

# **A significant improvement to the taxonomy of the gecko genus *Gekko* Laurenti, 1768 *sensu lato* to better reflect morphological diversity and ancient divergence within the group.**

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## **ABSTRACT**

The Asian gecko genus *Gekko* Laurenti, 1768 as recognized by most herpetologists in 2018 includes a significant array of sometimes large and spectacular species. About 60 described forms are currently recognized as species. However others await resurrection from synonymy or formal scientific description for the first time, meaning that as of 2018, species diversity is underestimated.

Various phylogenies published in the past decade (e.g. Heinicke *et al.* 2012, Pyron *et al.* 2013, Oliver *et al.* 2017) have shown the genus *Gekko* to be of ancient origin and other morphologically similar genera to place within the *Gekko* tree.

Even species within *Gekko sensu stricto* Heinicke *et al.* (2012) show divergence between taxa in excess of 50 MYA., while Oliver *et al.* (2017) claim divergences well in excess of 30 MYA.

Rather than merge dozens more disparate species into an even greater-sized genus, this paper is one of a series dividing the complex of genera into monophyletic species groups at the genus level based on divergence and morphology. The division of groups in this and other papers published at the same time dealing with the complex is extremely conservative relative to dates of divergence splits in other widely recognized reptile genera

This paper deals with the genus *Gekko* Laurenti, 1768 as currently recognized, excluding those species closely associated with the taxon originally described as *Gekko vittatus* Houttuyn, 1782, which is dealt with in another paper.

In summary the genus *Gekko* is herein split along lines similar to the species groups identified by Rösler *et al.* (2011), with the most divergent groups being treated as genera and subgenera. The result is 6 genera (including the *Gekko vittatus* Houttuyn, 1782 species group) and further subgenera.

Four genera and six subgenera are formally named for the first time according to the rules of the *International Code of Zoological Nomenclature* (Ride *et al.* 1999).

**Keywords:** Gecko; taxonomy; reptile; nomenclature; Asia; *Gekko*; *Luperosaurus*; *Pseudogekko*; *Lepidodactylus*; *Ptychozoon*; *Scelotretus*; new genus; *Sparsuscolotes*; *Lautusdigituscolotes*; *Magnaocellus*; *Extentusventersquamus*; New subgenus; *Sinogekko*; *Aurumgekko*; *Glanduliscrusgekko*; *Cavernagekko*; *Foderetdorsumgekko*.

## **INTRODUCTION**

The Asian gecko genus *Gekko* Laurenti, 1768 as recognized by most herpetologists in 2018 includes a significant array of sometimes large and spectacular species. About 60 described forms are currently recognized as species. However others await resurrection from synonymy or formal scientific description for the first time, meaning that species diversity of the genus as recognized is underestimated.

This paper arose out of a global audit of the planet's herpetofauna, including the geckos, with a view to correcting the genus-level classification in light of information that has emerged in the past century.

Since the publication of major texts by Boulenger and contemporaries at the end of the 1800's, much of the genus-

level taxonomy of the world's reptiles has not been changed or updated to better reflect phylogeny and divergences between groups of species.

To that end, various phylogenies published in the past decade (e.g. Heinicke *et al.* 2012 or Pyron *et al.* 2013) have shown the genus *Gekko* as recognized in 2018 to be of ancient origin and other morphologically similar genera to place within the *Gekko* tree.

Even within *Gekko sensu stricto* Heinicke *et al.* (2012) show divergence between taxa in excess of 50 MYA, while Oliver *et al.* (2017) claim divergences in excess of 30 MYA.

Rather than merge dozens more disparate species into an even greater-sized genus, this paper is one of a series dividing the

complex of genera into monophyletic species groups at the genus level based on divergence and morphology. The division of groups in this and other papers published at the same time dealing with the complex is extremely conservative relative to divergence splits in other reptile genera as recognized by most herpetologists in 2018.

This paper effectively deals with the genus *Gekko* Laurenti, 1768 as currently recognized, excluding those species closely associated with the taxon originally described as *Gekko vittatus* Houttuyn, 1782, which is dealt with in another paper.

That species group have also been associated with species in the putative genus *Luperosaurus* Gray, 1845, with it in fact not being particularly close to either the main *Gekko* or *Luperosaurus* lineages.

In summary the genus *Gekko* is herein split along lines similar to the species groups identified by Rösler *et al.* (2011), with the most divergent groups being treated as genera and subgenera. The result is approximately 6 genera and further subgenera. A number are formally named for the first time according to the rules of the *International Code of Zoological Nomenclature* (Ride *et al.* 1999).

#### MATERIALS, METHODS AND RESULTS

These are inferred in both the abstract and introduction, but as a matter of trite I spell them out in a little more explicit detail.

The available literature was examined relevant to the genus *Gekko*, as well as closely related genus groups, such as *Lepidodactylus* Fitzinger, 1843, *Luperosaurus* Gray, 1845, *Pseudogekko* Taylor, 1922 and *Ptychozoon* Kuhl and van Hasselt, 1822 as defined by most authors in the previous 200 years. Those putative genera are dealt with in papers published at the same time as this paper.

Additional to this has been inspection of specimens as required and possible in order to ascertain the classification of the genera and all known species within them.

Available information in the form of photos of specimens with good available data and other information was also utilized in this study.

As an intellectual exercise it was straight forward and while there is a vast body of available literature relied upon in terms of the conclusions herein, the final configuration of genera and species laid out herein can be effectively found in the more recent molecular studies such as Heinicke *et al.* (2012), Pyron *et al.* (2013) and Rösler *et al.* (2011).

Those studies effectively painted the road map for the genus level arrangement herein, which also happens to match the morphological divergences of each group and characters common to each.

*Gekko* Laurenti, 1768 *sensu lato* is split into six genera, including the *G. vittatus* group, which is placed in the genus *Scelotretus* Fitzinger, 1843. Four other genera are formally named for the first time according to the rules of the *International Code of Zoological Nomenclature* (Ride *et al.* 1999).

Further subgenera are also formally named for the first time.

During the course of this audit, I became aware of several undescribed species within *Gekko* Laurenti, 1768 *sensu lato* in the south-east Asian realm. I have however deferred naming any of these taxa as I was informed of others intending to name them and I respect their position.

The *International Code of Zoological Nomenclature* fourth edition (Ride *et al.* 1999) recommends such naming actions to be taken within 12 months of statement of intent.

While a vast body of literature was audited to confirm the genus-level arrangement herein, I only cite the most significant ones here as these alone adequately support the taxonomy within this paper.

Key sources relied upon to corroborate the split of *Gekko sensu lato* as done herein include the following: Anderson (1871), Auliya (2006), Bauer *et al.* (2008), Bobrov and Semenov (2008), Bonetti (2002), Boulenger (1885, 1886, 1887a, 1887b, 1907),

Brown (1902), Brown *et al.* (2008, 2009, 2011, 2012), Brown and Alcalá (1962, 1978), Das (2004), De Lisle *et al.* (2013), de Rooij (1915), Duméril and Bibron (1836), Fitzinger (1843), Gaulke (2010, 2011), Goris and Maeda (2004), Gray (1831, 1842, 1845), Grismer (2011), Grossmann (2004, 2006), Grossmann and Ulber (1990), Günther (1864, 1867, 1888), Günther (1994), Han *et al.* (2001), Heinicke *et al.* (2012), Hofmann (2009), Houttuyn (1782), Jono *et al.* (2015), Kluge (2001), Koch (2012), Koch *et al.* (2009), Kraus (2009), Laurenti, (1768), Lin and Yao (2016), Linkem *et al.* (2010), Linnaeus (1758), Luu *et al.* (2014, 2015, 2017), Manthey and Grossman (1997), Matsui and Okada (1968), McCoy (2006, 2015), Meiri *et al.* (2017), Mertens (1955), Ngo and Gamble (2010, 2011), Ngo *et al.* (2009, 2015), Nguyen *et al.* (2010a, 2010b, 2013), Okada and Okawa (1994), Okada (1956), Oliver and Huggall (2017), Oliver *et al.* (2017), Oshima (1912), Ota and Nabhitabhata (1991), Ota *et al.* (1991, 1995), Panitvong *et al.* (2010), Phung and Ziegler (2011), Pope (1928, 1935), Pyron *et al.* (2013), Ride *et al.* (1999), Rösler (2000, 2001, 2005a, 2005b, 2017), Rösler and Tiedemann (2007), Rösler *et al.* (2004, 2005, 2006, 2011, 2012), Russell (1979), Sang (2010), Sang *et al.* (2009), Schmidt (1927), Schneider (1979), Shang (2001), Shaw and Nodder (1992), Shcherbak and Nekrasova (1994), Sluiter (1893), Smedley (1931), Smith (1923a, 1923b, 1935), Song (1985), Stejneger (1907a, 1907b), Swinhoe (1863), Taylor (1919, 1922a, 1922b, 1925, 1944, 1962, 1963), Toda and Hikida (2011), Toda *et al.* (1997, 2001a, 2001b, 2008), Tytler (1865), Unterhössel (1902), Utsunomiya *et al.* (1996), Vesely (1999), Vogt (1922), Vogel (2014), Wermuth (1965), Woerdeman (1919), Yang (2015), Yang *et al.* (2012), Zhang (1986), Zhang *et al.* (2014), Zhao and Adler (1993), Zhou and Liu (1982), Zhou and Wang (2008) and sources cited therein.

