is largely ignored for the purposes of this paper. The same applies in terms of *Paracalotes* Bourret, 1939, also tentatively recognized here as a subgenus within *Pseudocalotes*. Assignment of species to this subgenus is also tentative, noting mixed results emerging from cited molecular and morphological studies.

Ceratophora Gray 1835, is divided in three, with the divergent taxa, *C. aspera* Günther, 1864 and *C. karu* Pethiyagoda and Manamendra-Arachchi, 1998 each placed in a new monotypic genus. The remaining *Ceratophora* is split into two obvious subgenera.

Bronchocela Kaup, 1827 is divided into two subgenera, the new one named *Ferebronchocela subgen. nov.*..

The taxon currently referred to as *Bronchocela cristatella* Kuhl, 1820 from the island of Halmahera, Indonesia is formally described herein as a new and closely related species.

Phoxophrys Hubrecht, 1881 is divided into three subgenera, one formally named for the first time.

Aphaniotis Peters, 1864 is subdivided into two subgenera as is *Ptyctolaemus* Peters, 1864.

Salea Gray, 1845 is divided into two subgenera for which a name is already available.

Draco Linnaeus, 1758 is herein divided nine ways into subgenera of which five are formally named for the first time.

Furthermore, the taxonomy and the nomenclature at the level between subfamily and genus is tidied up for the Draconinae. The result is the formal erection of ten tribes with some of these in turn divided into subtribes (6 subtribes being named).

Unlike authors such as Wallach *et al.* (2009), Baig *et al.* 2012., Bates *et al.* (2013), Reynolds *et al.* (2013a, 2013b and 2014), Hedges *et al.* (2014) and Thomas *et al.* (2014), I do not feel the need to dishonestly rehash other people's previously published data and present it as new to justify the taxonomic decisions herein or falsely claim the scientific basis underpinning these decisions is new.

Unlike these authors just cited and others in the group known as the Wüster gang, I do not find a need to step outside of the Zoological Code (Ride *et al.* 1999) to rename previously named taxa based on the research of others.

In this and all previous papers published by myself, I have always respected and used originally proposed names that have been named in a code compliant way, no matter how little evidence was provided as justification for the original descriptions (and in some cases this was none!).

Where names have been properly proposed, even if unused to date, they are used herein if appropriate and in total compliance with the established rules of zoology (Ride *et al.* 1999). In terms of newly defined taxa herein, I have formed the view that their placement in new groups, be they genus, subgenus or species is obvious based on one or more of the following: A/ The previously published literature on the relevant taxa, B/ The relevant published and publicly available molecular data as held at Genbank and readily tested via programs such as BEAST and C/ Direct inspection of specimens and photos of the relevant taxa.

I also note that at the species level, it is clear that there is considerable as yet undescribed biodiversity in the Asian lizards within the Agamidae, especially within the genus *Draco.*

Finally, as a taxonomist I am happy to be relegated to redescribing taxa improperly described by earlier authors, as complained about by the Wüster gang, (Kaiser 2012b, Kaiser *et al.* 2013), when they wrote "Taxonomists are relegated to "redescribing" valid taxa that were named prematurely in acts of mass naming or in deliberate acts of intellectual kleptoparasitism".

Holotype examples of names that I must validate that were created in "acts of mass naming" by authors seeking to describe taxa prematurely in order to establish "name rights", include the many names I use herein coined by John Edward Gray and Leopold Joseph Franz Johann Fitzinger, both of coined hundreds of names for taxa with little if any scientific evidence or basis in the clear hope that at least some would "stick".

However in stark contrast to Kaiser *et al.* 2013 I accept the reality of names and the Zoological Rules (Ride *et al.* 1999) and realise that the main issue at hand is not who first named given taxa, but rather that it is properly named.

While it would be nice for others to recognize my own work herein in terms of defining and diagnosing genera for the first time, including those for which I have had to use earlier coined names, it is evident that truth-haters like Kaiser et al. and others in the Wüster gang will do everything they can to avoid any positive citation or use of any of my herpetological publications spanning more than three decades and totalling well over1 million words.

UNLAWFUL THEFT OF MATERIALS AND DATA

I also note the following: In 2006 an online petition sponsored by a group of animal-hating pseudoscientists including Wolfgang Wüster, Mark O'Shea, David John Williams, Bryan Fry and others posted at: http://www.aussiereptileclassifieds.com/phpPETITION (Hunter *et al.* 2006) called for my successful wildlife education business and all my other herpetological activity to be shut down by the government of Victoria, Australia. These men were successful in that after a ruthless five-year campaign, on 17 August 2011, 11 heavily armed police and wildlife officers conducted a highly illegal and violent raid on our family home and research facility. Myself, my wife and two young daughters were assaulted without provocation, arrested at gunpoint and held captive in the kitchen of the house for nine hours. This was while the facility was ransacked. Besides the unspeakable acts of killing captive snakes and criminal damage to cages and household goods, the raiding officers illegally shut down our business and effectively placed myself under house arrest at gunpoint for some months after the raid.

An application by myself to the Supreme Court of Victoria led to the re-opening of our unlawfully shut down wildlife education business although the long term damage to the enterprise was irreparable.

Of greater relevance here is that at the time of the raid, research files spanning more than 40 years were taken and never returned, including materials and records relevant to this and other papers.

Material taken included all the computers, disks, hard drives, backups, cameras, books, scientific literature and other forms of information storage at the facility. All were loaded into the back of a truck and trailer and carted off.

Faced with the dilemma of deciding whether to spend another forty years gathering data, by which time I may be dead from old age, being aged 52 as of 2014, or publishing the relevant paper/s with minimal data, I have opted to publish.

Underlying this motivation has been an increasing concern that a delay to formally identify and name undescribed biodiversity may lead to its extinction before another scientist gets around to the matter.

O concur with the statements of Engstrom *et al.* (2002) who wrote: "The documentation of this diversity must be seen as an activity that is done not just for posterity but for immediate action and protection."

A number of authors including Kaiser (2012a, 2012b, 2013 and 2014), Kaiser *et al.* (2013), Naish (2013) and Wüster *et al.* (2014a), all part of the group of people effectively controlled by Wüster, have been highly critical of the fact that I have assigned names to unnamed clades of snakes. Their unscientific and childish attacks, continued incessantly on social media such as Facebook and Twitter are rejected herein as destabilizing the nomenclature and impeding the progress of science.

Their ridiculous comments and false and defamatory statements are systematically rebutted by Hoser (2013).

I also note that many taxa formally named by myself for the first time in earlier publications (e.g. Hoser 2000a, 2000b) are in fact threatened species.

Therefore I note the sensible remarks of Engstrom *et al.* (2002) as a perfectly reasonable explanation for the publishing of taxon descriptions for such unnamed groups. This remains the case even if a sizeable amount of my original research, files, photos and data have been stolen and therefore cannot be relied upon and incorporated into these contemporary publications.

While speaking about thefts, the following authors, namely Wallach *et al.* (2009), Baig *et al.* 2012., Bates *et al.* (2013), Reynolds *et al.* (2013a, 2013b and 2014), Hedges *et al.* (2014) and Thomas *et al.* (2014), all close associates of serial criminal Wolfgang Wüster, (based on Wales, UK) have all engaged in an attempted theft of my own research spanning some decades by publishing so-called papers that knowingly and deliberately step outside the zoological code to rename species and genera previously named by myself using the scientific method.

The deliberate creation of junior synonyms and promoting them as valid is a breach of numerous sections of the rules as spelt out in Ride *et al.* (1999), and both unscientific and unethical.

NOTES ON TAXA NAMED HEREIN

In the event a later author seeks to merge one or more taxon described within this paper, the order of priority should be by page priority in terms of this paper; that is the first name listed is the first to be used. Gender, spellings and the like of names or other perceived errors should not be altered in any way unless mandated by the Zoological Code, even if apparently wrong in the original descriptions herein, including by derivation or gender.

GONOCEPHALUS KAUP, 1825.

Gonocephalus, Kaup, 1825 as recognized to date has been shown to be paraphyletic by several authors using various criteria, including by Diong *et al.* (2000) and Pyron *et al.* (2013).

The obvious differences between the relevant taxa have been noted by many recent authors.

Diong *et al.* (2000) wrote: "The karyotype of *G. robinsonii*, while remarkably different from other congeneric karyotypes in exhibiting much smaller diploid (32) and biarmed macrochromosome numbers (12), share these and other chromosomal characteristics with several Australian species. It seems unlikely for the karyotype of *G. robinsonii* to directly emerge from other congeneric karyotypes or *vice versa*. We conclude that the inclusion of this species in *Gonocephalus* would render the genus paraphyletic."

Pyron *et al.* (2013) wrote: "In contrast, within draconine agamids (Figure 16), many intergeneric relationships are weakly supported, and some genera are non-monophyletic (Figure 16; see also [142]), including *Gonocephalus* (*G. robinsonii* is only distantly related to other *Gonocephalus*) and *Japalura* (with species distributed among three distantly related clades, including one allied with *Ptyctolaemus*, another with *G. robinsonii*, and a third with *Pseudocalotes*).

Yet in spite of the obvious, no one has bothered to assign the taxon *Gonocephalus robinsonii* (Boulenger, 1908), originally described as *Gonyocephalus robinsonii* to a genus of its own. As there is no pre-existing available name for this taxon, it is placed in a new genus, formally named herein as *Daraninagama gen. nov.*.

The species *Gonocephalus mjobergi* Smith, 1935 is also placed in its own monotypic genus, namely *Doongagama gen. nov.*.

The nominate genus *Gonocephalus* (that is the remaining species) is divided five ways into subgenera, three being formally named for the first time. For one of the other groups the available name *Dilophyrus* Gray, 1845 is resurrected for the type species of his genus namely *grandis*, this being the only taxon in the subgenus. The division of species within subgenera is essentially that as identified by Manthey and Denzer (2006) and Denzer and Manthey (2009) with numerous authors including Boulenger (1885) and Cochran (1922), Grismer (2011), Denzer and Manthey (1991) and Taylor (1953) quite adequately separating the relevant species from one another using obvious morphological characters.

Note also that the three Philippine Islands species are placed in their own subgenus on the basis of well-defined morphological differences as outlined by Boulenger (1885) and others.

While Denzer and Manthey (2009) recognized *Gonocephalus* as being diverse and noted obvious species groups, I note they also said the following: “Morphologically the genus *Gonocephalus* is highly diverse and solely defined by a few characters, i. e. basal scales adjacent to the nuchal and dorsal crests, a transverse gular fold, a sharp canthus rostralis and an “angled” supraciliary ridge. Some of these characters are not well developed in several of the species groups above. The most resemblance

to these generic features is exhibited by members of the *G. chamaeleontinus* species group.”

They also spelt out the taxa they believed should be in each species group, but did not assign them taxonomically.

The various genera and subgenera are therefore defined and named formally below.

Noting significant biological differences between taxa within each species group, these became relevant in identifying the relevant species groups by means other than physical. In summary, they were able to be separated by physical appearances and morphology, molecular evidence and habits. Key publications relevant to the taxonomy adopted within this paper in terms of *Gonocephalus sensu lato* as defined to date include the following: Alcala (1986), Auliya (2006), Barbour (1912), Barts and Wilms (2003), Bauer *et al.* (1995), Beolens *et al.* (2011), Berg *et al.* (2013), Bleeker (1860), Boettger (1892a, 1892b, 1893a), Bonetti (2002), Bong Heang (1987), Boulenger (1885, 1887b, 1908, 1920), Campbell *et al.* (2011), Chan-ard *et al.* (1999), Cochran (1922), Cox *et al.* (1998), Das (2004), Das and Yaakob (2007), Denzer and Manthey (2009), de Rooij (1915), Denzer (1996), Denzer and Manthey (2009), Dieckmann (2013), Diong *et al.* (2002), Dring (1979), Duméril and Bibron (1837), Evers (2010, 2013), Fischer (1886), Gaulke (2001, 2011), Gaulke and Demegillo (2005a, 2005b, 2008), Grandison (1972), Gray (1845), Grismer (2011), Grismer *et al.* (2010), Grossmann and Tillack (2004a, 2004b), Günther (1868, 1872a), Hallermann (2005a, 2005b), Hien *et al.* (2001), Hendrickson (1966), Hoffmann (1998), Hölßig (2012), Iskandar and Erdelen (2006), Kahl and Schmidt (1980), Kober (2003), Kopstein (1938), Laurenti (1768), Lim and Ng (1999), Macey *et al.* (2000), Malkmus *et al.* (2002), Manthey (1983, 1991, 2011, 2013), Manthey and Denzer (1982, 1991, 1992, 1993, 2006, 2009), Manthey and Grossmann (1997), Manthey and Schuster (1999), McLeod *et al.* (2011), Nabhitabhata *et al.* (2000), Peters (1867, 1871), Pianka and Vitt (2003), Pyron *et al.* (2013), Schlegel (1848), Siler and Brown (2010), Siler *et al.* (2011), Smedley (1931b), Smith (1925, 1931), Sworder (1933), Taylor (1922, 1923, 1963), Thireau *et al.* (1998), Tiedemann *et al.* (1994), Tweedie (1954), Voris (1977), Wilms (2004) and sources cited within.

GENUS *GONOCEPHALUS* KAUP, 1825

Type species: *Iguana chamaeleontina* Laurenti, 1768.

Diagnosis: Tympanum distinct. Body compressed. Dorsal scales small, uniform or intermixed with enlarged ones. A dorsal crest, A strong transverse gular fold. Males with a gular sac. No praeanal or femoral pores. Basal scales are adjacent to the nuchal and dorsal crests, a transverse gular fold, a sharp canthus rostralis and an “angled” supraciliary ridge. Some of these characters are not well developed in some of the subgenera defined herein.

Distribution: South-east Asia.

Content: *Gonocephalus chamaeleontinus* (Laurenti, 1768) (type species); *Gonocephalus abbotti* Cochran, 1922; *Gonocephalus bellii* (Duméril and Bibron, 1837); *Gonocephalus beyschlagi* (Boettger, 1892); *Gonocephalus bornensis* (Schlegel, 1848); *Gonocephalus chamaeleontinus* (Laurenti, 1768); *Gonocephalus doriae* (Peters, 1871); *Gonocephalus grandis* (Gray, 1845); *Gonocephalus interruptus* (Boulenger, 1885); *Gonocephalus klossi* (Boulenger, 1920); *Gonocephalus kuhlii* (Schlegel, 1848); *Gonocephalus lacunosus* Manthey and Denzer, 1991; *Gonocephalus liogaster* (Günther, 1872); *Gonocephalus megalepis* (Bleeker, 1860); *Gonocephalus semperi* (Peters, 1867); *Gonocephalus sophiae* (Gray, 1845).

SUBGENUS *GONOCEPHALUS* KAUP, 1825

Type species: *Iguana chamaeleontina* Laurenti, 1768.

Diagnosis: The subgenus *Gonocephalus* Kaup, 1825 is herein defined for the first time and separated from the other subgenera by having a supraciliary border strongly raised, forming an angular projection posteriorly, (as opposed to the supraciliary border being normal).

The subgenus *Dilophyrus* Gray, 1845 are separated from all other *Gonocephalus* by the following suite of characters: Snout longer than the diameter of the orbit; canthus rostralis and supraciliary edge sharp, projecting; tympanum nearly as large as the eye-opening; upper head-scales very small, bluntly keeled, enlarged on the canthus rostralis and the supraciliary and supraorbital borders; one or two enlarged tubercles on each side behind the occiput; ten to twelve upper and as many lower labials. Gular

sac moderately large, without serrated anterior edge; gular scales smaller than ventrals, which are smooth. Nuchal and dorsal crests subcontinuous, separated by a deep notch, composed of long lanceolate spines united together, free only at the tips, with smaller triangular smooth spines at the base; in the male, the height of the nuchal crest nearly equals the length of the snout, and the dorsal crest is a little lower; in the female, the former is scarcely developed and the latter is reduced to a slight serration.

Dorsal scales very small, with the points directed upwards and backwards; ventral scales rather small, smooth. Limbs above with equal smooth or very feebly keeled scales; third and fourth fingers equal; the adpressed hind limb reaches between the eye and the tip of the snout. Tail strongly compressed, with sharp serrated upper edge; caudal scales smooth, with two rows of enlarged strongly keeled ones inferiorly; the length of the tail about twice and a half that of head and body. Brown or olive above, with or without darker cross bands; flanks with roundish yellow spots; throat sometimes with blue lines.

Honlamagama subgen. nov. are readily separated from the other subgenera within *Gonocephalus* by the following suite of characters: A normal supraciliary border; strongly keeled ventral scales and strongly keeled gular scales.

Mantheyagama subgen. nov. are readily separated from the other subgenera within *Gonocephalus* by the following suite of characters: A normal supraciliary border; smooth or very feebly keeled ventral scales and smooth or very feebly keeled gular scales.

Denzeragama subgen. nov. are readily separated from the other subgenera within *Gonocephalus* by the following suite of characters: Supraciliary border is normal; smooth ventral scales; nuchal crest is strongly separated from the dorsal crest and is not continuous with it.

Distribution: Thailand, West Malaysia, Pahang (Pulau Tioman), Indonesia (Mentewei Island, Sumatra, Bangka, Natuna Island, Java, Nias, Sipora, Siberut, Bangkaru, Tuangku, Banyak Islands, Tanahmasa, Borneo),

Content: *Gonocephalus chamaeleontinus* (Laurenti, 1768) (type species); *Gonocephalus abbotti* Cochran, 1922; *Gonocephalus doriae* (Peters, 1871); *Gonocephalus kuhlii* (Schlegel, 1848).

SUBGENUS *DILOPHYRUS* GRAY, 1845.

Type species: *Dilophyrus grandis*, Gray, 1845.

Diagnosis: The subgenus *Dilophyrus* Gray, 1845 are separated from all other *Gonocephalus* by the following suite of characters: Snout longer than the diameter of the orbit; canthus rostralis and supraciliary edge sharp, projecting; tympanum nearly as large as the eye-opening; upper head-scales very small, bluntly keeled, enlarged on the canthus rostralis and the supraciliary and supraorbital borders; one or two enlarged tubercles on each side behind the occiput; ten to twelve upper and as many lower labials. Gular

sac moderately large, without serrated anterior edge; gular scales smaller than ventrals, which are smooth. Nuchal and dorsal crests subcontinuous, separated by a deep notch, composed of long lanceolate spines united together, free only at the tips, with smaller triangular smooth spines at the base; in the male, the height of the nuchal crest nearly equals the length of the snout, and the dorsal crest is a little lower; in the female, the former is scarcely developed and the latter is reduced to a slight serration.

Dorsal scales very small, with the points directed upwards and backwards; ventral scales rather small, smooth. Limbs above with equal smooth or very feebly keeled scales; third and fourth fingers equal; the adpressed hind limb reaches between the eye and the tip of the snout. Tail strongly compressed, with sharp serrated upper edge; caudal scales smooth, with two rows of enlarged strongly keeled ones inferiorly; the length of the tail about twice and a half that of head and body. Brown or olive above, with or without darker cross bands; flanks with roundish yellow spots; throat sometimes with blue lines.

Moleclular evidence strongly supports the view that *Dilophyrus* should be recognized as a separate genus to *Gonocephalus* (e.g. Pyron *et al.* 2013). However I have taken the conservative position herein and classified the group as a subgenus.

Distribution: Southern Thailand, Vietnam, West Malaysia, Pulau Tioman, Pulau Pinang, Indonesia including Sumatra, Borneo, Nias, Mentawei Island, Nako, Sipora.

Content: *Gonocephalus* (*Dilophyrus*) *grandis* (Gray, 1845) (monotypic).

SUBGENUS *HONLAMAGAMA SUBGEN. NOV.*

Type species: *Tiaris sophiae* Gray, 1845.

Diagnosis: *Honlamagama subgen. nov.* are readily separated from the other subgenera within *Gonocephalus* by the following suite of characters: A normal supraciliary border; strongly keeled ventral scales and strongly keeled gular scales.

Distribution: Phillippine Islands.

Etymology: Named in honour of Mr. Hon Lam of Park Orchards, Victoria, Australia, in recognition of his logistical support for wildlife conservation through his helping Snakebusters, Australia's best wildlife displays.

Content: *Gonocephalus* (*Honlamagama*) *sophiae* (Gray, 1845) (type species); *G.* (*Honlamagama*) *interruptus* (Boulenger, 1885); *G.* (*Honlamagama*) *semperi* (Peters, 1867).

SUBGENUS *MANTHEYAGAMA SUBGEN. NOV.*

Type species: *Lophyrus bornensis* Schlegel, 1848.

Diagnosis: *Mantheyagama subgen. nov.* are readily separated from the other subgenera within *Gonocephalus* by the following suite of characters: A normal supraciliary border; smooth or very feebly keeled ventral scales and smooth or very feebly keeled gular scales.

Distribution: The Island of Borneo (Indonesia/Malaysia).

Etymology: Named in honour of Ulrich Manthey in recognition of his work on south-east Asian agamids.

Content: *Gonocephalus bornensis* (Schlegel, 1848) (type species); *Gonocephalus beyschlagi* (Boettger, 1892); *Gonocephalus bellii* (Duméril and Bibron, 1837); *Gonocephalus liogaster* (Günther, 1872).

SUBGENUS *DENZERAGAMA SUBGEN. NOV.*

Type species: *Lophyrus megalepis* Bleeker, 1860.

Diagnosis: *Denzeragama subgen. nov.* are readily separated from the other subgenera within *Gonocephalus* by the following suite of characters: Supraciliary border is normal; smooth ventral scales; nuchal crest is strongly separated from the dorsal crest and is not continuous with it.

Denzeragama subgen. nov. is further diagnosed as follows: Snout as long as the diameter of the orbit; canthus rostralis and supraciliary edge sharp, projecting; tympanum as large as the eye opening; occiput concave; upper head-scales small, strongly keeled; usually twelve upper and ten lower labials. Gular sac rather small, without serrated anterior edge; gular scales smooth, smaller than ventrals; a large subconical tubercle below the tympanum. Nuchal crest not continuous with dorsal, its greatest height somewhat exceeding the length of the snout; it is composed of lanceolate spines directed backwards, very small anteriorly, gradually becoming very large; these spines implanted on a dermal fold covered on each side with three or four rows of keeled pointed scales directed upwards; dorsal crest formed of large lanceolate spines like the posterior nuchals, with a basal series of smaller feebly keeled scales. Dorsal scales smooth or very feebly keeled, with the points directed upwards, intermixed with irregularly scattered enlarged ones; ventral scales moderately large, smooth. Limbs above with subequal feebly keeled scales; fourth finger slightly longer than third; the adpressed hind limb reaches the eye. Tail very strongly compressed, with an upper crest composed of triangular lobes gradually decreasing in size towards the end; caudal scales large, the upper feebly, the lower strongly keeled; length of the tail not twice that of head and body. Olive, with very indistinct brown spots; gular fold black (Boulenger, 1885).

Distribution: Sumatra, Indonesia.

Etymology: Named in honour of Wolfgang Denzer in recognition of his work on south-east Asian agamids.

Content: *Gonocephalus* (*Denzeragama*) *megalepis* (Bleeker, 1860) (type species); *G.* (*Denzeragama*) *klossi* (Boulenger, 1920); *G.* (*Denzeragama*) *lacunosus* Manthey and Denzer, 1991.

GENUS *DARANINAGAMA GEN. NOV.*

Type species: *Gonyocephalus robinsonii* Boulenger, 1908.

Diagnosis: *Daraninagama gen. nov.* is separated from all other *Gonocephalus* species by karyotypic differences. In *Daraninagama gen. nov.* there are 2n=32 chromosomes. Of the diploid chromosomes, 12 (pairs 1-6) are metacentric macrochromosomes, whereas the remaining 20 (pairs 7-16) were microchromosomes. Therefore, the arm number in macrochromosomes of this karyotype equaled 24.

By contrast for all species of *Gonocephalus* the configuration is 2n=42 chromosomes, including 22

macrochromosomes (pairs 1-11) and 20 microchromosomes (pairs 12-21).

Doongagama gen. nov. (defined herein and formerly included in *Gonocephalus*) are separated from all species of *Gonocephalus* and *Daraninagama gen. nov.* as defined herein by the unique presence of two parallel longitudinal gular folds, a trait seen in none of the other species as well as the other diagnostic characters outlined in the description below.

Daraninagama gen. nov. and *Doongagama gen. nov.* are both separated from *Gonocephalus* by their enlarged gular fold.

Daraninagama gen. nov. is readily identifiable and separated from all other *Gonocephalus* and *Doongagama gen. nov.* by the unique combination of having a distinctive white lower jaw and greatly enlarged gular fold.

In the wild *Daraninagama gen. nov.* are found in montane forest at 1,000m and above, usually near flowing water, resting on thin trees and also among ferns along paths.

Distribution: The highlands of West Malaysia.

Etymology: Named in honour of Dara Nin, of Ringwood, Melbourne, Victoria, Australia in recognition of his contributions to herpetology in Australia, in particular through his work with Snakebusters, Australia's best reptiles shows and educational displays.

This work has included at our educational "reptile parties", a concept I invented back in the 1970's.

In terms of this, I was derided by many people for many years, including being held up for public ridicule and hatred for daring to bring live reptiles to kids parties. Sticking to my guns I registered the Australian trademark "reptile parties" (2 of them) with no opposition from anyone else, because, as already mentioned, the general perception of other so-called herpetologists was that the idea was stupid.

However the general public couldn't get enough of the concept.

So now four decades later I find hundreds of other reptile enthusiasts imitating the concept of "reptile parties" globally and countless herpetologists accepting that the "reptile parties" concept was a winner!

However the real winners are the reptiles themselves, who are de-demonized by our displays and those that imitate them. The result is a better conservation outcome for all our biodiversity.

Content: *Daraninagama robinsonii* (Boulenger, 1908) (monotypic).

GENUS *DOONGAGAMA GEN. NOV.*

Type species: *Gonocephalus mjobergi* Smith, 1925.

Diagnosis: *Doongagama gen. nov.* (monotypic for the species *Doongagama mjobergi* Smith, 1925), are separated from all species of *Gonocephalus* and *Daraninagama gen. nov.* as defined herein by the unique presence of two parallel longitudinal gular folds, a trait seen in none of the other species.

In more detail the genus *Doongagama gen. nov.* is defined as follows: A feature clearly distinguishing *D. mjobergi* from all other *Gonocephalus* is the possession of enlarged dorsolateral scales forming oblique rows. The first row is located in the shoulder region and two distinct rows can be seen. Dorsolaterally enlarged scales are present in some species of *Gonocephalus* from Sumatra, in particular *G. megalepis* (Bleeker, 1860), *G. klossi* Boulenger, 1920 and *G. lacunosus* Manthey and Denzer, 1991 but never in such a geometrical arrangement as can be found in the type specimen of *D. mjobergi*. Another feature in *D. mjobergi* is the possession of an enlarged platelike scale below the tympanum which is separated from the tympanum by two rows of small scales.

As already mentioned, *D. mjobergi* possesses two parallel longitudinal gular folds. No other *Gonocephalus* species possesses this particular character.

Both folds start on the distal part of the gular region approximately bordering the serrated edge in the middle line of the pouch. The outer one runs nearly parallel to the centre line of the gular pouch and continues onto the anterior part of the chest. It partially conceals the *Gonocephalus*-type typical transverse fold as seen in these lizards. The inner folds are shorter and curve inside towards the centre line. This feature is very similar to the longitudinal gular folds known from species of the genera *Ptyctolaemus* Peters, 1864 and *Mantheyus* Ananjeva and Stuart, 2001. Ananjeva and Stuart (2001) depict the gular region of the latter two genera. The arrangement and colouration in *D. mjobergi* is rather comparable to that in *Ptyctolaemus.* It consists of two rows (grayish white in alcohol) with dark colouration of the skin in between. This indicates that this character independently developed in *Ptyctolaemus*, *Mantheyus* and *D. mjobergi* and seems to be an autapomorphy. All three also lack a transverse gular fold present in *Gonocephalus*.

However, *D. mjobergi* is by no means congeneric with either *Ptyctolaemus* or *Mantheyus*. Both genera *Ptyctolaemus* and *Mantheyus* have scaled tympani as opposed to *D. mjobergi*; additionally, *Mantheyus* has femoral pores. Within this cluster of genera only *D. mjobergi* shows oblique rows of enlarged dorsolateral scales. Because of the type specimen of *D. mjobergi* is a female it has been hypothesized that the gular sac will be even larger in male specimens which would distinguish it further from the genera discussed here with the exception of *Daraninagama robinsonii.*

Distribution: Currently only known from a single specimen found at Mount Murud (7000 feet = (2134 m elevation), Sarawak, Borneo, Malaysia.

Etymology: Named in honour of Dr. Nicholas Doong, General Practitioner of Burwood in Sydney, Australia, for his many decades of service to medicine and public health in Australia often in the most testing of circumstances. These situations including a huge number of sick patients waiting for hours to receive his attention and Dr. Doong commonly working for more hours a day than is good for his own health.

Content: *Doongagama mjobergi* Smith, 1925 (monotypic).

JAPALURA GRAY, 1853

Japalura Gray, 1853 as recognized to date (2013) has been shown to be paraphyletic by several authors using various criteria. Recent authors doing so include Stuart-Fox and Owens (2003), Mahony (2009), most recently by Pyron *et al.* (2013). These authors between them show at least three widely separated clades currently labelled within this genus, each group in fact being more closely related to other genera than one another within *Japalura* as currently defined. Notwithstanding the obvious results, each group also is too divergent to be placed in the genus with closest related taxa within other genera.

Besides the obvious molecular results of Pyron *et al.* (2013), morphologically each species group is readily identified and separated, thereby creating a need for these groups to be split into appropriate genera and taxonomically recognized.

Claims by Kaiser (2012a, 2012b) and Kaiser *et al.* (2013) that there is no need to split such genera are rejected as being obviously foolish and reckless.

The type species for the genus *Japalura* is *Japalura variegata* Gray, 1853, meaning others within the western clade remain within that genus.

Oriotiaris Günther, 1864 was originally created as a monotypic genus for *Tiaris elliotti* (Günther, 1860)

but is in fact a junior synonym of *Calotes tricarinatus* Blyth, 1853 (now known as *Japalura tricarinata* (Blyth, 1853).

In the face of molecular data and morphological differences between the so-called *Oriotiaris* group and the nominate clade group of *Japalura*, it is a borderline decision as to whether or not the group should be split at the full genus level. Taking a conservative position, I herein recognize *Oriotiaris* as a valid subgenus within *Japalura* in order to give the group proper taxonomic recognition within the Zoological Code.

One divergent taxon can be placed within a genus for which a name is available, namely *Diploderma* Hallowell, 1861, for the taxon described originally as *Diploderma polygonatum* Hallowell, 1861 and in my view erroneously placed in *Japalura* by most authors ever since.

The divergent species group including *Japalura splendida* Barbour and Dunn, 1919 and *Japalura flaviceps* Barbour and Dunn, 1919 do not have a genus name available, most likely due to the fact that many herpetologists have assumed them to be closely related to *Diploderma polygonatum* Hallowell, 1861, which they are not. The confusion arose due to the fact that both groups have a China-centric distribution. Hence the *splendida* / *flaviceps* group are formally placed within a newly diagnosed genus herein according to the Zoological Code (Ride *et al.* 1999).

This group, is in turn split into subgenera defined herein.

Relevant literature in terms of *Japalura sensu lato* include Ananjeva *et al.* (2011a), Anderson (1879), Annandale (1905), Annandale (2012), Athreya (2006), Barbour (1909), Barbour and Dunn (1919), Barts and Wilms (2003), Bauer and Günther (1992), Bhosale *et al.* (2013), Blyth (1854), Bobrov (1995), Bobrov and Semenov (2008), Boettger (1885, 1904), Boulenger (1885, 1890, 1906, 1918), Boulenger *et al.* (1907), Bourret (1937), Constable (1949), Das *et al.* (2009), Deng (1988), Gao *et al.* (2006), Gao (2001), Goa and Hou (2002), Goris and Maeda (2004), Gray (1853), Gressitt (1936), Gruber (1975), Günther (1860, 1864), Hallermann (2005a, 2005b), Hallowell (1861), Hu (1966), Inger (1960), Jamdar (1985), Jerdon (1870), Jono *et al.* (2013), Kästle and Schleich (1998), Kunz (2012), Laue (2005, 2009a, 2009b, 2011), Lenz (2012), Li (2001), Li *et al.* (2001), Li *et al.* (1981, 2000), Li *et al.* (2003), Lin and Lu (1982), Liu-Yu (1970), LiVigni (2013), Kunte and Manthey (2009), Macey *et al.* (2000), Mahony (2009, 2010), Manthey (2011, 2013), Manthey (2008), Manthey and Denzer (2012), Manthey *et al.* (2012), Mathew (2004, 2006), McGuire and Kiew (2001), Mertens (1926), Nanhoe and Ouboter (1987), Norval and Mao (2008), Ota (1988, 1989a, 1989b, 1989c, 1991a, 1991b, 2000a, 2000b, 2003), Ota and Weidenhofer (1992), Ota *et al.* (1998), Pope (1935), Saikia *et al.* (2007), Sang *et al.* (2009), Schleich and Kästle (2002), Scharf and Meiri (2013), Schradin (2004), Schulte II *et al.* (2004), Shah (1995), Simpson (1961), Slevin and Leviton (1956), Smith (1935), Song (1987), Stejneger (1898, 1907, 1910, 1924), Swan and Leviton (1962), Tanaka and Nishihira (1981), Van Denburgh (1912), Venugopal (2010), Waltner (1975), Wettstein (1938), Wogan *et al.* (2008), Wu *et al.* (2005), Zhao and Adler (1993) and sources cited therein.

GENUS *JAPALURA* GRAY, 1853.

Type species: *Japalura variegata* Gray, 1853.

Diagnosis: Tympanum hidden or unhidden. Body compressed. Dorsal scales heterogeneous. A dorsal crest. Gular pouch small or absent. An oblique fold in front of the shoulder; gular fold present or absent. Tail feebly compressed. No praeanal or femoral pores. An enlarged subocular scale row is absent, or if present is not large enough to cover the space between the supralabials and orbit, thus a moderately enlarged row and one or two smaller rows are present.

Diploderma Hallowell, 1861 is separated from *Japalura* by having the third and fourth fingers of equal length and only seven upper labials.

