

A long overdue genus-level division of the gecko genus *Hemiphyllodactylus* Bleeker, 1860 *sensu lato*.

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ABSTRACT

The gecko genus *Hemiphyllodactylus* Bleeker, 1860 as defined by most recent authors is an assemblage of Asian geckos of conservative morphological divergence. Notwithstanding this, numerous molecular studies have shown the group to consist of a number of significantly ancient divergent lineages. This warrants a split of the genus as is currently recognized in accordance with the rules of the *International Code of Zoological Nomenclature* (Ride *et al.* 1999).

To bring the taxonomy of the group into line with other geckos, the genus *Hemiphyllodactylus* is divided four ways. The largest group of species remains in *Hemiphyllodactylus* but this is divided into two subgenera, the second formally named for the first time.

The available name *Cainodactylus* Barbour, 1924 is resurrected for the *Gehyra yunnanensis* Boulenger, 1903 species group, with it also being divided into two subgenera, the second formally named for the first time.

The so-called *Lepidodactylus harterti* Werner, 1900 group, most recently treated as part of *Hemiphyllodactylus* is split into two newly named genera, one split into two subgenera, all formally named for the first time.

Keywords: Geckos; Taxonomy; nomenclature; Asia; *Gehyra*; *Hemiphyllodactylus*; *Lepidodactylus*; *Cainodactylus*; new genera; *Cassandracambellea*; *Malayacolotes*; new subgenera; *Ferehemiphyllodactylus*; *Maculacruscalotes*; *Titiwangsaacolotes*; new species; *cassandracambellae*.

INTRODUCTION

The Asian gecko genus *Hemiphyllodactylus* Bleeker, 1860 as defined by most recent authors is an assemblage of Asian geckos of conservative morphological divergence.

Over the past two centuries, geckos in this genus and morphologically similar species have been treated as being in a number of different genera including *Gehyra* Gray, 1834, *Hemidactylus* Oken, 1817 and *Lepidodactylus* Fitzinger, 1843.

Molecular studies have largely resolved the overall placement of species within the current taxonomy and available genus group names. However those remaining in the genus *Hemiphyllodactylus* as generally defined as of 2018 are one of a number of putative genus-level groups shown to be deeply divergent in terms of dates of common ancestry.

The relevant species groups are also morphologically divergent from one another.

In combination, this warrants a split of the genus as is currently recognized in accordance with the rules of the *International Code of Zoological Nomenclature* (Ride *et al.* 1999).

As part of a global audit of the planet's herpetofauna and to bring the taxonomy of the group into line with other geckos, the genus *Hemiphyllodactylus* is divided four ways. The largest group of species remains in *Hemiphyllodactylus* but this is divided into two subgenera, the second formally named for the first time.

The available name *Cainodactylus* Barbour, 1924 is resurrected for

the *Gehyra yunnanensis* Boulenger, 1903 species group, with it also being divided into two subgenera, the second formally named for the first time.

The so-called *Lepidodactylus harterti* Werner, 1900 group, most recently treated as part of *Hemiphyllodactylus* is split into two newly named genera, one split into two subgenera, all formally named for the first time.

MATERIALS, METHODS AND RESULTS

These are summarized in the introduction. The basis of the results came from an audit of the relevant species in terms of relevant literature over the past 200 years, combined with examinations of specimens when required.

As mentioned already, *Hemiphyllodactylus* is divided into four genera.

This is in an arrangement that matches phylogenies published by Grismer *et al.* (2017) and where relevant, also Pyron *et al.* (2013). Two genera are formally named for the first time. 6 subgenera are also identified with three being formally named for the first time. Even if a reclassification is done at the most conservative of levels, *Hemiphyllodactylus* would need to be split, with the second genus-level grouping being the so-called *Lepidodactylus harterti* Werner, 1900 group as identified by Grismer *et al.* 2017. However divergences between the two main clades are sufficiently deep to warrant a full genus-level split between the two.