In terms of the nomenclature adopted within this paper, the following points should also be noted.

Spellings of new names should not be altered in any way unless absolutely mandatory according to the rules of the *International Code of Zoological Nomenclature* (Ride *et al.* 1999). Gender or alleged gender of names should not be altered unless mandatory. In the unlikely event that a later author or so-called "first reviser" seeks to merge named taxa, then the name to be used should be that first used in this paper, as dictated by page priority and order in the keywords of the abstract.

Material may be repeated in sequential descriptions in order to ensure that each complies wholly with the rules of the *International Code of Zoological Nomenclature* (Ride *et al.* 1999).

Most of the diagnostic information for each species group identified as newly named genera herein has been taken directly from Rösler *et al.* (2011) or modified from it.

In colloquial terms, there is no need to re-invent the wheel!

As the primary source of this diagnostic information is cited in the correct way, any allegations of plagiarism by pseudoscientists such as Wolfgang Wüster as detailed by Hoser (2015a-f) cannot be sustained.

#### GENUS GEKKO LAURENTI, 1768.

**Type species:** *Gekko verticillatus* Laurenti, 1768, now known as *Gekko gekko* (Laurenti, 1768).

**Diagnosis:** Species within the genus *Gekko sensu lato*, including all the other genera identified within this paper, until now treated as being within *Gekko* are separated from all other gekkoes by the following suite of characters: SVL 50-191 mm; snout-vent length being the same or smaller than tail length; head dorsoventrally depressed, but to different degrees depending on species; head distinctly set off from neck; snout concave in region of the paired nasals and single frontal; body cylindrical to

slightly dorsoventrally depressed; belly flat; hind limbs larger than fore limbs; tibia longer than forearm; webbing between toes from rudimentary to distinct; head, body, limbs and tail without significant skin flaps; tail base not or only slightly

thickened; tail base round or slightly dorsoventrally depressed; unregenerated tail with more or less distinct whorls; rostral wider than long; nares with or without rostral contact, mostly surrounded by 3 (2-4) nasals; ciliary spines present or lacking; rostral wider than mental; two enlarged postmentals present in most cases; tubercles on head, body, limbs and dorsal tail surface present or lacking; dorsals granular; ventrals flat, imbricate; lateral folds

slightly developed (i.e. discernible transition from large and flat ventrals towards smaller and more or less raised lateral scales); lateral folds without tubercles (except for *G. vittatus* and associated species herein placed in the genus *Scelotretus* Fitzinger, 1843); toes apically extended, with undivided, broadened subdigital lamellae; fingers and toes except for digit one of both manus and pes (hind foot) with apical, dorsal claws; dorsum of finger one and toe one with apically enlarged scale; subcaudals distinctly enlarged (medially subdivided in different degrees according to species), arranged in a longitudinal row; subcaudals with repeating arrangement of two slightly and one greatly widened plates or with subcaudals slightly or not widened; hemipenis is elongate, apically divided and with two lobes of same size; sulcus spermaticus bordered by voluminous skin bulges; small to large calyces with smooth or denticulated seams (Unterhössel 1902, Zhang 1986, Utsunomiya *et al.* 1996, Shang 2001, Rösler *et al.* 2005); eyes covered by transparent brille; pupil vertical when iris is closed; anteriorly and posteriorly denticulated pupil margins.

Base coloration is mainly brown in different degrees, combined with gray, yellow, green and red, with only a few species with uniform gray, brown or green base coloration. Head with or without pattern (most often Y- or W-shaped patterns). Dorsum mainly with bands or flecks, some species also show symmetrical or asymmetrical light dorsal blotches. Striped pattern rare (e.g. *Scelotretus* Fitzinger, 1843). Tail more or less banded. Juveniles usually with distinct, strongly contrasting light and dark tail bands. Embryo with paired egg teeth in apical contact (Sluiter 1893, Woerdeman 1919).

Species within the genus *Gekko* as defined herein are those that conform with the so-called *Gekko gekko* group as defined by Rösler *et al.* (2011).

They are separated from the other species previously included in the genus *Gekko* by the following suite of characters: 150.0-191.0 mm SVL; nares, except for *G. verreauxi* Tytler, 1865, not in contact with rostral; nasals 3-6; postmentals relatively low (largest in *G. siamensis* Grossmann and Ulber, 1990), dorsal tubercle rows 10-19; precloacal pores 10-16; postcloacal tubercles 2-4 (rarely single); webbing between fingers and toes lacking; tubercles present on fore and hind limbs; lateral fold without tubercles; subcaudals enlarged, in two parallel rows; iris yellow, green, blue or brick red; Y-shaped head pattern usually discernible; light (white), more or less transversally arranged, symmetrical dorsal and lateral blotches.

**Distribution:** From India and Nepal to China, southwards to Indonesia (Rösler *et al.* 2011). Feral populations exist in the Caribbean, in Belize, on Hawaii and in Florida (Kraus 2009).

**Content:** *Gekko gekko* (Linnaeus, 1758) (type species); *G. albobasialis* (Günther, 1867); *G. nutaphandi* Bauer, Sumontha and Pauwels, 2008; *G. reevesii* (Gray, 1831); *G. siamensis* Grossmann and Ulber, 1990; *G. smithii* Gray, 1842; *G. verreauxi* Tytler, 1865.

#### GENUS *SPARSUSCOLOTES* GEN. NOV.

**Type species:** *Platydactylus japonicus* Schlegel, 1836.

**Diagnosis:** Species within the genus *Sparsuscolotes* gen. nov. as defined herein are those that conform with the so-called *Gekko japonicus* group as defined by Rösler *et al.* (2011).

They are separated from the other species previously included in the genus *Gekko* as defined elsewhere in this paper, by the following suite of characters: 58.9-99.2 mm SVL; nares in contact with rostral (except for *S. auriverrucosus*); nasals 3 (rarely 2 in *S. chinensis*); postmentals relatively small (except in

*S. similignum*), largest in *S. canhi*, *S. chinensis*, *S. palmatus*, *S. scientiadventura*; 0-21 dorsal tubercle rows; 0-32 precloacal pores; postcloacal tubercles 1-4; webbing between fingers and toes weakly developed to extensive (*S. chinensis*, *S. melli*, *S. palmatus*, *S. scientiadventura*, *S. similignum*, *S. subpalmatus*); tubercles present on fore and hind limbs, hind limbs only, or lacking all together; lateral fold without tubercles; subcaudals enlarged, in a longitudinal row (in *S. yakuensis* medially subdivided); head pattern present or not, without figure-shape (UU- to W-shaped in *S. melli* and W-shaped in *S. scientiadventura*); vertebral region with relatively large, light flecks, blotches or bands.

Species within the genus *Gekko sensu lato*, including all the other genera identified within this paper, until now treated as being within *Gekko* are separated from all other geckoes by the following suite of characters: SVL 50-191 mm; snout-vent length being the same or smaller than tail length; head dorsoventrally depressed, but to different degrees depending on species; head distinctly set off from neck; snout concave in region of the paired nasals and single frontal; body cylindrical to

slightly dorsoventrally depressed; belly flat; hind limbs larger than fore limbs; tibia longer than forearm; webbing between toes from rudimentary to distinct; head, body, limbs and tail without significant skin flaps; tail base not or only slightly thickened; tail base round or slightly dorsoventrally depressed; unregenerated tail with more or less distinct whorls; rostral wider than long; nares with or without rostral contact, mostly surrounded by 3 (2-4) nasals; ciliary spines present or lacking; rostral wider than mental; two enlarged postmentals present in most cases; tubercles on head, body, limbs and dorsal tail surface present or lacking; dorsals granular; ventrals flat, imbricate; lateral folds

slightly developed (i.e. discernible transition from large and flat ventrals towards smaller and more or less raised lateral scales); lateral folds without tubercles (except for *G. vittatus* and associated species herein placed in the genus *Scelotretus* Fitzinger, 1843); toes apically extended, with undivided, broadened subdigital lamellae; fingers and toes except for digit one of both manus and pes (hind foot) with apical, dorsal claws; dorsum of finger one and toe one with apically enlarged scale; subcaudals distinctly enlarged (medially subdivided in different degrees according to species), arranged in a longitudinal row; subcaudals with repeating arrangement of two slightly and one greatly widened plates or with subcaudals slightly or not widened; hemipenis is elongate, apically divided and with two lobes of same size; sulcus spermaticus bordered by voluminous skin bulges; small to large calyces with smooth or denticulated seams (Unterhössel 1902, Zhang 1986, Utsunomiya *et al.* 1996, Shang 2001, Rösler *et al.* 2005); eyes covered by transparent brille; pupil vertical when iris is closed; anteriorly and posteriorly denticulated pupil margins.

Base coloration is mainly brown in different degrees, combined with gray, yellow, green and red, with only a few species with uniform gray, brown or green base coloration. Head with or without pattern (most often Y- or W-shaped patterns). Dorsum mainly with bands or flecks, some species also show symmetrical or asymmetrical light dorsal blotches. Striped pattern rare (e.g. *Scelotretus* Fitzinger, 1843). Tail more or less banded. Juveniles usually with distinct, strongly contrasting light and dark tail bands. Embryo with paired egg teeth in apical contact (Sluiter 1893, Woerdeman 1919).