Maxhoseragama gen. nov. are readily separated from *Japalura* (the genus in which it was previously placed) and *Diploderma* by the following suite of characters: having infracaudal scales larger than ventrals; the third and fourth fingers of equal length; does not have seven upper labials. Furthermore this genus is separated from *Japalura* by the fact that an enlarged subocular scale row is present and prominent or at least moderately so.

Distribution: Southern Asia.

Content: *Japalura variegata* Gray, 1853 (type species); *J. andersoniana* Annandale, 1905; *J. dasi* (Shah and Kästle, 2002); *J. kumaonensis* (Annandale, 1907); *J. major* (Jerdon, 1870); *J. otai* Mahony, 2009; *J. planidorsata* Jerdon, 1870; *J. sagittifera* Smith, 1940; *J. tricarinata* (Blyth, 1853).

SUBGENUS *ORIOTIARIS* GÜNTHER, 1864.

Type species: *Tiaris elliotti* (Günther, 1860) (a junior synonym of *Calotes tricarinatus* Blyth, 1853).
Currently known as *Japalura tricarinata* (Blyth, 1853).

Diagnosis: Tympanum naked (as opposed to hidden in the subgenus *Japalura*). Back and sides covered with very small scales, between which larger keeled ones are scattered; a tubercle behind the superciliary edge. Dorsal crest very low, formed by a series of larger, keeled, not prominent scales. Gular sack none. Tail not compressed, with keeled scales below, which are almost as broad as long. Hence this subgenus differs from the nominate subgenus *Japalura* in the details of a concealed tympanum, ability of males to raise a nuchal crest and possession of a small gular pouch in the later. The subgenus *Oriotiaris* is further separated from the nominate subgenus *Japalura* by the absence (vs. presence) of dorsal chevrons and presence (vs. absence) of a coloured gular region, concealed tympanum, large crest spines in males and erectile nuchal crest (roach), in members of *Japalura*.

The diagnosis for the nominate subgenus *Japalura* is simply a reversal of this diagnosis.

Distribution: South Asia.

Content: *Japalura* (*Oriotiaris*) *tricarinata* (Blyth, 1853) (type for subgenus); *J.* (*Oriotiaris*) *dasi* (Shah and Kästle, 2002); *J.* (*Oriotiaris*) *kumaonensis* (Annandale, 1907); *J.* (*Oriotiaris*) *major* (Jerdon, 1870).

SUBGENUS *JAPALURA* GRAY, 1853.

Type species: *Japalura variegata* Gray, 1853.

Diagnosis: The diagnosis for the nominate subgenus *Japalura* is simply a reversal of the diagnosis for *Oriotiaris* above.

Distribution: South Asia.

Content: *Japalura variegata* Gray, 1853 (type for subgenus); *J. andersoniana* Annandale, 1905; *J. otai* Mahony, 2009; *J. planidorsata* Jerdon, 1870; *J. sagittifera* Smith, 1940.

GENUS *DIPLODERMA* HALLOWELL, 1861.

Type species: *Diploderma polygonatum* Hallowell, 1861.

Diagnosis: As for *Japalura*, this genus is diagnosed with the following suite of characters: Body compressed. Dorsal scales heterogeneous. A dorsal crest. Gular pouch small or absent. An oblique fold in front of the shoulder; gular fold present or absent. Tail feebly compressed. No praeanal or femoral pores.

This genus has a hidden tympanum.

Diploderma Hallowell, 1861 is separated from *Japalura* by having the third and fourth fingers of equal length and only seven upper labials.

Maxhoseragama gen. nov. are readily separated from *Japalura* (the genus in which it was previously placed) and *Diploderma* by the following suite of characters: having infracaudal scales larger than ventrals; the third and fourth fingers of equal length; does not have seven upper labials.

Distribution: Japan (Ryukyu Archipelago), China (Taiwan).

Content: *Diploderma polygonatum* Hallowell, 1861 (monotypic).

GENUS *MAXHOSERAGAMA GEN. NOV.*

Type species: *Japalura splendida* Barbour and Dunn, 1919.

Diagnosis: *Maxhoseragama gen. nov.* are readily separated from *Japalura* (the genus in which it was previously placed) and *Diploderma* by the following suite of characters: having infracaudal scales larger than ventrals; the third and fourth fingers of equal length; does not have seven upper labials.

Furthermore this genus is separated from *Japalura* by the fact that an enlarged subocular scale row is present and usually prominent, or at least moderately so.

This genus is also identified by the following suite of characters: Tympanum hidden. Body compressed. Dorsal scales heterogeneous. A dorsal crest. Gular pouch small or absent. An oblique fold in front of the shoulder; gular fold present or absent. Tail feebly compressed. No praeanal or femoral pores.

Distribution: East Asia (mainly China).

Etymology: Named in honour of my cousin, Max Hoser of Campbelltown, NSW, for his long term contributions to herpetology and public welfare in Australia.

Content: *Maxhoseragama splendida* (Barbour and Dunn, 1919) (type species); *M. batangensis* (Li, Deng, Wu and Wang, 2001); *M. brevicauda* (Manthey, Denzer, Hou and Wang, 2012); *M. brevipes* (Gressitt, 1936); *M. chapaensis* (Bourret, 1937); *M. dymondi* (Boulenger, 1906); *M. fasciata* (Mertens, 1926); *M. flaviceps* (Barbour and Dunn, 1919); *M. grahami* (Stejneger, 1924); *M. hamptoni* (Smith, 1935); *M. luei* (Ota, Chen and Shang, 1998); *M. makii* (Ota, 1989); *M. micangshanensis* (Song, 1987); *M. swinhonis* (Günther, 1864); *M. varcoae* (Boulenger, 1918); *M. yulongensis* (Manthey, Denzer, Hou and Wang, 2012); *M. yunnanensis* (Anderson, 1878); *M. zhaoermii* (Goa and Hou, 2002).

SUBGENUS *EKSTEINAGAMA SUBGEN. NOV.*

Type species: *Japalura swinhonis* Günther, 1864.
Diagnosis: The subgenus *Eksteinagama subgen. nov.* is readily separated from *Maxhoseragama subgen. nov.* by the obvious

lack of a transverse gular fold and the fact that the tibia is as long as the skull.

In the subgenus *Maxhoseragama subgen. nov.* there is an obvious transverse gular fold and the tibia is noticeably shorter than the skull.

Distribution: Taiwan.

Etymology: Named in honour of Robert Ekstein of Sydney, New South Wales, with an importing business at Wetherill Park, NSW, for services to herpetology spanning some decades.

Content: *Maxhoseragama* (*Eksteinagama*) *swinhonis* (Günther, 1864) (type species); *M.* (*Eksteinagama*) *brevipes* (Gressitt, 1936); *M.* (*Eksteinagama*) *luei* (Ota, Chen and Shang, 1998); *M.* (*Eksteinagama*) *makii* (Ota, 1989).

SUBGENUS *MAXHOSERAGAMA SUBGEN. NOV.*

Type species: *Japalura splendida* Barbour and Dunn, 1919.

Diagnosis: In the subgenus *Maxhoseragama subgen. nov.* there is an obvious transverse gular fold and the tibia is noticeably shorter than the skull.

The subgenus *Eksteinagama subgen. nov.* is readily separated from *Maxhoseragama subgen. nov.* by the obvious lack of a transverse gular fold and the fact that the tibia is as long as the skull.

Distribution: East Asia.

Etymology: See for the genus *Maxhoseragama gen. nov.*.

Content: *Maxhoseragama* (*Maxhoseragama*) *splendida* (Barbour and Dunn, 1919) (type for genus); *M.* (*Maxhoseragama*) *batangensis* (Li, Deng, Wu and Wang, 2001); *M.* (*Maxhoseragama*) *brevicauda* (Manthey, Denzer, Hou and Wang, 2012); *M.* (*Maxhoseragama*) *chapaensis* (Bourret, 1937); *M.* (*Maxhoseragama*) *dymondi* (Boulenger, 1906); *M.* (*Maxhoseragama*) *fasciata* (Mertens, 1926); *M.* (*Maxhoseragama*) *flaviceps* (Barbour and Dunn, 1919); *M.* (*Maxhoseragama*) *grahami* (Stejneger, 1924)

M. (*Maxhoseragama*) *hamptoni* (Smith, 1935); *M.* (*Maxhoseragama*) *micangshanensis* (Song, 1987); *M.* (*Maxhoseragama*) *varcoae* (Boulenger, 1918); *M.* (*Maxhoseragama*) *yulongensis* (Manthey, Denzer, Hou and Wang, 2012); *M.* (*Maxhoseragama*) *yunnanensis* (Anderson, 1878); *M.* (*Maxhoseragama*) *zhaoermii* (Goa and Hou, 2002).

CALOTES DAUDIN, 1802.

While there is no question that the genus *Calotes* as currently recognized forms a broadly monopyletic group, as compared to other agamid genera, the genus as currently recognized is paraphyletic if genera are assigned on the basis of the level of divergences used to define other agamid genera. A good example is seen in the genera *Salea* Gray, 1845, *Sitana* Cuvier, 1829 and *Otocryptis* Wagler, 1830, treated individually as separate genera by most recent authors, but most clearly as a sister clade to the greater *Calotes* as shown in Pyron *et al.* (2013) and earlier phylogentic studies.

It is therefore not consistent to treat *Calotes* as a single genus any longer and it is therefore divided herein on the basis of the obvious morphological differences, which happens to coincide with the molecular results of Pyron *et al.* (2013) and earlier authors.

The most logical configuration for the relevant species are three genera, one with an estimated divergence calibrated at 10 MYA and the other two diverging at calibrated date of between 7-10 MYA.

The nominate genus is further divided five ways into subgenera. The second new genus herein named *Crottyagama gen. nov.* is divided into four subgenera. The third genus contains just two species from India. Other than the original nominate one/s, all genera and subgenera are formally named and defined herein for the first time.

I note also that for a number of the more widely distriburted species within *Calotes sensu lato*, many are in fact species complexes.

The literature in terms of *Calotes* as recognized in 2013 is extensive and key papers and books include Amarasinghe and Karunarathna (2007, 2008), Amarasinghe *et al.* (2009a, 2009b, 2011, 2014), Andersson (1900), Andrews *et al.* (2013), Annandale (1905, 1909), Asana (1931), Asela *et al.* (2007, 2012), Auffenberg and Rehman (1993, 1995), Bahir and Maduwage (2005), Bahir and Surasinghe (2005), Baier (2005), Baig *et al.* (2008), Barts and Wilms (2003), Bauer and Günther (1992), Bergmann *et al.* (2004), Biswas (1975), Blyth (1852, 1854), Bobrov and Semenov (2008), Botejue *et al.* (2012), Boulenger (1885, 1890), Boulenger *et al.* (1907), Chan-ard *et al.* (1999), Chandramouli (2009b), Chou (1994), Clark *et al.* (1969), Cox *et al.* (1998), de Sliva (1994), de Sliva *et al.* (2005), Das *et al.* (2009), Das (1999), Das and Palden 2000), Das *et al.* (2008), Daudin (1802), Denzer *et al.* (1997), de Rooij (1915), Devasahayam and Devasahayam (1989), Dieckmann and Dieckmann (2011), Duméril and Bibron (1837), Erdelen (1978, 1984), Gabadage *et al.* (2009), Ganesh and Chandramouli (2013), Ganesh *et al.* (1997), Geissler (2013), Geissler *et al.* (2011), Gray (1845, 1846), Grismer (2011), Grismer *et al.* (2007, 2008, 2010), Grossmann (2008, 2011), Günther (1864, 1869, 1870, 1872b, 1875), Hallermann (2000a, 2005a, 2005b), Hardwicke and Gray (1827), Harlan (1824), Hartmann *et al.* (2013a, 2013b), Huang *et al.* (2013), Islam and Saikia (2013), Janzen (2003, 2011), Janzen and Bopage (2011), Janzen *et al.* (2007b), Jaquemont (1814), Jerdon (1854), Jestrzemski *et al.* (2013), Ji *et al.* (2002), Karthikeyan *et al.* (1993), Karunarathna and Amarasinghe (2008a), Karunarathna *et al.* (2009a, 2009b, 2011a, 2011b), Kramer (1979), Krishnan (2008), Kuhl (1820), Lenz (2012), Linnaeus (1758), Lönnberg (1896), Macey *et al.* (1997, 2000), Mahony and Ali Reza (2007), Mahony *et al.* (2009), Manthey and Grossmann (1997), Manthey and Schuster (1999), Merrem (1820), Meshaka (2011), Moody (1980), Müller (1887), Murthy (1990, 2010), Neang *et al.* (2010), Nanhoe and Ouboter (1987), Nevill (1887), Pandav *et al.* (2010, 2012), Pauwels *et al.* (2000, 2003), Pawlowski and Krämer (2007), Peters (1860), Pradeep and Amarasinghe (2009), Pyron *et al.* (2013), Quah *et al.* (2011), Radder *et al.* (2002), Rastegar-Pouyani *et al.* (2008), Ride *et al.* (1999), Rogner (2006), Sandera and Starastová (2009), Sang *et al.* (2009), Schleich and Kästle (2002), Schmidt (1925), Shanbhag *et al.* (2010), Sharma (2010), Sindaco and Jeremcenko (2008), Smedley (1932), Smith (1935), Somaweera and Somaweera (2009), Stuart and Emmett (2006), Stuart *et al.* (2006), Subramanean and Reddy (2012), Sura (1989), Sworder (1933), Taylor (1935, 1963), Teo and Rajathurai (1997), Theobold (1876), Thireau *et al.* (1998), Tiedemann *et al.* (1994), Tiwaru and Schiavina (1990), Tsetan and Ramanibai (2011), Turpon and Probst (1996), Upadhye *et al.* (2012), van der Kooij (2001), Venugopal (2010), Vindum *et al.* (2003), Vyas (2007, 2011a, 2011b), Wall (1908b), Waltner (1975), Werner (1896), Zhao and Adler (1993), Zhao and Li (1984, 1987), Ziegler (2002), Zug *et al.* (1998, 2006, 2009, 2010), and sources cited therein.

GENUS *CALOTES* DAUDIN, 1802.

Type species: *Lacerta calotes* Linnaeus, 1758.

Diagnosis: Formerly including species now included in other genera such as *Pseudocalotes* Fitzinger, 1843, *Bronchocela*, Kaup, 1827 and *Hypsicalotes* Manthey and Denzer, 2000; *Calotes* is herein defined as follows: Tympanum distinct; body compressed, covered with equal-sized scales; a dorso-nuchal crest; a more or less developed gular sac in the male; no transverse gular fold, or a very feebly marked one. Tail round or feebly compressed. No femoral or preanal pores.

There is no long transversal fold in front of the shoulder extending across the throat or two slender spines on the back of the head as seen in *Skrijelus gen. nov.* which comprises the species formerly known as *Calotes rouxii* Duméri and Bibron, 1837 and *Calotes ellioti* Günther, 1864.

Crottyagama gen. nov. formally described below is separated from *Calotes* Cuvier, 1817 and *Skrijelus gen. nov.* by the following characters: An oblique fold or triangle pit in front of shoulder covered with small scales, not extending across the throat and dorsal scales larger than ventrals and keeled. In addition to this, each of the relevant subgenera within *Crottyagama gen. nov.* are further diagnosed and separated from the other genera by one or other of: A/ No post orbital spine present; fourth toe much longer than the third; relatively large specimens up to about 140 mm snout-vent length; pit in front of the shoulders light brown or not coloured; white or yellow stripe above lip extending to the shoulder (subgenus *Crottyagama gen. nov.*); or B/ A post orbital spine present (*Freudcalotes subgen. nov.*); or C/ Two parallel rows of compressed spines above the tympanum and a dorsal colour of green in life (*Khasicalotes subgen. nov.*); or D/ Pit in front of shoulders is black, no white or yellow stripe is above the lip (*Amboncalotes subgen. nov.*).

Skrijelus gen. nov. formally described below is readily separated from both *Calotes* and *Crottyagama gen. nov.* by the presence of a long transversal fold in front of the shoulder extending across the throat and two slender spines on the back of the head.

It appears that all subgenera described below within the genus *Calotes* are of Pliocene divergences.

Distribution: The lower Indian subcontinent, including Sri Lanka, across southern Asia to east Asia including China.

Content: *Calotes calotes* (Linnaeus, 1758) (type species); *C. aurantolabium* Krishnan, 2008; *C. bhutanensis* Biswas, 1975; *C. ceylonensis* Müller, 1887; *C. desilvai* Bahir and Maduwage, 2005; *C. grandisquamis* Günther, 1875; *C. htunwini* Zug and Vindum, 2006; *C. irawadi* Zug, Brown, Schulte and Vindum, 2006; *C. liocephalus* Günther, 1872; *C. liolepis* Boulenger, 1885; *C. maria* Gray, 1845; *C. medogensis* Zhao and Li, 1984; *C. nemoricola* Jerdon, 1853; *C. nigrilabris* Peters, 1860; *C. pethiyagodai* Amarasinghe, Karunarathna and Hallermann, 2014; *C. versicolor* (Daudin, 1802).

SUBGENUS *CALOTES* DAUDIN, 1802.

Type species: *Lacerta calotes* Linnaeus, 1758.

Diagnosis: The species within the subgenus *Calotes* are separated from the other subgenera defined and formally named herein by the following suite of characters: An oblique fold or pit covered with small granular scales in front of the shoulder, not extending across the throat; dorsal scales as large as or smaller than the ventrals; lateral scales pointing upwards and backwards.

Specimens within the subgenus *Calotes* are further defined as follows: Upper head-scales smooth, imbricate, enlarged on supraorbital region; two groups of spines on each side of the head, between the ear and the nuchal crest; tympanum nearly half the diameter of the orbit. Gular sac not developed; gular scales feebly keeled, nearly as large as ventrals. A short oblique fold in front of the shoulder. Dorso-nuchal crest composed of closely set lanceolate spines directed backwards, with smaller ones at the base; in the male the height of the crest on the nape equals or exceeds the diameter of the orbit, and decreases gradually on the back. Thirtyone to thirtyfive scales round the middle of the body; dorsal scales very feebly keeled, or even quite smooth, with the points directed upwards and backwards; ventral scales larger than dorsals, very strongly keeled and mucronate. The adpressed hind limb reaches the anterior border of the orbit or a little beyond; third and fourth fingers nearly equal. Tail round. Green above, frequently with blackish-green cross bands, broader than the interspaces between them; young sometimes with a whitish longitudinal band on each side of the back.

The species within this subgenus have at times been placed within the so-called *versicolor* group, with which they share affinities, but may be readily separated from them by the fact that the latter group does not have an oblique fold or pit covered with small granular scales in front of the shoulder.

Those lizards are described below as the subgenus *Rubercalotes subgen. nov.*.

Distribution: Sri Lanka, Southern India, Burma.

Content: *Calotes* (*Calotes*) *calotes* (Linnaeus, 1758) (type species); *C.* (*Calotes*) *htunwini* Zug and Vindum, 2006.

SUBGENUS *RUBERCALOTES SUBGEN. NOV.*

Type species: *Agama versicolor* Daudin, 1802.

Diagnosis: *Rubercalotes subgen. nov.* are readily separated from all other *Calotes* subgenera by the following suite of characters: No fold in front of the shoulder; lateral scales pointing backwards and upwards.

Rubercalotes subgen. nov. are further diagnosed as follows: Upper head-scales rather large, smooth or feebly keeled, imbricate, more or less enlarged on supraorbital region; two well-separated spines (seldom absent or scarcely distinct) on each side of the back of the head, above the ear; tympanum is roughly half the diameter of the orbit, usually being slightly larger or smaller. Gular pouch not developed; gular scales smoother feebly keeled, as large as or larger than ventrals, largest and mucronate in the adult male. No oblique fold in front of the shoulder. Dorsonuchal crest well developed in the male, composed of lanceolate spines gradually decreasing in size towards the posterior part of the back. Thirty-five to sixty-one scales round the middle of the body; dorsal scales more or less distinctly keeled, larger than ventrals, all directed upwards and backwards; ventral scales strongly keeled. The adpressed hind limb reaches the temple or the anterior part of the eye; fourth finger a little longer than third or roughly equal. Tail round. Light brownish or yellowish, to green, uniform or with dark transverse bands or spots, or dark olive-brown with light spots or longitudinal lines, most notably and consistently present on the limbs; belly sometimes with dark longitudinal lines.

Distribution: Southern Asia, from south-east Iran to China. Feral populations now also exist in Borneo, Celebes, Maldives, Seychelles, Florida, USA, Mauritius (Reunion, Rodrigues) and Oman.

Etymology: Named in reference to the frequent appearance of red in specimens and the genus within which these lizards have traditionally been placed.

Content: *Calotes* (*Rubercalotes*) *versicolor* (Daudin, 1802) (type species); *C.* (*Rubercalotes*) *bhutanensis* Biswas, 1975; *C.* (*Rubercalotes*) *irawadi* Zug, Brown, Schulte and Vindum, 2006; *C.* (*Rubercalotes*) *maria* Gray, 1845; *C.* (*Rubercalotes*) *medogensis* Zhao and Li, 1984.

SUBGENUS *GHATSCALOTES SUBGEN. NOV.*

Type species: *Calotes nemoricola* Jerdon, 1853.

Diagnosis: *Ghatscalotes subgen. nov.* are readily separated from all other *Calotes* by the following suite of characters: An oblique fold or pit covered with small granular scales in front of the shoulder, not extending across the throat; dorsal scales larger than ventrals, smooth; lateral scales pointing upwards and backwards; 29 to 43 scales round the middle of the body.

Ghatscalotes subgen. nov. is further diagnosed as follows: Upper head-scales smooth or very feebly keeled, imbricate, enlarged on supraorbital region; three or four small to very small spines above the tympanum; latter measuring half, or just under half the diameter of the orbit; a gular pouch; lateral gular scales larger than ventrals, smooth or very feebly keeled. A short oblique fold in front of the shoulder. Dorso-nuchal crest formed of large lanceolate spines, the longest of which (in the male) equals from 3/4 to the full diameter of the orbit, gradually decreasing in height on the back; in the female the dorsal crest is reduced to a very feebly serrated ridge. Twenty-nine to fourty-three scales around the middle of the body; dorsal scales between three and four times as large as ventrals, squarish, smooth, pointing backwards and upwards; ventral scales strongly keeled. The adpressed hind limb reaches either almost the tympanum or slightly beyond; third and fourth fingers equal. Tail compressed. Green, uniform, or with broad black transverse bands on the back, occasionally each scale within the black bands has a central orange-coloured spot; or alternatively the colour is olive above, with indistinct darker markings; a black streak from the eye to above the tympanum; dark lines radiating from the eye; gular sac pink.

Distribution: The Western Ghats of India.

Etymology: Named in recognition of the region the species come from and also the genus with which they have been traditionally placed within.

Content: *Calotes* (*Ghatscalotes*) *nemoricola* Jerdon, 1853 (type species); *C.* (*Ghatscalotes*) *grandisquamis* Günther, 1875.

SUBGENUS *LACCADIVECALOTES SUBGEN. NOV.*

Type species: *Calotes nigrilabris* Peters, 1860

Diagnosis: *Laccadivecalotes subgen. nov.* is readily separated from the other subgenera of *Calotes* by the following suite of characters: One or other of: 1/ An oblique fold or pit covered with small granular scales in front of the shoulder, not extending across the throat; dorsal scales much smaller than ventrals; lateral scales pointing downwards and backwards (*Calotes* (*Laccadivecalotes*) *nigrilabris* Peters, 1860); or: 2/ An oblique fold or pit covered with small granular scales in front of the shoulder, not extending across the throat; dorsal scales larger than ventrals, smooth; lateral scales pointing downwards and backwards (*C.* (*Laccadivecalotes*) *liolepis* Boulenger, 1885).

Laccadivecalotes subgen. nov. is further separated from the other subgenera of *Calotes* by the following suites of characters: One of other of:

1/ Upper head-scales smooth, imbricate, not or but slightly enlarged on supraorbital region; a short series of three to six small spines above and behind the posterior part of the tympanum; latter measuring half, or more than half, the diameter of the orbit. Gular pouch not developed; gular scales more or less distinctly keeled, as large as ventrals. A strong oblique fold or pit in front of the shoulder. Dorso-nuchal crest composed of small lanceolate spines, the longest of which, on the nape, measure about two thirds the diameter of the orbit; on the back the crest is very distinct, but the spines gradually decrease in size. Forty-three to forty-seven scales round the middle of the body; dorsal scales rather feebly keeled, the upper pointing straight backwards, the others downwards and backwards; ventral scales much larger than dorsals, very strongly keeled, mucronate. The adpressed hind limb reaches the eye; third and fourth fingers equal. Tail round; in the males the scales on the basal part of the tail very- large and hard, those of the median upper row forming a slightly serrated ridge. Green, uniform on the back and tail, or with angular whitish black-edged angular cross bars or ocelli, with or without a reddish-brown vertebral band; lips and sides of head with a broad black band or variegated with black in the male; female usually with a white, black-edged horizontal streak below the eye (*Calotes* (*Laccadivecalotes*) *nigrilabris* Peters, 1860), or:

2/ Upper head-scales smooth, imbricate, strongly enlarged on supra-orbital region; two distant spines on each side of the back of the head, between the ear and the nuchal crest; diameter of the tympanum nearly half that of the orbit. Gular sac not developed; gular scales strongly keeled, as large as ventrals. A short oblique fold in front of the shoulder. Nuchal crest formed of narrow separated spines, the longest of which measure about the diameter of the tympanum; dorsal crest quite indistinct. Thirty-five or thirty-nine scales around the middle of the body; dorsal scales three times as large as ventrals, squarish, smooth, pointing backwards and downwards; ventral scales strongly keeled. The adpressed hind limb reaches hardly reaches the tympanum; third and fourth fingers equal. Tail round in cross-section. Dorsally, pale olive, with indistinct brown transverse bands on the back; brown lines radiating from the eye, the lower ones reaching down to the lower lip (*Calotes* (*Laccadivecalotes*) *liolepis* Boulenger, 1885 and *C.* (*Laccadivecalotes*) *desilvai* Bahir and Maduwage, 2005).

Distribution: Sri Lanka (Ceylon).

Etymology: Named in reference to the region in which the subgenus occurs, that being immediately east of the Laccadive Sea and the genus from which the species have been traditionally placed.

Content: *Calotes* (*Laccadivecalotes*) *nigrilabris* Peters, 1860 (type species); *C.* (*Laccadivecalotes*) *desilvai* Bahir and Maduwage, 2005; *C.* (*Laccadivecalotes*) *liolepis* Boulenger, 1885.

SUBGENUS *CEYLONCALOTES SUBGEN. NOV.*

Type species: *Calotes liocephalus* Günther, 1872.

Diagnosis: *Ceyloncalotes subgen. nov.* is readily separated from the other subgenera of *Calotes* by the following suite of characters: One or other of:

1/ An oblique fold or pit covered with small granular scales in front of the shoulder, not extending across the throat; dorsal scales as large as or smaller than ventrals; lateral scales pointing downwards and backwards; no spines whatsoever on the head (*Calotes* (*Ceyloncalotes*) *liocephalus* Günther, 1872 and *C.* (*Ceyloncalotes*) *pethiyagodai* Amarasinghe, Karunarathna and Hallermann, 2014); or:
2/ An oblique fold or pit covered with small granular scales in front of shoulder, not extending across throat; dorsal scales larger than ventrals, smooth or nearly so; lateral scales pointing upwards and backwards, or straight backwards; 60 scales round middle of body (*Calotes* (*Ceyloncalotes*) *ceylonensis* Müller, 1887).

Ceyloncalotes subgen. nov. is further separated from the other subgenera of *Calotes* by the following suites of characters: One of other of:

1/ Upper head-scales smooth, imbricate, enlarged on supraorbital region; no spines whatever on the side of the head; tympanum measuring a little more than half the diameter of the orbit. Gular pouch not developed; gular scales much larger than ventrals and rather feebly keeled. An oblique fold in front of the shoulder; nuchal crest composed of narrow spines the length of which equals the diameter of the tympanum; dorsal crest a mere serrated ridge. Forty-five scales around the middle of the body; dorsal scales feebly keeled, the upper ones pointing straight backwards or slightly upwards, the others downwards and backwards; ventral scales strongly keeled, nearly the same size as the dorsals. The adpresed hind limb reaches the eye; third and fourth fingers equal. Tail round, the scales of its basal part very large and hard, those of the median upper row forming a serrated edge. Pale olive-green, above with transverse bands of a darker green; four angular reddish-brown cross bands on the back; a dark streak from the eye to above the tympanum; limbs and tail with alternate lighter and darker cross bands (*Calotes* (*Ceyloncalotes*) *liocephalus* Günther, 1872 and *C.* (*Ceyloncalotes*) *pethiyagodai* Amarasinghe, Karunarathna and Hallermann, 2014); or:

2/ Upper head-scales smooth, imbricate, considerably enlarged on the supraorbital region; two small spines on each side above the tympanum; diameter of the tympanum half that of the orbit. No gular sac; gular scales very strongly keeled, much smaller than dorsals. A few small spines form a short nuchal crest; no dorsal crest. 60 scales round the middle of the body, dorsals largest and smooth or indistinctly keeled; on the anterior half of the body the scales point upwards and backwards, on the hind half nearly straight backwards; ventrals two thirds the size of dorsals, mucronate. The hind limb reaches the posterior border of the orbit. Dorsally, greenish, with six large orange spots across the back, separated by dark bands; sides with a black network; black lines radiate from the eye (*Calotes* (*Ceyloncalotes*) *ceylonensis* Müller, 1887).

Distribution: Sri Lanka (Ceylon).

Etymology: Named in recognition of the location that the subgenus occurs (Ceylon), and the genus from which the species have been traditionally placed.

Content: *Calotes* (*Ceyloncalotes*) *liocephalus* Günther, 1872 (type species); *C.* (*Ceyloncalotes*) *ceylonensis* Müller, 1887; *C.* (*Ceyloncalotes*) *pethiyagodai* Amarasinghe, Karunarathna and Hallermann, 2014.

SUBGENUS *TAMILNADUCALOTES SUBGEN. NOV.*

Type species: *Calotes aurantolabium* Krishnan, 2008.

Diagnosis: The subgenus *Tamilnaducalotes subgen. nov.* is separated from all other *Calotes* by the following suite of characters: It has an orange streak above each row of supralabials, green body; acutely keeled scales over body (dorsally and ventrally), head, and throat; posteroventral orientation of the dorsal scales; antehumeral pit absent; 63 scales around midbody; small tympanum (5.5% HL); toe 3 and 4 are subequal. Distinguished from the species until recently known as "*Calotes andamanensis*" or "*Pseudocalotes andamanensis*" (now placed in a new genus described herein as *Notacalotes gen. nov.*) in having acutely keeled dorsals, all of which are directed posteroventrally; antehumeral pit absent; acutely keeled ventrals, limb and head scales; smaller occipital, nuchal, temporal regions. Distinguished from all known species of the so called "*Calotes versicolour*" group (herein described as *Rubercalotes subgen. nov.*) in having posteroventral orientation of dorsal scales (posterodorsal in *Rubercalotes subgen. nov.*). Distinguished from species of the so-called "*Calotes liocephalus*" group (herein described as *Ceyloncalotes subgen. nov.*) in lacking antehumeral pit, and in having a proportionately smaller head, ulnar length proportionately longer, tibial length proportionately shorter. Distinguished from *Skrijelus gen. nov.* described within this paper, (including the two species formerly known as *Calotes rouxi* and *Calotes elliotti*) in lacking antehumeral folds and spines; toe 4 longer than toe 3 in *Skrijelus gen. nov.*.

Distribution: Only known from the type locality Kalakad Mundanthurai Tiger Reserve, Tamil Nadu, India. **Etymology:** Named in recognition of the location that the subgenus occurs (Tamil Nadu, India), and the genus from which the species has been traditionally placed.

Content: *Calotes* (*Tamilnaducalotes*) *aurantolabium* Krishnan, 2008 (monotypic).

CROTTYAGAMA GEN. NOV.

Type species: *Calotes mystaceus* Duméri and Bibron, 1837.

Diagnosis: *Crottyagama gen. nov.* is separated from *Calotes* Cuvier, 1817 and *Skrijelus gen. nov.* by the following characters: An oblique fold or triangle pit in front of shoulder covered with small scales, not extending across the throat and dorsal scales larger than ventrals and keeled. In addition to this, each of the relevant subgenera are further diagnosed and separated from the other genera by one or other of: A/ No post orbital spine present; fourth toe much longer than the third; relatively large specimens up to about 140 mm snout-vent length; pit in front of the shoulders light brown or not coloured; white or yellow stripe above lip extending to the shoulder (subgenus *Crottyagama subgen. nov.*); or B/ A long spine behind the supraciliary edge, and two others above the ear (*Freudcalotes subgen. nov.*); or C/ Two parallel rows of compressed spines above the tympanum and a dorsal colour of green in life (*Khasicalotes subgen. nov.*); or D/ Pit in front of shoulders is black, no white or yellow stripe is above the lip (*Amboncalotes subgen. nov.*).

Skrijelus gen. nov. formally described below is readily separated from both *Calotes* and *Crottyagama gen. nov.* by the presence of a long transversal fold in front of the shoulder extending across the throat and two slender spines on the back of the head.

With a divergence from *Calotes* estimated at about 10 MYA (calibrated, refer to Schulte *et al.* 2002 and Pyron *et al.* 2013), for *Crottyagama gen. nov.* it is entirely appropriate that the species group herein be recognized at the genus level.

Distribution: Southern Asia.

Etymology: Named in honour of my deceased pet dog, *Crotalus* (named "Crotty" for short) in recognition of his loyal protection of research files and property for more than a decade. *Crotalus* is also a generic name for a North American genus of Pitvipers. I might add that the concept that all 40-dd recognized species of rattlesnake should be placed in the genus *Crotalus* Linnaeus, 1758 is patently ridiculous (Hoser 2009, 2012, 2013).

Content: *Crottyagama mystaceus* (Duméri and Bibron, 1837) (type species); *C. bachae* (Hartmann, Geissler, Poyarkov, Ihlow, Galoyan, Rodder and Bohme, 2013); *C. emma* (Gray, 1845); *C. chincollium* (Vindum, 2003); *C. jerdoni* (Günther, 1870); *C. nigriplicatus* (Hallermann, 2000).

SUBGENUS *CROTTYAGAMA SUBGEN. NOV.*

Type species: *Calotes mystaceus* Duméri and Bibron, 1837.