More than ten unnamed species have been identified in the

literature cited herein, but due to statements within these papers by the relevant authors that they intend formally naming them, they have been left unnamed and effectively ignored for the purposes of this paper.

Exceptional to this is a single species treated until now as a subpopulation of "*Hemiphyllodactylus titiwangsaensis* Zug, 2010" herein placed in a newly named genus, which no author has yet stated an intent on naming.

Relevant literature in terms of the taxonomic decisions herein include the following: Baker (2018), Barbour (1924), Bauer and Das (1999), Beddome (1870), Bleeker (1860), Bobrov and Semenov (2008), Boulenger (1885, 1887, 1900, 1903), Brongersma (1931), Brown and Alcalá (1978), Chan-ard *et al.* (2015), Chandramouli *et al.* (2012), Cox *et al.* (1998), Daniels (1994), Das (2004), de Rooij (1915), Gaulke (2011), Gray (1842, 1845), Grismer (2011a, 2011b), Grismer, *et al.* (2010, 2013, 2014, 2015, 2017), Günther (1872), Guo *et al.* (2015), Koch (2012), Malkmus *et al.* (2002), Manthey and Grossmann (1997), Mertens (1930), Pyron *et al.* (2013), Röhl (2006), Rösler (1995, 2017), Sang *et al.* (2009), Schröder and Röhl (2004), Smith (1935), Somaweera and Somaweera (2009), Sukprasert *et al.* (2018), Sung *et al.* (2018), Taylor (1918, 1922, 1953, 1963), Tri *et al.* (2014), Werner (1900), Zhao and Adler (1993), Zhou and Liu (1981), Zhou *et al.* (1996), Zug (1991, 2010), Zug and Kaiser (2014) and sources cited therein.

In terms of the descriptions below the following should be noted. Spellings of names, gender or similar 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). 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).

HEMIPHYLLODACTYLUS BLEEKER, 1860

Type species: *Hemiphyllodactylus typus* Bleeker, 1860.

Diagnosis: The genus *Hemiphyllodactylus* Bleeker, 1860 *sensu lato*, as defined to date is separated from other Asian gecko genera by the following suite of characters: Numerous adhesive lamellae on widened digits; tail is not lobulate; no skin fringe on the side of the body; terminal joints of digits are not united with the widened lamellae, subdigital lamellae are always divided; inner digit is vestigial, without free terminal joint; the claw is minute and often concealed.

Hemiphyllodactylus has now been divided into four genera, two named for the first time and while all conform to the preceding diagnosis, can be separated from one another by the following additional character suites:

Hemiphyllodactylus Bleeker, 1860 type species *H. typus*, as defined herein is separated from the other three genera by one or other of the following five suites of characters:

1/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black; adult females with actively secreting precloacal and femoral pores; unisexual species, all individuals are females; adult size often more than 36 mm SVL, (subgenus *Hemiphyllodactylus* part), or:

2/ Six chin scales; no enlarged postmentals; five circumnasal scales; three or four scales between the supranasals; 12 supralabials; 24 or 25 dorsal scales; 14 ventral scales; a lamellar forefoot formula of 4-5-5-4, 5-5-5-4 or 4-4-5-4; a contiguous femoroprecloacal pore series of 42; five cloacal spurs in males; no enlarged subcaudal scales; no dark postorbital stripes or striping on body; small dark blotches on the upper body; a yellowish postsacral mark bearing anteriorly projecting arms; and a pigmented caecum and gonads (subgenus *Hemiphyllodactylus* part), or:

3/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black, adult females with no or fewer than five secreting precloacal pores; adult size seldom greater than 38 mm SVL; three or four U-shaped digital lamellae under fourth digit of forefoot; dorsal trunk pattern muted, faded and small dark blotches or widely separated dark spots; postsacral mark with U- or V-shaped outer edge of yellow or red; dorsolateral spots yellow or red, (subgenus *Hemiphyllodactylus* part) or:

4/ Chin scales bordering mental scale posteriorly distinctly enlarged, appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series separate; females commonly with precloacal pores; forefoot digital lamellar formula usually 4-4-4-4, (subgenus *Ferehemiphyllodactylus* subgen. nov. part), or:

5/ Chin scales bordering mental scale posteriorly distinctly enlarged appear as a pair of scales usually labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4; adults moderate size, usually less than 42 mm SVL; hindfoot digital lamellar formula usually 3-4-4-4, occasionally higher; postsacral mark without anterior arms; trunk usually without dark dorsolateral stripe; precloacal and femoral pore series continuous usually with less than 23 pores; precloacal and femoral pore series usually more than 18 pores (subgenus *Ferehemiphyllodactylus* subgen. nov. part).

The genera *Cainodactylus* Barbour, 1924, *Cassandrampbellaea* gen. nov. and *Malayacolotes* gen. nov. are each separated from *Hemiphyllodactylus* and *Ferehemiphyllodactylus* subgen. nov. as defined below.

The genus *Cainodactylus* Barbour, 1924, type species *Cainodactylus yunnanensis* Barbour, 1924 is separated from the other three genera by one or other of the following three suites of characters:

1/ Chin scales bordering mental scale posteriorly distinctly enlarged appear as a pair of scales usually labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4; adults moderate size, usually less than 42 mm SVL; hindfoot digital lamellar formula usually 3-4-4-4, occasionally higher; postsacral mark without anterior arms; trunk usually without dark dorsolateral stripe; precloacal and femoral pore series continuous usually with less than 26 pores; precloacal and femoral pore series usually more than 23 pores; postsacral mark of anterior dark blotch and posterior larger light bar or alternatively this marking may be absent (subgenus *Cainodactylus* part), or:

2/ less than 39.5 mm SV length in adults; 7-10 chin scales; 5 circumnasal scales; 1-5 scales between supranasals; 9-12 supralabials; 8-11 infralabials; 16-18 dorsal scale rows; 8-10 ventral scale rows; lamellar formula on forefoot 4-4-4-4; lamellar formula on hindfoot 4-5-5-5; femoral pores absent in both sexes, 9 precloacal pores in males; 1 or 2 cloacal spurs on each side present in both sexes; dark postorbital stripe; no anteriorly projecting arms of postsacral mark, (subgenus *Cainodactylus* part), or:

3/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black; adult females with no or fewer than five secreting precloacal pores; adult size seldom greater than 38 mm SVL; usually two U-shaped digital lamellae under the fourth digit of forefoot; dorsal trunk pattern is bold, transverse dark blotches, longitudinal series of white dorsolateral spots and postsacral mark of dark brown and orange, (subgenus *Maculacruscalotes* subgen. nov.).

The genus *Cassandrampbellaea* gen. nov. type species *Lepidodactylus harterti* Werner, 1900, is separated from the other three genera by the following suite of characters: Chin scales bordering mental scale posteriorly distinctly enlarged and appear

as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, rarely higher; adults of moderate size, usually less than 42 mm SVL; postsacral mark without anterior arms; trunk usually with a distinct dark dorsolateral stripe; precloacal and femoral pore series continuous with 44-45 pores in males and a single cloacal spur.

The genus *Malayacolotes* gen. nov. type species *Gehyra larutensis* Boulenger, 1900 is separated from the other three genera by one or other of the following suites of characters:

1/ Chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, rarely higher; adults of moderate size, usually less than 42 mm SVL; postsacral mark without anterior arms; trunk usually with a distinct dark dorsolateral stripe; precloacal and femoral pore series continuous with 2-36 pores in males and two to three cloacal spurs (subgenus *Malayacolotes* gen. nov.), or:

2/ Adults large, usually more than 45 mm SVL; chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous usually more than 22 (17-39) pores; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, hindfoot digital lamellar formula is usually 4-4-5-5 or 4-5-5-5; postsacral mark with anterior arms (subgenus *Tituwangsacolotes* subgen. nov.).