**Distribution:** China, Japan, Korea, Taiwan and Vietnam including offshore islands; possibly Laos (Rösler *et al.* 2011).

**Etymology:** *Sparsuscolotes* is Latin for mottled gecko, in reflection of the common dorsal patterning of most species.

**Content:** *Sparsuscolotes japonicus* (Schlegel, 1836) (type species); *S. aaronbaueri* (Tri, Thai, Phimvohan, David and Teynié, 2015); *S. adleri* (Nguyen, Wang, Yang, Lehmann, Le, Ziegler and Bonkowski, 2013); *S. auriverrucosus* (Zhou and Liu, 1982); *S. bonkowskii* (Luu, Calame, Nguyen, Le and Ziegler,



2015); *S. canhi* Rösler, (Nguyen, Doan, Ho and Ziegler 2010); *S. chinensis* (Gray, 1842); *S. guishanicus* (Lin and Yao, 2016); *S. hokouensis* (Pope, 1928); *S. kwangsiensis* (Yang, 2015); *S. liboensis* (Zhou and Li, 1982); *S. melli* (Vogt, 1922); *S. nadenensis* (Luu, Nguyen, Le, Bonkowski and Ziegler, 2017); *S. palmatus* (Boulenger, 1907); *S. scientiadventura* (Rösler, Ziegler, Vu, Herrmann and Böhme, 2004); *S. scabridus* (Liu and Zhou, 1982); *S. sengchanthavongi* (Luu, Calame, Nguyen, Le and Ziegler, 2015); *S. shibatai* (Toda, Sengoku, Hikida and Ota, 2008); *S. similignum* (Smith, 1923); *S. subpalmatus* (Günther, 1864); *S. swinhonis* (Günther, 1864); *S. taibaiensis* (Song, 1985); *S. tawaensis* (Okada, 1956); *S. thakhekensis* (Luu, Calame, Nguyen, Le, Bonkowski and Ziegler, 2014); *S. truongi* (Phung and Ziegler, 2011); *S. vertebralis* (Toda, Sengoku, Hikida and Ota, 2008); *S. vietnamensis* (Sang, 2010); *S. wenxianensis* (Zhou and Wang, 2008); *S. yakuensis* (Matsui and Okada, 1968).

#### SUBGENUS *SINOGEKKO* SUBGEN. NOV.

**Type species:** *Gekko chinensis* Gray, 1842.

**Diagnosis:** Lizards in the subgenus *Sinogekko subgen. nov.* are readily separated from all other species in the genus *Sparsuscolotes gen. nov.* by the following: weakly developed webbing between the toes, versus moderately to extensive in all other species of *Sparsuscolotes gen. nov.*; as well as nares in contact with rostral; 2-3 nasals; subcaudals enlarged, in an undivided medially longitudinal row; the presence of limb tubercles (versus absence in the morphologically similar *S. palmatus*); internasals same size or larger than nasorostrals in *S. chinensis* versus always smaller in *S. palmatus*; 8-10 scales around the midbody (versus 11-13 in the morphologically similar *S. similignum*); 1-10 and 9-12 lamellae on the first and fourth toes (versus 11-13 and 12-14 in the morphologically similar *S. similignum*).

Species within the genus *Sparsuscolotes gen. nov.* as defined herein are those that conform with the so-called *Gekko japonicus* group as defined by Rösler *et al.* (2011).

They are separated from the other species previously included in the genus *Gekko* as defined elsewhere in this paper, by the following suite of characters: 58.9-99.2 mm SVL; nares in contact with rostral (except for *S. auriverrucosus*); nasals 3 (rarely 2 in *S. chinensis*); postmentals relatively small (e.S., *S. similignum*), largest in *S. canhi*, *S. chinensis*, *S. palmatus*, *S. scientiadventura*; 0-21 dorsal tubercle rows; 0-32 precloacal pores; postcloacal tubercles 1-4; webbing between fingers and toes weakly developed to extensive (*S. chinensis*, *S. melli*, *S. palmatus*, *S. scientiadventura*, *S. similignum*, *S. subpalmatus*); tubercles present on fore and hind limbs, hind limbs only, or lacking all together; lateral fold without tubercles; subcaudals enlarged, in a longitudinal row (in *S. yakuensis* medially subdivided); head pattern present or not, without figure-shape (UU- to W-shaped in *S. melli* and W-shaped in *S. scientiadventura*); vertebral region with relatively large, light flecks, blotches or bands.

Species within the genus *Gekko sensu lato*, including all the other genera identified within this paper, until now treated as being within *Gekko* are separated from all other geckoes by the following suite of characters: SVL 50-191 mm; snout-vent length being the same or smaller than tail length; head dorsoventrally depressed, but to different degrees depending on species; head distinctly set off from neck; snout concave in region of the paired nasals and single frontal; body cylindrical to slightly dorsoventrally depressed; belly flat; hind limbs larger than fore limbs; tibia longer than forearm; webbing between toes from rudimentary to distinct; head, body, limbs and tail without significant skin flaps; tail base not or only slightly thickened; tail base round or slightly dorsoventrally depressed; unregenerated tail with more or less distinct whorls; rostral wider than long; nares with or without rostral contact, mostly surrounded by 3 (2-4) nasals; ciliary spines present or lacking; rostral wider than mental; two enlarged postmentals present in

most cases; tubercles on head, body, limbs and dorsal tail surface present or lacking; dorsals granular; ventrals flat, imbricate; lateral folds

slightly developed (i.e. discernible transition from large and flat ventrals towards smaller and more or less raised lateral scales); lateral folds without tubercles (except for *G. vittatus* and associated species herein placed in the genus *Scelotretus* Fitzinger, 1843); toes apically extended, with undivided, broadened subdigital lamellae; fingers and toes except for digit one of both manus and pes (hind foot) with apical, dorsal claws; dorsum of finger one and toe one with apically enlarged scale; subcaudals distinctly enlarged (medially subdivided in different degrees according to species), arranged in a longitudinal row; subcaudals with repeating arrangement of two slightly and one greatly widened plates or with subcaudals slightly or not widened; hemipenis is elongate, apically divided and with two lobes of same size; sulcus spermaticus bordered by voluminous skin bulges; small to large calyces with smooth or denticulated seams (Unterhössel 1902, Zhang 1986, Utsunomiya *et al.* 1996, Shang 2001, Rösler *et al.* 2005); eyes covered by transparent brille; pupil vertical when iris is closed; anteriorly and posteriorly denticulated pupil margins.

Base coloration is mainly brown in different degrees, combined with gray, yellow, green and red, with only a few species with uniform gray, brown or green base coloration. Head with or without pattern (most often Y- or W-shaped patterns). Dorsum mainly with bands or flecks, some species also show symmetrical or asymmetrical light dorsal blotches. Striped pattern rare (e.g. *Scelotretus* Fitzinger, 1843). Tail more or less banded. Juveniles usually with distinct, strongly contrasting light and dark tail bands. Embryo with paired egg teeth in apical contact (Sluiter 1893, Woerdeman 1919).

Molecular studies as cited (e.g. Oliver *et al.* 2017), have consistently shown this subgenus (*Sinogekko subgen. nov.*) to have diverged from the other species in the genus (*Sparsuscolotes gen. nov.*) more than 20 million years before present, warranting genus-level recognition. The designation as a subgenus for this group is the most conservative step allowable in order to taxonomically recognize the group within the rules of the *International Code of Zoological Nomenclature*, beyond mere species level designation.

**Distribution:** Apparently confined to southern China and immediately adjacent areas.

**Etymology:** Named in reflection of where the subgenus mainly occurs (China).

**Content:** *Sparsuscolotes (Sinogekko) chinensis* (Gray, 1842).

#### GENUS *LAUTUSDIGITUSCOLOTES* GEN. NOV.

**Type species:** *Gekko grossmanni* Günther, 1994.

**Diagnosis:** Species within the genus *Lautusdigituscolotes gen. nov.* as defined herein are those that conform with the so-called *Gekko petricolus* group as defined by Rösler *et al.* (2011).

They are separated from the other species previously included in the genus *Gekko* as defined elsewhere in this paper (or by Rösler *et al.* 2011), by the following suite of characters: 82.9-108.5 mm SVL; nares in contact with rostral; nasals 3; postmentals relatively large; dorsal tubercle rows 8-18; precloacal pores 8-15; postcloacal tubercles 1-3; no webbing between fingers and toes; fore and hind limbs without tubercles (but present on hind limbs of *L. petricolus*); lateral folds without tubercles; subcaudals enlarged, in a longitudinal row; head without pattern or with blotches or short stripes, but not forming a distinctive UU- or W-shaped pattern; back banded (*L. badenii*) or more or less symmetrically blotched (*L. canaensis*, *L. grossmanni*, *L. lauhachindaei*, *L. petricolus*, *L. russelltraini*, *L. takouensis*).

Lizards in *Aurumgekko subgen nov.* are readily separated from all other species in the genus *Lautusdigituscolotes gen. nov.* by colouration. *Aurumgekko subgen nov.* have a dorsal pattern incorporating banding on the back and no flecks between them,

versus more or less symmetrically blotched in all other species. Geckos in the subgenus *Glanduliscrusgekko subgen. nov.* are readily separated from all other species in the genus *Lautusdigituscolotes gen. nov.* by the presence of tubercles on the hind legs (versus absence in the rest).