Diagnosis: The genus *Crottyagama gen. nov.* is separated from *Calotes* Cuvier, 1817 and *Skrijelus gen. nov.* by the following characters: An oblique fold or triangle pit in front of shoulder covered with small scales, not extending across the throat and dorsal scales larger than ventrals and keeled. In addition to this, each of the relevant subgenera are further diagnosed and separated from the other genera and subgenera by one or other of: A/ No post orbital spine present; fourth toe much longer than the third; relatively large specimens up to about 140 mm snout-vent length; pit in front of the shoulders light brown or not coloured; white or yellow stripe above lip extending to the shoulder (subgenus *Crottyagama subgen. nov.*); or B/ A long spine behind the supraciliary edge, and two others above the ear (*Freudcalotes subgen. nov.*); or C/ Two parallel rows of compressed spines above the tympanum and a dorsal colour of green in life (*Khasicalotes subgen. nov.*); or D/ Pit in front of shoulders is black, no white or yellow stripe is above the lip (*Amboncalotes subgen. nov.*).

Skrijelus gen. nov. formally described below is readily separated from both *Calotes* and *Crottyagama gen. nov.* by the presence of a long transversal fold in front of the shoulder extending across the throat and two slender spines on the back of the head.

Distribution: Southern Asia.

Etymology: See for genus.

Content: *Crottyagama* (*Crottyagama*) *mystaceus* (Duméri and Bibron, 1837) (type species); *C.* (*Crottyagama*) *bachae* (Hartmann, Geissler, Poyarkov, Ihlow, Galoyan, Rodder and Bohme, 2013).

SUBGENUS *FREUDCALOTES SUBGEN. NOV.*

Type species: *Calotes emma* Gray, 1845.

Diagnosis: The genus *Crottyagama gen. nov.* is separated from *Calotes* Cuvier, 1817 and *Skrijelus gen. nov.* by the following characters: An oblique fold or triangle pit in front of shoulder covered with small scales, not extending across the throat and dorsal scales larger than ventrals and keeled. In addition to this, each of the relevant subgenera are further diagnosed and separated from the other genera and subgenera by one or other of: A/ No post orbital spine present; fourth toe much longer than the third; relatively large specimens up to about 140 mm snout-vent length; pit in front of the shoulders light brown or not coloured; white or yellow stripe above lip extending to the shoulder (subgenus *Crottyagama subgen. nov.*); or B/ A long spine behind the supraciliary edge, and two others above the ear (*Freudcalotes subgen. nov.*); or C/ Two parallel rows of compressed spines above the tympanum and a dorsal colour of green in life (*Khasicalotes subgen. nov.*); or D/ Pit in front of shoulders is black, no white or yellow stripe is above the lip (*Amboncalotes subgen. nov.*).

Skrijelus gen. nov. formally described below is readily separated from both *Calotes* and *Crottyagama gen. nov.* by the presence of a long transversal fold in front of the shoulder extending across the throat and two slender spines on the back of the head.

Distribution: Southern Asia between Assam (India) and Yunnan (China).

Etymology: Named in honour of a Daschund cross Doberman I owned in my youth. His name was Freud, being named after the psychologist Sigmund Freud, this being the man born Sigismund Schlomo Freud on 6 May 1856, who died on 23 September 1939, was an Austrian neurologist and who became known as the founding father of psychoanalysis. The dog looked intelligent like the man himself and was in fact intelligent for a dog. The dog was a great pet and trained to efficiently hunt snakes and lizards which he did for about nine years. Further details as to his exploits are in Hoser (1989).

Contrary to the many hate posts by Wolfgang Wüster, Hinrich Kaiser, Robert Twombley, Wulf Schleip, Bryan Fry and Mark O'Shea on their facebook page "Herpetological Taxonomy" (see 51 pages of posts from 26 November 2013 to 8 March 2014) (Wüster *et al.* 2014b), I do not see a problem with assigning a patronym scientific name after a dog.
Unlike these people I actually "like" animals!

Content: *Crottyagama* (*Freudcalotes) emma* (Gray, 1845) (type species); *C.* (*Freudcalotes) chincollium* (Vindum, 2003).

SUBGENUS *KHASICALOTES SUBGEN. NOV.*

Type species: *Calotes jerdoni* Günther, 1870.

Diagnosis: The genus *Crottyagama gen. nov.* is separated from *Calotes* Cuvier, 1817 and *Skrijelus gen. nov.* by the following characters: An oblique fold or triangle pit in front of shoulder covered with small scales, not extending across the throat and dorsal scales larger than ventrals and keeled. In addition to this, each of the relevant subgenera are further diagnosed and separated from the other genera and subgenera by one or other of: A/ No post orbital spine present; fourth toe much longer than the third; relatively large specimens up to about 140 mm snout-vent length; pit in front of the shoulders light brown or not coloured; white or yellow stripe above lip extending to the shoulder (subgenus *Crottyagama subgen. nov.*); or B/ A long spine behind the supraciliary edge, and two others above the ear (*Freudcalotes subgen. nov.*); or C/ Two parallel rows of compressed spines above the tympanum and a dorsal colour of green in life (*Khasicalotes subgen. nov.*); or D/ Pit in front of shoulders is black, no white or yellow stripe is above the lip (*Amboncalotes subgen. nov.*).

Skrijelus gen. nov. formally described below is readily separated from both *Calotes* and *Crottyagama gen. nov.* by the presence of a long transversal fold in front of the shoulder extending across the throat and two slender spines on the back of the head.

Distribution: India (Khasi Hills in Assam and Shillong), Burma (Myanmar), Bhutan.

Etymology: Named in recognition of the main location from where the subgenus is known and in recognition of the genus from where it used to be placed.

Content: *Crottyagama* (*Khasicalotes) jerdoni* (Günther, 1870) (monotypic).

SUBGENUS *AMBONCALOTES SUBGEN. NOV.*

Type species: *Calotes nigriplicatus* Hallermann, 2000.

Diagnosis: The genus is monotypic for the type species.
It was formally described as a species of *Calotes* morphologically similar to "*C. mystaceus*" (herein referred to as *Crottyagama* (*Crottyagama*) *mystaceus*), with 57 scales around middle of body, ten subralabials and nine infralabials, body compressed, homogeneous scales arranged in regular rows, dorsal and dorsolateral scales larger than ventrals, strongly keeled, pointing backwards and upwards, ventral and gular scales strongly keeled; a small gular pouch is present. In front of the shoulder, there is a distinct oblique fold of skin covered with small granular black-coloured scales. Nuchal and dorsal crest continuously composed of erect triangular scales, the former lower than the latter. Head shape triangular, forehead feebly concave, its length one and a half times its width. No postorbital spines. Limbs slender, moderately long, fourth toe reaching the hind margin of orbit. Fourth toe longer than third, 18 scales under fourth finger, and 25 under fourth toe. *Crottyagama mystaceus* differs from *C. nigriplicatus* in having light brown or uncoloured small scales in the fold in front of the shoulder, a broad white or yellow band stretching over the upper lip and extending to the shoulder, falciform spines of nuchal and dorsal crests and much longer nuchal crest spines than in *C. nigriplicatus*. *Crottyagama emma* with a similar black fold has long postorbital spines. Other species of the genus *Calotes* have body scales pointing backwards (*ceylonensis*) or backwards and downwards (*liolepis*, *liocephalus*) or dorsal scales equal to ventrals with no spines on head (species *andamanensis* now placed in the genus *Notacalotes gen. nov.*), or one row of spines above tympanum (*calotes*, *nigrilabris*) or in the case of *Crottyagama jerdoni*, two rows. *Calotes nemoricola*, *C. medogenensis* and *C. grandisquamis* have the fourth toe scarcely longer than third and fewer scales around the body (27 to 43, Smith 1935, and 53-55 in *medogenensis*, Zhao and Li 1984). *C. versicolor*, *C. maria* and *C. bhutanensis* differ from *Crottyagama nigriplicatus* by lacking a fold in front of the shoulder (Biswas, 1975) (adapted from Hallermann 2000a).

The genus *Crottyagama gen. nov.* is separated from *Calotes* Cuvier, 1817 and *Skrijelus gen. nov.* by the following characters: An oblique fold or triangle pit in front of shoulder covered with small scales, not extending across the throat and dorsal scales larger than ventrals and keeled. In addition to this, each of the relevant subgenera are further diagnosed and separated from the other genera and subgenera by one or other of: A/ No post orbital spine present; fourth toe much longer than the third; relatively large specimens up to about 140 mm snout-vent length; pit in front of the shoulders light brown or not coloured; white or yellow stripe above lip extending to the shoulder (subgenus *Crottyagama subgen. nov.*); or B/ A long spine behind the supraciliary edge, and two others above the ear (*Freudcalotes subgen. nov.*); or C/ Two parallel rows of compressed spines above the tympanum and a dorsal colour of green in life (*Khasicalotes subgen. nov.*); or D/ Pit in front of shoulders is black, no white or yellow stripe is above the lip (*Amboncalotes subgen. nov.*).

Skrijelus gen. nov. formally described below is readily separated from both *Calotes* and *Crottyagama gen. nov.* by the presence of a long transversal fold in front of the shoulder extending across the throat and two slender spines on the back of the head.

Distribution: Known only from the holotype from Ambon Island, Moluccas, Indonesia.

Etymology: Named in recognition of the genus it was formerly a part of and the location from where the holotype came from.

Content: *Crottyagama* (*Amboncalotes*) *nigriplicatus* (Hallermann, 2000) (monotypic).

GENUS *SKRIJELUS GEN. NOV.*

Type species: *Calotes rouxii* Duméri and Bibron, 1837.

Diagnosis: *Skrijelus gen. nov.* is readily separated from both *Calotes* Cuvier, 1817 and *Crottyagama gen. nov.* by the presence of a long transversal fold in front of the shoulder extending across the throat and two slender spines on the back of the head.

Distribution: India (within the regions of Bombay Presidency, Travancore, West Bengala, Gujarat, Goa, Maharashtra, Karnataka, Western Ghats).

Etymology. Named in honour of Mehemet (Mick) Skrijel, most recently of Melbourne, Victoria, Australia who in the 1980's and

1990's put his life and that of his family at great risk by blowing the whistle on corrupt drug dealing Victorian Police and similar police corruption in South Australia, leading to a senior officer being jailed. Skrijel also exposed entrenched judicial corruption (as outlined in Hoser 1999).

Srijel was the first to expose former South Australian drug squad chief Barry Moyse as being a corrupt drug drealer.

Moyse was the face of Operation Noah in South Australia in the 1980's.

This was a ruse he invented to get members of the public to dob in drug dealing competitors to Moyce himself, a major drug trafficker. He was also a vice-president of the SA Police Association.

As a direct result of information from Skrijel, Moyse was arrested in September 1987 and later pleaded guilty to 17 charges relating to the sale, supply and possession of heroin, amphetamines and cannabis.

He was sentenced to 27 years jail, reduced to 21 on appeal.

Throughout the early 1980's Moyce also routinely rigged and "fixed" criminal trials with corrupt judges and magistrates in order to get whistleblowers and other innocent people jailed for bogus offences and at the same time beat charges laid against his own friends and criminal associates.

As a result of Skrijel's public interest disclosures, Moyce and other police retaliated by burning Skrijel's fishing boat and his home in Western Victoria and brutally attacking his young daughter.

Content: *Skrijelus rouxii* (Duméri and Bibron, 1837) (type species); *S. ellioti* (Günther, 1864).

CALOTES ANDAMENSIS BOULENGER, 1891.

The correct generic placement of the species first described by Boulenger in 1891 as *Calotes andamanensis* has long been uncertain.

Harikrishnan and Vasudevan (2013) analysed the type specimen and others and reassigned the species to the genus *Pseudocalotes* Fitzinger, 1843 on the basis of morphology and obvious similarities between the species.

The species within the genus *Pseudocalotes*, had until 1980 been generally placed within *Calotes* Daudin, 1802, whereupon Moody (1980) resurrected *Pseudocalotes* and transferred a number of species to the genus.

Pseudocalotes is readily separated from *Calotes* in having relatively weak limbs as may be noted in some of the species names, e.g. "*Calotes brevipes* Werner, 1904". *Pseudocalotes* posesses mixed orientation of dorsal scales and lacks spines on the head. It is distinguished from another morphologically similar genus *Bronchocela* Kaup, 1827 in lacking a cheek skin fold and in having short weak limbs. They do not have any enlarged compressed set of scales behind the orbit. Excluding the taxon, "*Calotes andamanensis*", known only from the Andaman Islands, *Pseudocalotes* does not occur west of Sumatra.

While it is clear that the species "*Calotes andamanensis"* is similar in many respects to *Pseudocalotes tympanistra* Gray, 1831, the type species for that genus, the species *andamanensis* is also sufficiently divergent to warrant being placed in a separate genus. This is formally defined and named below, according to the Zoological Code (Ride *et al.* 1999).

The new genus to accommodate "*Calotes andamanensis* Boulenger, 1891" is herein named *Notacalotes gen. nov.* for obvious reasons and with reference to the fact it was not properly placed within the genus *Calotes.*

In terms of the remaining *Pseudocalotes*, there are two well defined species groups, each worthy of subgenus-level recognition. These are the Sunda taxa (about 6 recognized species) and those from Indochina (about 10 recognized species including that identified herein as "*Pseudocalotes* (*Mictopholis*) *austeniana* (Annandale, 1908)"). The Sunda taxa carry the type species for the genus and therefore should retain the name *Pseudocalotes.*

The name *Paracalotes* Bourret, 1939 is available for the Indochinese group (type species being *Paracalotes poilani* Bourret, 1939) and the group is tentatively recognized within this paper as a subgenus.

The genus *Mictopholis* Smith, 1935 is also tentatively recognized as distinct herein as a subgenus although it may well in fact fall within one of the other subgenera (probably *Paracalotes*).

Relevant diagnostics, taxonomic and nomenclatural details for each species group within the genus *Pseudocalotes*, including *Paracalotes* and *Mictopholis* can be found in Ananjeva *et al.* (2007, 2011a), Anderson (1879), Annandale (1908), Athreya (2006), Bain *et al.* (2007), Barts and Wilms (2003), Bobrov and Semenov (2008), Boettger (1893c), Boulenger (1885, 1887c, 1887d, 1890, 1891a, 1912), Bourret (1939), Chan-ard *et al.* (2008), Cox *et al.* (1998), Das (2004), Das and Das (2007), Denzer and Mathey (1991), Denzer *et al.* (1997), de Rooij (1915), Duméril *et al.* (1837), Dunn (1927), Gray (1831), Grismer (2011), Grismer *et al.* (2011), Hallermann (2000a, 2005a, 2005b), Hallermann and Böhme (2000), Hallermann and McGuire (2001), Hallermann *et al.* (2010), Harikrishnan and Vasudevan (2013), Hubrecht (1879), Inger and Stuebing (1994), Ishwar and Das (1998), Kopstein (1938), Koshikawa (1982), Krishnan (2008), Lenz (2012), Macey *et al.* (2000), Mahony (2010), Manthey and Denzer (2000), Manthey and Grossmann (1997), Manthey and Schuster (1999), Mertens (1954), Milto and Barabanov (2012), Moody (1980), Nguyen and Ziegler (2010), Ota (1989c), Rendahl (1937), Sang *et al.* (2009), Smith (1924, 1930, 1935, 1937a, 1940, 1943), Taylor (1963), Tiedmann and Häupl (1980), Venugopal (2010), Vindum *et al.* (2003), Waltner (1975), Werner (1904), Yang *et al.* (1979), Ziegler *et al.* (2008), Zug *et al.* (2006) and sources cited therein. A molecular basis for subgeneric recognition of the relevant species groups can be seen in Pyron *et al.* (2013) and earlier molecular studies.

Key literature in terms of the monotypic genus as defined herein as *Notacalotes gen. nov.*, its taxonomy and nomenclature include the following, Boulenger (1891a), Hallermann (2000a), Harikrishnan and Vasudevan (2013), Ishwar and Das (1998), Krishnan (2008), Moody (1980), Murthy (1990), Pryon *et al.* (2013), Ride *et al.* (1999), Smith (1935), Venugopal (2010) and sources cited therein.

GENUS *NOTACALOTES GEN. NOV.*

Type species: *Calotes andamanensis* Boulenger, 1891.

Diagnosis: *Notacalotes gen. nov.* monotypic for the species originally described as "*Calotes andamanensis* Boulenger, 1891" is separated from similar species by having enlarged keeled scales on the posterior surface of the thigh, dorsal head scales obtusely keeled, smooth dorsal body scales (upper six rows directed posterodorsally, remainder posteroventrally), and lacking body crest, antehumeral pit present; nuchal crest well developed; 67 scales around the midbody; tympanum (11% HL); toe 3 shorter than toe 4. Distinguished from *Calotes* (*Tamilnaducalotes*) *aurantolabium* Krishnan, 2008 in having smooth dorsals, dorsal body scales unequal, upper six scale rows larger, remainder equal in size to ventral scales; three enlarged scales on caudal thigh; dorsal head scales obtusely keeled; parietal ridge raised; enlarged scale between nuchal crest and tympanum; antehumeral pit present; toe 4 longer than 3; stretched hindlimb reaches eye. Distinguished from other *Calotes* subgenera *Ceyloncalotes subgen. nov.* and *Rubercalotes subgen. nov.* as well as *Skrijelus gen. nov.* (species formerly within *Calotes*) by the presence of enlarged keeled scales on caudal surface of thigh. Distinguished from *Calotes* subgenus *Rubercalotes subgen. nov.* in scale orientation: distinguished from *Rubercalotes subgen. nov.* in having an antehumeral pit; distinguished from *Calotes* subgenus *Ghatscalotes subgen. nov.* in having equal size dorsal and ventral scales, toe 4 longer than toe 3, scales around midbody 67 (36-43 and 27-35 respectively); distinguished from the

Calotes subgenus *Calotes* as defined within this paper in lacking flattened spines in the nuchal region. Distinguished from *Skrijelus gen. nov.* (species formerly within *Calotes*) in having an antehumeral pit (instead of folds) and in lacking spines in the nuchal region. Distinguished from *Calotes* subgenera *Ceyloncalotes subgen. nov.* and *Laccadivecalotes subgen. nov.* in lacking spines in the nuchal region; distinguished from *Calotes* (*Ceyloncalotes*) *liocephalus* by midbody scale count and body crest scales.

This genus *Notacalotes gen. nov.* is alternatively defined as follows: relatively long head (hw: hl = 0.59); 56-67 longitudinal scale rows around midbody; dorsals and laterals smooth, sometimes weakly keeled near the sacral region; ventrals strongly keeled; dorsals of 4-7 paravertebral longitudinal rows larger than laterals, of irregular shape, pointing posterodorsally; laterals pointing posteroventrally; laterals and ventrals of similar size; ventrals slightly irregular; a row of enlarged scales between supralabials and orbit, bordered by one or two smaller scale rows; gular scales smaller than ventrals, weakly keeled; gular pouch present in males; antehumeral fold/pit weakly developed; nuchal crest composed of 11-15 lanceolate spines; dorsal crest a denticulate ridge; enlarged conical lamellae under the leading edge of third toe; 27-30 lamellae under fourth toe; hind limb length 70-75 % of svl; tail length 238-265% of svl, slightly compressed at the base (Harikrishnan and Vasudevan, 2013).

The species within *Notacalotes gen. nov.* can be distinguished from *Pseudocalotes* in having stronger and proportionately longer limbs (proportional antebrachial length not different); nuchal crest vertically directed compressed triangle scales, nuchal crest scales not intermittent as in several *Pseudocalotes*; presence of enlarged keeled scales on posterior surface of thigh. Distinguished from *Bronchocela* Kaup, 1827 and *Calotes* in having enlarged keeled scales on caudal surface of thigh. Distinguished from *Complicitus* Manthey and Grossmann, 1997 in having enlarged keeled scales on caudal face of thigh, lacking a gular pouch or dewlap, and having smaller head length and head height proportions. Distinguished from *Salea* Gray, 1845 in having predominantly uniform dorsal body scales, smooth body scales, lacks body crest, and laterally compressed body (depressed body in *Salea khakienensis*). Distinguished from *Dendragama* Doria, 1888 in lacking a lateral crest on either side of neck; lacking raised parietal ridges; lacking a row of enlarged keeled body scales; lacking keeled dorsal body scales; having flat forehead.

Distribution: Known only from the Andaman and Nicobar Islands (India).

Etymology: The new genus to accommodate "*Calotes andamanensis* Boulenger, 1891" is herein named *Notacalotes gen. nov.* for obvious reasons and with reference to the fact it is not properly placed within the genus *Calotes.*

Content: *Notacalotes andamanensis* (Boulenger, 1891) (monotypic).

***CERATOPHORA* GRAY, 1835**

In line with *Calotes* Daudin, 1802, *Ceratophora* Gray 1835 as currently recognized does form a monophyletic group.

However the degree of divergence of two species lineages, namely *C. aspera* Günther, 1864 and *C. karu* Pethiyagoda and Manamendra-Arachchi, 1998 are sufficient to warrent them each being placed in their own unique genera, if the relevant species are to be treated in a manner similar to other agamid species in terms of placement within genera. This divergence can be measured either by way of long recognized and significant morphological differences (including as cited by Boulenger 1885 and 1890 and then more recently and relevantly Pethiyagoda and Manamendra-Arachchi, 1988), or alternatively via the results of several molecular studies including that published by Schulte *et al.* (2002) and recently corroborated by Pyron *et al.* (2013), showing divergences in well excess of 10 MYA for each of the newly named genera as identified herein.

Ceratophora Gray 1835, is thus divided in three, with the divergent taxa, *C. aspera* Günther, 1864 (diverged at 13 MYA according to Schulte *et al.* 2002) and *C. karu* Pethiyagoda and Manamendra-Arachchi, 1998 (diverged at 10.8 MYA according to Schulte *et al.* 2002) each placed in a new monotypic genus named for the first time. The remaining *Ceratophora* is split into two obvious subgenera, with each group diverged at about 7.1 MYA (according to Schulte *et al.* 2002).

All are obviously united at the subtribe level of classification and higher.

Relevant literature in terms of the classification of *Ceratophora* Gray 1835 as recognized as of 2013 include the following: Amarasinghe *et al.* (2007, 2009), Bahir and Surasinghe (2005), Bartelt (1996), Bartelt and Janzen (2007), Botejue *et al.* (2012), Boulenger (1885, 1890), de Silva (1994), Dieckmann (2011), Gray (1835), Günther (1864), Janzen (2003), Janzen *et al.* (2007b), Kelaart (1854), Macey *et al.* (2000), Manthey (2011), Manthey and Schuster (1999), Pethiyagoda and Manamendra-Arachchi (1998), Pyron *et al.* (2013), Ride *et al.* (1999), Schulte *et al.* (2002), Simpson (1961), Smith (1935), Somaweera and Somaweera (2009), Taylor (1953) and sources cited therein.

GENUS *CERATOPHORA* GRAY, 1835.

Type species: *Ceratophora stoddartii* Gray, 1834.

Diagnosis: The genus *Ceratophora* Gray 1835 is diagnosed herein as follows: Tympanum hidden. Body more or less compressed, covered with unequal scales. No dorsal crest; a nuchal crest may be present or absent. No gular sac; no gular fold. A large rostral appendage, at least in the males. No femoral or praeanal pores. The gular scales larger than the ventrals, smooth or feebly keeled; lateral scales are large, equal or unequal; rostral appendage is either scaleless or scaly.

Pethiyagodaus gen. nov. is readily separated from *Ceratophora* (both subgenera) and *Manamendraarachchius gen. nov.* as defined herein by having gular scales smaller than the ventrals, strongly keeled; lateral scales small; rostral appendage scaly. It is separated from all other *Ceratophora sensu lato* by the presence of a visible and palpable squamosal process (absent in all *Ceratophora sensu lato* other species).

Manamendraarachchius gen. nov. (type species being *M. karu* Pethiyagoda and Manamendra-Arachchi, 1988) are separated from all other *Ceratophora sensu lato* (except *C.* (*Jamesschulteus*) *tennentii* and *Pethiyagodaus aspera*) by the rostral appendage being complex, comprising more scales than rostral scale alone (vs. rostral appendage restricted to rostral scale alone in *C. erdeleni* and *C. stoddartii*). It is distinguished from *C.* (*Jamesschulteus*) *tennentii* by the presence of prominent superciliary scales, versus absent in *C.* (*Jamesschulteus*) *tennentii*) and from *Pethiyagodaus aspera* by the absence of a palpable squamosal process versus squamosal process present in *P. aspera.*

Distribution: Sri Lanka (Ceylon).

Content: *Ceratophora stoddartii* Gray, 1834 (type species); *C. erdeleni* Pethiyagoda and Manamendra-Arachchi, 1998; *C. tennentii* Günther, 1861.

SUBGENUS JAMESSCHULTEUS SUBGEN. NOV.

Type species: *Ceratophora tennentii* Günther, 1861.

Diagnosis: The subgenus *Jamesschulteus* subgen. nov. is readily separated from the subgenus *Ceratophora* by having gular scales larger than the ventrals, feebly keeled; lateral scales large, equal; rostral appendage scaly, versus gular scales larger than the ventrals, and smooth; lateral scales large and of unequal sizes; rostral appendage scaleless in *Ceratophora.*

Distribution: Sri Lanka (Ceylon). This monotypic subgenus is restricted to the Knuckles range of mountains, separated from the Central Massif by the lowlands (500 m) of the valley of the Mahaweli River.

Etymology: Named in honour of James Schultz II of St. Louis, Missouri, USA in recognition of his recent work on the molecular biology of the relevant lizards in *Ceratophora sensu lato.*

Content: *Ceratophora* (*Jamesschulteus*) *tennentii* Günther, 1861 (monotypic).

SUBGENUS *CERATOPHORA* GRAY, 1835.

Type species: *Ceratophora stoddartii* Gray, 1834.

Diagnosis: The subgenus *Jamesschulteus subgen. nov.* (the only other subgenus in this genus) is readily separated from the subgenus *Ceratophora* by having gular scales larger than the ventrals, feebly keeled; lateral scales large, equal; rostral appendage scaly, versus gular scales larger than the ventrals, and smooth; lateral scales large and of unequal sizes; rostral appendage scaleless in *Ceratophora.*

Distribution: Sri Lanka (Ceylon).

Content: *Ceratophora* (*Ceratophora*) *stoddartii* Gray, 1834 (type species); *C.* (*Ceratophora*) *erdeleni* Pethiyagoda and Manamendra-Arachchi, 1998.

GENUS *PETHIYAGODAUS GEN. NOV.*

Type species: *Ceratophora aspera* Günther, 1864.

Diagnosis: *Pethiyagodaus gen. nov.* is readily separated from *Ceratophora* (both subgenera) and *Manamendraarachchius gen. nov.* as defined herein by having gular scales smaller than the ventrals, strongly keeled; lateral scales small; rostral appendage scaly. It is separated from all other *Ceratophora sensu lato* by the presence of a visible and palpable squamosal process (absent in all *Ceratophora sensu lato* other species). *Pethiyagodaus gen. nov.* also differs from *Ceratophora* (both subgenera) and *Manamendraarachchius gen. nov.* as defined herein by lacking a knob or boss at the dorsoanterior corner of the postorbital.

Manamendraarachchius gen. nov. are separated from all other *Ceratophora sensu lato* except (except *C.* (*Jamesschulteus*) *tennentii* and *Pethiyagodaus aspera*) by the rostral appendage being complex, comprising more scales than rostral scale alone (vs. rostral appendage restricted to rostral

scale alone in *C. erdeleni* and *C. stoddartii*). It is distinguished from *C.* (*Jamesschulteus*) *tennentii*

by the presence of prominent superciliary scales, versus absent in *C.* (*Jamesschulteus*) *tennentii*) and

from *Pethiyagodaus aspera* by the absence of a palpable squamosal process versus squamosal process present in *P. aspera* the sole representative of that genus.

Pethiyagodaus aspera and *Lyriocephalus scutatus* are the only two species in the subtribe *Pethiyagodaiina subtribe nov.* inhabiting lowland rain forest, the other species in this subtribe being restricted to montane cloud forests.

Distribution: Sri Lanka (Ceylon).

Etymology: Named in honour of Rohan Pethiyagoda of Sri Lanka in recognition of his taxonomic work on these lizards.

Content: *Pethiyagodaus aspera* (Günther, 1864) (monotypic).

GENUS *MANAMENDRAARACHCHIUS GEN. NOV.*

Type species: *Ceratophora karu* Pethiyagoda and Manamendra-Arachchi, 1988.

Diagnosis: *Manamendraarachchius gen. nov.* are separated from all other *Ceratophora sensu lato* except (except *C.* (*Jamesschulteus*) *tennentii* and *Pethiyagodaus aspera*) by the rostral appendage being complex, comprising more scales than rostral scale alone (vs. rostral appendage restricted to rostral

scale alone in *C. erdeleni* and *C. stoddartii*). It is distinguished from *C.* (*Jamesschulteus*) *tennentii*

by the presence of prominent superciliary scales, versus absent in *C.* (*Jamesschulteus*) *tennentii*) and

from *Pethiyagodaus aspera* by the absence of a palpable squamosal process versus squamosal process present in *P. aspera*.

Manamendraarachchius karu (monotypic for the genus) also shows an unusual behavioural trait in always holding its head well above the horizontal, its supraoccipital being recessed to facilitate this.

Further diatgnostic information for the monotypic genus is provided by Pethiyagoda and Manamendra-Arachchi (1988), in the original description of its sole species, that which they named as "*Ceratophora karu*".

Distribution: Sri Lanka (Ceylon). The sole species of this genus is known only from a very restricted region including the eastern side of the Sinharaja World Heritage Site at Morningside Forest Reserve, near Rakwana (06°24'N, 80°38'E, alt. 1060 m) and while apparently able to tolerate some habitat modification, must be regarded as a potentially threatened taxon. Due to the relative uniqueness of this taxon (the genus as defined herein is monotypic) and the lack of particularly closely related taxa, the nearest relatives having diverged more than 10 MYA, the species *Manamendraarachchius karu* should be accorded the highest possible conservation value in law.

Etymology: Named in honour of Kelum Manamendra-Arachchi from Sri Lanka in recognition of his taxonomic work on these lizards.

Content: *Manamendraarachchius karu* (Pethiyagoda and Manamendra-Arachchi, 1988).

***BRONCHOCELA* KAUP, 1827.**

This genus of lizards, formerly treated as part of *Calotes* Daudin, 1802 (e.g. Boulenger 1885), has since 1980 been treated as a single genus.

A detailed review of the genus and component species was conducted by Hallerman (2005c) and need not be repeated here. The 12 currently recognized species within the genus (including that formally described herein) appear to be associated with two main species groups, namely those similar to the type species for the genus *B. cristatella* (Kuhl, 1820) (*terra typica* from Java) and those associated with the taxon *B. jubata* Duméril and Bibron, 1837.

The latter group are both sympatric with the former and also sufficiently different to warrant recognition at the genus level. However in the absence of molecular data for the group, I hereby take a conservative position and herein place them in a new subgenus, formally named for the first time.

Because the genus *Bronchocela* is divided two ways only, there is no need to formally define the nominate subgenus, in that its definition and diagnosis is simply by way of elimination in terms of specimens of the newly named subgenus or a reversal of the new subgenus diagnosis.

The species *Bronchocela cristatella* Kuhl, 1820 has long been regarded as being composite and the species *B. moluccana* (Lesson, 1830) is herein regarded as being a separate species.

This is on the basis of both morphological differences as outlined by Boulenger (1885) and the allopatric distribution separated by a significant geographical barrier.

The form from Halmahera Island, while similar in many respects to the nominate form and *B. moluccana*, is regarded as being sufficiently divergent from them to be classified as a new species on the basis of similar reasons, these being consistent morphological differences and being found in a place separated by a deep water barrier.

This decision is also based the inspection of live animals and photos of numerous specimens of both the Halmahera form and the nominate one. It is therefore formally described as a new species below.

Relevant literature in terms of the newly diagnosed and defined subgenus *Ferebronchocela subgen. nov.* the remainder of *Bronchocela* and the newly named species below (*Bronchocela harradineus sp. nov.*) include Alcala (1986), Auliya (2006), Barts and Wilms (2003), Baumann (1913), Berthold (1840), Biswas (1984), Blanford (1878), Bobrov and Semenov (2008), Böhme (2012), Boulenger (1883, 1885, 1890), Brongersma (1948), Brown *et al.* (1970, 1996, 2013), Chan-ard *et al.* (1999), Cox *et* *al.* (1998), Das (1993, 1999, 2004, 2013), Das and Gemel (2000), de Rooij (1915), Diong and Lirn (1998), Duméril and Bibron (1837, 1851), Ferner *et al.* (2000), Fitzinger (1861), Flower (1899), Gaulke (1999, 2001, 2011), Gray (1845), Grismer (2011), Grismer *et al.* (2010), Grossmann (2009), Günther (1864, 1873), Hallermann (2004, 2005a, 2005b, 2005c, 2009), Heang (1987), Hendrickson (1966), Iskandar and Erdelen (2006), Koch *et al.* (2009), Kopstein (1938), Kuhl (1820), Lagat (2009), Lim and Ng (1999), Macey *et al.* (2000), Malkmus (2000), Malkmus and Kunkel (1992), Malkmus *et al.* (2002), Manthey (1993), Manthey and Grossmann (1997), Manthey and Schuster (1999), McLeod *et al.* (2011), Mertens (1930), Moody (1980), Müller (1895), Müller (1928), Murthy (1990), Nabhitabhata and Chan-ard (2005), Nabhitabhata *et al.* (2000), Pauwels *et al.* (2000, 2003), Peters (1867), Peters and Doria (1878), Pianka and Vitt (2003), Quah *et al.* (2012), Sang *et al.* (2009), Setiadi and Hamidy (2006), Sharma (2002), Siler and Brown (2010), Siler *et al.* (2011), Simpson (1961), Smedley (1931a), Smith (1935), Stuart *et al.* (2006), Taylor (1963), Teo and Rajathurai (1997), ter Borg (2005, 2007), Tikader and Sharma (1992), Tiwari and Biswas (1993), Venugopal (2010), Wanger *et al.* (2011), Wood *et al.* (2004) and sources cited therein.

SUBGENUS *FEREBRONCHOCELA SUBGEN. NOV.*

Type species: *Bronchocela jubata* Duméril and Bibron, 1837.

Diagnosis: The genus *Bronchocela* is defined and separated from similar agamid genera as follows: No fold in front of the shoulder; lateral scales pointing backwards and downwards; ventral scales larger than latero-dorsals; fourth finger nearly the same length as the fifth toe or rarely longer.