Distribution: South-east Asia, mainly Indonesia, but introduced elsewhere in south-east Asia and the Pacific.

Content: *Hemiphyllodactylus typus* Bleeker, 1860 (type species); *H. changningensis* Guo, Zhou, Yan and Li, 2015; *H. chiangmaiensis* Grismer, Wood and Cota, 2014; *H. engganoensis* Grismer, Riyanto, Iskander and McGuire, 2014; *H. ganoklonis* Zug, 2010; *H. insularis* Taylor, 1918; *H. jinpingensis* (Zhou and Liu, 1981); *H. khlonglanensis* Sukprasert, Sutthiwises, Lauhachinda and Taksintum, 2018; *H. linnwayensis* Grismer, Wood, Thura, Zin, Quah, Murdoch, Grismer, Li, Kyaw and Lwin, 2017; *H. longlingensis* (Zhou and Liu, 1981); *H. margarethae* Brongersma, 1931; *H. montawaensis* Grismer, Wood, Thura, Zin, Quah, Murdoch, Grismer, Li, Kyaw and Lwin, 2017; *H. tonywhiteni* Grismer, Wood, Thura, Zin, Quah, Murdoch, Grismer, Li, Kyaw and Lwin, 2017.

SUBGENUS FEREHEMIPHYLLODACTYLUS SUBGEN. NOV.

LSID urn:lsid:zoobank.org:act:41718D5B-5496-4215-9996-084000CF3FB1

Type species: *Hemiphyllodactylus yunnanensis jinpingensis* Zhou and Liu, 1981.

Diagnosis: The genus *Hemiphyllodactylus* Bleeker, 1860 *sensu lato*, as defined to date is separated from other Asian gecko genera by the following suite of characters: Numerous adhesive lamellae on widened digits; tail is not lobulate; no skin fringe on the side of the body; terminal joints of digits are not united with the widened lamellae, subdigital lamellae are always divided; inner digit is vestigial, without free terminal joint; the claw is minute and often concealed.

Hemiphyllodactylus has now been divided into four genera, two named for the first time and while all conform to the preceding diagnosis, can be separated from one another by the following additional character suites:

Hemiphyllodactylus Bleeker, 1860 type species *H. typus*, as defined herein is separated from the other three genera by one or other of the following five suites of characters:

1/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black; adult females with actively secreting precloacal and femoral pores; unisexual species, all individuals are females; adult size

often more than 36 mm SVL, (subgenus *Hemiphyllodactylus* part), or:

2/ Six chin scales; no enlarged postmentals; five circumnasal scales; three or four scales between the supranasals; 12 supralabials; 24 or 25 dorsal scales; 14 ventral scales; a lamellar forefoot formula of 4-5-5-4, 5-5-5-4 or 4-4-5-4; a contiguous femoroprecloacal pore series of 42; five cloacal

spurs in males; no enlarged subcaudal scales; no dark postorbital stripes or striping on body; small dark blotches on the upper body; a yellowish postsacral mark bearing anteriorly projecting arms; and a pigmented caecum and gonads (subgenus *Hemiphyllodactylus* part), or:

3/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black, adult females with no or fewer than five secreting precloacal pores; adult size seldom greater than 38 mm SVL; three or four U-shaped digital lamellae under fourth digit of forefoot; dorsal trunk pattern muted, faded and small dark blotches or widely separated dark spots; postsacral mark with U- or V-shaped outer edge of yellow or red; dorsolateral spots yellow or red, (subgenus *Hemiphyllodactylus* part) or:

4/ Chin scales bordering mental scale posteriorly distinctly enlarged, appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series separate; females commonly with precloacal pores; forefoot digital lamellar formula usually 4-4-4-4, (subgenus *Ferehemiphyllodactylus* subgen. nov. part), or:

5/ Chin scales bordering mental scale posteriorly distinctly enlarged appear as a pair of scales usually labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4; adults moderate size, usually less than 42 mm SVL; hindfoot digital lamellar formula usually 3-4-4-4, occasionally higher; postsacral mark without anterior arms; trunk usually without dark dorsolateral stripe; precloacal and femoral pore series continuous usually with less than 23 pores; precloacal and femoral pore series usually more than 18 pores (subgenus *Ferehemiphyllodactylus* subgen. nov. part).