Geckos in the nominate subgenus *Lautusdigituscolotes subgen. nov.* are readily separated from those in the other two subgenera by a body pattern of being more or less symmetrically blotched on the back (as opposed to banding) and an absence of tubercles on the hind legs.

Species within the genus *Gekko sensu lato*, including all the other genera identified within this paper, until now treated as being within *Gekko* are separated from all other geckoes by the following suite of characters: SVL 50-191 mm; snout-vent length being the same or smaller than tail length; head dorsoventrally depressed, but to different degrees depending on species; head distinctly set off from neck; snout concave in region of the paired nasals and single frontal; body cylindrical to

slightly dorsoventrally depressed; belly flat; hind limbs larger than fore limbs; tibia longer than forearm; webbing between toes from rudimentary to distinct; head, body, limbs and tail without significant skin flaps; tail base not or only slightly thickened; tail base round or slightly dorsoventrally depressed; unregenerated tail with more or less distinct whorls; rostral wider than long; nares with or without rostral contact, mostly surrounded by 3 (2-4) nasals; ciliary spines present or lacking; rostral wider than mental; two enlarged postmentals present in most cases; tubercles on head, body, limbs and dorsal tail surface present or lacking; dorsals granular; ventrals flat, imbricate; lateral folds slightly developed (i.e. discernible transition from large and flat ventrals towards smaller and more or less raised lateral scales); lateral folds without tubercles (except for *G. vittatus* and associated species herein placed in the genus *Scelotretus* Fitzinger, 1843); toes apically extended, with undivided, broadened subdigital lamellae; fingers and toes except for digit one of both manus and pes (hind foot) with apical, dorsal claws; dorsum of finger one and toe one with apically enlarged scale; subcaudals distinctly enlarged (medially subdivided in different degrees according to species), arranged in a longitudinal row; subcaudals with repeating arrangement of two slightly and one greatly widened plates or with subcaudals slightly or not widened; hemipenis is elongate, apically divided and with two lobes of same size; sulcus spermaticus bordered by voluminous skin bulges; small to large calyces with smooth or denticulated seams (Unterhössel 1902, Zhang 1986, Utsunomiya *et al.* 1996, Shang 2001, Rösler *et al.* 2005); eyes covered by transparent brille; pupil vertical when iris is closed; anteriorly and posteriorly denticulated pupil margins.

Base coloration is mainly brown in different degrees, combined with gray, yellow, green and red, with only a few species with uniform gray, brown or green base coloration. Head with or without pattern (most often Y- or W-shaped patterns). Dorsum mainly with bands or flecks, some species also show symmetrical or asymmetrical light dorsal blotches. Striped pattern rare (e.g. *Scelotretus* Fitzinger, 1843). Tail more or less banded. Juveniles usually with distinct, strongly contrasting light and dark tail bands. Embryo with paired egg teeth in apical contact (Sluiter 1893, Woerdeman 1919).

**Distribution:** Laos, Thailand and Vietnam (Rösler *et al.* 2011).

**Etymology:** *Lautusdigituscolotes* is Latin for clean digits gecko, in reflection of the lack of webbing between toes in this genus.

**Content:** *Lautusdigituscolotes grossmanni* (Günther, 1994) (type species); *L. boehmei* (Luu, Calame, Nguyen, Le and Ziegler, 2015); *L. canaensis* (Ngo and Gamble, 2011); *L. lauhachindai* (Panitvong, Sumontha, Konlek and Kunya, 2010); *L. petricolus* (Taylor, 1962); *L. russeltraini* (Ngo, Bauer, Wood and Grismer, 2009); *L. takouensis* (Ngo and Gamble, 2010); *L. badenii* (Szczerbak and Nekrasova, 1994).

**SUBGENUS AURUMGEKKO SUBGEN. NOV.**

**Type species:** *Gekko badenii* Szczerbak and Nekrasova, 1994.

**Diagnosis:** Lizards in *Aurumgekko subgen nov.* are readily separated from all other species in the genus *Lautusdigituscolotes gen. nov.* by colouration. *Aurumgekko subgen nov.* have a dorsal pattern incorporating banding on the back and no flecks between them, versus more or less symmetrically blotched in all other species. Geckos in the subgenus *Glanduliscrusgekko subgen. nov.* are readily separated from all other species in the genus *Lautusdigituscolotes gen. nov.* by the presence of tubercles on the hind legs (versus absence in the rest).

Geckos in the nominate subgenus *Lautusdigituscolotes subgen. nov.* are readily separated from those in the other two subgenera by a body pattern of being more or less symmetrically blotched on the back (as opposed to banding), and an absence of tubercles on the hind legs.

Species within the genus *Lautusdigituscolotes gen. nov.* as defined herein are those that conform with the so-called *Gekko petricolus* group as defined by Rösler *et al.* (2011).

They are separated from the other species previously included in the genus *Gekko* as defined elsewhere in this paper and Rösler *et al.* (2011), by the following suite of characters: 82.9-108.5 mm SVL; nares in contact with rostral; nasals 3; postmentals relatively large; dorsal tubercle rows 8-18; precloacal pores 8-15; precloacal tubercles 1-3; no webbing between fingers and toes; fore and hind limbs without tubercles (but present on hind limbs of *L. petricolus*); lateral folds without tubercles; subcaudals enlarged, in a longitudinal row; head without pattern or with blotches or short stripes, but not forming a distinctive UU- or W-shaped pattern; back banded (*L. badenii*) or more or less symmetrically blotched (*L. canaensis*, *L. grossmanni*, *L. lauhachindai*, *L. petricolus*, *L. russeltraini*, *L. takouensis*).

**Distribution:** Southern Vietnam.

**Etymology:** Named in reflection of the colour of most specimens. Name in Latin literally means "Gold Gecko".

**Content:** *Lautusdigituscolotes (Aurumgekko) badenii* (Szczerbak and Nekrasova, 1994).

**SUBGENUS GLANDULISCRUSGEKKO SUBGEN. NOV.**

**Type species:** *Gekko petricolus* Taylor, 1962.

**Diagnosis:** Geckos in the subgenus *Glanduliscrusgekko subgen. nov.* are readily separated from all other species in the genus *Lautusdigituscolotes gen. nov.* (both other subgenera) by the presence of tubercles on the hind legs (versus absence in the rest). Lizards in *Aurumgekko subgen nov.* are readily separated from all other species in the genus *Lautusdigituscolotes gen. nov.* by colouration. *Aurumgekko subgen nov.* have a dorsal pattern incorporating banding on the back and no flecks between them, versus more or less symmetrically blotched in all other species.

Geckos in the nominate subgenus *Lautusdigituscolotes subgen. nov.* are readily separated from those in the other two subgenera by a body pattern of being more or less symmetrically blotched on the back (as opposed to banding), and an absence of tubercles on the hind legs.

Species within the genus *Lautusdigituscolotes gen. nov.* as defined herein are those that conform with the so-called *Gekko petricolus* group as defined by Rösler *et al.* (2011).

They are separated from the other species previously included in the genus *Gekko* as defined elsewhere in this paper and by Rösler *et al.* (2011), by the following suite of characters: 82.9-108.5 mm SVL; nares in contact with rostral; nasals 3; postmentals relatively large; dorsal tubercle rows 8-18; precloacal pores 8-15; precloacal tubercles 1-3; no webbing between fingers and toes; fore and hind limbs without tubercles (but present on hind limbs of *L. petricolus*); lateral folds without tubercles; subcaudals enlarged, in a longitudinal row; head without pattern or with blotches or short stripes, but not forming a distinctive UU- or W-shaped pattern; back banded (*L. badenii*) or more or less symmetrically blotched (*L. canaensis*, *L.*

*grossmanni*, *L. lauhachindaei*, *L. petricolus*, *L. russelltraini*, *L. takouensis*).

**Distribution:** Thailand, Laos, Cambodia.

**Etymology:** *Glanduliscrusgekko* in Latin means tubercles on legs Gekko, as a perfect diagnostic description of the subgenus.

**Content:** *Lautusdigituscolotes* (*Glanduliscrusgekko*) *petricolus* (Taylor, 1962) (type species); *L. (Glanduliscrusgekko) boehmei* (Luu, Calame, Nguyen, Le and Ziegler, 2015).

#### SUBGENUS LAUTUSDIGITUSCOLOTES SUBGEN. NOV.

**Type species:** *Gekko grossmanni* Günther, 1994.

**Diagnosis:** Geckos in the nominate subgenus *Lautusdigituscolotes* subgen. nov. are readily separated from those in the other two subgenera by a body pattern of being more or less symmetrically blotched on the back (as opposed to banding), and an absence of tubercles on the hind legs.

Geckos in the subgenus *Glanduliscrusgekko* subgen. nov. are readily separated from all other species in the genus *Lautusdigituscolotes* gen. nov. (both other subgenera) by the presence of tubercles on the hind legs (versus absence in the rest).

Lizards in *Aurumgekko* subgen. nov. are readily separated from all other species in the genus *Lautusdigituscolotes* gen. nov. by colouration. *Aurumgekko* subgen. nov. have a dorsal pattern incorporating banding on the back and no flecks between them, versus more or less symmetrically blotched in all other species.

Species within the genus *Lautusdigituscolotes* gen. nov. as defined herein are those that conform with the so-called *Gekko petricolus* group as defined by Rösler *et al.* (2011).