The subgenus *Ferebronchocela subgen. nov.* is separated from the nominate genus by the fact that only the scales of the row at the base of the dorsal crest point upwards, versus all the upper dorsal scales pointing upwards and backwards in *Bronchocela*. The dorsal crest gives the appearance as if it is composed of tiny hairs as opposed to scales (as seen in *Bronchocela*).

The subgenus *Ferebronchocela subgen. nov.* is further diagnosed as follows: Relatively large species of 88.7-135.6 mm SVL, (mean 112.90, n=51) and a long tail (ratio tail svl=344.74, n=35). Tympanum large, more than half diameter of orbit. There are 5-6 scales along canthus rostralis between nasal scale and front border of orbit. Two larger keeled scales on rostral border of tympanum, and a row of compressed scales (3-4) behind hind corner of orbit. Gular sac large, extending under forelegs, covered with large keeled scales. Nuchal crest scales large, falciform and directed backwards, about as large as diameter of orbit or larger in adults. Dorsal crest lower than nuchal crest, continuing back to base of tail. Body scales rather large, strongly keeled in 44-59 midbody scales (mean: 49.21, n=51), the uppermost scale row next to dorsal crest pointing upwards, 1-3 rows directed parallel, others scale row downwards. Ventrals large, strongly keeled. It can be distinguished from other congeners in the nominate subgenus (*Bronchocela*) by the combination of 5-6 scales between nasal and orbit along canthus rostralis, large keeled body scales, with only uppermost scale row pointing upwards, a prominent nuchal and dorsal crest, and a large gular sac in males.

Distribution: South-east Asia.

Etymology: *Fere* being Latin for “not quite” or “nearly”, the name reflecting the species being “not quite” *Bronchocela sensu stricto.*

Content: *Bronchocela* (*Ferebronchocela*) *jubata* (Duméril and Bibron, 1837) (type species); *B.* (*Ferebronchocela*) *orlovi* Hallermann, 2004.

BRONCHOCELA HARRADINEUS SP. NOV.

Holotype: Reptile specimen number 237431 at the United States National Museum (USNM), Washington DC, USA, collected at Kampung Pasir Putih, Jailolo District, Halmahera Island, Indonesia. The USNM is a government controlled facillity that allows access to specimens by researchers.

Paratypes: Specimen numbers 237430, 237432, 237433, 237434, 237435, 215789, 215790 and 215791 at the United States National Museum (USNM), Washington, DC, USA, all collected at Kampung Pasir Putih, Jailolo District, Halmahera Island, Indonesia. The USNM is a government controlled facillity that allows access to specimens by researchers.

Diagnosis: The species *Bronchocela harradineus sp. nov*. has until now been identified as a variant of the species *Bronchocela cristatella* Kuhl, 1820 or perhaps as *B. moluccana* (Lesson, 1830).

The species *Bronchocela harradineus sp. nov*. shares characteristics of both taxa, but is readily separated from both by the following unique suite of characters: Dorsal colour in healthy living adults is greenish all over and not punctuated by a distinct pattern of flecks or bars (as seen in both *B. cristatella* and *B. moluccana*); there is minimal dark pigment encircling the eye and what is present is black and only within the folds of the eye socket (as opposed to extending beyond this in both *B. cristatella* and *B. moluccana*); the nuchal crest is characterized by distinct yellowish-coloured scales, except for the last two which are usually the same green colour as the upper body (these are usually green in both *B. cristatella* and *B. moluccana*); the front toes are yellowish in colour and the rear ones a reddish-brown; there is a whitish patch at the back of the hind limbs on the lower flanks near the vent; the underside of the tail lacks the distinct line or border on each of the lower sides as seen in typical *B. cristatella* or the large red patches commonly seen on those species tails; the back of the upper lip below the tympanum has a feint flush of cream or yellow; there are usually just two scales between the nasal and the rostral, but in contrast to *B. moluccana* the rear one of the pair is considerably more elongate.

Typical (West Java) *C. cristatellus* has a very small rostral, separated from the nasal by three or four scales (all of similar size), the two first supralabials very small, the nasal being situated above the third labial, and eighty-one to ninety-seven scales round the middle of the body. *C. moluccanus* has the rostral larger, separated from the nasal by one or two scales, the nasal situated above the second labial, and fifty-nine to sixtythree scales.

B. harradineus sp. nov., *B. cristatella* and *B. moluccana*, including the potentially undescribed species currently referred to *B. cristatella* as cited below all share the following diagnostic features that separate them from other *Bronchocela*: Upper head-scales rather small, keeled, slightly enlarged on supraorbital

region; a few more or less distinct, erect, compressed scales behind the supraciliary edge; tympanum half, or more than half, the diameter of the orbit. 2-4 scales between the rostral and nasal. Gular pouch very small; gular scales keeled, smaller than ventrals, distinctly larger than latero-dorsals. No oblique fold in front of the shoidder. Nuchal crest composed of erect compressed spines, the longest never equalling the diameter of the orbit; dorsal crest a mere serrated ridge. 57 to 97 scales round the middle of the body; dorsal scales keeled, much smaller than ventrals, the upper ones directed upwards and backwards, the others downwards and backwards. The adpressed hind limb reaches between the eye and the tip of the snout; third and fourth fingers equal or nearly so, about as long as the fifth toe. Tail round, subtriangular at the base. Green, uniform or with reddish-white markings.

The genus *Bronchocela* is defined and separated from similar agamid genera as follows: No fold in front of the shoulder; lateral scales pointing backwards and downwards; ventral scales larger than latero-dorsals; fourth finger nearly the same length as the fifth toe or rarely longer.

The subgenus *Ferebronchocela subgen. nov.* (referred to by many as the “*jubata* group”) is separated from the nominate subgenus (including *B. harradineus sp. nov*., *B. cristatella* and *B. moluccana*) by the fact that only the scales of the row at the

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base of the dorsal crest point upwards, versus all the upper dorsal scales pointing upwards and backwards in *Bronchocela*. The dorsal crest gives the appearance as if it is composed of tiny hairs as opposed to scales (as seen in *Bronchocela*).

Comment: It appears that the specimens of *B. cristatella* Kuhl, 1820 in East Java and Bali may be a different species to those from West Java (herein treated as terra typica), due to observed consistent morphological differences. The specimens from West Java are similar in many respects to those of Peninsula Malaysia, Sumatra and parts of Borneo, although there appears to be significant local variation on Borneo, implying more than one species or subspecies present there. Specimens of *B. cristatella* from Timor and outliers (identified as *B. moluccana* by Boulenger, 1883) are also likely to be a distinct species.

Distribution: Halmahera and Morotai Islands, Indonesia.

Etymology: Named in honour of the recently late Richard William Brian Harradine (9 January 1935-14 April 2014), who served a long and distinguished political career in Australia, most notably in the Australian senate and as an independent senator, holding the balance of power at the time when the Howard Liberal Government sought to introduce the toxic “Goods and Services” tax (or GST).

This was an added regressive form of income tax on the population, over and above that which already existed, but being taxed on consumption instead of earnings, to be used to fund an ever-growing parasitic public service bureaucracy that time controlled by the long-disgraced Howard Liberal government.

In spite of Harradine’s action, taken on behalf of the majority of the Australian public, the two major parties later ganged up on the independents to force the tax through the legislature and both major parties (Liberal and Labor, who in effect act as a coalition while masquerading otherwise) ensured its perpetuation to the present time (2013). While the government claimed the GST was only 10% of the cost of goods and services, the means of compliance was so onerous that for many small businesses the real cost of the tax was about 25% and in effect made businesses of Australia tax-collectors for the bloated public service. This in turn made Australia a prohibitively expensive place to do business.

A decade after the introduction of the toxic GST tax, it has been shown to be an abject failure with manufacturing in Australia effectively destroyed due to the fact that the cost of doing business in Australia is now too high for most relvant companies and former companies. Transnationals have shifted operations to other lower tax countries with smaller government bureaucracies.

This includes all the transnational car manufacturers in Australia (including Chrysler, Toyota, Ford and Holden) who have either deserted Australia or have announced a timetable to do so.

At 3:07 pm on Friday 14th May 1999, Senator Brian Harradine rose to address the Australian Senate.

He made a speech that should be recorded for posterity as history has proved his view at the time and his statements to be correct.

The most relevant part of the speech was as follows:

“The question now in my mind is whether it is inherently regressive to such an extent that it should not be supported. The GST burdens the poor and those with the least capacity to pay. It discriminates against the poor and the pensioners who are living a hand-to-mouth existence and spending the bulk of their income on the necessities of life: food, clothing, rent, heating, power, bus fares and so on.

I have always been conscious of the fact that the true test of a civilised society is how it regards and treats its most vulnerable. But I do not claim here a monopoly on moral judgments in respect of this. I do not criticise the government, and I do not reflect upon the government or on any of its members. I just happen to believe that the inherently regressive nature of the GST does not achieve that test.

The regressive nature of the goods and services tax is why compensation is invariably needed to secure its passage wherever it is introduced throughout the world. The government’s genuine attempt to compensate and to lock in that compensation is something to be commended, but it cannot be guaranteed.

But one thing can be guaranteed, and that is that the goods and services tax, once enshrined in legislation, will never be removed. Decisions we make now on this issue are not for the next three years; we are making decisions here that will affect generations.

The question that I have to ask myself is whether I am going to be a party to imposing an impersonal, indiscriminate tax on my children, my grandchildren and their children for generations to come.

I cannot.”

PHOXOPHRYS HUBRECHT, 1881.

This genus was described along with the first species placed within it, namely *Phoxophrys tuberculata* Hubrecht, 1881. Since then five other morphologically similar species have been placed in the same genus, although one of them, *Phoxophrys grahami* Stejneger, 1924 was moved by Inger (1960) to *Japalura* and is herein placed within *Maxhoseragama gen. nov*. (see earlier in this paper).

The type species of the genus *Phoxophrys* as currently recognized comes from West Sumatra, while the other four species are all known from hillier parts of mainly northern Borneo.

Morphologically, both groups of species are very divergent from one another and almost certainly enough to warrant being placed in separate genera.

The same applies for one of the Borneo species, namely the radically different and divergent *Phoxophrys spiniceps* Smith, 1925 in terms of it and the other species from the same island.

Therefore I herein conservatively define the three groups as subgenera. The Sumatran taxon is monotypic for the nominate subgenus. *Pelturagonia* is available for *Phoxophrys cephalum* (Mocquard, 1890) and those species most closely related to it.

As there is no genus level name available for *Phoxophrys spiniceps* Smith, 1925, a new name is designated according to the Zoological Code (Ride *et al.* 1999).

While in the recent past a number of authors have defined *Phoxophrys* in terms of the relevant five species, no one has ever defined subgenera or until now seen a need to do so. *Pelturagonia* Mocquard, 1890 was synonymised with *Phoxophrys* by later authors, with the name *Pelturagonia* effectively unused since it was first proposed.

As there has never been a definition or diagnosis of *Pelturagonia* as a distinct genus or subgenus from *Phoxophrys*, it is important that I provide one herein for the first time.

The obvious morphological differences between species in the three subgenera as defined herein are significant and I believe they are highly likely of sufficient degree to warrant full genus-level division.

However in the absence of robust molecular data for the five species I take the most conservative position and define the three groups as subgenera only.

Relevant papers in terms of the taxonomy and nomenclature of the genus *Phoxophrys sensu lato* as defined herein include the following Ananjeva *et al.* (2011a), Auliya (2006), Barts and Wilms (2003), Boulenger (1885, 1891c, 1920), Das (2004, 2006), Das and Yaakob (2007), Denzer (1996), de Rooij (1915), Hallermann (2005a, 2005b), Hubrecht (1881), Inger (1960), Malkmus *et al.* (2002), Manthey (1983), Manthey and Grossmann (1997), Manthey and Schuster (1999), Manthey *et al.* (2012), Mocquard (1890), Peters (1864), Pope (1935), Smith (1925), Stejneger (1924) and sources cited therein.

GENUS *PHOXOPHRYS* HUBRECHT, 1881.

Type species: *Phoxophrys tuberculata* Hubrecht, 1881.

Diagnosis: *Phoxophrys* is readily separated from other Draconinae subgenera by the following suite of characters: The presence of a few large tubercular scales laterally (versus simply unicarinate scales in *Japalura*); the supraciliaries are juxtaposed or very slightly imbricate (noting that in *Japalura* species each supraciliary overlaps at least a third of its successor; the head is short and deep, versus long and flat in *Japlura*).

All species of *Japalura* have hair-like sense organs on the cephalic scales, whereas these are absent in *Phoxophrys.* The rostral scale in *Japalura* is 3 or 4 times as wide as high and occupies the entire end of the snout whereas by contrast in *Phoxophrys* the rostral, if distinguishable at all is at most twice as wide as high and occupies only the center at the end of the snout. The tail of the male of *Phoxophrys* is markedly swollen at the basal end. It is also flattened above and furnished with dorsolateral keels formed by enlarged angular scales. In male Japalura the tail is compresed, oval in cross section and not flattened above; usually a low mid-dorsal crest is formed by a median row of enlarged keeled scales.

Some *Maxhoseragama gen. nov.* (species formerly placed within *Japalura*) deviate from this pattern somewhat in having the tail flattened above, proximally at the base and slightly swollen. However in head scalation, these species are essentially the same as other *Japalura.*

The lateral superficial position of the extra columella of *Phoxophrys* is narrow (length being 5 times width) and corved, as opposed to wider (3-4 times width) and straight in *Japalura*, *Maxhoseragama gen. nov.* and *Diploderma.*

Distribution: West Sumatra (nominate subgenus); Borneo (Kalimantan) for both other subgenera.

Content: *Phoxophrys tuberculata* Hubrecht, 1881 (type species); *P. borneensis* Inger, 1960; *P. cephalum* (Mocquard, 1890); *P. nigrilabris* (Peters, 1864); *P. spiniceps* Smith, 1925.

SUBGENUS *PHOXOPHRYS* HUBRECHT, 1881.

Type species: *Phoxophrys tuberculata* Hubrecht, 1881.

Diagnosis: *Phoxophrys* as a subgenus is readily separated from the other subgenera by the fact that specimens of both sexes lack a nuchal crest. This was originally regarded as a diagnostic trait for the genus, however only the type species, this being that of the monotypic subgenus in fact has this condition. Specimens in both other subgenera have a nuchal crest.

Specimens in the subgenus *Phoxophrys* also lack a single scaled supraciliary spine.

The subgenus is further defined and diagnosed by the following suite of characters: the nasal contacts the first and second supralabials; there are two continuous rows of infraorbitals; supraciliary scales raised into a crest, but not in the form of a one scale supraciliary spine; several strongly compressed supraoculars; gular scales sharply keeled, mucronate; nuchal crest absent; vertebral scale row posteriorly lacks continuous series of enlarged scales; lateral caudal scales keeled; four rows of keeled subcaudals near base.

Distribution: West Sumatra only.

Content: *Phoxophrys* (*Phoxophrys*) *tuberculata* Hubrecht, 1881 (monotypic).

SUBGENUS *PELTURAGONIA* MOCQUARD, 1890.

Type species: *Pelturagonia cephalum* Mocquard, 1890.

Diagnosis: *Pelturagonia* are readily separated from both other subgenera by the presence of a nuchal crest in males and females and an absence of a supraciliary spine.

Distribution: The northern part of Borneo (Kalimantan).

Content: *Phoxophrys* (*Pelturagonia*) *cephalum* (Mocquard, 1890) (type species); *P.* (*Pelturagonia*) *borneensis* Inger, 1960; *P.* (*Pelturagonia*) *nigrilabris* (Peters, 1864).

SUBGENUS *OLORENSHAWAGAMA SUBGEN. NOV.*

Type species: *Phoxophrys spiniceps* Smith, 1925.

Diagnosis: *Olorenshawagama subgen. nov.* are readily separated form all species within the other two subgenera within *Phoxophrys* by the possession of a supraciliary spine and nuchal crest.

The subgenus is further diagnosed by the following unique suite of characters: the nasal contacts the second supralabial; there is a single continuous row of infraorbitals; a distinctive supraciliary spine is formed by a scale about three quarters the diameter of the eye; gular scales are keeled; nuchal crest with three spinose scales separated by two-six small, keeled scales; vertebral scale row posteriorly with widely separated, enlarged scales; lateral caudal scales keeled; two rows of keeled subcaudals near base (anterior end) of the tail.

Distribution: Relatively high altitude forested areas of northern Borneo.

Etymology: Named in honour of Dr Guy Olorenshaw of Vision Eye Institute in St Kilda Road, Melbourne, Victoria, Australia for his excellent work in rectifying defective eyesight in many thousands of Australians.

His patients have included my wife and myself, both of whom had bad and deteriorating eye-sight corrected by his excellent surgical skills. Without his surgery a large part of our ongoing herpetological research and wildlife conservation work in the post 2000 period would not have been possible.

Content: *Phoxophrys* (*Olorenshawagama*) *spiniceps* Smith, 1925 (monotypic).

APHANIOTIS PETERS, 1864.

This genus of south-east Asian agamids conisists of three similar species and is closely associated with the genus *Coryphophylax* Fitzinger, 1869, itself consisting just two species.

Of the three species within *Aphaniotis* Peters, 1864, one is clearly divergent from the other two and it is therefore placed in its own subgenus formally named and defined for the first time.

For the genus *Aphaniotis* Peters, 1864 and the closely allied genus *Coryphophylax* Fitzinger, 1869 key references include Ananjeva *et al.* (2011a), Barts and Wilms (2003), Blyth (1860), Boulenger (1885, 1890, 1891a), Chan-ard *et al.* (1999), Cox *et al.* (1998), Daan and Hillenius (1966), Das (2004), Das and Yaakob (2007), de Jong (1930), de Rooij (1915), Grandison (1972), Grismer (2011), Grismer *et al.* (2006, 2010), Hallermann (2005a, 2005b), Hallermann and McGuire (2001), Hallermann *et al.* (2010), Harikrishnan *et al.* (2012), Heang (1987), Hendrickson (1996), Lidth de Jeude (1893), Lim and Ng (1999), Macey *et al.* (2000), Malkmus (1994), Malkmus *et al.* (2002), Manthey (1983), Manthey and Grossmann (1997), Manthey and Schuster (1999), Modigliani (1889), Ota and Hikida (2000), Peters (1864), Smedley (1931a), Smith (1935), Stoliczka (1873b), Sworder (1933), Taylor (1963), Teo and Rajathurai (1997), Venugopal (2010), Werner (1900), Wood *et al.* (2004),

GENUS *APHANIOTIS* PETERS 1864.

Type species: *Otocryptis* (*Aphaniotis*) *fusca* Peters, 1864.

Diagnosis: The genus *Aphaniotis* Peters, 1864 is defined and separated from all other Draconinae by the following unique suite of characters: Body compressed, limbs very long and slender. Fifth toe much longer than first. All the scales keeled; the dorsals heterogeneous. A dorsal crest. Probably a gular pouch in the male. No gular fold. Ear concealed. No praeanal or femoral pores.

Distribution: South-east Asia.

Content: *Aphaniotis fusca* (Peters, 1864) (type species); *A. acutirostris* Modigliani, 1889; *A. ornata* (Lidth de Juede, 1893).

SUBGENUS *PROBOSCISAGAMA SUBGEN. NOV.*

Type species: *Japalura ornata* Lidth de Juede, 1893.

Currently known as *Aphaniotis ornata* (Lidth de Juede, 1893).

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Diagnosis: The subgenus *Proboscisagama subgen. nov*. is monotypic and readily separated from the other two species (of the nominate subgenus) by the fact that specimens have a distinct protrusion on the snout. This is absent on the other species in the genus.

In males this protrusion is conical and in females it is flat. The lizard's body colour is predominantly medium brown, with pale brown mottling, and the head is brown or olive green. The hind legs may also vary from brown to dark olive brown. Some specimens may possess vague, dark diagonal eye stripes.

Otherwise the genus diagnosis applies to this subgenus.

The genus *Aphaniotis* Peters, 1864 is defined and separated from all other Draconinae by the following unique suite of characters: Body compressed, limbs very long and slender. Fifth toe much

longer than first. All the scales keeled; the dorsals heterogeneous. A dorsal crest. No gular fold. Ear concealed. No praeanal or femoral pores.

There is probably a gular pouch in the male.

Distribution: Northern Borneo only.

Etymology: Named in reflection of the protrusion on the snout and the family the lizard is placed within.

Content: *Aphaniotis* (*Proboscisagama*) *ornata* (Lidth de Juede, 1893) (monotypic).

PTYCTOLAEMUS PETERS, 1864.

The genus *Ptyctolaemus* Peters, 1864 as currently recognized consists just two species from southern Asia. However both species have significant morphological and genetic divergence from one another, so it is a "no-brainer' in terms of the need to split the genus in terms of recognition of the species.

While other genera have been divided on the basis of equivalent differences between species, I am loathe to create two monotypic genera for two species that are clearly closely related and until now have been placed in the same genus. Therefore I herein describe a new subgenus to accommodate the currently unnamed (at the genus-level) lineage.

For the genus *Ptyctolaemus* Peters, 1864 key references include Ahsan *et al.* (2008), Ananjeva and Boulenger (1885, 1890), Huang (1980), Islam and Saikia (2013), Lenz (2012), Mahony *et al.* (2009), Stuart (2001), Moody (1980), Peters (1864), Pyron *et al.* (2013), Schulte *et al.* (2004), Shreve (1940), Smith (1935, 1940), Venugopal (2010), Wall (1908a), Zhao and Adler (1993) and sources cited therein.

GENUS *PTYCTOLAEMUS* PETERS, 1864.

Type species: *Otocryptis* (*Ptyctolaemus*) *gularis* Peters, 1864.

Diagnosis: The most obvious character that distinguishes the genus *Ptyctolaemus* from other genera of the subfamily Draconinae (*sensu* Macey *et al.* 2000) or Group V agamids (*sensu* Moody 1980) of mainland southeast Asia is that the male *Ptyctolaemus* have longitudinal gular folds on either side of the midline with the posterior portion of the folds curving medially on each side of the throat. However, these folds are only evident when the gular pouch is in a relaxed position (as seen in preserved specimens). The folds are formed when the gular pouch is relaxed in an accordion-like fashion, the folds become more pronounced because the scales within the folds are darkly pigmented.

The only other southeast Asian genus with gular folds is *Mantheyus* Ananjeva and Stuart, 2001; however it has rounded "U"-shaped folds encompassing the gular sac. *Mantheyus,* monotypic for *M. phuwuanensis* also differs from *Ptyctolaemus* and all other draconines by the presence of femoral pores (Ananjeva and Stuart 2001).

The species *Ptyctolaemus collicristatus* Schulte and Vindum, 2004 (subgenus *Mindatagama subgen. nov.*) can be distinguished from *P. gularis* (subgenus *Ptyctolaemus*) by having a more prominent nuchal crest comprised of larger, flattened, triangular, scales, consisting of fewer scales in adult males (15-16 versus 17-30 scales); a shorter tail, with an average Tail length:SVL ratio of 1.99 versus 2.24; stouter and shorter limbs; and more heterogeneity among dorsal and lateral scales.

Distribution: Southern Asia, including: far North-east India, Bangladesh, Burma and nearby parts of south-west China.

Content: *Ptyctolaemus gularis* (Peters, 1864) (type species); *P. collicristatus* Schulte and Vindum, 2004.

SUBGENUS *MINDATAGAMA SUBGEN. NOV.*

Type species: *Ptyctolaemus collicristatus* Schulte and Vindum, 2004.

Diagnosis: The species *Ptyctolaemus collicristatus* Schulte and Vindum, 2004 (subgenus *Mindatagama subgen. nov.*) can be distinguished from *P. gularis* (subgenus *Ptyctolaemus*) by having a more prominent nuchal crest comprised of larger, flattened, triangular, scales, consisting of fewer scales in adult males (15-16 versus 17-30 scales); a shorter tail, with an average Tail length:SVL ratio of 1.99 versus 2.24; stouter and shorter limbs; and more heterogeneity among dorsal and lateral scales.

The most obvious character that distinguishes the genus *Ptyctolaemus* from other genera of the subfamily Draconinae (*sensu* Macey *et al.* 2000) or Group V agamids (*sensu* Moody 1980) of mainland southeast Asia is that the male *Ptyctolaemus* have longitudinal gular folds on either side of the midline with the posterior portion of the folds curving medially on each side of the throat. However, these folds are only evident when the gular pouch is in a relaxed position (as seen in preserved specimens). The folds are formed when the gular pouch is relaxed in an accordion-like fashion, the folds become more pronounced because the scales within the folds are darkly pigmented.

The only other southeast Asian genus with gular folds is *Mantheyus* Ananjeva and Stuart, 2001; however it has rounded "U"-shaped folds encompassing the gular sac. *Mantheyus,* monotypic for *M. phuwuanensis* also differs from *Ptyctolaemus* and all other draconines by the presence of femoral pores (Ananjeva and Stuart 2001).

Distribution: Chin Chin Hills, Min Dat District, Burma (Myanmar).

Etymology: Named in reference to the type locality for the type species and also the family of lizards from which it is within.

Content: *Ptyctolaemus* (*Mindatagama*) *collicristatus* Schulte and Vindum, 2004.

SALEA GRAY, 1845.

The genus *Salea* Gray, 1845 as currently recognized includes three recognized species.

These are *Salea horsfieldii* Gray, 1845 (the type species); *S. anamallayana* (Beddome, 1878) and *S. gularis* Blyth, 1854. The last of these is of uncertain status and included herein only tentatively, also being placed provisionally in association with the species *Salea horsfieldii* Gray, 1845 in terms of generic and subgeneric placement, noting that this is only done 1/ In the absence of contrary evidence and 2/ Noting it does not otherwise affect the taxonomy and nomenclature within this paper.

Of the remaining two species, both are very divergent morphologically and noting the conservatism of morphology of the subfamily Draconinae my immediate inclination would be to place each in a monotypic genus.

Mitigating against this is the general aversion to the creation of monotypic genera for species that share obvious affinities as well as the absence of comparative and calibrated molecular data for both taxa.

Therefore in order to accord proper recognition of the divergence of the forms and to maintain nomenclatural stability, I treat both species as being within the same genus and of different subgenera.

Salea Gray, 1845 is attached to the type species *Salea* *horsfieldii* Gray, 1845.

The other taxon *S. anamallayana* (Beddome, 1878) was originally described as *Lophosalea anamallayana*, with the genus name being available for the subgenus containing this species.

As neither the genus *Salea* Gray, 1845 or the subgenus *Lophosalea* Beddome, 1878 being properly defined to date in terms of the Agamidae or the Draconinae, this is done herein for the first time.

GENUS *SALEA* GRAY, 1845.

Type species: *Salea horsfieldii* Gray, 1845.

Diagnosis: The genus Salea is defined and separated from all other agamidae as follows: Mouth large; teeth erect in both jaws. Incisors small and conical. No praeanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895); five toes; no fold across the throat; dorsal scales large, unequal; males with a gular pouch; tympanum distinct. Body compressed, covered with unequalsized imbricate keeled scales. Male with a dorso- nuchal crest and a gular sac. No transverse gular fold. Tail compressed.

The subgenus *Salea* Gray, 1845 is further defined and separated from *Lophosalea* Beddome, 1878 as follows: Snout not more than once and a half as long as the diameter of the orbit, which equals about twice that of the tympanum; upper head-scales large, rugose, with a more or less marked curved series of regular ones bordering the supraorbital region internally; a row of three or four enlarged scales from the eye to above the tympanum. Gular scales lanceolate, keeled, ending in a spine as large as or a little larger than the ventrals. No fold in front of the shoulder. Nuchal crest, in the male composed of a few lanceolate spines directed backwards, the longest measuring nearly the length of the snout, with smaller ones at the base; in the female this crest is reduced to a double row of alternate oblique short spines; dorsal crest not continuous with nuchal, composed of similar slightly shorter lanceolate spines in the male, absent in the female. Dorsal scales large, rhomboidal, strongly keeled, pointing straight backwards; they are nearly always of unequal size, larger ones being scattered on the sides; ventral scales very strongly imbricate, strongly keeled and ending in a spine, nearly as large as the dorsals.

Limbs moderately elongate, the adpressed hind Hmb reaching between the shoulder and the tympanum. Tail compressed, and with a small upper crest in the male, scarcely compressed, and without a crest in the- female; caudal scales subequal, strongly keeled. Pale olive above, with irregular dark-brown cross bands, which may be broken up by a band of the light-brown colour running along each side of the back; the enlarged scales on the sides frequently white; a blackish band, edged below with white, extends from the eye to the fore limb, passing through the tympanum; tail usually with regular dark-brown annuli (modified from Boulenger 1885).

The subgenus *Lophosalea* is defined immediately below.

Distribution: Southern India.

Content: *Salea* (*Salea*) *horsfieldii* Gray, 1845 (type species); *S. gularis* Blyth, 1854 (added herein tentatively).

SUBGENUS *LOPHOSALEA* BEDDOME, 1878.

Type species: *Lophosalea anamallayana* Beddome, 1878.

Diagnosis: The subgenus *Lophosalea* is defined and separated from the subgenus *Salea* by the following unique suite of characters: Snout long, measuring nearly twice the diameter of the orbit (as opposed to being not more than once and a half as long as the diameter of the orbit in the subgenus *Salea*); tympanum once and two thirds or once and three fifths the diameter of the orbit; upper head-scales rather large, feebly keeled, with a regular curved series of enlarged scales bordering the supraorbital region internally; an enlarged tubercle behind the supraciliary edge and a few others scattered on the back of the head; a row of three or four enlarged scales from the eye to above the tympanum. Gular scales are a little larger than ventrals, smooth or keeled.

A well marked curved fold on each side of the neck, in front of the shoulder. Dorso-nuchal crest continuous, composed of large lanceolate spines. Dorsal scales of unequal size, their arrangement varying considerably, strongly keeled, the upper ones pointing upwards and backwards, the others straight backwards or backwards and downwards; ventral scales very strongly imbricate, strongly keeled,

and ending in a spine. The adpressed hind limb reaches the neck.

Tail strongly compressed, in its anterior half with an upper crest nearly as much developed as the dorsal; caudal scales rather unequal in size, keeled. Pale olive above, with four broad angular dark-brown cross bands on the back, separated by narrow interspaces; head to the lip dark brown, with small light spots; limbs and tail with more or less regular dark-brown cross bars.

Distribution: Southern India.

Content: *Salea* (*Lophosalea*) *anamallayana* Beddome, 1878 (monotypic).

DRACO LINNAEUS, 1758.

The genus *Draco* Linnaeus, 1758, better known as the flying lizards, has been universally recognized as a distinct assemblage of species by herpetologists ever since Linnaeus first created the genus.

Morphologically all are similar in form as well as similar in habits. As a result most publishing authors have treated all species as being within the same genus (Musters 1983).

However recent phylogenetic studies published including McGuire and Heang (2001) and the more recent composite study of Pyron *et al.* (2013) have shown that it is clearly appropriate to taxonomically recognize subgroups within *Draco sensu lato.*

The usual mass-namers of the 1800's coined names for various species or groups as new genera, but with little if any scientific basis to do so and so most were quickly relegated to the synonomy of *Draco* by later workers.

This is of course the correct way to deal with taxonomic and nomenclatural vandalism and remain within the zoological code (Ride *et al.* 1999, Hoser, 2013).

One of the most prolific namers of reptile genera of the time, the 1800's, John Edward Gray even created a junior synonym for a group that already had an established name. This was *Dracocella*, Gray 1845, type species, *Draco dussumieri* Duméril and Bibron, 1837, a junior synonym of *Pterosaurus* Fitzinger, 1843.

Another prolific namer, Leopold Joseph Franz Johann Fitzinger coined the name *Pleuropterus* Fitzinger, 1843 with the type species *Draco haematopogon* Gray, 1831. However this is a genus name pre-occupied by a mammal genus *Pleuropterus* Burnett, 1829 and for that matter the insect genus *Pleuropterus* Westwood 1841 and is therefore unavailable.

Notwithstanding this the names proposed by these 1800's authors that are for otherwise unoccupied taxa and themselves not homonyms are available under the zoological code, provided they are at any stage found to match an otherwise unnamed and defined genus-level group.

Unlike the taxonomic and nomenclatural vandals in the group Wüster *et. al.*, best defined in terms of their *modus operandi* in the publication known as Kaiser (2012a, 2012b), Kaiser *et al.* (2013), and Wüster *et al.* (2014a, 2014b) I do not misrepresent the Zoological Rules (Ride *et al.* 1999) to attempt to justify the overwriting of properly established names with names of my own coining for the purpose of self aggradisment.

Quite properly and ethically, I resurrect old names coined by earlier authors, regardless of the merit of their previous works or the scientific basis underpinning their taxonomic and nomenclatural decisions of the time.

This means that in terms of *Draco* as widely known to date, the following names are available should the genus need to be split and provided they actually match relevant species groups.

Draco Linnaeus, 1758 (Type species: *Draco volans* Linnaeus, 1758);

Dracontoides Fitzinger, 1843 (Type species: *Draco lineatus* Daudin, 1802);

Rhacodracon Fitzinger, 1843 (Type species: *Draco fimbriatus* Kuhl, 1820).

Pterosaurus Fitzinger, 1843 (Type species: *Draco dussumieri* Dumeril and Bibron, 1837).

Relying on a number of recently published molecular phylogenies, including McGuire and Heang (2001) and the composite of Pyron *et al.* (2013), it is clear that the 45 currently recognized species of *Draco* can be split into more than one distinct clade dating in excess of 8 MYA. I also note here that recent studies also indicate the present number of recognized species is well short of the actual number.

However the divergence time for the entire genus as presently recognized is clearly recent being estimated at well under 15 MYA and 10 MYA or less for all but two small species groups. Therefore in spite of the size of the genus (number of species), it is probably not appropriate that the clades be given full genus recognition.

Taking a conservative position, the nine obvious clades dated in excess of 8 MYA are each accorded subgenus status. I note however that were these lizards mammals, there would be no hesitation in placing each defined group in a separate full genus.

The four available names as given above can each be used as the appropriate name for each relevant clade.

The remaining five clades are at present unnamed according to the Zoological Code (Ride *et al.* 1999) and are therefore defined and named for the first time herein.

The four subgenera which in combination account for about half the recognized species in the genus *Draco*, and have available names are as follows: *Draco* Linnaeus, 1758; *Dracontoides* Fitzinger, 1843; *Rhacodracon* Fitzinger, 1843 and *Pterosaurus* Fitzinger, 1843.