The genus *Cainodactylus* Barbour, 1924, type species *Cainodactylus yunnanensis* Barbour, 1924 is separated from the other three genera by one or other of the following three suites of characters:

1/ Chin scales bordering mental scale posteriorly distinctly enlarged appear as a pair of scales usually labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4; adults moderate size, usually less than 42 mm SVL; hindfoot digital lamellar formula usually 3-4-4-4, occasionally higher; postsacral mark without anterior arms; trunk usually without dark dorsolateral stripe; precloacal and femoral pore series continuous usually with less than 26 pores; precloacal and femoral pore series usually more than 23 pores; postsacral mark of anterior dark blotch and posterior larger light bar or alternatively this marking may be absent (subgenus *Cainodactylus* part), or:

2/ less than 39.5 mm SV length in adults; 7-10 chin scales; 5 circumnasal scales; 1-5 scales between supranasals; 9-12 supralabials; 8-11 infralabials; 16-18 dorsal scale rows; 8-10 ventral scale rows; lamellar formula on forefoot 4-4-4-4; lamellar formula on hindfoot 4-5-5-5; femoral pores absent in both sexes, 9 precloacal pores in males; 1 or 2 cloacal spurs on each side present in both sexes; dark postorbital stripe; no anteriorly projecting arms of postsacral mark, (subgenus *Cainodactylus* part), or:

3/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black; adult females with no or fewer than five secreting precloacal pores; adult size seldom greater than 38 mm SVL; usually two U-shaped

digital lamellae under the fourth digit of forefoot; dorsal trunk pattern is bold, transverse dark blotches, longitudinal series of white dorsolateral spots and postsacral mark of dark brown and orange, (subgenus *Maculacruscalotes* subgen. nov.).

The genus *Cassandraccampbellae* gen. nov. type species *Lepidodactylus harterti* Werner, 1900, is separated from the other three genera by the following suite of characters: Chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, rarely higher; adults of moderate size, usually less than 42 mm SVL; postsacral mark without anterior arms; trunk usually with a distinct dark dorsolateral stripe; precloacal and femoral pore series continuous with 44-45 pores in males and a single cloacal spur.

The genus *Malayacolotes* gen. nov. type species *Gehyra larutensis* Boulenger, 1900 is separated from the other three genera by one or other of the following suites of characters:

1/ Chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, rarely higher; adults of moderate size, usually less than 42 mm SVL; postsacral mark without anterior arms; trunk usually with a distinct dark dorsolateral stripe; precloacal and femoral pore series continuous with 2-36 pores in males and two to three cloacal spurs (subgenus *Malayacolotes* gen. nov.), or:

2/ Adults large, usually more than 45 mm SVL; chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous usually more than 22 (17-39) pores; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, hindfoot digital lamellar formula is usually 4-4-5-5 or 4-5-5-5; postsacral mark with anterior arms (subgenus *Titiwangsacolotes* subgen. nov.).

Distribution: Southern China, Thailand and Myanmar.

Etymology: In Latin *Ferehemiphyllodactylus* means not quite *Hemiphyllodactylus*.