They are separated from the other species previously included in the genus *Gekko* as defined elsewhere in this paper and by Rösler *et al.* (2011), by the following suite of characters: 82.9-108.5 mm SVL; nares in contact with rostral; nasals 3; postmentals relatively large; dorsal tubercle rows 8-18; precloacal pores 8-15; postcloacal tubercles 1-3; no webbing between fingers and toes; fore and hind limbs without tubercles (but present on hind limbs of *L. petricolus*); lateral folds without tubercles; subcaudals enlarged, in a longitudinal row; head without pattern or with blotches or short stripes, but not forming a distinctive UU- or W-shaped pattern; back banded (*L. badenii*) or more or less symmetrically blotched (*L. canaensis*, *L. grossmanni*, *L. lauhachindaei*, *L. petricolus*, *L. russelltraini*, *L. takouensis*).

**Distribution:** Believed to be restricted to southern Vietnam, Laos, Cambodia and Thailand.

**Etymology:** As for genus.

**Content:** *Lautusdigituscolotes* (*Lautusdigituscolotes*) *grossmanni* (Günther, 1994) (type species); *L. (Lautusdigituscolotes) canaensis* (Ngo and Gamble, 2011); *L. (Lautusdigituscolotes) lauhachindaei* (Panitvong, Sumontha, Konlek and Kunya, 2010); *L. (Lautusdigituscolotes) russelltraini* (Ngo, Bauer, Wood and Grismer, 2009); *L. (Lautusdigituscolotes) takouensis* (Ngo and Gamble, 2010).

#### GENUS SCLOTRETUS FITZINGER, 1843.

**Type species:** *Gekko vittatus* Houttuyn, 1782.

**Diagnosis:** The genus *Luperosaurus* Gray, 1845 as recognized to date is a paraphyletic assemblage of morphologically similar species with affinities to the species associated with the taxon presently known as "*Gekko vittatus* Houttuyn, 1782", which herein is treated as more correctly being in a separate genus to *Gekko* and dealt with here. Therefore *Luperosaurus* Gray, 1845 was split by Hoser (2018) into four genera.

*Scelotretus* Fitzinger, 1843 is the one of the four relevant genera which happens to include the "*Gekko vittatus* Houttuyn, 1782" species group (being resurrected from synonymy by Hoser (2018) and in this paper), and so is properly diagnosed and described herein as it is relevant to this paper.

This is a modified diagnosis from Hoser (2018).

All four genera, formerly included in *Luperosaurus*, namely *Luperosaurus*, *Scelotretus* Fitzinger, 1843, a genus named in

honour of publisher Charles Pierson and a genus named in honour of athlete George Mariolis are readily separated from all other geckos by the following suite of characters: Digits strongly dilated, half webbed (excluding a subgenus named in honour of herpetologist Harold Cogger, a subgenus of *Scelotretus* Fitzinger, 1843 which has only slight webbing between the toes or none), with undivided, angularly curved lamellae below; all but thumb and inner toe with a very short, compressed, distal phalanx, with retractile claw; legs bordered with cutaneous lobes; upper and lower surfaces covered with juxtaposed granular scales; pupil vertical; males with preanal pores.

The genera *Scelotretus* Fitzinger, 1843 and a genus named in honour of athlete George Mariolis are readily separated from the other two genera (*Luperosaurus* and a genus named in honour of publisher Charles Pierson) by the presence of a distinctly elongate head, elongate versus robust body shape (in the other genera) and the presence of enlarged interstitial granules.

The genera *Luperosaurus* and a genus named in honour of publisher Charles Pierson are separated from *Scelotretus* Fitzinger, 1843 (described here) and a genus named in honour of athlete George Mariolis by the presence of beadlike, granular dorsals, a stout and robust, stout body and deeply notched to divided penultimate subdigital scansors.

The genus named in honour of publisher Charles Pierson is most easily separated from the genus *Luperosaurus* (as well as *Scelotretus* Fitzinger, 1843 and the genus named in honour of athlete George Mariolis) by the presence of strongly spinose dorsal tubercles.

The species originally described as *Luperosaurus palawanensis* Brown and Alcalá, 1978 has many characteristics intermediate between that seen in members of the genera, the genus named in honour of publisher Charles Pierson and *Luperosaurus*, most notably weakly spinose dorsal scales and it is placed in the genus *Luperosaurus*, even though no other members of the genus *Luperosaurus* have spinose dorsal scales of any sort. It is likely it may need to be eventually assigned to a separate genus or subgenus.

The genus named in honour of George Mariolis is readily separated from *Scelotretus* Fitzinger, 1843 by having a small round to ovoid auricular opening, versus a narrow elliptical or vertical slit-like opening in *Scelotretus* Fitzinger, 1843.

The genus named in honour of George Mariolis is further separated from *Scelotretus* Fitzinger, 1843 by having 11-15 supralabials, versus 16 in *Scelotretus* Fitzinger, 1843 and 10-14 infralabials, versus 15-18 in *Scelotretus* Fitzinger, 1843.

The genus named in honour of George Mariolis has round-hexagonal, flat convex dorsal body scales, versus hexagonal flat dorsal body scales in *Scelotretus* Fitzinger, 1843.

The genus named in honour of George Mariolis has flat or convex dorsal body tubercles, versus flat only in *Scelotretus* Fitzinger, 1843.

The genus named in honour of George Mariolis has 28-40 preanofemorals versus 12 or less in *Scelotretus* Fitzinger, 1843, 11-13 scansors on toe 1, versus 10 in *Scelotretus* Fitzinger, 1843 and small anteriormost chinshields, versus slightly enlarged in *Scelotretus* Fitzinger, 1843.

The subgenus *Scelotretus* is further defined and separated from the subgenus named in honour of herpetologist Harold Cogger and all other geckos by the following suite of characters: Maximum SVL 140.0 mm; nares in contact with rostral; nasals 3-4; postmentals relatively small; dorsal tubercle rows 12-14; precloacal pores 14-58; postcloacal tubercles 1-3; no webbing between fingers and toes; fore and hind limbs with tubercles; lateral folds with tubercles; subcaudals not enlarged; head unicolored, without pattern; nominate form with white, anteriorly bifurcated dorsal stripe (derived from Rösler *et al.* 2011).

The preceding diagnosis in similar form is published as a formal description with the newly assigned correct genus names in Hoser (2018) in accordance with the rules of the *International Code of Zoological Nomenclature* (Ride *et al.* 1999).



**Distribution:** Sulawesi and Palawan (subgenus named after Harold Cogger), Indonesia, extending to the Solomon Islands and the Vanuatu Islands (subgenus *Scelotretus* Fitzinger, 1843).

**Content:** *Scelotretus vittatus* (Houttuyn, 1782) (type species) including three species first formally named by Hoser (2018) that had previously been treated as populations of the former; *S. gulat* (Brown, Diesmos, Duya, Garcia and Rico, 2010); *S. iskandari* (Brown, Supriatna and Ota, 2000); *S. remotus* (Rösler, Ineich, Wilms and Böhme, 2012).

#### GENUS MAGNAOCELLUS GEN. NOV.

**Type species:** *Gekko athymus* Brown and Alcalá, 1962.

**Diagnosis:** Phylogenetically, the genus *Magnaocellus* gen. nov. is most closely related to the Philippines genus

*Extentusventersquamus* gen. nov., (Rösler et al. 2011), although morphologically it more closely resembles the genera *Gekko* and *Sparsuscolotes* gen. nov..

*Magnaocellus* gen. nov. as defined herein was placed in a separate group on its own by Rösler et al. (2011). It is separated from all other species within *Gekko sensu lato* as defined by Rösler et al. (2011), by having broad webbing between the fingers and toes (unlike the genus *Extentusventersquamus* gen. nov.), and differs from the morphologically similar genus *Sparsuscolotes* gen. nov. by having a relatively large SVL (> 100 mm), a higher number of lamellae below the fourth toe (18-22, versus less than 18) and more precloacal pores (20-24 versus less than 19).

Species within the genus *Gekko* as defined herein are those that conform with the so-called *Gekko gekko* group as defined by Rösler et al. (2011).

They are separated from the other species previously included in the genus *Gekko* by the following suite of characters: 150.0-191.0 mm SVL; nares, except for *G. verreauxi* Tytler, 1865, not in contact with rostral; nasals 3-6; postmentals relatively low (largest in *G. siamensis* Grossmann and Ulber, 1990), dorsal tubercle rows 10-19; precloacal pores 10-16; postcloacal tubercles 2-4 (rarely single); webbing between fingers and toes lacking; tubercles present on fore and hind limbs; lateral fold without tubercles; subcaudals enlarged, in two parallel rows; iris yellow, green, blue or brick red; Y-shaped head pattern usually discernible; light (white), more or less transversally arranged, symmetrical dorsal and lateral blotches.

Species within the genus *Sparsuscolotes* gen. nov. as defined herein are those that conform with the so-called *Gekko japonicus* group as defined by Rösler et al. (2011).