These are also properly defined herein for the first time and within the context of the entire genus *Draco* as presently recognized and with respect to all recognized species.

The subgenera for which names are available already are defined after the descriptions of the five new subgenera.

As it happens, the diagnostic species key for the genus *Draco* as defined by Boulenger (1885) also readily separates all the subgenera as defined herein, with the exception of the subgenera *Macguiredraco subgen. nov.* and *Engannodraco subgen. nov.*, both of which would key out in that document as being "*Draco lineatus*". McGuire *et al.* (2007) provide diagnostic information that separates the three relevant subgenera *Pterosaurus* Fitzinger, 1843, *Macguiredraco subgen. nov.* and *Engannodraco subgen. nov.*.

Both these documents are available for free download on the internet as of end 2013.

Key references relevant to the taxonomy proposed herein for *Draco* include the following; Alcock (1895), Ananjeva *et al.* (2011a), Andersson (1900), Auffenberg (1980), Auliya (2006), Barbour (1909), Bartlett (1895), Barts and Wilms (2003), Beukema (2011), Blanford (1878), Bobrov (1995), Bobrov and Semenov (2008), Boettger (1893a, 1893b), Boistel *et al.* (2011), Boulenger (1885, 1887a, 1887c, 1890, 1891a, 1891b, 1893, 1897, 1900a, 1900b, 1908), Brygoo (1988), Burden (1927), Cantor (1847), Capocaccia (1961), Chan-ard *et al.* (1999), Colbert (1967), Cox *et al.* (1998), Daan and Hillenius (1966), Das (2004), Das and Lim (2001), Daudin (1802), De Jong (1926), Denzer and Manthey (1991), De Queiroz (1998), De Rooij (1915), Despax (1912), de Witte (1933), Diong and Soon (1999), Duméril *et al.* (1837), Evans *et al.* (2003), Ferner *et al.* (2000), Fitzinger (1843), Flower (1896), Gaulke (2011), Goin *et al.* (1978), Grandison (1972), Gray (1835, 1845), Grismer (2008, 2011), Grismer *et al.* (2007, 2008, 2010), Grossmann and Tillack (2004a), Günther (1861a, 1864, 1872a), Hairston (1957), Hallermann (1998, 2005a, 2005b), Hardwicke and Gray (1827), Hartmann (2012), Heang (1987), Hecht *et al.* (2013), Hendrickson (1966), Hennig (1936), Honda *et al.* (1999, 2000), Inger (1983), Islam and Saikia (2013), Iskandar and Erdelen (2006), Iskandar and Tjan (1996), Jong (1926), Koch (2011), Koch *et al.* (2007), Kopstein (1927, 1938), Kuhl (1820), Lazell (1982, 1987, 1992), Lenz (2012), Lesson (1834), Leviton *et al.* (1985), Lim and Ng (1999), Linnaeus (1758), Macey *et al.* (2000), Mägdefrau (1991), Mahony *et al.* (2009), Malkmus (2000), Malkmus *et al.* (2002), Manthey (1983, 2008), Manthey and Grossmann (1997), Manthey and Schuster (1999), McGuire and Alcala (2000), McGuire and Dudley (2011), McGuire and Heang (2001), McGuire and Kiew (2001), McGuire *et al.* (2007), McLeod *et al.* (2011), Mertens (1930), Mocquard (1890), Mori and Hikida (1993), Murthy (1990, 2010), Musters (1983), Neang *et al.* (2010), Onn *et al.* (2009), Pauwels *et al.* (2000, 2003), Peters (1867), Peters and Doria (1878), Pyron *et al.* (2013), Quah *et al.* (2011), Ride *et al.* (1999), Ross and Lazell (1991), Sang *et al.* (2009), Sathiamurthy and Voris (2006), Schlegel (1837), Shaw and Nodder (1790), Shine (1998), Simpson (1961), Smedley (1931a), Smith (1993), Smith (1946), Smith (1927, 1928, 1935, 1937b), Smith and Kloss (1915a, 1915b), Smith and Procter (1921), Stejneger (1908), Stone (1913), Stoliczka (1873a), Stuart and Emmett (2006), Taylor (1922, 1934, 1963), Teo and Rajathurai (1997), Treitschke (1839), van Rooijen and van Rooijen (2002), Venugopal (2010), Vinciguerra (1892), Waltner (1975), Wanger *et al.* (2011), Weber (1890), Wermuth (1967), Werner (1910), Wiegmann (1834a, 1834b), Wood *et al.* (2004), Zhao and Adler (1993), Ziegler (2002) and sources cited therein.

GENUS *DRACO* LINNAEUS, 1758.

Type species: *Draco volans* Linnaeus, 1758.

Diagnosis: The species within the genus *Draco* are readily distinguished from all other lizards by the fact that the body is depressed and with a large lateral wing-like membrane, supported by the much-expanded five or six posterior ribs, folding like a fan. A gular appendage, and a lateral smaller one on each side. Tympanum distinct or covered with scales. Tail long. No femoral or preanal pores.

Distribution: Wetter parts of southern and south-east Asia.

Content: *Draco volans* Linnaeus, 1758 (type species); *D. abbreviatus* Hardwicke and Gray, 1827; *D. affinis* Bartlett, 1895; *D. beccarii* Peters and Doria, 1878; *D. biaro* Lazell, 1987; *D. bimaculatus* Günther, 1864; *D. blanfordii* Blanford, 1878; *D. boschmai* Hennig, 1936; *D. bourouniensis* Lesson, 1834; *D. caerulhians* Lazell, 1992; *D. cornutus* Günther, 1864; *D. cristatellus* Günther, 1872; *D. cyanopterus* Peters, 1867; *D. divergens* Taylor, 1934; *D. dussumieri* Duméril and Bibron, 1837; *D. fimbriatus* Kuhl, 1820; *D. formosus* Boulenger, 1900; *D. guentheri* Boulenger, 1885; *D. haematopogon* Gray, 1831; *D. haasei* Boettger, 1893; *D. indochinensis* Smith, 1928; *D. iskandari* McGuire, Brown, Mumpini, Riyanto and Andayani, 2007; *D. jareckii* Lazell, 1992; *D. lineatus* Daudin, 1802; *D. maculatus* (Gray, 1845); *D. maximus* Boulenger, 1893; *D. melanopogon* Boulenger, 1887; *D. mindanensis* Stejneger, 1908; *D. modiglianii* Vinciguerra, 1892; *D. norvillii* Alcock, 1895; *D. obscurus* Boulenger, 1887; *D. ornatus* (Gray, 1845); *D. palawanensis* McGuire and Alcala, 2000; *D. quadrasi* Boettger, 1893; *D. quinquefasciatus* Hardwicke and Gray, 1827; *D. reticulatus* Günther, 1864; *D. rhytisma* Musters, 1983; *D. spilonotus* Günther, 1872; *D. spilopterus* (Wiegmann, 1834); *D. sumatranus* Schlegel, 1844; *D. supriatnai* McGuire, Brown, Mumpini, Riyanto and Andayani, 2007; *D. taeniopterus* Günther, 1861; *D. timorensis* Kuhl, 1820; *D. walkeri* Boulenger, 1891; *D. whiteheadi* Boulenger, 1900.

SUBGENUS *MACGUIREDRAGO SUBGEN. NOV.*

Type species: *Draco bourouniensis* Lesson, 1834.

Diagnosis: *Macguiredraco subgen. nov.* is comprised of nine Wallacean species (*bourouniensis*, *beccarii*, *biaro*, *caerulhians*, *iskandari*, *rhytisma*, *spilonotus*, *supriatnai*, and *walkeri*), treated by most herpetologists to date as being within the so-called "*lineatus* group" (subgenus *Dracontoides* Fitzinger, 1843) but phylogenetically quite distinct and divergent from the species *D. lineatus*. *Macguiredraco subgen. nov.* is diagnosed and defined on the basis of the following features: (1) a strong statistical mode of five ribs supporting each wing (versus six), (2) absence of lacrimal bones (versus presence), (3) nostrils oriented laterally (versus posterodorsally), and (4) dewlap scalation small and undifferentiated (versus enlarged distally). The only *Draco* species that cannot be distinguished from *Macguiredraco subgen. nov.* on the basis of these characters is *D. bimaculatus* of the southern Philippines (herein placed in the monotypic subgenus *Philippinedraco subgen. nov.*) and separated from *Macguiredraco subgen. nov.* below and also *D. lineatus* (placed in the subgenus *Dracontoides* Fitzinger, 1843), herein regarded as a composite species.

Most *Macguiredraco subgen. nov.* species can be distinguished primarily on the basis of adult male coloration because these lizards are characterized by granular squamation that is apparently not conducive either to the evolution or the discovery of heritable species-specific differences.

Philippinedraco subgen. nov. is separated from *Macguiredraco subgen. nov.* by the following suite of characters: an adult snout-vent length of 73 mm; 8-10 supralabials; tympanum usually covered with smooth skin; lateral pouches with slightly enlarged scales; 122-150 dorsals; five ribs in patagium; and the presence of a black, white-centred spot between the tympanum and the corner of the mouth (not seen in *Macguiredraco subgen. nov.*).

Draco lineatus (*sensu lato*) (treated here as a complex of morphologically similar species) (subgenus *Dracontoides* Fitzinger, 1843), can be distinguished from all other members of *Macguiredraco subgen. nov.*, *Philippinedraco subgen. nov.* and *Engannodraco subgen. nov*. as defined within this paper by the following combination of characteristics: (1) the dorsal patagial coloration of males with five pale brown radial bands on a vivid yellow field, or with several radial bands comprised of pale white or tan spots on a gray field, (2) male dewlap short and rounded distally, (3) dewlap in males bright yellow in coloration, (4) males and females with large yellow spots on a brown field on the side of the neck and base of the dewlap, (5) melanic interorbital spot usually absent in males, (6) large rhomboidal melanic nuchal spot usually absent from both sexes, (7) melanic postnuchal spot usually absent from males, usually present in females, (8) absence of white pigments in association with variably present nuchal and posnuchal spots in both sexes, (8) variable presence in males and absence in females of melanic 'eye spots' (dark spots with associated white or pale pigments) on the supraorbital semicircles, (9) parietal lens usually present (32 of 34 specimens examined), and (10) tympana at least partially covered with scales (usually completely covered) (adapted from McGuire *et al.* 2007).

Distribution: Confined to islands within Wallacea, eastern Indoneasia.

Etymology: Named in honour of Jimmy McGuire of California, USA in recognition of his published works on this group of lizards, until now merely referred to by most authors as a part of the so-called "*lineatus"* group.

Content: *Draco* (*Macguiredraco*) *bourouniensis* Lesson, 1834 (type species); *D.* (*Macguiredraco*) *beccarii* Peters and Doria, 1878; *D.* (*Macguiredraco*) *biaro* Lazell, 1987; *D.* (*Macguiredraco*) *caerulhians* Lazell, 1992; *D.* (*Macguiredraco*) *iskandari* McGuire, Brown, Mumpini, Riyanto and Andayani, 2007; *D.* (*Macguiredraco*) *rhytisma* Musters, 1983; *D.* (*Macguiredraco*) *spilonotus* Günther, 1872; *D.* (*Macguiredraco*) *supriatnai* McGuire, Brown, Mumpini, Riyanto and Andayani, 2007; *D.* (*Macguiredraco*) *walkeri* Boulenger, 1891.

SUBGENUS *PHILIPPINEDRACO SUBGEN. NOV.*

Type species: *Draco bimaculatus* Günther, 1864.

Diagnosis: *Philippinedraco subgen. nov.* is separated from *Macguiredraco subgen. nov.* and *Dracontoides* Fitzinger, 1843, both defined above, by the following suite of characters: an adult snout-vent length of 73 mm; 8-10 supralabials; tympanum usually covered with smooth skin; lateral pouches with slightly enlarged scales; 122-150 dorsals; five ribs in patagium; and the presence of a black, white-centred spot between the tympanum and the corner of the mouth (not seen in *Macguiredraco subgen. nov.*).

Macguiredraco subgen. nov. (and this genus) is diagnosed and defined on the basis of the following features: (1) a strong statistical mode of five ribs supporting each wing (versus six), (2) absence of lacrimal bones (versus presence), (3) nostrils oriented laterally (versus posterodorsally), and (4) dewlap scalation small and undifferentiated (versus enlarged distally). The only *Draco* species that cannot be distinguished from *Macguiredraco subgen. nov.* on the basis of these characters is *D. bimaculatus* of the southern Philippines (herein placed in the monotypic subgenus *Philippinedraco subgen. nov.*) and separated from *Macguiredraco subgen. nov.* above and below.

Most *Macguiredraco subgen. nov.* species can be distinguished primarily on the basis of adult male coloration because these lizards are characterized by granular squamation that is apparently not conducive either to the evolution or the discovery of heritable species-specific differences.

Draco lineatus (*sensu lato*) (treated here as a complex of morphologically similar species) (subgenus *Dracontoides* Fitzinger, 1843), can be distinguished from all other members of *Macguiredraco subgen. nov.*, *Philippinedraco subgen. nov.* and *Engannodraco subgen. nov*. as defined within this paper by the following combination of characteristics: (1) the dorsal patagial coloration of males with five pale brown radial bands on a vivid yellow field, or with several radial bands comprised of pale white or tan spots on a gray field, (2) male dewlap short and rounded distally, (3) dewlap in males bright yellow in coloration, (4) males and females with large yellow spots on a brown field on the side of the neck and base of the dewlap, (5) melanic interorbital spot usually absent in males, (6) large rhomboidal melanic nuchal spot usually absent from both sexes, (7) melanic postnuchal spot usually absent from males, usually present in females, (8) absence of white pigments in association with variably present nuchal and posnuchal spots in both sexes, (8) variable presence in males and absence in females of melanic 'eye spots' (dark spots with associated white or pale pigments) on the supraorbital semicircles, (9) parietal lens usually present (32 of 34 specimens examined), and (10) tympana at least partially covered with scales (usually completely covered) (adapted from McGuire *et al.* 2007).

Philippinedraco subgen. nov. is also separated from all other *Draco* species on the basis of the following unique suite of characters: Head small; snout very short, hardly as long as the diameter of the orbit; nostril lateral, directed outwards; tympanum naked, much smaller than the eye-opening. Upper head-scales unequal, strongly keeled; eight to ten upper labials. The male's gular appendage shorter than the head. Male with a very slight nuchal crest. Dorsal scales rather regular, feebly keeled, a little larger than the ventrals; on each side a more or less distinct series of enlarged keeled distant scales. The fore limb stretched forwards extends considerably beyond the tip of the snout; the adpressed hind limb reaches the axil or a little beyond. Upper surfaces greenish grey with metallic gloss, and more or less defined broad blackish cross bars; a black interorbital spot; a large round black spot, with a white scale in the centre, behind the angle of the mouth; wing-membranes above blue-green, reticulated with black, with four or five more or less indistinct broad blackish transverse bands, and numerous pale longitudinal lines; wing-membranes inferiorly with irregular large black spots; throat and base of gular appendage with dark reticulation; female with two black cross bars under the neck; belly sometimes with a few blackish dots (adapted from Boulenger 1885).

Distribution: Known only from the Philippines Islands.

Etymology: Named in reflection of the origin of the subgenus and the generic root it comes from.

Content: *Draco bimaculatus* Günther, 1864 (monotypic).

SUBGENUS *ENGANNODRACO SUBGEN. NOV.*

Type species: *Draco modiglianii* Vinciguerra, 1892.

Diagnosis: *Engannodraco subgen. nov.* is similar in most respects to *Macguiredraco subgen. nov.* as defined above, but is separated from this subgenus and all other *Draco* species by the following suite of characters: An adult snout-vent length of about 71 mm; 6-9 supralabials; tympanum usually covered with smooth skin; lateral pouch with slightly enlarged scales; 110-135 dorsals; six or seven ribs in patagium; lateral parts of nuchal region in males with light spots.

Distribution: Known only from Enganno Island, off the south-west coast of Sumatra, Indonesia.

Etymology: Named in reflection of the origin of the subgenus and the generic root it comes from.

Content: *Draco* (*Engannodraco*) *modiglianii* Vinciguerra, 1892 (monotypic).

SUBGENUS *SOMNIADRACO SUBGEN. NOV.*

Type species: *Draco blanfordii* Blanford, 1878.

Diagnosis: Species within the subgenus *Somniadraco subgen. nov.* are readily separated from all other *Draco* species and subgenera by the following suite of characters, being one or other of the following three:

1/ The nostril is pierced vertically and directed upwards; the tympanum is naked; the adpressed hind limb does not reach beyond the axil and the tympanum is smaller than the eye opening; or:

2/ The nostril is pierced vertically and directed upwards; the tympanum is naked; the adpressed hind limb reaches beyond the axil (and wing-membranes above have five transverse black bands, inferiorly without markings); or:

3/ The nostril is pierced vertically and directed upwards; the tympanum is scaly (and wing-membranes above and below with, five regular transverse black bands).

Alternatively, this subgenus may be defined by exclusion of the other subgenera as defined within this paper.

Distribution: South-east Asia.

Etymology: Named in reflection of the colourful nature of many species within this subgenus and the genus from which they are derived ("somnia" being Latin for "dreams").

Content: *D.* (*Somniadraco*) *blanfordii* Blanford, 1878 (type species); *D.* (*Somniadraco*) *formosus* Boulenger, 1900; *D.* (*Somniadraco*) *haematopogon* Gray, 1831; *D.* (*Somniadraco*) *indochinensis* Smith, 1928; *D.* (*Somniadraco*) *obscurus* Boulenger, 1887; *D.* (*Somniadraco*) *maximus* Boulenger, 1893; *D.* (*Somniadraco*) *melanopogon* Boulenger, 1887; *D.* (*Somniadraco*) *mindanensis* Stejneger, 1908; *D.* (*Somniadraco*) *norvillii* Alcock, 1895; *D.* (*Somniadraco*) *quinquefasciatus* Hardwicke and Gray, 1827;

D. (*Somniadraco*) *taeniopterus* Günther, 1861.

SUBGENUS *SPOTTYDRACO GEN. NOV.*

Type species: *Dracunculus maculatus* Gray, 1845.

Diagnosis: *Spottydraco subgen. nov.* is readily separated from all other *Draco* species and subgenera by the following suite of characters: Head small; snout a little longer than the diameter of the orbit; nostril lateral, directed outwards; tympanum scaly. Upper headscales unequal, strongly keeled; a compressed prominent scale on the posteri or part of the supraciliary region; seven to eleven upper labials. The male's gular appendage very large, always much longer than and frequently twice as long as, the head; female also with a well-developed but smaller gular sac. Male with a very small nuchal crest. Dorsal scales little larger than the ventrals, irregular, smooth or very feebly keeled; on each side of the back a series of large trihedral keeled distant scales. The fore limb stretched forwards reaches bevond the tip of the snout; the adpressed hind limb reaches a little beyond the elbow of the adpressed fore limb, or the axilla. Greyish above, with more or less distinct darker markings; a more or less distinct darker interorbital spot; wing-membranes above with numerous small round black spots, which are seldom confluent, inferiorly immaculate or with a few black spots; a blue spot on each side the base of the gular appendage.

Distribution: Continental south-east Asia.

Etymology: Named in reflection of the spotted nature of the type species and the generic root it comes from, noting that the species name *maculatus* also refers to the spots in Latin, and noting that only a minority of English-speaking users of the nomenclature would know this.

Content: *Draco* (*Spottydraco*) *maculatus* Gray, 1845 (type species); *D.* (*Spottydraco*) *divergens* Taylor, 1934; *D.* (*Spottydraco*) *haasei* Boettger, 1893; *D.* (*Spottydraco*) *whiteheadi* Boulenger, 1900.

SUBGENUS *DRACO* LINNAEUS, 1758.

Type species: *Draco volans* Linnaeus, 1758.

Diagnosis: In the recent literature this clade or subgenus has been generally referred to as the "*volans* group" (e.g. Inger, 1983). They are defined and separated from other *Draco* species by the following suite of characters: six ribs supporting the patagium; nostrils pointed laterally; males without a caudal crest; dewlap in males covered with small scales and tapering continuously from its base.

I had considered following Hennig (1936) and dividing the subgenus into two main groups, this being the species he grouped under the species *volans* and the other group of species he grouped under *spilopterus*. However molecular studies show the divergence to be recent and the radiation of species within that time quite dramatic and so I have deferred naming a new subgenus herein on the basis of recent divergences.

Distribution: Wetter parts of southern and south-east Asia.

Content: *Draco* (*Draco*) *volans* Linnaeus, 1758 (type species); *D.* (*Draco*) *affinis* Bartlett, 1895; *D.* (*Draco*) *boschmai* Hennig, 1936; *D.* (*Draco*) *cornutus* Günther, 1864; *D.* (*Draco*) *cyanopterus* Peters, 1867; *D.* (*Draco*) *guentheri* Boulenger, 1885; *D.* (*Draco*) *jareckii* Lazell, 1992; *D.* (*Draco*) *ornatus* (Gray, 1845); *D.* (*Draco*) *palawanensis* McGuire and Alcala, 2000; *D.* (*Draco*) *quadrasi* Boettger, 1893; *D.* (*Draco*) *reticulatus* Günther, 1864; *D.* (*Draco*) *spilopterus* (Wiegmann, 1834); *D.* (*Draco*) *sumatranus* Schlegel, 1844; *D.* (*Draco*) *timorensis* Kuhl, 1820.

SUBGENUS *DRACONTOIDES* FITZINGER, 1843.

Type species: *Draco lineatus* Daudin, 1802.

Diagnosis: *Macguiredraco subgen. nov.* is comprised of nine Wallacean species (*bourouniensis*, *beccarii*, *biaro*, *caerulhians*, *iskandari*, *rhytisma*, *spilonotus supriatnai*, and *walkeri*), treated by most herpetologists to date as being within the so-called "*lineatus* group" (subgenus *Dracontoides* Fitzinger, 1843) but phylogenetically quite distinct and divergent from the species *D. lineatus. Macguiredraco subgen. nov.* is diagnosed and defined on the basis of the following features: (1) a strong statistical mode of five ribs supporting each wing (versus six), (2) absence of lacrimal bones (versus presence), (3) nostrils oriented laterally (versus posterodorsally), and (4) dewlap scalation small and undifferentiated (versus enlarged distally). The only *Draco* species that cannot be distinguished from *Macguiredraco subgen. nov.* on the basis of these characters is *D. bimaculatus* of the southern Philippines (herein placed in the monotypic subgenus *Philippinedraco subgen. nov.*) and separated from *Macguiredraco subgen. nov.* below and also *D. lineatus* (placed in the subgenus *Dracontoides* Fitzinger, 1843), herein regarded as a composite species.

Most *Macguiredraco subgen. nov.* species can be distinguished primarily on the basis of adult male coloration because these lizards are characterized by granular squamation that is apparently not conducive either to the evolution or the discovery of heritable species-specific differences.

Philippinedraco subgen. nov. is separated from *Macguiredraco subgen. nov.* by the following suite of characters: an adult snout-vent length of 73 mm; 8-10 supralabials; tympanum usually covered with smooth skin; lateral pouches with slightly enlarged scales; 122-150 dorsals; five ribs in patagium; and the presence of a black, white-centred spot between the tympanum and the corner of the mouth (not seen in *Macguiredraco subgen. nov.*).

Draco lineatus (*sensu lato*) (treated here as a complex of morphologically similar species) (subgenus *Dracontoides* Fitzinger, 1843), can be distinguished from all other members of *Macguiredraco subgen. nov.*, *Philippinedraco subgen. nov.* and *Engannodraco subgen. nov*. as defined within this paper by the following combination of characteristics: (1) the dorsal patagial coloration of males with five pale brown radial bands on a vivid yellow field, or with several radial bands comprised of pale white or tan spots on a gray field, (2) male dewlap short and rounded distally, (3) dewlap in males bright yellow in coloration, (4) males and females with large yellow spots on a brown field on the side of the neck and base of the dewlap, (5) melanic interorbital spot usually absent in males, (6) large rhomboidal melanic nuchal spot usually absent from both sexes, (7) melanic postnuchal spot usually absent from males, usually present in females, (8) absence of white pigments in association with variably present nuchal and posnuchal spots in both sexes, (8) variable presence in males and absence in females of melanic ‘eye spots’ (dark spots with associated white or pale pigments) on the supraorbital semicircles, (9) parietal lens usually present (32 of 34 specimens examined), and (10) tympana at least partially covered with scales (usually completely covered) (adapted from McGuire *et al.* 2007).

Distribution: Indonesia.

Content: *Draco (Dracontoides*) *lineatus* Daudin, 1802 (monotypic).

SUBGENUS *RHACODRACON* FITZINGER, 1843.

Type species: *Draco fimbriatus* Kuhl, 1820.

Diagnosis: *Rhacodracon* are readily separated from all other *Draco* by the following suite of characters: Nostril lateral, directed outwards; tympanum naked; the adpressed hind limb reaches at least to halfway between the elbow of the adpressed fore limb and the axil; dorsal scales all smaller than the ventrals.

The species *Draco maculatus* Gray, 1845 (*Spottydraco subgen. nov.*) is readily separated from *Rhacodracon* by the fact that the dorsal scales are a little larger than, or as large as, the ventrals; on each side of the back is a series of enlarged, keeled, distant scales and the male’s gular appendage is much longer than the head.

Distribution: Malaysia (Borneo, Pulau Tioman), Indonesia (Sunda Islands, Natuna), Philippines
Southern Thailand.

Content: *Draco (Rhacodracon*) *fimbriatus* Kuhl, 1820 (type species); *D. (Rhacodracon*) *abbreviatus* Hardwicke and Gray, 1827; *D. (Rhacodracon*) *cristatellus* Günther, 1872.

SUBGENUS *PTEROSAURUS* FITZINGER, 1843.

Type species: *Draco dussumieri* Dumeril and Bibron, 1837.

Diagnosis: *Pterosaurus* is easily the most divergent of the subgenera within *Draco* and of all the subgenera is the single one for which the argument for full genus status is strongest.

It is separated from all other *Draco* by the following suite of characters: Nostril pierced vertically, directed upwards; Tympanum naked and as large as the eye-opening; the adpressed hind limb does not reach beyond the axil; wing-membranes black above with round light spots, inferiorly with a series of large black spots near the margin.

The subgenus *Pterosaurus* is further defined and diagnosed as follows: Head small; snout constricted, as long as the diameter of the orbit; nostril directed upwards, perfectly vertical; tympanum naked, as large as the eye-opening. Upper head-scales unequal, keeled; a spinose conical scale at the posterior corner of the orbit; nine to twelve upper labials, the last twice or thrice as large as the preceding. The male’s gular appendage much longer than the head; male with a slight nuchal fold; dorsal scales scarcely larger than

ventrals, unequal, smooth, or very slightly keeled; on each side of the back a series of small tubercular prominences, each being composed of several small scales. The fore-limb stretched forwards

extends beyond the tip of the snout; the adpressed hind limb reaches the axil or not quite so far. Grey-brown above; a series of more or less distinct dark circles on the back; wing-membranes above

purplish black, enclosing round light spots, inferiorly with a series of large black spots near the margin; throat with irregular dark spots.

Distribution: Southern India (India (Goa, Madras, Malabar coast, Nilghiri Hills, Travancore, Western Ghats & Eastern Ghats, Gujarat).

Content: *Draco (Pterosaurus) dussumieri* Dumeril and Bibron, 1837 (monotypic).

SUBFAMILY DRACONINAE FITZINGER, 1826

The subfamily Draconinae has been recognized for nearly two centuries. The number of genera placed within the subfamily has steadily increased as the phylogenetic relationships of the group have become better known.

With roughly 30 genera now recognized within the subfamily (this paper and excluding defined subgenera), it makes eminent sense to divide them into groups on the basis of relationships to one another at a higher level. In other words the subfamily should be properly devided up into tribes.

The use of tribes in herpetology as a useful identifier of taxon groups has been relatively unusual until the present time, but besides myself, who has made use of tribes in a number of papers from 2012 onwards an increasing number of other herpetologists are making use of this classification level when discussing taxa (e.g. Zaher *et al.* 2009, Grazziotin *et al.* 2012).

Therefore I break up the Draconinae along obvious phylogenetic lines into ten well-defined tribes. Some of these are further divided into six well-defined subtribes.

The key references in terms of most species within the Draconinae have already been given and do not need to be repeated in terms of what has been relied upon in terms of diagnosing and defining the tribes herein.

However for the recognized genera within the subfamily Draconinae not dealt with above, I think it is appropriate that I list the most relevant previously published studies relied upon to establish the relevant positions of the clades within phylogenies and also other relevant information in terms of the classification of the said lizards, this including molecular evidence, morphological evidence and relavent ecological and distributional attributes of the same taxa.

For the genus *Acanthosaura* Gray, 1831, key references include Akeret (2010), Ananjeva *et al.* (2008, 2011b), Barts and Wilms (2003), Bobrov (2013), Bobrov and Semenov (2008), Bonetti (2002), Boulenger (1885, 1890, 1900b), Brygoo (1988), Chanard *et al.* (1999), Cox *et al.* (1998), Cuvier (1829), Denzer *et al.*

(1997), de Rooij (1915), Duméril *et al.* (1937), Geissler (2012), Grismer (2011), Grismer *et al.* (2007, 2010), Grossmann and Tillack (2004a), Günther (1861a, 1861b, 1864), Hallermann (2000b, 2005a, 2005b), Hardwicke and Gray (1827), Hecht *et al.* (2013), Hendrickson (1966), Jestrzemski *et al.* (2013), Kwet (2012), Leong *et al.* (2003), Lim and Ng (1999), LiVigni (2013), Macey *et al.* (2000), Manthey (2008), Manthey and Grossmann (1997), Manthey and Schuster (1999), Mell (1952), Milto and Barabanov (2012), Nabhitabhata *et al.* (2000), Neang *et al.* (2010), Okajima and Kumazawa (2010), Orlov *et al.* (2006), Pauwels *et al.* (2000, 2003), Sang *et al.* (2009), Smith (1935), Smits (2004), Stuart and Emmett (2006), Stuart *et al.* (2006, 2010), Taylor (1963), Vogt (1914), Werner (1904), Wöhrle (1996), Wood *et al.* (2009, 2010), Zhao and Adler (1993), Ziegler (2002) and sources cited therein.

For the genus *Dendragama* Doria, 1888, key references include Ahl (1926), de Rooij (1915), Doria (1888), Hallermann (2005a, 2005b), Manthey and Grossmann (1997), Manthey and Schuster (1999), Mertens (1954) and sources cited therein.

For the monotypic genus *Complicitus* Manthey and Grossmann, 1997, key references include Barts and Wilms (2003), Boulenger (1891a), Das (2004), Das and Lakim (2008), Harikrishnan and Vasudevan (2013), Malkmus (1994), Malkmus *et al.* (2002), Manthey and Grossmann (1997), Ota and Hikida (1991), and sources cited therein.

For the genus *Cophotis* Peters, 1861, key references include Amarasinghe *et al.* (2009b), Bahir and Surasinghe (2005), Barts and Kwet (2007), Barts and Wilms (2003), Boulenger (1885, 1890), De Silva (1990, 1994), Hallermann (2005a, 2005b), Hallermann and Böhme (2007), Janzen *et al.* (2007b), Karunarathna and Amarasinghe (2009), Kästle (1996), Macey *et al.* (2000), Manamendra-Arachchi *et al.* (2006), Manthey and Schuster (1999), Marx (1958), Mohr and Cabrera (2013), Peters (1861a, 1861b), Samarawickrama *et al.* (2006), Schulte *et al.* (2000, 2002), Smith (1935), Somaweera and Somaweera (2009), Taylor (1953), and sources cited therein.

For the genus *Pseudocophotis* Manthey and Grossmann, 1997 key references include Ananjeva *et al.* (2007), Bain *et al.* (2007), Bobrov and Semenov (2008), Boulenger (1885), de Rooij (1915), Hallermann and Böhme (2000), Hallermann and McGuire (2001), Hallermann *et al.* (2010), Hubrecht (1879), Manthey and Grossmann (1997), Manthey and Schuster (1999), Milto *et. al.* (2012), Ota (1989c), Sang *et al.* (2009) and sources cited therein.

For the monotypic genus *Lophocalotes* Günther, 1872 key references include Ananjeva *et al.* (2011a), Bleeker (1860), Boulenger (1885, 1887b), de Rooij (1915), Hallermann *et al.* (2004), Manthey and Grossmann (1997), Manthey and Schuster (1999) and sources cited therein.

For the monotypic genus *Lyriocephalus* Merrem, 1820 key references include Amarasinghe *et al.* (2009), Bahir and Surasinghe (2005), Bambaradeniya *et al.* (1997), Bandara (2012), Bartelt (2003), Bartelt and de Bitter (2004, 2005a, 2005b), Barts and Wilms (2003), Boulenger (1885, 1890), Cuvier (1831), Duméril *et al.* (1837), Goonawardene and de Silva (2005), Gray (1835), Hallermann (2005a, 2005b), Janzen (2011), Janzen and Bopage (2011), Janzen *et al.* (2007a, 2007b), Karunarathna and Amarasinghe (2013), Kelaart (1852), Kiehlmann (1980), Linnaeus (1758), Macey *et al.* (2000), Manthey and Schuster (1999), Pachmann (2008), Prinz and Prinz (1986), Pyron *et al.* (2013), Schulte *et al.* (2002), Smith (1935), Somaweera and Somaweera (2009), Taylor (1953) and sources cited therein.

For the genus *Mantheyus* Ananjeva and Stuart, 2001 key references include Ananjeva and Stuart (2001), Ananjeva *et al.* (2011), Barts and Wilms (2003), Hallermann and Böhme (2003), Manthey and Nabhitabhata (1991), Manthey and Manthey (2005a, 2005b), Manthey and Schuster (1999), Schulte *et al.* (2004) and sources cited therein.

For the monotypic genus *Oriocalotes* Günther, 1864 key references include Boulenger (1885, 1890), Gray (1845), Günther (1864), Lenz (2012), Manthey and Schuster (1999), Smith (1935), Venugopal (2010), Zhao and Adler (1993) and sources cited therein.