Content: *Hemiphyllodactylus* (*Ferehemiphyllodactylus*) *jinpingensis* (Zhou and Liu, 1981) (type species); *H. (Ferehemiphyllodactylus) changningensis* Guo, Zhou, Yan and Li, 2015; *H. (Ferehemiphyllodactylus) Chiangmaiensis* Grismer, Wood and Cota, 2014; *H. (Ferehemiphyllodactylus) khlonglanensis* Sukprasert, Sutthiwise, Lauhachinda and Taksintum, 2018; *H. (Ferehemiphyllodactylus) linnwayensis* Grismer, Wood, Thura, Zin, Quah, Murdoch, Grismer, Li, Kyaw and Lwin, 2017; *H. (Ferehemiphyllodactylus) longlingensis* (Zhou and Liu, 1981); *H. (Ferehemiphyllodactylus) montawaensis* Grismer, Wood, Thura, Zin, Quah, Murdoch, Grismer, Li, Kyaw and Lwin, 2017; *H. (Ferehemiphyllodactylus) tonywhitteni* Grismer, Wood, Thura, Zin, Quah, Murdoch, Grismer, Li, Kyaw and Lwin, 2017.

Content of the nominate subgenus *Hemiphyllodactylus*

Bleeker, 1860: *Hemiphyllodactylus typus* Bleeker, 1860 (type species); *H. (Hemiphyllodactylus) engganoensis* Grismer, Riyanto, Iskander and McGuire, 2014; *H. (Hemiphyllodactylus) ganoklonis* Zug, 2010; *H. (Hemiphyllodactylus) insularis* Taylor, 1918; *H. (Hemiphyllodactylus) margarethae* Brongersma, 1931.

GENUS CAINODACTYLUS BARBOUR, 1924.

Type species: *Gehyra yunnanensis* Boulenger, 1903.

Diagnosis: The genus *Hemiphyllodactylus* Bleeker, 1860 *sensu lato*, as defined to date is separated from other Asian gecko genera by the following suite of characters: Numerous adhesive lamellae on widened digits; tail is not lobulate; no skin fringe on the side of the body; terminal joints of digits are not united with the widened lamellae, subdigital lamellae are always divided; inner digit is vestigial, without free terminal joint; the claw is minute and often concealed.

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2/ Six chin scales; no enlarged postmentals; five circumnasal scales; three or four scales between the supranasals; 12 supralabials; 24 or 25 dorsal scales; 14 ventral scales; a lamellar forefoot formula of 4-5-5-4, 5-5-5-4 or 4-4-5-4; a contiguous femoroprecloacal pore series of 42; five cloacal

spurs in males; no enlarged subcaudal scales; no dark postorbital stripes or striping on body; small dark blotches on the upper body; a yellowish postsacral mark bearing anteriorly projecting arms; and a pigmented caecum and gonads (subgenus *Hemiphyllodactylus* part), or:

3/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black, adult females with no or fewer than five secreting precloacal pores; adult size seldom greater than 38 mm SVL; three or four U-shaped digital lamellae under fourth digit of forefoot; dorsal trunk pattern muted, faded and small dark blotches or widely separated dark spots; postsacral mark with U- or V-shaped outer edge of yellow or red; dorsolateral spots yellow or red, (subgenus *Hemiphyllodactylus* part) or:

4/ Chin scales bordering mental scale posteriorly distinctly enlarged, appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series separate; females commonly with precloacal pores; forefoot digital lamellar formula usually 4-4-4-4, (subgenus *Ferehemiphyllodactylus* subgen. nov. part), or:

5/ Chin scales bordering mental scale posteriorly distinctly enlarged appear as a pair of scales usually labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4; adults moderate size, usually less than 42 mm SVL; hindfoot digital lamellar formula usually 3-4-4-4, occasionally higher; postsacral mark without anterior arms; trunk usually without dark dorsolateral stripe; precloacal and femoral pore series continuous usually with less than 23 pores; precloacal and femoral pore series usually more than 18 pores (subgenus *Ferehemiphyllodactylus* subgen. nov. part).

The genera *Cainodactylus* Barbour, 1924, *Cassandraccampbellae* gen. nov. and *Malayacolotes* gen. nov. are each separated from *Hemiphyllodactylus* and *Ferehemiphyllodactylus* subgen. nov. as defined below.