They are separated from the other species previously included in the genus *Gekko* as defined elsewhere in this paper, by the following suite of characters: 58.9-99.2 mm SVL; nares in contact with rostral (except for *S. auriverrucosus*); nasals 3 (rarely 2 in *S. chinensis*); postmentals relatively small (e.S., *S. similignum*), largest in *S. canhi*, *S. chinensis*, *S. palmatus*, *S. scientiadvventura*; 0-21 dorsal tubercle rows; 0-32 precloacal pores; postcloacal tubercles 1-4; webbing between fingers and toes weakly developed to extensive (*S. chinensis*, *S. melli*, *S. palmatus*, *S. scientiadvventura*, *S. similignum*, *S. subpalmatus*); tubercles present on fore and hind limbs, hind limbs only, or lacking all together; lateral fold without tubercles; subcaudals enlarged, in a longitudinal row (in *S. yakuensis* medially subdivided); head pattern present or not, without figure-shape (UU- to W-shaped in *S. melli* and W-shaped in *S. scientiadvventura*); vertebral region with relatively large, light flecks, blotches or bands.

Species within the genus *Lautusdigituscolotes* gen. nov. as defined herein are those that conform with the so-called *Gekko petricolus* group as defined by Rösler et al. (2011).

They are separated from the other species previously included in the genus *Gekko* as defined elsewhere in this paper, by the following suite of characters: 82.9-108.5 mm SVL; nares in contact with rostral; nasals 3; postmentals relatively large; dorsal tubercle rows 8-18; precloacal pores 8-15; postcloacal tubercles 1-3; no webbing between fingers and toes; fore and hind limbs

without tubercles (but present on hind limbs of *L. petricolus*); lateral folds without tubercles; subcaudals enlarged, in a longitudinal row; head without pattern or with blotches or short stripes, but not forming a distinctive UU- or W-shaped pattern; back banded (*L. badenii*) or more or less symmetrically blotched (*L. canaensis*, *L. grossmanni*, *L. lauhachindaei*, *L. petricolus*, *L. russelltraini*, *L. takouensis*).

Species within the genus *Lautusdigituscolotes* gen. nov. as defined herein are those that conform with the so-called *Gekko petricolus* group as defined by Rösler et al. (2011).

They are separated from the other species previously included in the genus *Gekko* as defined elsewhere in this paper (or by Rösler et al. 2011), by the following suite of characters: 82.9-108.5 mm SVL; nares in contact with rostral; nasals 3; postmentals relatively large; dorsal tubercle rows 8-18; precloacal pores 8-15; postcloacal tubercles 1-3; no webbing between fingers and toes; fore and hind limbs without tubercles (but present on hind limbs of *L. petricolus*); lateral folds without tubercles; subcaudals enlarged, in a longitudinal row; head without pattern or with blotches or short stripes, but not forming a distinctive UU- or W-shaped pattern; back banded (*L. badenii*) or more or less symmetrically blotched (*L. canaensis*, *L. grossmanni*, *L. lauhachindaei*, *L. petricolus*, *L. russelltraini*, *L. takouensis*).

The genus *Luperosaurus* Gray, 1845 as recognized to date is a paraphyletic assemblage of morphologically similar species with affinities to the species associated with the taxon presently known as "*Gekko vittatus* Houttuyn, 1782", which herein is treated as more correctly being in a separate genus to *Gekko* and dealt with here. Therefore *Luperosaurus* Gray, 1845 was split by Hoser (2018) into four genera.

*Scelotretus* Fitzinger, 1843 is the one of the four relevant genera which happens to include the "*Gekko vittatus* Houttuyn, 1782" species group (being resurrected from synonymy by Hoser 2018), and so is properly diagnosed and described herein as it is relevant to this paper.

All four genera, formerly included in *Luperosaurus*, namely *Luperosaurus*, *Scelotretus* Fitzinger, 1843, a genus named in honour of publisher Charles Pierson and a genus named in honour of athlete George Mariolis are readily separated from all other geckos by the following suite of characters: Digits strongly dilated, half webbed (excluding a subgenus named in honour of herpetologist Harold Cogger, a subgenus of *Scelotretus* Fitzinger, 1843 which has only slight webbing between the toes or none), with undivided, angularly curved lamellae below; all but thumb and inner toe with a very short, compressed, distal phalanx, with retractile claw; legs bordered with cutaneous lobes; upper and lower surfaces covered with juxtaposed granular scales; pupil vertical; males with preanal pores.

The genera *Scelotretus* Fitzinger, 1843 and a genus named in honour of athlete George Mariolis are readily separated from the other two genera (*Luperosaurus* and a genus named in honour of publisher Charles Pierson) by the presence of a distinctly elongate head, elongate versus robust body shape (in the other genera) and the presence of enlarged interstitial granules.

The genera *Luperosaurus* and a genus named in honour of publisher Charles Pierson are separated from *Scelotretus* Fitzinger, 1843 (described here) and a genus named in honour of athlete George Mariolis by the presence of beadlike, granular dorsals, a stout and robust, stout body and deeply notched to divided penultimate subdigital scancers.

The genus named in honour of publisher Charles Pierson is most easily separated from the genus *Luperosaurus* (as well as *Scelotretus* Fitzinger, 1843 and the genus named in honour of athlete George Mariolis) by the presence of strongly spinose dorsal tubercles.

The species originally described as *Luperosaurus palawanensis* Brown and Alcalá, 1978 has many characteristics intermediate between that seen in members of the genera the genus named in honour of publisher Charles Pierson and *Luperosaurus*, most

notably weakly spinose dorsal scales and it is placed in the genus *Luperosaurus*, even though no other members of the genus *Luperosaurus* have spinose dorsal scales of any sort. It is likely it may need to be eventually assigned to a separate genus or subgenus.

The genus named in honour of George Mariolis is readily separated from *Scelotretus* Fitzinger, 1843 by having a small round to ovoid auricular opening, versus a narrow elliptical or vertical slit-like opening in *Scelotretus* Fitzinger, 1843.

The genus named in honour of George Mariolis is further separated from *Scelotretus* Fitzinger, 1843 by having 11-15 supralabials, versus 16 in *Scelotretus* Fitzinger, 1843 and 10-14 infralabials, versus 15-18 in *Scelotretus* Fitzinger, 1843.

The genus named in honour of George Mariolis has round-hexagonal, flat convex dorsal body scales, versus hexagonal flat dorsal body scales in *Scelotretus* Fitzinger, 1843.

The genus named in honour of George Mariolis has flat or convex dorsal body tubercles, versus flat only in *Scelotretus* Fitzinger, 1843.

The genus named in honour of George Mariolis has 28-40 preanofemorals versus 12 or less in *Scelotretus* Fitzinger, 1843, 11-13 scansors on toe 1, versus 10 in *Scelotretus* Fitzinger, 1843 and small anteriormost chinshields, versus slightly enlarged in *Scelotretus* Fitzinger, 1843.

The subgenus *Scelotretus* is further defined and separated from the subgenus named in honour of herpetologist Harold Cogger and all other geckos by the following suite of characters: Maximum SVL 140.0 mm; nares in contact with rostral; nasals 3-4; postmentals relatively small; dorsal tubercle rows 12-14; precloacal pores 14-58; postcloacal tubercles 1-3; no webbing between fingers and toes; fore and hind limbs with tubercles; lateral folds with tubercles; subcaudals not enlarged; head unicolored, without pattern; nominate form with white, anteriorly bifurcated dorsal stripe (Rösler *et al.* 2011).

Species within the genus *Gekko sensu lato*, including all the other genera identified within this paper, until now treated as being within *Gekko* are separated from all other geckoes by the following suite of characters: SVL 50-191 mm; snout-vent length being the same or smaller than tail length; head dorsoventrally depressed, but to different degrees depending on species; head distinctly set off from neck; snout concave in region of the paired nasals and single frontal; body cylindrical to

slightly dorsoventrally depressed; belly flat; hind limbs larger than fore limbs; tibia longer than forearm; webbing between toes from rudimentary to distinct; head, body, limbs and tail without significant skin flaps; tail base not or only slightly thickened; tail base round or slightly dorsoventrally depressed; unregenerated tail with more or less distinct whorls; rostral wider than long; nares with or without rostral contact, mostly surrounded by 3 (2-4) nasals; ciliary spines present or lacking; rostral wider than mental; two enlarged postmentals present in most cases; tubercles on head, body, limbs and dorsal tail surface present or lacking; dorsals granular; ventrals flat, imbricate; lateral folds

slightly developed (i.e. discernible transition from large and flat ventrals towards smaller and more or less raised lateral scales); lateral folds without tubercles (except for *G. vittatus* and associated species herein placed in the genus *Scelotretus* Fitzinger, 1843); toes apically extended, with undivided, broadened subdigital lamellae; fingers and toes except for digit one of both manus and pes (hind foot) with apical, dorsal claws; dorsum of finger one and toe one with apically enlarged scale; subcaudals distinctly enlarged (medially subdivided in different degrees according to species), arranged in a longitudinal row; subcaudals with repeating arrangement of two slightly and one greatly widened plates or with subcaudals slightly or not widened; hemipenis is elongate, apically divided and with two lobes of same size; sulcus spermaticus bordered by voluminous skin bulges; small to large calyces with smooth or denticulated seams (Unterhössel 1902, Zhang 1986, Utsunomiya *et al.* 1996,

Shang 2001, Rösler *et al.* 2005); eyes covered by transparent brille; pupil vertical when iris is closed; anteriorly and posteriorly denticulated pupil margins.