For the genus *Otocryptis* Wagler, 1830 key references include Amarasinghe *et al.* (2009b), Bahir and de Silva (2005), Bahir and Gabadage (2009), Bahir and Surasinghe (2005), Barts and Wilms (2003), Bauer (1998), Boulenger (1885, 1890), Chandramouli (2009a), Duméril *et al.* (1837), Hallermann (2005a, 2005b), Janzen (2003, 2011), Janzen and Bopage (2011), Janzen *et al.* (2007), Jose *et al.* (2007), Karunarathna and Amarasinghe (2008b, 2011), Macey *et al.* (2000), Manthey and Schuster (1999), Murthy (1990), Pachmann (2012), Pyron *et al.* (2013), Smith (1935), Somaweera and Somaweera (2009), Taylor (1953), Wagler (1830), Wiegmann (1831), Venugopal (2010) and sources cited therein.

For the genus *Salea* Gray, 1845 key references include Barts and Wilms (2003), Beddome (1878), Boulenger (1885, 1890), Duméril and Duméril (1851), Ganesh and Aengals (2011), Gray (1845), Günther (1864), Jerdon (1854), Macey *et al.* (2000), Manthey and Schuster (1999), Murthy (1990, 2010), Smith (1935), Venugopal (2010) and sources cited therein.

For the genus *Sitana* Cuvier, 1829 key references include Amarasinghe *et al.* (2009), Bahir and Surasinghe (2005), Boulenger (1885, 1890), Cuvier (1829), Deraniyagala (1953), Duméril *et al.* (1837), Günther (1864), Hallermann (2005a, 2005b), Janzen *et al.* (2007b), Jerdon (1870), Karunarathna and Amarasinghe (2011a), Kelaart (1854), Macey *et al.* (2000), Manthey and Schuster (1999), Murthy (2010), Pal *et al.* (2010, 2011), Patankar *et al.* (2013), Saikia *et al.* (2007), Schleich and Kästle (1998a, 1998b, 2002), Schleich *et al.* (1998), Smith (1935), Somaweera and Somaweera (2009), Subramanean and Reddy (2012), Tsetan and Ramanibai (2011), Upadhye *et al.* (2012), Venugopal (2010), Vitt and Pianka (2006), Vyas (2007, 2011a, 2011b) Wiegmann (1834a) and sources cited therein.

For the genus *Hypsicalotes* Manthey and Denzer, 2000, key references include Das (2004), Hallermann (2000a), Inger and Lakim (1998), Malkmus (1994), Manthey (1983, 2012), Manthey and Denzer (2000), Moody (1980), Ota and Hikida (1996) and sources cited therein.

As already mentioned earlier, should a later author seek to merge one or more of the tribes described herein, then the order of priority should be that as presented herein.

TRIBE DRACOIINI *TRIBE NOV.*

(Terminal taxon: *Draco volans* Linnaeus, 1758)

Diagnosis: The tribe Dracoiini *tribe nov.* consists the same species as the genus *Draco* Linnaeus, 1758 in that the tribe is monotypic and therefore the definition for each is one and the same.

Dracoiini *tribe nov.* and *Draco* Linnaeus, 1758 are readily distinguished from all other lizards by the fact that the body is depressed and with a large lateral wing-like membrane, supported by the much-expanded five or six posterior ribs, folding like a fan. A gular appendage and a lateral smaller one on each side. Tympanum distinct or covered with scales. Tail long. No femoral or preanal pores in the true sense of the term.

Distribution: Wetter parts of southern and south-east Asia.

Content: *Draco* Linnaeus, 1758 (including all nine subgenera, namely *Draco* Linnaeus, 1758; *Dracontoides* Fitzinger, 1843; *Rhacodracon* Fitzinger, 1843; *Pterosaurus* Fitzinger, 1843; *Macguiredraco subgen. nov.*; *Philippinedraco subgen. nov.*; *Engannodraco subgen. nov.*; *Somniadraco subgen. nov.* and *Spottydraco subgen. nov.*).

As mentioned elsewhere in this paper, there is a strong argument in favour of elevating all named subgenera within *Draco* as recognized herein to the status of genus, leaving the tribe as defined herein unchanged and consisting of nine genera rather than one.

TRIBE MAXHOSERAGAMAIINI *TRIBE NOV.*

(Terminal taxon: *Japalura splendida* Barbour and Dunn, 1919)

Diagnosis: The tribe Maxhoseragamiini *tribe nov.* is best defined by the diagnosis of each of the component genera. The tribe is therefore defined as one or other of the following eight genera defined herein:

1/ *Maxhoseragama gen. nov*. are readily separated from *Japalura* Gray, 1853 (the genus in which it was previously placed) and *Diploderma* Hallowell, 1861 (neither in this tribe) by the following suite of characters: having infracaudal scales larger than ventrals; the third and fourth fingers of equal length; does not have seven upper labials.

Furthermore this genus is separated from *Japalura* by the fact that an enlarged subocular scale row is present and usually prominent, or at least moderately so.

This genus is also identified by the following suite of characters: Tympanum hidden. Body compressed. Dorsal scales heterogeneous. A dorsal crest. Gular pouch small or absent. An oblique fold in front of the shoulder; gular fold present or absent. Tail feebly compressed. No praeanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895).

Notacalotes gen. nov. monotypic for the species originally described as "*Calotes andamanensis* Boulenger, 1891" is separated from similar species by having enlarged keeled scales on the posterior surface of the thigh, dorsal head scales obtusely keeled, smooth dorsal body scales (upper six rows directed posterodorsally, remainder posteroventrally), and lacking body crest, antehumeral pit present; nuchal crest well developed; 67 scales around midbody; tympanum (11% HL); toe no. 3 shorter than no. 4. Distinguished from *Calotes* (*Tamilnaducalotes*) *aurantolabium* Krishnan, 2008 in having smooth dorsals, dorsal body scales unequal, upper six scale rows larger, remainder equal in size to ventral scales; three enlarged scales on caudal thigh; dorsal head scales obtusely keeled; parietal ridge raised; enlarged scale between nuchal crest and tympanum; antehumeral pit present; toe 4 longer than 3; stretched hindlimb reaches eye. Distinguished from other *Calotes* subgenera *Ceyloncalotes subgen. nov.* and *Rubercalotes subgen. nov*. as well as *Skrijelus gen. nov*. (species formerly within *Calotes*) by the presence of enlarged keeled scales on caudal surface of thigh. Distinguished from *Calotes* subgenus *Rubercalotes subgen. nov*. in scale orientation: distinguished from *Rubercalotes subgen. nov*. in having an antehumeral pit; distinguished from *Calotes* subgenus *Ghatscalotes subgen. nov.* in having equal size dorsal and ventral scales, toe no. 3 longer than no. 4, scales around midbody 67 (36-43 and 27-35 respectively); distinguished from the *Calotes* subgenus *Calotes* as defined within this paper in lacking flattened spines in the nuchal region. Distinguished from *Skrijelus gen. nov*. (species formerly within *Calotes*) in having an antehumeral pit (instead of folds) and in lacking spines in the nuchal region; or:

2/ *Notacalotes gen. nov.* is distinguished from *Calotes* subgenera *Ceyloncalotes subgen. nov.* and *Laccadivecalotes subgen. nov.* in lacking spines in the nuchal region; distinguished from *Calotes* (*Ceyloncalotes*) *liocephalus* by midbody scale count and body crest scales.

This genus *Notacalotes gen. nov.* is alternatively defined and separated from all other agamidae as follows: relatively long head (hw: hl = 0.59); 56-67 longitudinal scale rows around midbody; dorsals and laterals smooth, sometimes weakly keeled near the sacral region; ventrals strongly keeled; dorsals of 4-7 paravertebral longitudinal rows larger than laterals, of irregular shape, pointing posterodorsally; laterals pointing posteroventrally; laterals and ventrals of similar size; ventrals slightly irregular; a row of enlarged scales between supralabials and orbit, bordered by one or two smaller scale rows; gular scales smaller than ventrals, weakly keeled; gular pouch present in males; antehumeral fold/pit weakly developed; nuchal crest composed of 11-15 lanceolate spines; dorsal crest a denticulate ridge; enlarged conical lamellae under the leading edge of third toe; 27-30 lamellae under fourth toe; hind limb length 70-75 % of svl; tail length 238-265% of svl, slightly compressed at the base (Harikrishnan and Vasudevan, 2013).

The species within *Notacalotes gen. nov.* can be distinguished from *Pseudocalotes* in having stronger and proportionately longer limbs (proportional antebrachial length not different); nuchal crest vertically directed compressed triangle scales, nuchal crest scales not intermittent as in several *Pseudocalotes*; presence of enlarged keeled scales on posterior surface of thigh. Distinguished from *Bronchocela* Kaup, 1827 and *Calotes* in having enlarged keeled scales on caudal surface of thigh. Distinguished from *Complicitus* Manthey and Grossmann, 1997 in having enlarged keeled scales on caudal face of thigh, lacking a gular pouch or dewlap, and having smaller head length and head height proportions. Distinguished from *Salea* Gray, 1845 in having predominantly uniform dorsal body scales, smooth body scales, lacks body crest, and laterally compressed body (depressed body in *Salea khakienensis*). Distinguished from *Dendragama* Doria, 1888 in lacking a lateral crest on either side of neck; lacking raised parietal ridges; lacking a row of enlarged keeled body scales; lacking keeled dorsal body scales; having flat forehead; or:

3/ *Pseudocalotes* Fitzinger, 1843 (herein treated as including *Paracalotes* Bourret, 1939 and *Mictopholis* Smith, 1935) are readily separated from *Calotes* Cuvier, 1817 in having relatively weak limbs as may be noted in some of the species names, e.g. "*Calotes brevipes* Werner, 1904". *Pseudocalotes* posesses mixed orientation of dorsal scales, and lacks spines on the head. It is distinguished from another morphologically similar genus *Bronchocela* Kaup, 1827 (not in this tribe) in lacking a cheek skin fold and in having short weak limbs. They do not have any enlarged compressed set of scales behind the orbit. Excluding the taxon, "*Calotes andamanensis*", known only from the Andaman Islands and herein treated as within the genus *Notacalotes gen. nov.*, *Pseudocalotes* does not occur west of Sumatra. In turn *Pseudocalotes* and *Calotes* (the latter genus being in tribe Crottyagamaiini *tribe nov.*) are both defined and separated from all other Agamidae (as a pair of genera) as follows: Tympanum distinct. Body compressed, covered with equal-sized scales. A dorso-nuchal crest. A more or less developed gular sac in the male; no transverse gular fold, or a very feebly marked one. Tail round or feebly compressed. No femoral or prseanal pores. The genus *Bronchocela* Kaup, 1827 (in tribe Doongagamaiini *tribe nov.*) is defined and separated from similar agamid genera as follows: No fold in front of the shoulder; lateral scales pointing backwards and downwards; ventral scales larger than latero-dorsals; fourth finger nearly the same length as the fifth toe or rarely longer; (These three genera, namely *Pseudocalotes* Fitzinger, 1843 (herein treated as including *Paracalotes* Bourret, 1939), *Notacalotes gen. nov.* and *Maxhoseragama gen. nov.* form the subtribe Maxhoseragamaiina *subtribe nov.*); or:

4/ The genus *Sitana* Cuvier, 1829 is defined and separated from all other Agamidae as follows: Mouth large; teeth erect in both jaws.Incisors small, conical. No true praeanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895). No wing-like lateral expansion. Body not depressed and slightly compressed; limbs long and four toes only.Scales all keeled, regular, smallest on the flanks. No dorsal crest. Male with a slight nuchal fold and a large folding gular appendage extending backwards to the belly and covered with large scales. No gular fold. Ear exposed; or:

5/ The genus *Otocryptis* Wagler, 1830 is separated from all other Agamid genera as follows: Mouth large; teeth erect in both jaws. Incisors small and conical. No true preanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895). No wing-like lateral expansion. Fifth toe very short, not longer than the first; no dorsal crest. Body compressed, limbs very long. All the scales keeled, the dorsals heterogeneous. No gular fold. Male with a low nuchal crest and a large folding gular appendage extending backwards to the belly, and covered with large scales. Ear concealed; (These two genera namely *Sitana* Cuvier, 1829 and *Otocryptis* Wagler, 1830 form the subtribe Sitanaiina *subtribe nov.*); or:

6/ The genus *Acanthosaura* Gray, 1831 is separated from all other Agamid genera as follows: Mouth large; teeth erect in both jaws. Incisors small and conical. No true preanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895). No wing-like lateral expansion. Tympanum exposed. No fold across the throat ; dorsal scales unequal; no gular pouch. Body generally compressed, limbs more or less elongate. Dorsal scales heterogeneous, small or moderate. A dorsal crest. No gular fold, but a more or less distinct oblique fold in front of the shoulder. No gular sac. The nuchal crest is separated from dorsal crest, or if continuous then there is a spine on each side of the neck and the small dorsal scales are much smaller than the ventrals; or:

7/ The genus *Oriocalotes* Günther, 1864 is separated from all other Agamid genera as follows: Mouth large; teeth erect in both jaws. Incisors small and conical. No true preanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895). No wing-like lateral expansion. Tympanum exposed. No fold across the throat; dorsal scales unequal; no gular pouch. Body generally compressed, limbs more or less elongate. Dorsal scales heterogeneous, small or moderate. A dorsal crest. No gular fold, but a more or less distinct oblique fold in front of the shoulder. No gular sac. The nuchal crest is continuous and there is a spine on each side of the neck and the smaller dorsal scales are larger than the ventrals: The morphologically similar genus *Calotes* Cuvier, 1817 and all other genera within the tribe Crottyagamaiini *tribe nov.* are separated from both *Acanthosaura* and *Oriocalotes* by having no spine on the side of the neck; (These two genera; namely *Acanthosaura* Gray, 1831 and *Oriocalotes* Günther, 1864 form the subtribe Acanthosauriina *subtribe nov.*); or:

8/ The genus *Salea* Gray, 1845 is separated from all other Agamid genera as follows: Mouth large; teeth erect in both jaws. Incisors small and conical. No true preanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895). Tympanum distinct. No transverse gular fold; dorsal scales large, unequal; males with a gular pouch; body compressed, covered with unequal-sized imbricate keeled scales. Male with a dorso-nuchal crest and a gular sac. Tail compressed; (The genus *Salea* Gray, 1845 including the subgenus *Lophosalea* Beddome, 1878 monotypically forms the subtribe Saleaiina *subtribe nov.*).

Distribution: Southern and south-east Asia.

Content: *Maxhoseragama gen. nov.*; *Notacalotes gen. nov.*; *Pseudocalotes* Fitzinger, 1843 (herein treated as including as subgenera *Paracalotes* Bourret, 1939 and *Mictopholis* Smith, 1935) (subtribe Maxhoseragamaiina *subtribe nov.*); *Sitana* Cuvier, 1829; *Otocryptis* Wagler, 1830 (subtribe Sitanaiina *subtribe nov.*); *Acanthosaura* Gray, 1831; *Oriocalotes* Günther 1864 (Acanthosauriina *subtribe nov.*); *Salea* Gray, 1845 (Saleaiina *subtribe nov.*).

SUBTRIBE MAXHOSERAGAMAIINA *SUBTRIBE NOV.*

(Terminal taxon: *Japalura splendida* Barbour and Dunn, 1919)

Diagnosis: The subtribe Maxhoseragamiina *subtribe nov.* is best defined by the diagnosis of each of the component genera. The tribe is therefore defined as one or other of the following three genera defined herein:

1/ *Maxhoseragama gen. nov.* are readily separated from *Japalura* Gray, 1853 (the genus in which it was previously placed) and *Diploderma* Hallowell, 1861 (neither in this tribe) by the following suite of characters: having infracaudal scales larger than ventrals; the third and fourth fingers of equal length; does not have seven upper labials.

Furthermore this genus is separated from *Japalura* by the fact that an enlarged subocular scale row is present and usually prominent, or at least moderately so.

This genus is also identified by the following suite of characters: Tympanum hidden. Body compressed. Dorsal scales heterogeneous. A dorsal crest. Gular pouch small or absent. An oblique fold in front of the shoulder; gular fold present or absent. Tail feebly compressed. No praeanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895); or:

2/ *Notacalotes gen. nov.* monotypic for the species originally described as "*Calotes andamanensis* Boulenger, 1891" is separated from similar species by having enlarged keeled scales on the posterior surface of the thigh, dorsal head scales obtusely keeled, smooth dorsal body scales (upper six rows directed posterodorsally, remainder posteroventrally), and lacking body crest, antehumeral pit present; nuchal crest well developed; 67 scales around midbody; tympanum (11% HL); toe no. 3 shorter than no. 4. Distinguished from *Calotes* (*Tamilnaducalotes*) *aurantolabium* Krishnan, 2008 in having smooth dorsals, dorsal body scales unequal, upper six scale rows larger, remainder equal in size to ventral scales; three enlarged scales on caudal thigh; dorsal head scales obtusely keeled; parietal ridge raised; enlarged scale between nuchal crest and tympanum; antehumeral pit present; toe 4 longer than 3; stretched hindlimb reaches eye. Distinguished from other *Calotes* subgenera *Ceyloncalotes subgen. nov.* and *Rubercalotes subgen. nov.* as well as *Skrijelus gen. nov.* (species formerly within *Calotes*) by the presence of enlarged keeled scales on caudal surface of thigh. Distinguished from *Calotes* subgenus *Rubercalotes subgen. nov.* in scale orientation: distinguished from *Rubercalotes subgen. nov.* in having an antehumeral pit; distinguished from *Calotes* subgenus *Ghatscalotes subgen. nov.* in having equal size dorsal and ventral scales, toe no. 3 longer than no. 4, scales around midbody 67 (36-43 and 27-35 respectively); distinguished from the *Calotes* subgenus *Calotes* as defined within this paper in lacking flattened spines in the nuchal region. Distinguished from *Skrijelus gen. nov.* (species formerly within *Calotes*) in having an antehumeral pit (instead of folds) and in lacking spines in the nuchal region. *Notacalotes gen. nov.* is distinguished from *Calotes* subgenera *Ceyloncalotes subgen. nov.* and *Laccadivecalotes subgen. nov.* in lacking spines in the nuchal region; distinguished from *Calotes* (*Ceyloncalotes*) *liocephalus* by midbody scale count and body crest scales.

This genus *Notacalotes gen. nov.* is alternatively defined and separated from all other agamidae as follows: relatively long head (hw: hl = 0.59); 56-67 longitudinal scale rows around midbody; dorsals and laterals smooth, sometimes weakly keeled near the sacral region; ventrals strongly keeled; dorsals of 4-7 paravertebral longitudinal rows larger than laterals, of irregular shape, pointing posterodorsally; laterals pointing posteroventrally; laterals and ventrals of similar size; ventrals slightly irregular; a row of enlarged scales between supralabials and orbit, bordered by one or two smaller scale rows; gular scales smaller than ventrals, weakly keeled; gular pouch present in males; antehumeral fold/pit weakly developed; nuchal crest composed of 11-15 lanceolate spines; dorsal crest a denticulate ridge; enlarged conical lamellae under the leading edge of third toe; 27-30 lamellae under fourth toe; hind limb length 70-75 % of svl; tail length 238-265% of svl, slightly compressed at the base (Harikrishnan and Vasudevan, 2013).

The species within *Notacalotes gen. nov.* can be distinguished from *Pseudocalotes* in having stronger and proportionately longer limbs (proportional antebrachial length not different); nuchal crest vertically directed compressed triangle scales, nuchal crest scales not intermittent as in several *Pseudocalotes*; presence of enlarged keeled scales on posterior surface of thigh. Distinguished from *Bronchocela* Kaup, 1827 and *Calotes* in having enlarged keeled scales on caudal surface of thigh. Distinguished from *Complicitus* Manthey and Grossmann, 1997 in having enlarged keeled scales on caudal face of thigh, lacking a gular pouch or dewlap, and having smaller head length and head height proportions. Distinguished from *Salea* Gray, 1845 in having predominantly uniform dorsal body scales, smooth body scales, lacks body crest, and laterally compressed body (depressed body in *Salea khakienensis*). Distinguished from *Dendragama* Doria, 1888 in lacking a lateral crest on either side of neck; lacking raised parietal ridges; lacking a row of enlarged keeled body scales; lacking keeled dorsal body scales; having flat forehead; or:

3/ *Pseudocalotes* Fitzinger, 1843 (herein treated as including as subgenera *Paracalotes* Bourret, 1939 and *Mictopholis* Smith, 1935) are readily separated from *Calotes* Cuvier, 1817 in having relatively weak limbs as may be noted in some of the species names, e.g. "*Calotes brevipes* Werner, 1904". *Pseudocalotes* posesses mixed orientation of dorsal scales, and lacks spines on the head. It is distinguished from another morphologically similar genus *Bronchocela* Kaup, 1827 (not in this tribe) in lacking a cheek skin fold and in having short weak limbs. They do not have any enlarged compressed set of scales behind the orbit. Excluding the taxon, "*Calotes andamanensis*", known only from the Andaman Islands and herein treated as within the genus *Notacalotes gen. nov.*, *Pseudocalotes* does not occur west of Sumatra. In turn *Pseudocalotes* and *Calotes* (the latter genus being in tribe Crottyagamaiini *tribe nov.*) are both defined and separated from all other Agamidae (as a pair of genera) as follows: Tympanum distinct. Body compressed, covered with equal-sized scales. A dorso-nuchal crest. A more or less developed gular sac in the male; no transverse gular fold, or a very feebly marked one. Tail round or feebly compressed. No femoral or prseanal pores. The genus *Bronchocela* Kaup, 1827 (in tribe Doongagamaiini *tribe nov.*) is defined and separated from similar agamid genera as follows: No fold in front of the shoulder; lateral scales pointing backwards and downwards; ventral scales larger than latero-dorsals; fourth finger nearly the same length as the fifth toe or rarely longer.

Distribution: South-east Asia.

Content: *Maxhoseragama gen. nov.*; *Pseudocalotes* Fitzinger, 1843 (herein treated as including as subgenera *Paracalotes* Bourret, 1939 and *Mictopholis* Smith, 1935); *Notacalotes gen. nov.*.

SUBTRIBE SITANAIINA *SUBTRIBE NOV.*

(Terminal taxon: *Sitana ponticeriana* Cuvier, 1829)

Diagnosis: The subtribe Sitanaiina *subtribe nov.* is best defined by the diagnosis of each of the component genera. The tribe is therefore defined as one or other of the following two genera defined herein:

1/ The genus *Sitana* Cuvier, 1829 is defined and separated from all other Agamidae as follows: Mouth large; teeth erect in both jaws.Incisors small, conical. No true praeanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895). No wing-like lateral expansion. Body not depressed and slightly compressed; limbs long and four toes only.Scales all keeled, regular, smallest on the flanks. No dorsal crest. Male with a slight nuchal fold and a large folding gular appendage extending backwards to the belly and covered with large scales. No gular fold. Ear exposed; or:

2/ The genus *Otocryptis* Wagler, 1830 is separated from all other Agamid genera as follows: Mouth large; teeth erect in both jaws. Incisors small and conical. No true preanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895). No wing-like lateral expansion. Fifth toe very short, not longer than the first; no dorsal crest. Body compressed, limbs very long. All the scales keeled, the dorsals heterogeneous. No gular fold. Male with a low nuchal crest and a large folding gular appendage extending backwards to the belly, and covered with large scales. Ear concealed.

Distribution: The region encompassing the Indian subcontinent.

Content: *Sitana* Cuvier, 1829; *Otocryptis* Wagler, 1830.

SUBTRIBE ACANTHOSAURIINA *SUBTRIBE NOV.*

(Terminal taxon: *Agama armata* Gray, 1827)

Diagnosis: The subtribe Acanthosauriina *subtribe nov.* is best defined by the diagnosis of each of the component genera. The tribe is therefore defined as one or other of the following two genera defined herein:

1/ The genus *Acanthosaura* Gray, 1831 is separated from all other Agamid genera as follows: Mouth large; teeth erect in both jaws. Incisors small and conical. No true preanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895). No wing-like lateral expansion. Tympanum exposed. No fold across the throat; dorsal scales unequal; no gular pouch. Body generally compressed, limbs more or less elongate. Dorsal scales heterogeneous, small or moderate. A dorsal crest. No gular fold, but a more or less distinct oblique fold in front of the shoulder. No gular sac. The nuchal crest is separated from dorsal crest, or if continuous then there is a spine on each side of the neck and the small dorsal scales are much smaller than the ventrals; or:

2/ The genus *Oriocalotes* Günther, 1864 is separated from all other Agamid genera as follows: Mouth large; teeth erect in both jaws. Incisors small and conical. No true preanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895). No wing-like lateral expansion. Tympanum exposed. No fold across the throat; dorsal scales unequal; no gular pouch. Body generally compressed, limbs more or less elongate. Dorsal scales heterogeneous, small or moderate. A dorsal crest. No gular fold, but a more or less distinct oblique fold in front of the shoulder. No gular sac. The nuchal crest is continuous and there is a spine on each side of the neck and the smaller dorsal scales are larger than the ventrals.

Note that the morphologically similar genus *Calotes* Cuvier, 1817 and all other genera within the tribe Crottyagamaiini *tribe nov.)* are separated from both *Acanthosaura* and *Oriocalotes* by having no spine on the side of the neck.

Distribution: South-east Asia.

Content: *Acanthosaura* Gray, 1831; *Oriocalotes* Günther, 1864.

SUBTRIBE SALEAIINA *SUBTRIBE NOV.*

(Terminal taxon: *Salea horsfieldii* Gray, 1845)

Diagnosis: The subtribe Saleaiina *subtribe nov.* is best defined by the diagnosis of the single genus within the monotypic tribe. This tribe and the genus *Salea* Gray, 1845 are separated from all other Agamid genera as follows: Mouth large; teeth erect in both jaws. Incisors small and conical. No true preanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895). Tympanum distinct. No transverse gular fold; dorsal scales large, unequal; males with a gular pouch; body compressed, covered with unequal-sized imbricate keeled scales. Male with a dorso-nuchal crest and a gular sac. Tail compressed.

The subgenus *Lophosalea* Beddome, 1878 is included in this diagnosis.

Distribution: Southern India.

Content: *Salea* Gray, 1845.

TRIBE *CROTTYAGAMAIINI TRIBE NOV.*

(Terminal taxon: *Calotes mystaceus* Duméri and Bibron, 1837)

Diagnosis: The tribe Crottyagamiini *tribe nov.* is best defined by the diagnosis of each of the component genera. The tribe is therefore defined as one or other of the following three genera defined herein:

1/ *Calotes* Daudin, 1802 is herein defined as follows: Tympanum distinct; body compressed, covered with equal-sized scales; a dorso-nuchal crest; a more or less developed gular sac in the male; no transverse gular fold, or a very feebly marked one. Tail round or feebly compressed. No femoral or preanal pores.

There is no long transversal fold in front of the shoulder extending across the throat or two slender spines on the back of the head as seen in *Skrijelus gen. nov.* which comprises the species formerly known as *Calotes rouxii* Duméri and Bibron, 1837 and *Calotes ellioti* Günther, 1864; or:

2/ *Crottyagama gen. nov.* formally described within this paper is separated from *Calotes* Cuvier, 1817 and *Skrijelus gen. nov*. by the following characters: An oblique fold or triangle pit in front of shoulder covered with small scales, not extending across the throat and dorsal scales larger than ventrals and keeled. In addition to this, each of the relevant subgenera within *Crottyagama gen. nov.* are further diagnosed and separated from the other genera by one or other of: A/ No post orbital spine present; fourth toe much longer than the third; relatively large specimens up to about 140 mm snout-vent length; pit in front of the shoulders light brown or not coloured; white or yellow stripe above lip extending to the shoulder (subgenus *Crottyagama gen. nov.*); or B/ A post orbital spine present (*Freudcalotes subgen. nov.*); or C/ Two parallel rows of compressed spines above the tympanum and a dorsal colour of green in life (*Khasicalotes subgen. nov.*); or D/ Pit in front of shoulders is black, no white or yellow stripe is above the lip (*Amboncalotes subgen. nov.*); or:

3/ *Skrijelus gen. nov*. formally described below is readily separated from both *Calotes* and *Crottyagama gen. nov*. by the presence of a long transversal fold in front of the shoulder extending across the throat and two slender spines on the back of the head.

Distribution: South and south-east Asia.

Content: *Crottyagama gen. nov.*; *Calotes* Daudin, 1802; *Skrijelus gen. nov.*.

TRIBE *DARANINAGAMAIINI TRIBE NOV.*

(Terminal taxon: *Gonyocephalus robinsonii* Boulenger, 1908)

Referred to now as *Daraninagama robinsonii* (Boulenger, 1908).

Diagnosis: The tribe Daraninagamaiini *tribe nov.* is best defined by diagnosis of the two component genera. Hence the tribe is defined as being one or other of:

1/ *Daraninagama gen. nov.* is separated from all other *Gonocephalus* Kaup, 1825 species by karyotypic differences. In *Daraninagama gen. nov.* there are 2n=32 chromosomes. Of the diploid chromosomes, 12 (pairs 1-6) are metacentric macrochromosomes, whereas the remaining 20 (pairs 7-16) were microchromosomes. Therefore, the arm number in macrochromosomes of this karyotype equaled 24.

By contrast for all species of *Gonocephalus* the configuration is 2n=42 chromosomes, including 22

macrochromosomes (pairs 1-11) and 20 microchromosomes (pairs 12-21).

Doongagama gen. nov. (defined herein and formerly included in *Gonocephalus*) are separated from all species of *Gonocephalus* and *Daraninagama gen. nov*. as defined herein by the unique presence of two parallel longitudinal gular folds, a trait seen in none of the other species as well as the other diagnostic characters outlined in the description below.

Daraninagama gen. nov. and *Doongagama gen. nov.* are both separated from *Gonocephalus* by their enlarged gular fold. *Daraninagama gen. nov.* is readily identifiable and separated from all other *Gonocephalus* and *Doongagama gen. nov.* by the unique combination of having a distinctive white lower jaw and greatly enlarged gular fold.

Daraninagama gen. nov., *Doongagama gen. nov.* and *Gonocephalus* Kaup, 1825 are separated from all other agamids by the following suite of characters: Tympanum distinct. Body compressed. Dorsal scales small, uniform or intermixed with enlarged ones. A dorsal crest, A strong transverse gular fold. Males with a gular sac. No praeanal or femoral pores.

2/ The genus *Diploderma* Hallowell, 1861 is diagnosed as follows: As for *Japalura* Gray, 1853, this genus has the following suite of characters: Body compressed. Dorsal scales heterogeneous. A dorsal crest. Gular pouch small or absent. An oblique fold in front of the shoulder; gular fold present or absent. Tail feebly compressed. No praeanal or femoral pores. This genus has a hidden tympanum.

Diploderma is separated from *Japalura* by having the third and fourth fingers of equal length and only seven upper labials.

Maxhoseragama gen. nov. are readily separated from *Japalura* (the genus in which it was previously placed) and *Diploderma* by the following suite of characters: having infracaudal scales larger than ventrals; the third and fourth fingers of equal length; does not have seven upper labials.

Distribution: The highlands of West Malaysia (*Daraninagama gen. nov.*) and Japan (Ryukyu Archipelago) and China (North Taiwan only) (*Diploderma* Hallowell, 1861).

Content: *Daraninagama gen. nov.*; *Diploderma* Hallowell, 1861.

TRIBE *PETHIYAGODAIINI TRIBE NOV.*

(Terminal taxon: *Ceratophora aspera* Günther, 1864)

Herein referred to as: *Pethiyagodaus aspera* (Günther, 1864).

Diagnosis: This tribe is best defined by diagnosis of the component genera. Hence the tribe consists of one or other of the following 13 suites of characters as defined below:

1/ The genus *Ceratophora* Gray 1835 is diagnosed herein as follows: Tympanum hidden. Body more or less compressed, covered with unequal scales. No dorsal crest; a nuchal crest may be present or absent. No gular sac; no gular fold. A large rostral appendage, at least in the males. No femoral or praeanal pores. The gular scales larger than the ventrals, smooth or feebly keeled; lateral scales are large, equal or unequal; rostral appendage is either scaleless or scaly; or:

2/ *Pethiyagodaus gen. nov.* is readily separated from *Ceratophora* (both subgenera) (as defined above) and *Manamendraarachchius gen. nov.* as defined within this paper by having gular scales smaller than the ventrals, strongly keeled; lateral scales small; rostral appendage scaly. It is separated from all other *Ceratophora sensu lato* by the presence of a visible and palpable squamosal process (absent in all *Ceratophora sensu lato* other species); or:

3/ *Manamendraarachchius gen. nov.* (type species being *M. karu* Pethiyagoda and Manamendra-Arachchi, 1988) are separated from all other *Ceratophora sensu lato* (as defined above) (except *C.* (*Jamesschulteus*) *tennentii* and

Pethiyagodaus aspera) by the rostral appendage being complex, comprising more scales than rostral scale alone (vs. rostral appendage restricted to rostral scale alone in *C. erdeleni* and *C. stoddartii*). It is distinguished from *C.* (*Jamesschulteus*) *tennentii* by the presence of prominent superciliary scales, versus absent in *C.* (*Jamesschulteus*) *tennentii*) and from *Pethiyagodaus aspera* by the absence of a palpable squamosal process versus squamosal process present in *P. Aspera*; or:

4/ *Cophotis* Peters, 1861 is defined by the following suite of characters: Mouth large; teeth erect in both jaws. Incisors small and conical. No praeanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895); tympanum hidden. Five toes. A dorsal crest: tail prehensile. Body compressed, covered with large subequal irregular scales. A very small gular sac in both sexes; a slight transverse gular fold; or:

5/ *Pseudocophotis* Manthey and Grossmann, 1997 is defined as for the genus *Cophotis* Peters, 1861 (diagnosed above), but separated from it by the following suite of characters: A rostral appendage consisting of a small pointed horn-like scale; a fringe of elongated scales along the supraciliary edge. Nuchal crest composed of nine larger and several smaller lobes; dorsal crest composed of eighteen lobes; the crest extends on more than three fourths of the length of the tail. Caudal scales as large ventrally as dorsally. Body and tail with broad brown cross bands. Head marmorated with brown, or:

6/ *Lyriocephalus* Merrem, 1820 is defined by the following suite of characters: Mouth large; teeth erect in both jaws. Incisors small and conical. No praeanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895); tympanum hidden. Five toes. A dorsal crest; a V-shaped gular fold; a bony supraorbital arch. Body compressed, covered with small scales intermixed with enlarged ones. A nuchal and a dorsal crest. A gular sac and a V-shaped gular fold. Adult with a globular hump on the nose.