The genus *Cainodactylus* Barbour, 1924, type species *Cainodactylus yunnanensis* Barbour, 1924 is separated from the other three genera by one or other of the following three suites of characters:

1/ Chin scales bordering mental scale posteriorly distinctly enlarged appear as a pair of scales usually labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4; adults moderate size, usually less than 42 mm SVL; hindfoot digital lamellar formula usually 3-4-4-4, occasionally higher; postsacral mark without anterior arms; trunk usually without dark dorsolateral stripe; precloacal and femoral pore series continuous usually with less than 26 pores; precloacal and femoral pore series usually more than 23 pores; postsacral mark of anterior dark blotch

and posterior larger light bar or alternatively this marking may be absent (subgenus *Cainodactylus* part), or:

2/ less than 39.5 mm SV length in adults; 7-10 chin scales; 5 circumnasal scales; 1-5 scales between supranasals; 9-12 supralabials; 8-11 infralabials; 16-18 dorsal scale rows; 8-10 ventral scale rows; lamellar formula on forefoot 4-4-4-4; lamellar formula on hindfoot 4-5-5-5; femoral pores absent in both sexes, 9 precloacal pores in males; 1 or 2 cloacal spurs on each side present in both sexes; dark postorbital stripe; no anteriorly projecting arms of postsacral mark, (subgenus *Cainodactylus* part), or:

3/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black; adult females with no or fewer than five secreting precloacal pores; adult size seldom greater than 38 mm SVL; usually two U-shaped digital lamellae under the fourth digit of forefoot; dorsal trunk pattern is bold, transverse dark blotches, longitudinal series of white dorsolateral spots and postsacral mark of dark brown and orange, (subgenus *Maculacruscalotes* subgen. nov.).

The genus *Cassandrampellea* gen. nov. type species *Lepidodactylus harterti* Werner, 1900, is separated from the other three genera by the following suite of characters: Chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, rarely higher; adults of moderate size, usually less than 42 mm SVL; postsacral mark without anterior arms; trunk usually with a distinct dark dorsolateral stripe; precloacal and femoral pore series continuous with 44-45 pores in males and a single cloacal spur.

The genus *Malayacolotes* gen. nov. type species *Gehyra larutensis* Boulenger, 1900 is separated from the other three genera by one or other of the following suites of characters:

1/ Chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, rarely higher; adults of moderate size, usually less than 42 mm SVL; postsacral mark without anterior arms; trunk usually with a distinct dark dorsolateral stripe; precloacal and femoral pore series continuous with 2-36 pores in males and two to three cloacal spurs (subgenus *Malayacolotes* gen. nov.), or:

2/ Adults large, usually more than 45 mm SVL; chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous usually more than 22 (17-39) pores; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, hindfoot digital lamellar formula is usually 4-4-5-5 or 4-5-5-5; postsacral mark with anterior arms (subgenus *Titivangsacalotes* subgen. nov.).

Content: *Cainodactylus yunnanensis* (Boulenger, 1903) (type species); *C. aurantiacus* (Beddome, 1870);

C. banaensis (Tri, Grismer, Thai and Wood, 2014); *C. dushanensis* (Zhou and Liu, 1981); *C. flaviventris* (Sukprasert, Sutthiwiwes, Lanhachinda and Taksintum, 2018); *C. hongkongensis* (Sung, Lee, Ng, Zhang and Yang, 2018); *C. huishuiensis* (Yan, Lin, Guo, Li and Zhou, 2016); *C. kiziriani* (Nguyen, Botov, Le Duc, Nophaseud, Bonkowski and Zeigler, 2014); *C. zugi* (Nguyen, Lehmann, Le Duc, Duong, Bonkowski and Ziegler, 2013).

Distribution: Southern Asia from China to the Indian Subcontinent.

SUBGENUS MACULACRUSCALOTES SUBGEN. NOV.