Base coloration is mainly brown in different degrees, combined with gray, yellow, green and red, with only a few species with uniform gray, brown or green base coloration. Head with or without pattern (most often Y- or W-shaped patterns). Dorsum mainly with bands or flecks, some species also show symmetrical or asymmetrical light dorsal blotches. Striped pattern rare (e.g. *Scelotretus* Fitzinger, 1843). Tail more or less banded. Juveniles usually with distinct, strongly contrasting light and dark tail bands. Embryo with paired egg teeth in apical contact (Sluiter 1893, Woerdeman 1919).

**Distribution:** Philippines.

**Etymology:** *Magnaocellus* literally means large eye in Latin.

**Content:** *Magnaocellus athymus* (Brown and Alcalá, 1962) (monotypic).

#### GENUS *EXTENTUSVENTERSQUAMUS* GEN. NOV.

**Type species:** *Platydactylus monarchus* Schlegel, 1836.

**Diagnosis:** Species within the genus *Extentusventersquamus* gen. nov. as defined herein are those that conform with the so-called *Gekko monarchus* group and the *Gekko porosus* group as defined by Rösler *et al.* (2011). They are separated from the other species previously included in the genus *Gekko* as defined elsewhere in this paper (or by Rösler *et al.* 2011), by the following suite of characters: One or other of the following: 1/ 63.0-100.0 mm SVL; nares in contact with rostral; nasals 3 (rarely 4 in *E. ernstkelleri* being subgenus *Cavernagekko* subgen. nov.); postmentals relatively large; dorsal tubercle rows 10-24; precloacal pores 32-70; postcloacal tubercles 2-3 (1 in *E. carusadensis* and *E. palawanensis*); no webbing between fingers and toes; tubercles on fore and hind limbs (not on fore limbs of *E. ernstkelleri* which separates the subgenus *Cavernagekko* subgen. nov. from the subgenus *Extentusventersquamus* subgen. nov.) lateral folds without tubercles; subcaudals mostly enlarged, in a longitudinal row; more or less distinct, W-shaped head pattern; light (white to gray), mostly asymmetrically arranged dorsal and lateral flecks, (subgenera *Extentusventersquamus* subgen. nov. and *Cavernagekko* subgen. nov.), or:

2/ 89.2-108.2 mm SVL; nares in contact with rostral; nasals 3; postmentals relatively large; dorsal tubercle rows 12-22; precloacal pores 52-88; postcloacal tubercle single; no webbing between fingers and toes; tubercles present on fore and hind limbs; lateral folds without tubercles; subcaudals enlarged, in a longitudinal row; green to blue coloration of the iris; head pattern without a distinctive (i.e. W-shaped) pattern; dorsum with flecks or in *E. gigante* indistinctly banded, (subgenus *Foderetdorsumgekko* subgen. nov.).

**Distribution:** The genus is restricted to the Philippines, except for one species endemic to Lanyu Island, Taiwan and another from Burma, eastwards to include most of Indonesia to Irian Jaya.

**Etymology:** In Latin, *Extentusventersquamus* means "enlarged belly scales", in reflection of the enlarged size of the ventral scales in members of the genus.

**Content:** *Extentusventersquamus monarchus* (Schlegel, 1836) (type species); *E. carusadensis* (Linkem, Siler, Diesmos, Sy and Brown, 2010); *E. coi* (Brown, Siler, Oliveros, Diesmos and Alcalá, 2011); *E. crombota* (Brown, Oliveros, Siler and Diesmos, 2008); *E. (Cavernagekko) ernstkelleri* (Rösler, Siler, Brown, Demeglio and Gaulke, 2006); *E. gigante* (Brown and Alcalá, 1978); *E. kikuchii* (Oshima, 1912); *E. mindorensis* (Taylor, 1919); *E. palawanensis* (Taylor, 1925); *E. porosus* (Taylor, 1922); *E. romblon* (Brown and Alcalá, 1978); *E. rossi* (Brown, Oliveros, Siler and Diesmos, 2009).

#### SUBGENUS *CAVERNAGEKKO* SUBGEN. NOV.

**Type species:** *Gekko ernstkelleri* Rösler, Siler, Brown, Demeglio and Gaulke, 2006.



**Diagnosis:** Species within the genus *Extentusventersquamus* *gen. nov.* as defined herein are those that conform with the so-called *Gekko monarchus* group and the *Gekko porosus* group as defined by Rösler *et al.* (2011). They are separated from the other species previously included in the genus *Gekko* as defined elsewhere in this paper (or by Rösler *et al.* 2011), by the following suite of characters: One or other of the following:

1/ 63.0-100.0 mm SVL; nares in contact with rostral; nasals 3 (rarely 4 in *E. ernstkelleri* being subgenus *Cavernagekko subgen. nov.*); postmentals relatively large; dorsal tubercle rows 10-24; precloacal pores 32-70; postcloacal tubercles 2-3 (1 in *E. carusadensis* and *E. palawanensis*); no webbing between fingers and toes; tubercles on fore and hind limbs (not on fore limbs of *E. ernstkelleri* which separates the subgenus *Cavernagekko subgen. nov.* from the subgenus *Extentusventersquamus subgen. nov.*) lateral folds without tubercles; subcaudals mostly enlarged, in a longitudinal row; more or less distinct, W-shaped head pattern; light (white to gray), mostly asymmetrically arranged dorsal and lateral flecks, (subgenera *Extentusventersquamus subgen. nov.* and *Cavernagekko subgen. nov.*), or:

2/ 89.2-108.2 mm SVL; nares in contact with rostral; nasals 3; postmentals relatively large; dorsal tubercle rows 12-22; precloacal pores 52-88; postcloacal tubercle single; no webbing between fingers and toes; tubercles present on fore and hind limbs; lateral folds without tubercles; subcaudals enlarged, in a longitudinal row; green to blue coloration of the iris; head pattern without a distinctive (i.e. W-shaped) pattern; dorsum with flecks or in *E. gigante* indistinctly banded, (subgenus *Foderetdorsumgekko subgen. nov.*).

It is the absence of tubercles on the fore limbs that separates *Cavernagekko subgen. nov.* from the morphologically similar *Extentusventersquamus subgen. nov.* species.

**Distribution:** Known only from near the type locality in Panay, Philippines.

**Etymology:** In Latin *Cavernagekko* means "Cave Gekko".

**Content:** *Extentusventersquamus (Cavernagekko) ernstkelleri* (Rösler, Siler, Brown, Demeglio and Gaulke, 2006) (monotypic).

#### **SUBGENUS FODERETDORSUMGEKKO SUBGEN. NOV.**

**Type species:** *Gekko porosus* Taylor, 1922.

**Diagnosis:** Species within the genus *Extentusventersquamus* *gen. nov.* as defined herein are those that conform with the so-called *Gekko monarchus* group and the *Gekko porosus* group as defined by Rösler *et al.* (2011). They are separated from the other species previously included in the genus *Gekko* as defined elsewhere in this paper (or by Rösler *et al.* 2011), by the following suite of characters: One or other of the following:

1/ 89.2-108.2 mm SVL; nares in contact with rostral; nasals 3; postmentals relatively large; dorsal tubercle rows 12-22; precloacal pores 52-88; postcloacal tubercle single; no webbing between fingers and toes; tubercles present on fore and hind limbs; lateral folds without tubercles; subcaudals enlarged, in a longitudinal row; green to blue coloration of the iris; head pattern without a distinctive (i.e. W-shaped) pattern; dorsum with flecks or in *E. gigante* indistinctly banded, (subgenus *Foderetdorsumgekko subgen. nov.*) the preceding paragraph being a diagnosis for the subgenus *Foderetdorsumgekko subgen. nov.*.

2/ 63.0-100.0 mm SVL; nares in contact with rostral; nasals 3 (rarely 4 in *E. ernstkelleri* being subgenus *Cavernagekko subgen. nov.*); postmentals relatively large; dorsal tubercle rows 10-24; precloacal pores 32-70; postcloacal tubercles 2-3 (1 in *E. carusadensis* and *E. palawanensis*); no webbing between fingers and toes; tubercles on fore and hind limbs (not on fore limbs of *E. ernstkelleri* which separates the subgenus *Cavernagekko subgen. nov.* from the subgenus *Extentusventersquamus subgen. nov.*) lateral folds without tubercles; subcaudals mostly enlarged, in a longitudinal row; more or less distinct, W-shaped head pattern; light (white to

gray), mostly asymmetrically arranged dorsal and lateral flecks, (subgenera *Extentusventersquamus subgen. nov.* and *Cavernagekko subgen. nov.*).

*Foderetdorsumgekko subgen. nov.* is the *Gekko porosus* group as defined by Rösler *et al.* (2011).

**Distribution:** Philippines only.

**Etymology:** *Foderetdorsumgekko* in Latin means flecked dorsum in reflection of the colouration of most specimens of most species in the genus.

**Content:** *Extentusventersquamus (Foderetdorsumgekko) porosus* (Taylor, 1922) (type species); *E. (Foderetdorsumgekko) coi* (Brown, Siler, Oliveros, Diesmos and Alcalá, 2011); *E. (Foderetdorsumgekko) crombota* (Brown, Oliveros, Siler and Diesmos, 2008); *E. (Foderetdorsumgekko) gigante* (Brown and Alcalá, 1978); *E. (Foderetdorsumgekko) romblon* (Brown and Alcalá, 1978); *E. (Foderetdorsumgekko) rossi* (Brown, Oliveros, Siler and Diesmos, 2009).