Pre and post-orbital bones forming an arch limiting a supraorbital fossa. (These six genera namely *Ceratophora* Gray 1835, *Pethiyagodaus gen. nov.*, *Manamendraarachchius gen. nov.*, *Cophotis* Peters, 1861, *Pseudocophotis* Manthey and Grossmann, 1997 and *Lyriocephalus* Merrem, 1820 form the subtribe *Pethiyagodaiina subtribe nov.*); or:

7/ *Gonocephalus* Kaup, 1825 is defined as follows: Tympanum distinct. Body compressed. Dorsal scales small, uniform or intermixed with enlarged ones. A dorsal crest, A strong transverse gular fold. Males with a gular sac. No praeanal or femoral pores. Basal scales are adjacent to the nuchal and dorsal crests, a transverse gular fold, a sharp canthus rostralis and an “angled” supraciliary ridge; or:

8/ *Doongagama gen. nov.* (monotypic for the species *Doongagama mjobergi* Smith, 1925), are separated from all species of *Gonocephalus* and *Daraninagama gen. nov.* (within the tribe Daraninagamaiini *tribe nov.*) as defined within this paper by the unique presence of two parallel longitudinal gular folds, a trait seen in none of the other species.

In more detail the genus *Doongagama gen. nov.* is defined as follows: A feature clearly distinguishing *D. mjobergi* from all other *Gonocephalus* is the possession of enlarged dorsolateral scales forming oblique rows. The first row is located in the shoulder region and two distinct rows across the can be seen. Dorsolaterally enlarged scales are present in some species of *Gonocephalus* from Sumatra, in particular *G. megalepis* (Bleeker, 1860), *G. klossi* Boulenger, 1920 and *G. lacunosus* Manthey and Denzer, 1991 but never in such a geometrical arrangement as can be found in the type specimen of *D. mjobergi*. Another feature in *D. mjobergi* is the possession of an enlarged platelike scale below the tympanum which is separated from the tympanum by two rows of small scales.

As already mentioned, *D. mjobergi* possesses two parallel longitudinal gular folds. No other *Gonocephalus* species possesses this particular character.

Both folds start on the distal part of the gular region approximately bordering the serrated edge in the middle line of the pouch. The outer one runs nearly parallel to the centre line of the gular pouch and continues onto the anterior part of the chest. It partially conceals the *Gonocephalus*-type typical transverse fold as seen in these lizards. The inner folds are shorter and curve inside towards the centre line. This feature is very similar to the longitudinal gular folds known from species of the genera *Ptyctolaemus* Peters, 1864 and *Mantheyus* Ananjeva and Stuart, 2001. Ananjeva and Stuart (2001) depict the gular region of the latter two genera. The arrangement and colouration in *D. mjobergi* is rather comparable to that in *Ptyctolaemus.* It consists of two rows (grayish white in alcohol) with dark colouration of the skin in between. This indicates that this character independently developed in *Ptyctolaemus*, *Mantheyus* and *D. mjobergi* and seems to be an autapomorphy. All three also lack a transverse gular fold present in *Gonocephalus*. However, *D. mjobergi* is by no means congeneric with either *Ptyctolaemus* or *Mantheyus*. Both genera *Ptyctolaemus* and *Mantheyus* have scaled tympani as opposed to *D. mjobergi*; additionally, *Mantheyus* has femoral pores. Within this cluster of genera (each of different tribe) only *D. mjobergi* shows oblique rows of enlarged dorsolateral scales. Because of the type specimen of *D. mjobergi* is a female it has been hypothesized that the gular sac will be even larger in male specimens which would distinguish it further from the genera discussed here with the exception of *Daraninagama robinsonii*; or:

9/ The genus *Bronchocela* Kaup, 1827 (including subgenus *Ferebronchocela subgen. nov.*) is defined and separated from other agamid genera as follows: No fold in front of the shoulder; lateral scales pointing backwards and downwards; ventral scales larger than latero-dorsals; fourth finger nearly the same length as the fifth toe or rarely longer; or:

10/ The genus *Complicitus* Manthey and Grossmann, 1997 includes a single species formerly placed within *Bronchocela* Kaup, 1827, but now monotypic in a separate genus. *Complicitus* is separated from *Bronchocela* by having a unique combination of lateral gular sac pockets and almost granular scutellation of the gular sac; or:

11/ The genus *Hypsicalotes* Manthey and Denzer, 2000 was defined by these authors in detail. The following diagnosis is adapted from their paper and is produced herein, noting that the placement of this genus within this tribe (and defined subtribe) is tentatitive. The monotypic genus *Hypsicalotes* Manthey and Denzer, 2000, known only from three specimens taken at Mt. Kinabalu, Sabah, Malaysia is thus defined as follows: A large species (up to 145 mm SVL), morphometrically similar to *Calotes* with medium sized hindlimbs (44% SVL) and tail (230% SVL); dorsal scales heterogeneous in size, form and arrangement, larger than ventrals; side of head below tympanum covered with an extremely enlarged plate approximately same size as orbit of eye (see Fig. 1 in Manthey and Denzer 2000); nuchal and dorsal crest clearly separated, present at least in males and continuing on tail; males with well developed gular pouch with long lanceolate scales along anterior edge (see Fig. 2 in Manthey and Denzer 2000); scales on gular pouch minute, heterogeneous in shape (oval to rhombic) and size; scalation on lower surface of head extremely heterogeneous in shape and size. Tail swollen behind base, posterior part strongly compressed.

Hypsicalotes differs from all other agamid genera (except *Hypsilurus* Peters, 1867) by the possession of large plates on both sides of head, heterogeneous, partly very large scalation on lower surface of head, by distinctive, lanceolate scales along midline of gular pouch of males as well as minute, mainly oval gular pouch scalation. It is expected that the plate on the sides of the head will be smaller in females as this is true for similar species such as *Hypsicalotes schultzewestrumi.* Additionally to all these characteristics it differs from the following genera as follows:

Calotes Cuvier, 1817 by heterogeneous, somewhat irregularly arranged dorsal scalation (vs homogeneous, regularly arranged dorsal scalation) and the separation of nuchal and dorsal crest in males (vs a continued vertebral crest);

Bronchocela Kaup, 1827 by absent lateral skinfolds on both sides of neck supported by hyoid apparatus (vs present), inhomogeneous, somewhat irregularly arranged dorsal scalation (vs homogeneous, regularly arranged dorsal scalation) and ventrals smaller than dorsals (vs ventrals larger than dorsals);

Complicitus Manthey and Grossmann, 1997 by absent lateral pockets on the gular pouch (vs present);

Dendragama Doria, 1888 by absent bony ridges on occipital region (vs present);

Lophocalotes Günther, 1872 by keeled subdigital scales (vs smooth subdigital scales);

Pseudocalotes Fitzinger, 1843 by the possession of a strongly developed nuchal crest consisting of scales in close neighbourhood (vs single standing scales or a poorly developed nuchal crest);

Pseudocophotis Manthey and Grossmann, 1997 by a present tympanum (vs absent), an absent prehensile tail (vs present), and absent erected superciliary scales (vs present);

As regards the large plates on both sides of head and throat, as well as lanceolate scales along midline of gular pouch *Hypsicalotes* reveals similarities to *Hypsilurus* Peters, 1867.

In *Hypsilurus schultzewestrumi* (Urban, 1999) from Papua New Guinea, plates on both sides of head and on ventral surface of head are also present (see Figs. 3-4 in Manthey and Denzer 2000). With the exception of tail length, additional morphometric data are similar to those of *Hypsicalotes*. Other undescribed and described *Hypsilurus* species only possess strongly enlarged scales on both sides of the head (e.g., *H. papuensis*) or lanceolate scales along median line of gular pouch are present (e.g., *H. dilophus* and *H. boydii*).

The development of the latter two characters are clearly evolutionary convergence in *Hypsicalotes* and *Hypsilurus*.

Hypsicalotes differs from *Hypsilurus* by the possession of hair-like sense organs (vs lens-like sense organs); a significantly larger dorsal scalation; an absent oblique fold when the gular pouch is adpressed (vs present, see fig. 4 in Manthey and Denzer 2000); equally sized scalation in the anterior and posterior part of the gular pouch (vs a different scalation in the anterior and posterior part of the gular pouch); or:

12/ The genus *Coryphophylax* Fitzinger, 1869 is separated from all other agamids by the following suite of characters: Tympanum distinct. Body compressed. Dorsal scales small, uniform or intermixed with enlarged ones. A dorsal crest, A strong transverse gular fold. Males with a gular sac. No praeanal or femoral pores. Supraciliary border normal. Enlarged scales scattered among the dorsals. Nuchal and dorsal crests subcontinuous. Limbs above with subequal scales; or:

13/ The genus *Aphaniotis* Peters, 1864 (including the subgenus *Proboscisagama subgen. nov.*) is defined by the following unique suite of characters: Body compressed, limbs very long and slender. Fifth toe much longer than first. All the scales keeled; the dorsals heterogeneous. A dorsal crest. Probably a gular pouch in the male. No gular fold. Ear concealed. No praeanal or femoral pores. (These seven genera namely *Gonocephalus* Kaup, 1825, *Doongagama gen. nov.*, *Bronchocela* Kaup, 1827 (including subgenus *Ferebronchocela subgen. nov.*), *Complicitus* Manthey and Grossmann, 1997, *Hypsicalotes* Manthey and Denzer, 2000, *Coryphophylax* Fitzinger, 1869 and *Aphaniotis* Peters, 1864 (including the subgenus *Proboscisagama subgen. nov.*) form the subtribe *Doongagamaiina subtribe nov.*).

Distribution: Southern and south-east Asia.

Content: *Pethiyagodaus gen. nov.; Ceratophora* Gray 1835; *Manamendraarachchius gen. nov.*; *Cophotis* Peters, 1861; *Pseudocophotis* Manthey and Grossmann, 1997; *Lyriocephalus* Merrem, 1820 (subtribe *Pethiyagodaiina subtribe nov.*); *Doongagama gen. nov.*; *Gonocephalus* Kaup, 1825; *Bronchocela* Kaup, 1827 (including subgenus *Ferebronchocela subgen. nov.*); *Complicitus* Manthey and Grossmann, 1997; *Hypsicalotes* Manthey and Denzer, 2000; *Coryphophylax* Fitzinger, 1869; *Aphaniotis* Peters, 1864 (including the subgenus *Proboscisagama subgen. nov.*) (subtribe *Doongagamaiina subtribe nov.*).

SUBTRIBE PETHIYAGODAIINA *SUBTRIBE NOV.*

(Terminal taxon: *Ceratophora aspera* Günther, 1864)

Herein referred to as: *Pethiyagodaus aspera* Günther, 1864)

Diagnosis: This subtribe is best defined by diagnosis of the component genera. Hence the subtribe consists of one or other of the following six:

1/ The genus *Ceratophora* Gray 1835 is diagnosed herein as follows: Tympanum hidden. Body more or less compressed, covered with unequal scales. No dorsal crest; a nuchal crest may be present or absent. No gular sac; no gular fold. A large rostral appendage, at least in the males. No femoral or praeanal pores. The gular scales larger than the ventrals, smooth or feebly keeled; lateral scales are large, equal or unequal; rostral appendage is either scaleless or scaly; or:

2/ *Pethiyagodaus gen. nov.* is readily separated from *Ceratophora* (both subgenera) (as defined above) and *Manamendraarachchius gen. nov.* as defined within this paper by having gular scales smaller than the ventrals, strongly keeled; lateral scales small; rostral appendage scaly. It is separated from all other *Ceratophora sensu lato* by the presence of a visible and palpable squamosal process (absent in all *Ceratophora sensu lato* other species); or:

3/ *Manamendraarachchius gen. nov.* (type species being *M. karu* Pethiyagoda and Manamendra-Arachchi, 1988) are separated from all other *Ceratophora sensu lato* (as defined above) (except *C.* (*Jamesschulteus*) *tennentii* and *Pethiyagodaus aspera*) by the rostral appendage being complex, comprising more scales than rostral scale alone (vs. rostral appendage restricted to rostral scale alone in *C. erdeleni* and *C. stoddartii*). It is distinguished from *C.* (*Jamesschulteus*) *tennentii* by the presence of prominent superciliary scales, versus absent in *C.* (*Jamesschulteus*) *tennentii*) and from *Pethiyagodaus aspera* by the absence of a palpable squamosal process versus squamosal process present in *P. Aspera*; or:

4/ *Cophotis* Peters, 1861 is defined by the following suite of characters: Mouth large; teeth erect in both jaws. Incisors small and conical. No praeanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895); tympanum hidden. Five toes. A dorsal crest: tail prehensile. Body compressed, covered with large subequal irregular scales. A very small gular sac in both sexes; a slight transverse gular fold; or:

5/ *Pseudocophotis* Manthey and Grossmann, 1997 is defined as for the genus *Cophotis* Peters, 1861 (diagnosed above), but separated from it by the following suite of characters: A rostral appendage consisting of a small pointed horn-like scale; a fringe of elongated scales along the supraciliary edge. Nuchal crest composed of nine larger and several smaller lobes; dorsal crest composed of eighteen lobes; the crest extends on more than three fourths of the length of the tail. Caudal scales as large ventrally as dorsally. Body and tail with broad brown cross bands. Head marmorated with brown, or:

6/ *Lyriocephalus* Merrem, 1820 is defined by the following suite of characters: Mouth large; teeth erect in both jaws. Incisors small and conical. No praeanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895); tympanum hidden. Five toes. A dorsal crest; a V-shaped gular fold; a bony supraorbital arch. Body compressed, covered with small scales intermixed with enlarged ones. A nuchal and a dorsal crest. A gular sac and a V-shaped gular fold. Adult with a globular hump on the nose.

Pre and post-orbital bones forming an arch limiting a supraorbital fossa.

Distribution: Southern and South-east Asia.

Content: *Pethiyagodaus gen. nov.*; *Ceratophora* Gray 1835; *Manamendraarachchius gen. nov.*; *Cophotis* Peters, 1861; *Pseudocophotis* Manthey and Grossmann, 1997; *Lyriocephalus* Merrem, 1820.

SUBTRIBE DOONGAGAMAIINA *SUBTRIBE NOV.*
(Terminal taxon: *Gonocephalus mjobergi* Smith, 1925)

Identified herein as *Doongagama mjobergi* (Smith, 1925)

Diagnosis: This subtribe is best defined by diagnosis of the seven component genera. Hence the subtribe consists of one or other of the following seven:

1/ *Gonocephalus* Kaup, 1825 is defined as follows: Tympanum distinct. Body compressed. Dorsal scales small, uniform or intermixed with enlarged ones. A dorsal crest, A strong transverse gular fold. Males with a gular sac. No praeanal or femoral pores. Basal scales are adjacent to the nuchal and dorsal crests, a transverse gular fold, a sharp canthus rostralis and an “angled” supraciliary ridge; or:

2/ *Doongagama gen. nov.* (monotypic for the species *Doongagama mjobergi* Smith, 1925), are separated from all species of *Gonocephalus* and *Daraninagama gen. nov.* (within the tribe Daraninagamaiini *tribe nov.*) as defined within this paper by the unique presence of two parallel longitudinal gular folds, a trait seen in none of the other species.

In more detail the genus *Doongagama gen. nov.* is defined as follows: A feature clearly distinguishing *D. mjobergi* from all other *Gonocephalus* is the possession of enlarged dorsolateral scales forming oblique rows. The first row is located in the shoulder region and two distinct rows across the can be seen. Dorsolaterally enlarged scales are present in some species of *Gonocephalus* from Sumatra, in particular *G. megalepis* (Bleeker, 1860), *G. klossi* Boulenger, 1920 and *G. lacunosus* Manthey and Denzer, 1991 but never in such a geometrical arrangement as can be found in the type specimen of *D. mjobergi*. Another feature in *D. mjobergi* is the possession of an enlarged platelike scale below the tympanum which is separated from the tympanum by two rows of small scales.

As already mentioned, *D. mjobergi* possesses two parallel longitudinal gular folds. No other *Gonocephalus* species possesses this particular character.

Both folds start on the distal part of the gular region approximately bordering the serrated edge in the middle line of the pouch. The outer one runs nearly parallel to the centre line of the gular pouch and continues onto the anterior part of the chest. It partially conceals the *Gonocephalus*-type typical transverse fold as seen in these lizards. The inner folds are shorter and curve inside towards the centre line. This feature is very similar to the longitudinal gular folds known from species of the genera *Ptyctolaemus* Peters, 1864 and *Mantheyus* Ananjeva and Stuart, 2001. Ananjeva and Stuart (2001) depict the gular region of the latter two genera. The arrangement and colouration in *D. mjobergi* is rather comparable to that in *Ptyctolaemus.* It consists of two rows (grayish white in alcohol) with dark colouration of the skin in between. This indicates that this character independently developed in *Ptyctolaemus*, *Mantheyus* and *D. mjobergi* and seems to be an autapomorphy. All three also lack a transverse gular fold present in *Gonocephalus*. However, *D. mjobergi* is by no means congeneric with either *Ptyctolaemus* or *Mantheyus*. Both genera *Ptyctolaemus* and *Mantheyus* have scaled tympani as opposed to *D. mjobergi*; additionally, *Mantheyus* has femoral pores. Within this cluster of genera (each of different tribe) only *D. mjobergi* shows oblique rows of enlarged dorsolateral scales. Because of the type specimen of *D. mjobergi* is a female it has been hypothesized that the gular sac will be even larger in male specimens which would distinguish it further from the genera discussed here with the exception of *Daraninagama robinsonii*; or:

3/ The genus *Bronchocela* Kaup, 1827 (including subgenus *Ferebronchocela subgen. nov.*) is defined and separated from other agamid genera as follows: No fold in front of the shoulder; lateral scales pointing backwards and downwards; ventral scales larger than latero-dorsals; fourth finger nearly the same length as the fifth toe or rarely longer; or:

4/ The genus *Complicitus* Manthey and Grossmann, 1997 includes a single species formerly placed within *Bronchocela* Kaup, 1827, but now monotypic in a separate genus. *Complicitus* is separated from *Bronchocela* by having a unique combination of lateral gular sac pockets and almost granular scutellation of the gular sac; or:

5/ The genus *Hypsicalotes* Manthey and Denzer, 2000 was defined by these authors in detail. The following diagnosis is adapted from their paper and is produced herein, noting that the placement of this genus within this tribe (and defined subtribe) is tentatitive. The monotypic genus *Hypsicalotes* Manthey and Denzer, 2000, known only from three specimens taken at Mt. Kinabalu, Sabah, Malaysia is thus defined as follows: A large species (up to 145 mm SVL), morphometrically similar to *Calotes* with medium sized hindlimbs (44% SVL) and tail (230% SVL); dorsal scales heterogeneous in size, form and arrangement, larger than ventrals; side of head below tympanum covered with an extremely enlarged plate approximately same size as orbit of eye (see Fig. 1 in Manthey and Denzer 2000); nuchal and dorsal crest clearly separated, present at least in males and continuing on tail; males with well developed gular pouch with long lanceolate scales along anterior edge (see Fig. 2 in Manthey and Denzer 2000); scales on gular pouch minute, heterogeneous in shape (oval to rhombic) and size; scalation on lower surface of head extremely heterogeneous in shape and size. Tail swollen behind base, posterior part strongly compressed.

Hypsicalotes differs from all other agamid genera (except *Hypsilurus* Peters, 1867) by the possession of large plates on both sides of head, heterogeneous, partly very large scalation on lower surface of head, by distinctive, lanceolate scales along midline of gular pouch of males as well as minute, mainly oval gular pouch scalation. It is expected that the plate on the sides of the head will be smaller in females as this is true for similar species such as *Hypsicalotes schultzewestrumi*. Additionally to all these characteristics it differs from the following genera as follows:

Calotes Cuvier, 1817 by heterogeneous, somewhat irregularly arranged dorsal scalation (vs homogeneous, regularly arranged dorsal scalation) and the separation of nuchal and dorsal crest in males (vs a continued vertebral crest).

Bronchocela Kaup, 1827 by absent lateral skinfolds on both sides of neck supported by hyoid apparatus (vs present), inhomogeneous, somewhat irregularly arranged dorsal scalation (vs homogeneous, regularly arranged dorsal scalation) and ventrals smaller than dorsals (vs ventrals larger than dorsals).

Complicitus Manthey and Grossmann, 1997 by absent lateral pockets on the gular pouch (vs present).

Dendragama Doria, 1888 by absent bony ridges on occipital region (vs present).

Lophocalotes Günther, 1872 by keeled subdigital scales (vs smooth subdigital scales).

Pseudocalotes Fitzinger, 1843 by the possession of a strongly developed nuchal crest consisting of scales in close neighbourhood (vs single standing scales or a poorly developed nuchal crest).

Pseudocophotis Manthey and Grossmann, 1997 by a present tympanum (vs absent), an absent prehensile tail (vs present), and absent erected superciliary scales (vs present).

As regards the large plates on both sides of head and throat, as well as lanceolate scales along midline of gular pouch *Hypsicalotes* reveals similarities to *Hypsilurus* Peters, 1867.

In *Hypsilurus schultzewestrumi* (Urban, 1999) from Papua New Guinea, plates on both sides of head and on ventral surface of head are also present (see Figs. 3-4 in Manthey and Denzer 2000). With the exception of tail length, additional morphometric data are similar to those of *Hypsicalotes*. Other undescribed and described *Hypsilurus* species only possess strongly enlarged scales on both sides of

the head (e.g., *H. papuensis*) or lanceolate scales along median line of gular pouch are present

(e.g., *H. dilophus* and *H. boydii*).

The development of the latter two characters are clearly evolutionary convergence in *Hypsicalotes* and

Hypsilurus.

Hypsicalotes differs from *Hypsilurus* by the possession of hair-like sense organs (vs lens-like sense organs); a significantly larger dorsal scalation; an absent oblique fold when the gular pouch is adpressed (vs present, see fig. 4 in Manthey and Denzer 2000); equally sized scalation in the anterior and posterior part of the gular pouch (vs a different scalation in the anterior and posterior part of the gular pouch); or:

6/ The genus *Coryphophylax* Fitzinger, 1869 is separated from all other agamids by the following suite of characters: Tympanum distinct. Body compressed. Dorsal scales small, uniform or intermixed with enlarged ones. A dorsal crest, A strong transverse gular fold. Males with a gular sac. No praeanal or femoral pores. Supraciliary border normal. Enlarged scales scattered among the dorsals. Nuchal and dorsal crests subcontinuous. Limbs above with subequal scales; or:

7/ The genus *Aphaniotis* Peters, 1864 (including the subgenus *Proboscisagama subgen. nov.*) is defined by the following unique suite of characters: Body compressed, limbs very long and slender. Fifth toe much longer than first. All the scales keeled; the dorsals heterogeneous. A dorsal crest. Probably a gular pouch in the male. No gular fold. Ear concealed. No praeanal or femoral pores.

Distribution: Mainly south-east Asia.

Content: *Doongagama gen. nov.*; *Gonocephalus* Kaup, 1825; *Bronchocela* Kaup, 1827 (including subgenus *Ferebronchocela subgen. nov.*); *Complicitus* Manthey and Grossmann, 1997; *Hypsicalotes* Manthey and Denzer, 2000; *Coryphophylax* Fitzinger, 1869; *Aphaniotis* Peters, 1864 (including the subgenus *Proboscisagama subgen. nov.*).

TRIBE JAPALURAIINI *TRIBE NOV.*

(Terminal taxon: *Japalura variegata* Gray, 1853)

Diagnosis: The tribe Japaluraiini *tribe nov.* is best defined by way of diagnosis of the two component genera. In other words the tribe consists of one of other of:

1/ *Japalura* Gray, 1853 (including the subgenus *Oriotiaris* Günther, 1864) is herein defined as follows: Tympanum hidden or unhidden. Body compressed. Dorsal scales heterogeneous. A dorsal crest. Gular pouch small or absent. An oblique fold in front of the shoulder; gular fold present or absent. Tail feebly compressed. No praeanal or femoral pores. An enlarged subocular scale row is absent, or if present is not large enough to cover the space between the supralabials and orbit, thus a moderately enlarged row and one or two smaller rows are present. *Diploderma* Hallowell, 1861 is separated from *Japalura* by having the third and fourth fingers of equal length and only seven upper labials. *Maxhoseragama gen. nov.* are readily separated from *Japalura* (the genus in which it was previously placed) and *Diploderma* by the following suite of characters: having infracaudal scales larger than ventrals; the third and fourth fingers of equal length; does not have seven upper labials. Furthermore this genus is separated from *Japalura* by the fact that an enlarged subocular scale row is present and prominent or at least moderately so; or:

2/ The genus *Ptyctolaemus* Peters, 1864 (including the subgenus *Mindatagama subgen. nov.*) is diagnosed as follows: The most obvious character that distinguishes the genus *Ptyctolaemus* from other genera of the subfamily Draconinae (*sensu* Macey *et al.* 2000) or Group V agamids (*sensu* Moody 1980) of mainland southeast Asia is that the male *Ptyctolaemus* have longitudinal gular folds on either side of the midline with the posterior portion of the folds curving medially on each side of the throat. However, these folds are only evident when the gular pouch is in a relaxed position (as seen in preserved specimens). The folds are formed when the gular pouch is relaxed in an accordion-like fashion, the folds become more pronounced because the scales within the folds are darkly pigmented.

The only other southeast Asian genus with gular folds is *Mantheyus* Ananjeva and Stuart, 2001; however it has rounded “U”-shaped folds encompassing the gular sac.

Mantheyus, monotypic for *M. phuwuanensis* also differs from *Ptyctolaemus* and all other draconines by the presence of femoral pores (Ananjeva and Stuart 2001).

The species *Ptyctolaemus collicristatus* Schulte and Vindum, 2004 (subgenus *Mindatagama subgen. nov.*) can be distinguished from *P. gularis* (subgenus *Ptyctolaemus*) by having a more prominent nuchal crest comprised of larger, flattened, triangular, scales, consisting of fewer scales in adult males (15-16 versus 17-30 scales); a shorter tail, with an average Tail length:SVL ratio of 1.99 versus 2.24; stouter and shorter limbs; and more heterogeneity among dorsal and lateral scales.

Distribution: Southern Asia.

Content: *Japalura* Gray, 1853; *Ptyctolaemus* Peters, 1864.

TRIBE *LOPHOCALOTESIINI TRIBE NOV.*

(Terminal taxon: *Calotes Ludekingi* Bleeker, 1860)

(Now usually referred to as: *Lophocalotes ludekingi* (Bleeker, 1860)

Diagnosis: The tribe is monotypic for the genus *Lophocalotes* Günther, 1872, which is in turn monotypic for the species *Lophocalotes ludekingi* (Bleeker, 1860). All three are readily separated from all other agamids by the following suite of characters: Mouth large; teeth erect in both jaws. Incisors small and conical. No true preanal or femoral pores (as opposed to the callous pore-like swelling of the preanal scales of the males in the genera *Agama* Daudin, 1802, *Uromastix* Merrem, 1820 and *Xenagama* Boulenger, 1895). Tympanum large and distinct. Body compressed, covered with large subequal keeled scales. A dorsal crest. No gular sac; a transverse gular fold. Digits are not keeled inferiorly, these being smooth subdigital lamellae on fingers and toes. The head is large and expanded below the ears.

Distribution: Highlands of central west Sumatra.

Content: *Lophocalotes* Günther, 1872.

TRIBE PHOXOPHRYIINI *TRIBE NOV.*

(Terminal taxon: *Phoxophrys tuberculata* Hubrecht, 1881)

Diagnosis: Phoxophryiini *tribe nov.* are separated from all other agamids by the following unique suite of characters: Mouth large; teeth erect in both jaws. Incisors small and conical. No true praeanal or femoral pores. No dorsal crest; tympanum hidden. Back and sides covered with small smooth scales, intermixed with larger keeled ones, and with very large multicarinate conical tubercles. A row of longer crest-scales above the eye. Upper surface of head covered with conical tubercles.

Distribution: Sumatra and Borneo only.

Content: *Phoxophrys* Hubrecht, 1881 (including the three subgenera as identified within this paper).

TRIBE MANTHEYIINI *TRIBE NOV.*

(Terminal taxon: *Ptyctolaemus phuwuanensis* Manthey and Nabhitabhata, 1991)

Diagnosis: Mantheyiini *tribe nov.* monotypic for the genus *Mantheyus* Ananjeva and Stuart, 2001 and monotypic for the species *M. phuwuanensis* Manthey and Nabhitabhata, 1991 differs from the morphologically similar *Ptyctolaemus* Peters, 1864 and all other draconines by the presence of femoral pores, and from all other agamids by having the combination of femoral pores and haired skin sense organs.

Distribution: North eastern Thailand and west central Laos.

Content: *Mantheyus* Ananjeva and Stuart, 2001.

TRIBE *DENDRAGAMAIINI TRIBE NOV.*

(Terminal taxon *Dendragama boulengeri* Doria, 1888)

Diagnosis: Dendragamaiini *tribe nov.* is defined as follows: Body compressed; covered with equal or slightly unequal scales. Tympanum distinct; a slight dorsal crest; a gular sac; no fold across the throat; no fold in front of the shoulder; no preanal or femoral pores. Further details of the diagnostics of the relevant species within the genus (as an added part of this diagnosis) are in de Rooij (1915) available on the internet.

Distribution: Java and Sumatra (Indonesia) only.

Content: *Dendragama* Doria, 1888.

CONFLICT OF INTEREST

This author reports no conflict of interest in terms of any material within this paper.

Species list for the Subfamily Draconinae Fitzinger, 1826.

Tribe Dracoiini *tribe nov.*

Genus *Draco* Linnaeus, 1758.

Subgenus *Draco* Linnaeus, 1758.

Draco (*Draco*) *volans* Linnaeus, 1758 (type species);
D. (*Draco*) *affinis* Bartlett, 1895;
D. (*Draco*) *boschmai* Hennig, 1936;
D. (*Draco*) *cornutus* Günther, 1864;
D. (*Draco*) *cyanopterus* Peters, 1867;
D. (*Draco*) *guentheri* Boulenger, 1885;
D. (*Draco*) *jareckii* Lazell, 1992;
D. (*Draco*) *ornatus* (Gray, 1845);
D. (*Draco*) *palawanensis* McGuire and Alcala, 2000;
D. (*Draco*) *quadrasi* Boettger, 1893;
D. (*Draco*) *reticulatus* Günther, 1864;
D. (*Draco*) *spilopterus* (Wiegmann, 1834);
D. (*Draco*) *sumatranus* Schlegel, 1844;
D. (*Draco*) *timorensis* Kuhl, 1820.

Subgenus *Macguiredraco subgen. nov.*

Draco (*Macguiredraco*) *bourouniensis* Lesson, 1834 (type species);
D. (*Macguiredraco*) *beccarii* Peters and Doria, 1878;
D. (*Macguiredraco*) *biaro* Lazell, 1987;
D. (*Macguiredraco*) *caerulhians* Lazell, 1992;
D. (*Macguiredraco*) *iskandari* McGuire, Brown, Mumpini, Riyanto and Andayani, 2007;
D. (*Macguiredraco*) *rhytisma* Musters, 1983;
D. (*Macguiredraco*) *spilonotus* Günther, 1872;
D. (*Macguiredraco*) *supriatnai* McGuire, Brown, Mumpini, Riyanto and Andayani, 2007;
D. (*Macguiredraco*) *walkeri* Boulenger, 1891.

Subgenus *Somniadraco subgen. nov.*

Draco (*Somniadraco*) *blanfordii* Blanford, 1878 (type species);
D. (*Somniadraco*) *formosus* Boulenger, 1900;
D. (*Somniadraco*) *haematopogon* Gray, 1831;
D. (*Somniadraco*) *indochinensis* Smith, 1928;
D. (*Somniadraco*) *obscurus* Boulenger, 1887;
D. (*Somniadraco*) *maximus* Boulenger, 1893;
D. (*Somniadraco*) *melanopogon* Boulenger, 1887;
D. (*Somniadraco*) *mindanensis* Stejneger, 1908;
D. (*Somniadraco*) *norvillii* Alcock, 1895;
D. (*Somniadraco*) *quinquefasciatus* Hardwicke and Gray, 1827;
D. (*Somniadraco*) *taeniopterus* Günther, 1861.

Subgenus *Rhacodracon* Fitzinger, 1843.

Draco (*Rhacodracon*) *fimbriatus* Kuhl, 1820 (type species);
D. (*Rhacodracon*) *abbreviatus* Hardwicke and Gray, 1827;
D. (*Rhacodracon*) *cristatellus* Günther, 1872.

Subgenus *Dracontoides* Fitzinger, 1843.

Draco (Dracontoides) *lineatus* Daudin, 1802 (monotypic).

Subgenus *Pterosaurus* Fitzinger, 1843.

Draco (*Pterosaurus*) *dussumieri* Duméril and Bibron, 1837 (monotypic).

Subgenus *Philippinedraco subgen. nov.*

Draco (*Philippinedraco*) *bimaculatus* Günther, 1864 (monotypic).

Subgenus *Engannodraco subgen. nov.*
Draco (*Engannodraco*) *modiglianii* Vinciguerra, 1892 (monotypic).

Subgenus *Spottydraco subgen. nov.*
Draco (*Spottydraco*) *maculatus* (Gray, 1845) (type species);
D. (*Spottydraco*) *divergens* Taylor, 1934;
D. (*Spottydraco*) *haasei* Boettger, 1893;
D. (*Spottydraco*) *whiteheadi* Boulenger, 1900.

Tribe Maxhoseragamiini *tribe nov.*

Subtribe Maxhoseragamaiina *subtribe nov.*

Genus *Maxhoseragama gen. nov.*
Subgenus *Maxhoseragama subgen. nov.*

Maxhoseragama (*Maxhoseragama*) *splendida* (Barbour and Dunn, 1919) (type species);
M. (*Maxhoseragama*) *batangensis* (Li, Deng, Wu and Wang, 2001);
M. (*Maxhoseragama*) *brevicauda* (Manthey, Denzer, Hou and Wang, 2012);
M. (*Maxhoseragama*) *chapaensis* (Bourret, 1937);
M. (*Maxhoseragama*) *dymondi* (Boulenger, 1906);
M. (*Maxhoseragama*) *fasciata* (Mertens, 1926);
M. (*Maxhoseragama*) *flaviceps* (Barbour and Dunn, 1919);
M. (*Maxhoseragama*) *grahami* (Stejneger, 1924);
M. (*Maxhoseragama*) *hamptoni* (Smith, 1935);
M. (*Maxhoseragama*) *micangshanensis* (Song, 1987);

M. (*Maxhoseragama*) *varcoae* (Boulenger, 1918);

M. (*Maxhoseragama*) *yulongensis* (Manthey, Denzer, Hou and Wang, 2012);

M. (*Maxhoseragama*) *yunnanensis* (Anderson, 1878);

M. (*Maxhoseragama*) *zhaoermii* (Goa and Hou, 2002).

Subgenus *Eksteinagama subgen. nov.*

Maxhoseragama (*Eksteinagama*) *swinhonis* (Günther, 1864) (type species);

M. (*Eksteinagama*) *brevipes* (Gressitt, 1936);

M. (*Eksteinagama*) *luei* (Ota, Chen and Shang, 1998);

M. (*Eksteinagama*) *makii* (Ota, 1989).

Genus *Notacalotes gen. nov.*

Notacalotes andamanensis (Boulenger, 1891) (monotypic).

Genus *Pseudocalotes* Fitzinger, 1843.

Subgenus *Pseudocalotes* Fitzinger, 1843.

Pseudocalotes (*Pseudocalotes*) *tympanistriga* (Gray, 1831) (type species);

P. (*Pseudocalotes*) *dringi* Hallermann and Böhme, 2000;

P. (*Pseudocalotes*) *flavigula* (Smith, 1924);

P. (*Pseudocalotes*) *larutensis* Hallermann and McGuire, 2001;

P. (*Pseudocalotes*) *saravacensis* Inger and Stuebing, 1994;

P. (*Pseudocalotes*) *sumatrana* (Hubrecht, 1879).

Subgenus *Paracalotes* Bourret, 1939.

Pseudocalotes (*Paracalotes*) *poilani* (Bourret, 1939) (type species);

P. (*Paracalotes*) *brevipes* (Werner, 1904);

P. (*Paracalotes*) *floweri* (Boulenger, 1912);

P. (*Paracalotes*) *kakhienensis* (Anderson, 1879);

P. (*Paracalotes*) *khaonanensis* Chan-ard, Cota, Makchai and Laoteow, 2008;

P. (*Paracalotes*) *kingdonwardi* (Smith, 1935);

P. (*Paracalotes*) *microlepis* (Boulenger, 1888);

P. (*Paracalotes*) *poilani* (Bourret, 1939);

P. (*Paracalotes*) *ziegleri* Hallermann, Truong, Orlov and Ananjeva, 2010.

Subgenus *Mictopholis* Smith, 1935.

Pseudocalotes (*Mictopholis*) *austeniana* (Annandale, 1908).

Subtribe Sitanaiina *subtribe nov.*

Genus *Sitana* Cuvier, 1829.

Sitana ponticeriana Cuvier, 1829 (type species);

S. fusca Schleich and Kästle, 1998;

S. schleichi Anders and Kästle, 2002;

S. sivalensis Schleich, Kästle and Shah, 1998.

Genus *Otocryptis* Wagler, 1830.

Otocryptis wiegmanni Wagler, 1830 (monotypic).

Subtribe Acanthosauriina *subtribe nov.*

Genus *Acanthosaura* Gray, 1831.

Acanthosaura armata (Gray, 1827) (type species);

A. bintangensis Wood, Grismer, Grismer, Ahmad, Onn and Bauer, 2009;

A. brachypoda Ananjeva, Orlov, Nguyen and Ryabov, 2011;

A. capra Günther, 1861;

A. cardamomensis Wood, Grismer, Grismer, Neang, Chav and Holden, 2010;

A. coronata Günther, 1861;

A. crucigera Boulenger, 1885;

A. lepidogaster (Cuvier, 1829);

A. nataliae Orlov, Truong and Sang, 2006;

A. titiwangsaensis Wood, Grismer, Grismer, Ahmad, Onn and Bauer, 2009.

Genus *Oriocalotes* Günther 1864.

Oriocalotes paulus Smith, 1935 (monotypic).

Subtribe Saleaiina *subtribe nov.*

Genus *Salea* Gray, 1845.

Subgenus *Salea* Gray, 1845.

Salea horsfieldii Gray, 1845 (type species);

S. gularis Blyth, 1854 (added tentatively).

Subgenus *Lophosalea* Beddome, 1878.

Salea (*Salea*) *anamallayana* (Beddome, 1878) (monotypic).

Tribe Crottyagamiini *tribe nov.*

Genus *Crottyagama gen. nov.*

Subgenus *Crottyagama gen. nov.*

Crottyagama (*Crottyagama*) *mystaceus* (Duméri and Bibron, 1837) (type species);

C. (*Crottyagama*) *bachae* (Hartmann, Geissler, Poyarkov, Ihlow, Galoyan, Rodder and Bohme, 2013).

Subgenus *Freudcalotes subgen. nov.*

Crottyagama (*Freudcalotes) emma* (Gray, 1845) (type species);

C. (*Freudcalotes) chincollium* (Vindum, 2003).

Subgenus *Khasicalotes subgen. nov.*

Crottyagama (*Khasicalotes) jerdoni* (Günther, 1870) (monotypic).

Subgenus *Amboncalotes subgen. nov.*

Crottyagama (*Amboncalotes*) *nigriplicatus* (Hallermann, 2000) (monotypic).

Genus *Skrijelus gen. nov.*

Skrijelus rouxii (Duméri and Bibron, 1837) (type species);

S. ellioti (Günther, 1864).

Genus *Calotes* Daudin, 1802.

Subgenus *Calotes* Daudin, 1802.

Calotes (*Calotes*) *calotes* (Linnaeus, 1758) (type species);

C. (*Calotes*) *htunwini* Zug and Vindum, 2006.

Subgenus *Rubercalotes subgen. nov.*

Calotes (*Rubercalotes*) *versicolor* (Daudin, 1802) (type species);

C. (*Rubercalotes*) *bhutanensis* Biswas, 1975;

C. (*Rubercalotes*) *irawadi* Zug, Brown, Schulte and Vindum, 2006;

C. (*Rubercalotes*) *maria* Gray, 1845;

C. (*Rubercalotes*) *medogensis* Zhao and Li, 1984.

Subgenus *Ghatscalotes subgen. nov.*

Calotes (*Ghatscalotes*) *nemoricola* Jerdon, 1853 (type species);

C. (*Ghatscalotes*) *grandisquamis* Günther, 1875.

Subgenus *Laccadivecalotes subgen. nov.*

Calotes (*Laccadivecalotes*) *nigrilabris* Peters, 1860 (type);

C. (*Laccadivecalotes*) *desilvai* Bahir and Maduwage, 2005;

C. (*Laccadivecalotes*) *liolepis* Boulenger, 1885.

Subgenus *Ceyloncalotes subgen. nov.*

Calotes (*Ceyloncalotes*) *liocephalus* Günther, 1872 (type species);

C. (*Ceyloncalotes*) *ceylonensis* Müller, 1887;

C. (*Ceyloncalotes*) *pethiyagodai* Amarasinghe, Karunarathna and Hallermann, 2014.

Subgenus *Tamilnaducalotes subgen. nov.*

Calotes (*Tamilnaducalotes*) *aurantolabium* Krishnan, 2008 (monotypic).

Tribe Daraninagamaini *tribe nov.*

Genus *Daraninagama gen. nov.*

Daraninagama robinsonii (Boulenger, 1908) (monotypic).

Genus *Diploderma* Hallowell, 1861.

Diploderma polygonatum Hallowell, 1861 (monotypic).

Tribe *Pethiyagodaiini tribe nov.*

Subribe *Pethiyagodaiina subtribe nov.*

Genus *Pethiyagodaus gen. nov.*

Pethiyagodaus aspera (Günther, 1864) (monotypic).

Genus *Ceratophora* Gray 1835.

Subenus *Ceratophora* Gray 1835.

Ceratophora (*Ceratophora*) *stoddartii* Gray, 1834 (type);

C. (*Ceratophora*) *erdeleni* Pethiyagoda and Manamendra-Arachchi, 1998.

Subgenus *Jamesschulteus* subgen. nov.

Ceratophora (*Jamesschulteus*) *tennentii* Günther, 1861 (monotypic).

Genus *Manamendraarachchius gen. nov.*

Manamendraarachchius karu (Pethiyagoda and Manamendra-Arachchi, 1988) (monotypic).

Genus: *Cophotis* Peters, 1861.

Cophotis ceylanica Peters, 1861 (type species);

Cophotis dumbara Samarawickrama, Ranawana, Rajapaksha, Ananjeva, Orlov, Ranasinghe and Samarawickrama, 2006.

Genus *Pseudocophotis* Manthey and Grossmann, 1997.

Pseudocophotis sumatrana (Hubrecht, 1879) (type species);

Pseudocophotis kontumensis Ananjeva, Orlov, Truong and Nazarov, 2007.

Genus *Lyriocephalus* Merrem, 1820.

Lyriocephalus scutatus (Linnaeus, 1758) (monotypic).

Subtribe *Doongagamaiina subtribe nov.*

Genus *Doongagama gen. nov.*

Doongagama mjobergi Smith, 1925 (monotypic).

Genus *Gonocephalus* Kaup, 1825.

Subgenus *Gonocephalus* Kaup, 1825.

Gonocephalus chamaeleontinus (Laurenti, 1768) (type);

Gonocephalus abbotti Cochran, 1922;

Gonocephalus doriae (Peters, 1871);

Gonocephalus kuhlii (Schlegel, 1848).

Subgenus *Dilophyrus* Gray, 1845.

Gonocephalus (*Dilophyrus*) *grandis* (Gray, 1845) (monotypic).

Subgenus *Honlamagama subgen. nov.*

Gonocephalus (*Honlamagama*) *sophiae* (Gray, 1845) (type species);

G. (*Honlamagama*) *interruptus* (Boulenger, 1885);

G. (*Honlamagama*) *semperi* (Peters, 1867).

Subgenus *Mantheyagama subgen. nov.*

Gonocephalus bornensis (Schlegel, 1848) (type species);

Gonocephalus beyschlagi (Boettger, 1892);

Gonocephalus bellii (Duméril and Bibron, 1837);

Gonocephalus liogaster (Günther, 1872).

Subgenus *Denzeragama subgen. nov.*

Gonocephalus (*Denzeragama*) *megalepis* (Bleeker, 1860) (type species);

G. (*Denzeragama*) *klossi* (Boulenger, 1920);

G. (*Denzeragama*) *lacunosus* Manthey and Denzer, 1991.

Genus *Bronchocela* Kaup, 1827.

Subgenus *Bronchocela* Kaup, 1827.

Bronchocela cristatella (Kuhl, 1820) (type species);

Bronchocela celebensis Gray, 1845;

Bronchocela danieli (Tiwari and Biswas, 1973);

Bronchocela harradineus sp. nov.;

Bronchocela hayeki (Müller, 1928);

Bronchocela marmorata Gray, 1845;

Bronchocela rubrigularis Hallermann, 2009;

Bronchocela smaragdina Günther, 1864;

Bronchocela vietnamensis Hallermann and Orlov, 2005.

Subgenus *Ferebronchocela subgen. nov.*

Bronchocela (*Ferebronchocela*) *jubata* (Duméril and Bibron, 1837) (type species);

B. (*Ferebronchocela*) *orlovi* Hallermann, 2004.

Genus *Complicitus* Manthey and Grossmann, 1997.

Complicitus nigrigularis (Ota and Hikida, 1991) (monotypic).

Genus *Hypsicalotes* Manthey and Denzer, 2000.

Hypsicalotes kinabaluensis (De Grijs, 1937) (monotypic).

Genus *Coryphophylax* Fitzinger, 1869.

Coryphophylax subcristatus (Blyth, 1860) (type species);

Coryphophylax brevicaudus Harikrishnan, Vasudevan, Chandramouli, Choudhury, Dutta and Das, 2012.

Genus *Aphaniotis* Peters, 1864.

Subgenus *Aphaniotis* Peters, 1864.

Aphaniotis fusca (Peters, 1864) (type species);

A. acutirostris Modigliani, 1889.

Subgenus *Proboscisagama subgen. nov.*

Aphaniotis (*Proboscisagama*) *ornata* (Lidth de Juede, 1893) (monotypic).

Tribe Japaluraiini *tribe nov.*

Genus *Japalura* Gray, 1853.

Subgenus *Japalura* Gray, 1853.

Japalura variegata Gray, 1853 (type for subgenus);

J. andersoniana Annandale, 1905;

J. otai Mahony, 2009;

J. planidorsata Jerdon, 1870;

J. sagittifera Smith, 1940.

Subgenus *Oriotiaris* Günther, 1864.

Japalura (*Oriotiaris*) *tricarinata* (Blyth, 1853) (type species);

J. (*Oriotiaris*) *dasi* (Shah and Kästle, 2002);

J. (*Oriotiaris*) *kumaonensis* (Annandale, 1907);

J. (*Oriotiaris*) *major* (Jerdon, 1870).

***Genus Ptyctolaemus* Peters, 1864.**

***Subgenus Ptyctolaemus* Peters, 1864.**

Ptyctolaemus gularis (Peters, 1864) (monotypic).

***Subgenus Mindatagama* subgen. nov.**

Ptyctolaemus (*Mindatagama*) *collicristatus* Schulte and Vindum, 2004 (monotypic).

Tribe *Lophocalotesiini tribe nov.*

Lophocalotes ludekingi (Bleeker, 1860) (monotypic).

Tribe Phoxophryiini *tribe nov.*

Genus *Phoxophrys* Hubrecht, 1881.

Subgenus *Phoxophrys* Hubrecht, 1881.

Phoxophrys (*Phoxophrys*) *tuberculata* Hubrecht, 1881 (monotypic).

Subgenus *Pelturagonia* Mocquard, 1890.

Phoxophrys (*Pelturagonia*) *cephalum* (Mocquard, 1890) (type)

P. (*Pelturagonia*) *borneensis* Inger, 1960;

P. (*Pelturagonia*) *nigrilabris* (Peters, 1864).

Subgenus *Olorenshawagama subgen. nov.*

Phoxophrys (*Olorenshawagama*) *spiniceps* Smith, 1925 (monotypic).

Tribe Mantheyiini *tribe nov.*

Genus *Mantheyus* Ananjeva and Stuart, 2001.

Mantheyus phuwuanensis Manthey and Nabhitabhata, 1991 (monotypic).

Tribe Dendragamaiini *tribe nov.*

Genus *Dendragama* Doria, 1888.

Dendragama boulengeri Doria, 1888.

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A review of the turtle genus *Pelochelys* Gray, 1864 (Trionychidae) including the division into two subgenera and the formal descriptions of two new species.

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ABSTRACT

This paper revises the taxonomy for the living turtles of the genus *Pelochelys*.
In line with well-defined morphological evidence, extant species from the Australasian region are placed in a new subgenus. Two regional and divergent forms of *Pelochelys cantorii* Gray, 1864 are also formally described and named herein as new species, these being the specimens from Kalimantan (Borneo) and those from the Ganges system of India and Bangladesh.

Keywords: Taxonomy; Australasia; Asia; Trionychidae; *Chitra*; *Pelochelys*; *cantorii; bibroni; signifera;* new subgenus; *Ferepelochelys*; new species; *clivepalmeri*; *telstraorum*.

INTRODUCTION

The Trionychid turtle genus *Pelochelys* Gray, 1864 has been known to science under this name for 150 years, with the first species within the genus described sometime earlier. That was *Trionyx* (*Gymnopus*) *bibroni* Owen, 1853.

For most of the intervening period, all species within the genus were referred to as the single species *Pelochelys cantorii* Gray, 1864, or more commonly under the earlier available name, *P. bibroni* Owen, 1853. However the most recent taxonomic treatment of the genus was that of Webb (2002), who recognized both Gray's *Pelochelys cantorii* Gray, 1864 and Owen's species, already recognized by earlier authors and placed in the same genus.

Webb (2002) also split the New Guinea species *bibroni* into two, these being the nominate form from south of the main cordillera and a newly described taxon from the north side, named as *Pelochelys signifera* Webb, 2002.

In terms of the southern and south-east Asian taxon, until now recognized by most authors as a single species, namely, *P. cantorii*, research has been hampered by several factors including the following: 1/ Difficulty in locating specimens for study on the basis of several factors including: A/ political instability and wars in relevant places where they may occir; B/ the habitat and habits of the species (i.e. bottom dwelling of crocodile-infested large rivers) making it relatively difficult to locate and catch and; C/ the common confusion with similar looking species, notably turtles of the genus *Chitra* Gray, 1844.

2/ Several synonyms in use for the species leading taxonomists to believe that any unrecognized forms probably already have available names, thereby leading them to look elsewhere for turtle groups to study for the purposes of naming new taxa.

3/ Ongoing confusion, caused by the literature giving inaccurate distribution information for the taxon, derived in part from erroneous and unchecked records, misinterpretation of data including the result being conclusions made that don't necessarily match the facts, as well as other similar issues.

The taxonomic confusion in terms of these turtles came to my attention in 1993 and in the nearly two decades post-dating that year I assembled a sizeable portfolio of data on the taxon *Pelochelys cantorii* Gray, 1864 including photos, records and the like from the entire known range of the taxon and including alleged marine records for the species as well. On 17 August 2011 this material was stolen (see below).

Noting that all regional forms of this taxon are threatened in some way, including being potentially endangered, I have opted to publish the following revision and scientific descriptions with a minimum of available data. The alternative of not doing so and taxa being unrecognized and potentially becoming extinct is not something I wish to entertain.

PELOCHELYS SENSU LATO

Until recently, all species within the genus were recognized as a single taxon, namely one or other of *P. bibroni* or *P. cantorii.* As mentioned already, Webb (2002) was the most recent author to change the taxonomy of the genus *Pelochelys* by dividing the New Guinea taxon, then widely recognized and known as *P. bibroni* (and excluding *P. cantorii* from west of Wallace's line). Webb's division was a north-south one with the central cordillera of the island being the dividing line of note. However this division was actually foreshadowed by Rhodin *et al.* (1993).

A number of authors, including Rhodin *et al.* (1993) have suggested a strong sea-water tolerance by *Pelochelys* species, but this is not supported by the evidence. Rhodin *et al.* (1993) conceded that the preferred habitat for the taxon was fresh-water river systems well away from estuarine habitats. See also Liem (1983), Liem and Haynes (1977) and Jones (1950). This is also the case for Asiatic *P. cantorii.*

The known riverine distribution for all *Pelochelys* species also indicates little salt-water tolerance. The physical evidence of the morphological differences between Asiatic *P. cantorii* and the New Guinea taxa indicates deep historical divergence. Noting this fact, the two following points are further noted.

The two New Guinea species were unable to regularly breach the sea-water barrier to the east of New Guinea along the coastline to intermingle as a single species in recent geological times. Secondly the Asiatic *P. cantorii* (as referred to by most recent authors to date) remains unknown from Java (Iskander 2004), and in spite of intensive searching of the island and is also not known to have ever been present in Sulawesi (see Webb 2002), which is also a heavily surveyed island. This being in spite of suitable riverine habitat there and a short physical distance from east Kalimantan (Borneo), where the taxon is relatively abundant and regularly seen. Of course, unlike the major islands from Borneo west to Asia, Sulawesi has no recent historical land bridge to Asia during recent glacial maxima.

Webb (2002) reports on a *Pelochelys* specimen sold in a market in Sulawesi, but this is not necessarily indicative of the taxon on the island, as it may potentially include any of several other factors such as an animal brought in from elsewhere or a vagrant found at sea as was apparently the case documented by Radhakrishnan and Badrudeen (1975).

The alleged marine record of Radhakrishnan and Badrudeen (1975) from southern India, was re-examined critically and found to be questionable in terms of the conclusion reached.

These authors asserted that because a specimen was trawled alive some 5 km offshore in Palk Bay, off Mandapam southern India, that their finding “proves beyond doubt that the species can tolerate the marine environment, as against the belief that it is purely a freshwater form.”

I subscribe that this finding does not in any way establish this fact.

Freshwater species are regularly washed to sea in floods and while then occurring in salt water and potentially being found alive there, invariably die within a relatively short time frame.

This is also exactly what happened to the specimen of *Pelochelys* found by these authors. In spite of their best efforts, the authors reported that their specimen refused all food offered and then died 14 days after capture.

In other words the animal was almost certainly very ill and in poor physical condition.

These facts indicate that the animal may have lost condition either as a result of the long-term sea-water immersion prior to capture, or alternatively, a lack of condition is what led to the animal being moved a considerable distance from the preferred habitat in the first instance.

What is however clear is that the animal in question was a non breeding specimen and not part of an established breeding population or an indication that the species regularly migrates across bodies of sea water.

The lack of salt-water tolerance demonstrated herein is relevant in terms of assessing the status of widely separated populations of *P. cantorii* with a view to assessing their taxonomy, nomenclature and in turn their long-term survival prospects, noting that some are found within the most (human) populated regions on earth. The distribution map for the genus *Chitra* Gray, 1844, as published by McCord and Pritchard (2002) is largely similar to that of that produced by Das (2008) for Asiatic *P. cantorii* (as referred to by most recent authors to date). While there are now known to be notable differences in terms of the Indonesian distribution with *Chitra* known from Java and Asiatic *P. cantorii* (as referred to by most recent authors to date) not known from there, the reverse for Kalimantan (Borneo) and alleged findings of subfossil *Chitra* remains on Sulawesi means that the significance of the maps is great.

Both maps demonstrate the restriction of modern living species in each genus to major river basins and an absence in the intervening regions.

Morphologically similar species within the genus *Chitra* have been split three ways in line with their main centres of distribution (as done by McCord and Pritchard in 2003). However for reasons not entirely clear, no such split has yet been done for the *P. cantorii* complex, even though the divisions are of near identical manner and each of the regional forms are sufficiently distinct as to warrant being placed in different species.

As a result of this anomaly and in order to resolve it, two regional forms, until now known as *P. cantorii* are hereby described as new species according to the Zoological Code (Ride *et al.* 1999).

The distributions of these newly named taxa are within large drainage regions separated by oceanic regions within enlarged river drainages as mapped out by Molengraaff (1921), Molengraaff and Weber (1921), Voris (2000) and sources cited therein according to the 120 metre sea depth level, which corresponded to the lowest approximate sea-level in recent ice-age maxima.

These drainage maps readily explain the modern distributions of these divergent forms.

Webb (2002), when publishing his description of the taxon, *P. signifera* Webb, 2002, detailed significant morphological differences between the two *Pelochelys* found east of Wallace’s Line versus *P. cantorii* as widely known from west of this biogeographical division.

In view of the facts that both eastern and western species are widely separated, likely to have been so for an extended geological time frame (as seen in the results of Sanders *et al.* 2010 for similarly separated fresh-water reptile species across the same geographical divide) and the obvious morphological differences between each species group the eastern taxa are formally placed in a separate subgenus, formally named for the first time.

The Australian fossil species *Murgonemys braithwaitei* White, 2001 is a significantly different Eocene taxon. Therefore that name is not available for the extant New Guinea taxa.

Pliocine/Pleistocine fossil and subfossil remains from Australia may or may not be attributable to the genus including the New Guinea taxa, until now known as *P. bibroni* and *P. signifera.*

While there are unconfirmed reports of *Pelochelys* from rivers in the Northern Territory of Australia, none have been caught and lodged in Australian museums to date.

The literature relevant to what is known about the species within the genus *Pelochelys* as defined to date, including relevant fossil taxa that have significant relationships to extant species include the following: Baur (1891), Bonin *et al.* (2006), Boulenger (1889, 1891), Brown *et al.* (2013), Chan-ard *et al.* (1999), Cogger and Zweifel (1998), Cox *et al.* (1998), Das (2008), Das and Maklarin (2006), de Rooij (1915), De Vis (1894), Diesmos *et al.* (2008), Ernst and Barbour (1989), Gaffney and Bartholomai (1979), Georges and Thomson (2006, 2010), Georges *et al.* (2008), Gray (1864), Iskander (2004), Jones (1950), Kowalski *et al.* (2011), Lehr and Holloway (2003), Liem (1983), Liem and Haynes (1977), Manthey and Grossmann (1997), McCord and Joseph-Ouni (2003), Meylan (1987), Molengraaff (1921), Molengraaff and Weber (1921), Murthy (2010), Owen (1853), Palot and Radhakrishnan (2011), Pauwels *et al.* (2003), Platt *et al.* (2008), Radhakrishnan and Badrudeen (1975), Rhodin *et al.* (1993), Riger *et al.* (2009), Rudolphi and Weser (1998), Sanders *et al.* (2010), Shiping *et al.* (2009), Smedley (1932), Vijaya (1982), Voris (2000), Waite (1903), Webb (1995, 1997, 2002) Xiao *et al.* (2013), Zhou and Li (2007) and sources cited therein.

As already mentioned, this genus, *Pelochelys* is closely allied to *Chitra* and specimens of each genus are regularly confused with one another by lay people. However *Pelochelys* may be readily distinguished from *Chitra* by the large and prominent orbits, which occupy a less anterior position on the skull.

THEFT OF MATERIALS TO IMPEDE SCIENCE AND WILDLIFE CONSERVATION

I note also the following: In 2006 an online petition sponsored by a group of animal-hating pseudoscientists including Wolfgang Wüster, Mark O’Shea, David John Williams, Bryan Fry and others posted at: http://www.aussiereptileclassifieds.com/phpPETITION (Hunter *et al.* 2006) called for my successful wildlife education business and all my other herpetological activity to be shut down by the government of Victoria, Australia. These men were successful in that after a ruthless five-year campaign, on 17 August 2011, 11 heavily armed police and wildlife officers conducted a highly illegal and violent raid on our family home and research facility. Myself, my wife and two young daughters were arrested at gunpoint and held captive in the kitchen of the house for nine hours while the facility was ransacked. Besides the unspeakable acts of killing captive snakes and criminal damage to cages and household goods, the raiding officers illegally shut down our business and effectively placed myself under house arrest at gunpoint for some months after the raid.

An application by myself to the Supreme Court of Victoria led to the re-opening of our unlawfully shut down wildlife education business, although much of the damage to the business and our reputation built up over more than 4 decades was irrepairable.

Of greater relevance here is that at the time of the raid, research files spanning more than 40 years were taken and never returned, including materials and records relevant to this paper.

Material taken included all the computers, disks, hard drives, backups, cameras, scientific literature and other forms of information and information storage at the facility. All were loaded into the back of a truck and trailer and carted off.

Faced with the dilemma of deciding whether to spend another forty years gathering data, by which time I may be dead from old age, being aged 52 as of 2014, or publishing the relevant paper/s with minimal data, I have opted to publish.

Underlying this motivation has been an increasing concern that a delay to formally identify and name undescribed biodiversity may lead to its extinction before another scientist gets around to the matter.

Engstrom *et al.* (2002) wrote: “The documentation of this diversity must be seen as an activity that is done not just for posterity but for immediate action and protection.”

A number of authors including Kaiser (2012a, 2012b, 2013 and 2014), Kaiser *et al.* (2013), Naish (2013) and Wüster *et al.* (2014), all part of the group of people effectively controlled by Wolfgang Wüster of Wales, UK, have been highly critical of the fact that I have assigned names to unnamed clades of snakes. Their unscientific and childish attacks, continued incessantly on social media such as Facebook and Twitter are rejected herein as destabilizing the nomenclature and impeding the progress of science.

Their ridiculous comments and false and defamatory statements are systematically rebutted by Hoser (2013).

I also note that many taxa formally named by myself for the first time in earlier publications (e.g. Hoser 2000a, 2000b) are in fact threatened species.

Therefore I note the sensible remarks of Engstrom *et al.* (2002) as a perfectly reasonable explanation for the publishing of taxon descriptions for such unnamed groups. This remains the case even if a sizeable amount of my original research, files, photos and data have been stolen and therefore cannot be relied upon and incorporated into these contemporary publications.

NOMENCLATURAL STATEMENT IN TERMS OF THE DESCRIPTIONS WITHIN THIS PAPER

Unless mandated by the zoological code, no names proposed within this paper should be amended in any way for the purposes of correction, gender change or the like. In terms of priority of names in the event of conflict, where more than one newly named taxon is deemed conspecific or within a single taxon group by a later author, the priority to be taken is by page priority, this meaning the first taxon described in full is the one to take precedent.

FEREPELOCHELYS SUBGEN. NOV.

Type species: *Trionyx* (*Gymnopus*) *bibroni* Owen, 1853.

Diagnosis: This subgenus differs from the nominate genus by the modal position of neural bone reversal (see also definitions by Meylan 1987 and Rhodin *et al.* 1993). In *Ferepelochelys subgen. nov.* this is at position 5/6, as opposed to being at 6 for *Pelochelys* from Asia (the nominate subgenus).

Furthermore all *Ferepelochelys gen. nov.* from New Guinea have 9 neurals (8 distinct bony elements, the fused first neural counting as 2) whereas in Asiatic *Pelochelys* may have 7, 8 or 9 neurals.

The two species within *Ferepelochelys subgen. nov.* are separated from *Pelochelys* species as follows:

Ferepelochelys signifera of northern New Guinea is separated from all other *Pelochelys* by the following suite of characters: Juvenile carapace smooth, except for low tubercles in nuchal region and longitudinal ridges over central bony disc area and covered with a distinct, dark pattern of close-set, small dots and markings; adult carapace uniformly brownish (no distinct pattern).

Ferepelochelys bibroni of southern New Guinea is separated from all other *Pelochelys* by the following suite of characters: Juveniles with overall rough-textured, tuberculate carapace; adults with yellow neck stripes and contrasting yellow markings on carapace.

By contrast *Pelochelys* species (grouped by most authors within the single species *cantorii*) are separated from *Ferepelochelys gen. nov.* by the following suite of characters:

Juvenile carapace smooth, except for low tubercles in nuchal region and longitudinal ridges over central bony disc area and lacking a distinct, close-set variegated pattern of dark markings, being mostly uniform brownish, but may have indistinct, pale spots; adult carapace uniformly brownish (no distinct pattern) (modified from Webb 2003).

Distribution: Known only from river drainages on the north side and south-side of island New Guinea.

Etymology: *Ferepelochelys* is in reference to these species being “not quite” *Pelochelys*.

PELOCHELYS CLIVEPALMERI SP. NOV.

Holotype: A skeletonised specimen number: BMNH 80.9.25.6, at the British Museum of Natural History, London, UK. The specimen was collected at “Koti’’ (equivalent to Kutai, 00.35 S, 117.17 E, Kalimantan Timur Province) within the Indonesian part of Borneo. This is a public facility that allows access to specimens by scientists.

Paratype: An adult specimen number: SP(P)285 at the Sabah Parks Zoological Museum, Kota Kinabalu, Sabah, Malaysia. It was collected at the junction of Sungei Kinarom and Sungei Serimsim, Sabah, Borneo, within a lowland rainforest, on 30 August 2001. This is a public facility that allows access to specimens by scientists.

Diagnosis: In the past *Pelochelys clivepalmeri sp. nov.* was identified as a variant of *P. cantorii.* However *Pelochelys clivepalmeri sp. nov.* is most readily separated from other *Pelochelys* species, including *P. cantorii* on the basis of colouration and other external features.

In *Pelochelys telstraorum sp. nov.* (from Bangladesh and India), described below the adult colouration is olive green with slightly darker dots, these darker dots being absent in *P. cantorii* and *P. clivepalmeri sp. nov.* or if present in these species are only prominent in the anterior part of the carapace and in subadult specimens. In *Pelochelys telstraorum sp. nov.* the neck and the head are lighter in colour with a distinct yellow tinge (as opposed to whitish-yellow in *P. cantorii* and *P. clivepalmeri sp. nov.*). The ventral side is whitish with a light-yellow tinge at angles. The plastron is whitish with light pink plastrol callosities.

P. cantorii adults have numerous closely placed raised tubercle-like structures on the upper anterior carapace. These are limited in number in widely scattered and of smaller size in both *Pelochelys telstraorum sp. nov.* and *P. clivepalmeri sp. nov.*. and can be used to separate the relevant species.

In *P. clivepalmeri sp. nov.* a noticeable light streak runs along both the upper and lower jaw as opposed to only on the lower jaw in *P. cantorii.*

Distribution: Known definitively only from eastern Kalimantan (Borneo). Thought to be the only *Pelochelys taxon* from Borneo.

Etymology: Named in honour of Australian politician Clive Palmer in recognition of his valiant attempts to shake up the duopoly of Liberal/Labor leadership of the country, which over many decades has descended into an evil culture of corruption and nepotism.

The shape of the carapace of the taxon also bears a passing similarity to Mr. Palmer’s physical shape (as of 2014).

PELOCHELYS TELSTRAORUM SP. NOV.

Holotype: A specimen number 1781 (skull only) in the herpetology collection lodged at the Museum of India 27, Jawaharlal Nehru Road, Park Street Area, Kolkata (Calcutta), West Bengal 700016, India, collected locally. This is a public facility that allows access to specimens by scientists.

Paratype: A specimen number 1886 (33a. A.S.B.) in the herpetology collection lodged at the Museum of India 27, Jawaharlal Nehru Road, Park Street Area, Kolkata (Calcutta), West Bengal 700016, India, collected locally. This is a public facility that allows access to specimens by scientists.

Diagnosis: In the past *Pelochelys telstraorum sp. nov.* was identified as a variant of *P. cantorii.* However *Pelochelys telstraorum sp. nov.* is most readily separated from other *Pelochelys* species, including *P. cantorii* on the basis of colouration and other external features.

In *Pelochelys telstraorum sp. nov.* the adult colouration is olive green with slightly darker dots, these darker dots being absent in *P. cantorii* and *P. clivepalmeri sp. nov.* or if present in these species are only prominent in the anterior part of the carapace and in subadult specimens. In *Pelochelys telstraorum sp. nov.* the neck and the head are lighter in colour with a distinct yellow tinge (as opposed to whitish-yellow in *P. cantorii* and *P. clivepalmeri sp. nov.*). The ventral side is whitish with a light-yellow tinge at angles. The plastron is whitish with light pink callosities.

P. cantorii adults have numerous raised tubercle-like structures on the upper anterior carapace. These are limited in number in widely scattered and of smaller size in both *Pelochelys telstraorum sp. nov.* and *P. clivepalmeri sp. nov.*.

Distribution: Known definitively only from the middle and lower Ganges River System in India/Bangladesh and nearby areas of the upper bay of Bengal in India and Bangladesh. Specimens retrieved from southern India appear to be of this taxon.

Etymology: Named in honour of the many Indian-based employees of the Australian company Telstra, in recognition for their efforts to sell Australians beneficial telecommunications services and make sense of complicated phone bills.

CONFLICT OF INTEREST

This author reports no conflict of interest in terms of any material within this paper.

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