#### **SUBGENUS EXTENTUSVENTERSQUAMUS SUBGEN. NOV.**

**Type species:** *Platydictylus monarchus* Schlegel, 1836.

**Diagnosis:** Species within the genus *Extentusventersquamus* *gen. nov.* as defined herein are those that conform with the so-called *Gekko monarchus* group and the *Gekko porosus* group as defined by Rösler *et al.* (2011). They are separated from the other species previously included in the genus *Gekko* as defined elsewhere in this paper (or by Rösler *et al.* 2011), by the following suite of characters: One or other of the following:

1/ 63.0-100.0 mm SVL; nares in contact with rostral; nasals 3 (rarely 4 in *E. ernstkelleri* being subgenus *Cavernagekko subgen. nov.*); postmentals relatively large; dorsal tubercle rows 10-24; precloacal pores 32-70; postcloacal tubercles 2-3 (1 in *E. carusadensis* and *E. palawanensis*); no webbing between fingers and toes; tubercles on fore and hind limbs (not on fore limbs of *E. ernstkelleri* which separates the subgenus *Cavernagekko subgen. nov.* from the subgenus *Extentusventersquamus subgen. nov.*) lateral folds without tubercles; subcaudals mostly enlarged, in a longitudinal row; more or less distinct, W-shaped head pattern; light (white to gray), mostly asymmetrically arranged dorsal and lateral flecks, (subgenera *Extentusventersquamus subgen. nov.* and *Cavernagekko subgen. nov.*), or:

2/ 89.2-108.2 mm SVL; nares in contact with rostral; nasals 3; postmentals relatively large; dorsal tubercle rows 12-22; precloacal pores 52-88; postcloacal tubercle single; no webbing between fingers and toes; tubercles present on fore and hind limbs; lateral folds without tubercles; subcaudals enlarged, in a longitudinal row; green to blue coloration of the iris; head pattern without a distinctive (i.e. W-shaped) pattern; dorsum with flecks or in *E. gigante* indistinctly banded, (subgenus *Foderetdorsumgekko subgen. nov.*), the preceding paragraph being diagnostic for the subgenus *Foderetdorsumgekko subgen. nov.*.

*Extentusventersquamus subgen. nov.* is the *Gekko monarchus* group as defined by Rösler *et al.* (2011), minus the species *E. ernstkelleri*, which is placed in a separate subgenus due to morphological divergence and molecular divergence.

**Distribution:** Mainly the Philippines, but including Burma to Irian Jaya and Lanyu Island, Taiwan.

**Etymology:** As for genus.

**Content:** *Extentusventersquamus (Extentusventersquamus) monarchus* (Schlegel, 1836) (type species); *E. (Extentusventersquamus) carusadensis* (Linkem, Siler, Diesmos, Sy and Brown, 2010); *E. (Extentusventersquamus) kikuchii* (Oshima, 1912); *E. (Extentusventersquamus) mindorensis* (Taylor, 1919); *E. (Extentusventersquamus) palawanensis* (Taylor, 1925).

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- CONFLICT OF INTEREST**  
There are no conflicts of interest in terms of this paper.
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- Genus and species list for *Gekko* Laurenti, 1768 sensu lato**
- GENUS GEKKO LAURENTI, 1769**  
*Gekko gecko* (Linnaeus, 1758) (type species)  
*Gekko albofasciolatus* (Günther, 1867)  
*Gekko nutaphandi* Bauer, Sumontha and Pauwels, 2008  
*Gekko reevesii* Gray, 1831  
*Gekko siamensis* Grossmann and Ulber, 1990  
*Gekko smithii* Gray, 1842  
*Gekko verreauxi* Tytler, 1865
- GENUS SPARSUSCOLOTES GEN. NOV.**  
*Sparsuscolotes japonicus* (Schlegel, 1836) (type species)  
*Sparsuscolotes aaronbaueri* (Tri, Thai, Phimvohan, David and Teynié, 2015)  
*Sparsuscolotes adleri* (Nguyen, Wang, Yang, Lehmann, Le, Ziegler and Bonkowski, 2013)  
*Sparsuscolotes auriverrucosus* (Zhou and Liu, 1982)  
*Sparsuscolotes bonkowskii* (Luu, Calame, Nguyen, Le and Ziegler, 2015)  
*Sparsuscolotes canhi* Rösler, (Nguyen, Doan, Ho and Ziegler 2010)  
*Sparsuscolotes guishanicus* (Lin and Yao, 2016)  
*Sparsuscolotes hokouensis* (Pope, 1928)  
*Sparsuscolotes kwangsiensis* (Yang, 2015)  
*Sparsuscolotes liboensis* (Zhou and Li, 1982)
- Sparsuscolotes melli* (Vogt, 1922)  
*Sparsuscolotes nadenensis* (Luu, Nguyen, Le, Bonkowski and Ziegler, 2017)  
*Sparsuscolotes palmatus* (Boulenger, 1907)  
*Sparsuscolotes scientiaventura* (Rösler, Ziegler, Vu, Herrmann and Böhme, 2004)  
*Sparsuscolotes scabridus* (Liu and Zhou, 1982)  
*Sparsuscolotes sengchanthavongi* (Luu, Calame, Nguyen, Le and Ziegler, 2015)  
*Sparsuscolotes shibatai* (Toda, Sengoku, Hikida and Ota, 2008)  
*Sparsuscolotes similignum* (Smith, 1923)  
*Sparsuscolotes subpalmatus* (Günther, 1864)  
*Sparsuscolotes swinhonis* (Günther, 1864)  
*Sparsuscolotes taibaiensis* (Song, 1985)  
*Sparsuscolotes tawaensis* (Okada, 1956)  
*Sparsuscolotes thakhekensis* (Luu, Calame, Nguyen, Le, Bonkowski and Ziegler, 2014)  
*Sparsuscolotes truongi* (Phung and Ziegler, 2011)  
*Sparsuscolotes vertebralis* (Toda, Sengoku, Hikida and Ota, 2008)  
*Sparsuscolotes vietnamensis* (Sang, 2010)  
*Sparsuscolotes wenxianensis* (Zhou and Wang, 2008)  
*Sparsuscolotes yakuensis* (Matsui and Okada, 1968)
- SUBGENUS SINOGEKKO SUBGEN. NOV.**  
*Sparsuscolotes (sinogekko) chinensis* (Gray, 1842)
- GENUS LATUSDIGITISCOLOTES GEN. NOV.**  
*Lautusdigituscolotes grossmanni* (Günther, 1994) (type species) (Vietnam)  
*Lautusdigituscolotes canaensis* (Ngo and Gamble, 2011)  
*Lautusdigituscolotes lauhachindai* (Panitvong, Sumontha, Konlek and Kunya, 2010)  
*Lautusdigituscolotes russelltraini* (Ngo, Bauer, Wood and Grismer, 2009)  
*Lautusdigituscolotes takouensis* (Ngo and Gamble, 2010)
- SUBGENUS AURUMGEKKO SUBGEN. NOV.**  
*Lautusdigituscolotes (Aurumgekko) badenii* (Szczerebak and Nekrasova, 1994)
- SUBGENUS GLANDULISCRUSGEKKO SUBGEN. NOV.**  
*Lautusdigituscolotes (Glanduliscrusgekko) petricolus* (Taylor, 1962) (type species)  
*Lautusdigituscolotes (Glanduliscrusgekko) boehmei* (Luu, Calame, Nguyen, Le and Ziegler, 2015)
- GENUS SCELOTRETUS FITZINGER, 1843**  
*Scelotretus vittatus* (Houttuyn, 1782) (type species)  
*Scelotretus remotus* (Rösler, Ineich, Wilms and Böhme, 2012). And three other species named by Raymond Hoser in honour of Dara Nin, Harold Cogger and Jen Anderson, as published in Hoser (2018).
- GENUS MAGNAOCELLUS GEN. NOV.**  
*Magnaocellus athymus* (Brown and Alcalá, 1962) (monotypic)
- GENUS EXTENTUSVENTERSQUAMUS GEN. NOV.**  
*Extentusventersquamus monarchus* (Schlegel, 1836) (type species)  
*Extentusventersquamus carusadensis* (Linkem, Siler, Diesmos, Sy and Brown, 2010)  
*Extentusventersquamus mindorensis* (Taylor, 1919)  
*Extentusventersquamus kikuchii* (Oshima, 1912)  
*Extentusventersquamus palawanensis* (Taylor, 1925)
- SUBGENUS CAVERNAGEKKO SUBGEN. NOV.**  
*Extentusventersquamus (Cavernagekko) ernstkelleri* (Rösler, Siler, Brown, Demeglio and Gaulke, 2006)
- SUBGENUS FODERETDORSUMGEKKO SUBGEN. NOV.**  
*Extentusventersquamus (Foderetdorsumgekko) porosus* (Taylor, 1922) (type species)  
*Extentusventersquamus (Foderetdorsumgekko) coi* (Brown, Siler, Oliveros, Diesmos and Alcalá, 2011)  
*Extentusventersquamus (Foderetdorsumgekko) crombota* (Brown, Oliveros, Siler and Diesmos, 2008)  
*Extentusventersquamus (Foderetdorsumgekko) gigante* (Brown and Alcalá, 1978)  
*Extentusventersquamus (Foderetdorsumgekko) romblon* (Brown and Alcalá, 1978)  
*Extentusventersquamus (Foderetdorsumgekko) rossii* (Brown, Oliveros, Siler and Diesmos, 2009)