LSID urn:lsid:zoobank.org:act:3DBAE10D-3395-4D61-8959-DCAFA332AF96

Type species: *Hemidactylus aurantiacus* Beddome, 1870.

Diagnosis: The genus *Hemiphyllodactylus* Bleeker, 1860 *sensu*

lato, as defined to date is separated from other Asian gecko genera by the following suite of characters: Numerous adhesive lamellae on widened digits; tail is not lobulate; no skin fringe on the side of the body; terminal joints of digits are not united with the widened lamellae, subdigital lamellae are always divided; inner digit is vestigial, without free terminal joint; the claw is minute and often concealed.

Hemiphyllodactylus has now been divided into four genera, two named for the first time and while all conform to the preceding diagnosis, can be separated from one another by the following additional character suites:

Hemiphyllodactylus Bleeker, 1860 type species *H. typus*, as defined herein is separated from the other three genera by one or other of the following five suites of characters:

1/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black; adult females with actively secreting precloacal and femoral pores; unisexual species, all individuals are females; adult size often more than 36 mm SVL, (subgenus *Hemiphyllodactylus* part), or:

2/ Six chin scales; no enlarged postmentals; five circumnasal scales; three or four scales between the supranasals; 12 supralabials; 24 or 25 dorsal scales; 14 ventral scales; a lamellar forefoot formula of 4-5-5-4, 5-5-5-4 or 4-4-5-4; a contiguous femoroprecloacal pore series of 42; five cloacal

spurs in males; no enlarged subcaudal scales; no dark postorbital stripes or striping on body; small dark blotches on the upper body; a yellowish postsacral mark bearing anteriorly projecting arms; and a pigmented caecum and gonads (subgenus *Hemiphyllodactylus* part), or:

3/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black, adult females with no or fewer than five secreting precloacal pores; adult size seldom greater than 38 mm SVL; three or four U-shaped digital lamellae under fourth digit of forefoot; dorsal trunk pattern muted, faded and small dark blotches or widely separated dark spots; postsacral mark with U- or V-shaped outer edge of yellow or red; dorsolateral spots yellow or red, (subgenus *Hemiphyllodactylus* part) or:

4/ Chin scales bordering mental scale posteriorly distinctly enlarged, appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series separate; females commonly with precloacal pores; forefoot digital lamellar formula usually 4-4-4-4, (subgenus *Ferehemiphyllodactylus* subgen. nov. part), or:

5/ Chin scales bordering mental scale posteriorly distinctly enlarged appear as a pair of scales usually labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4; adults moderate size, usually less than 42 mm SVL; hindfoot digital lamellar formula usually 3-4-4-4, occasionally higher; postsacral mark without anterior arms; trunk usually without dark dorsolateral stripe; precloacal and femoral pore series continuous usually with less than 23 pores; precloacal and femoral pore series usually more than 18 pores (subgenus *Ferehemiphyllodactylus* subgen. nov. part).

The genera *Cainodactylus* Barbour, 1924, *Cassandrampellea* gen. nov. and *Malayacolotes* gen. nov. are each separated from *Hemiphyllodactylus* and *Ferehemiphyllodactylus* subgen. nov. as defined below,

The genus *Cainodactylus* Barbour, 1924, type species *Cainodactylus yunnanensis* Barbour, 1924 is separated from the other three genera by one or other of the following three suites of characters:

1/ Chin scales bordering mental scale posteriorly distinctly enlarged appear as a pair of scales usually labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack

precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4; adults moderate size, usually less than 42 mm SVL; hindfoot digital lamellar formula usually 3-4-4-4, occasionally higher; postsacral mark without anterior arms; trunk usually without dark dorsolateral stripe; precloacal and femoral pore series continuous usually with less than 26 pores; precloacal and femoral pore series usually more than 23 pores; postsacral mark of anterior dark blotch and posterior larger light bar or alternatively this marking may be absent (subgenus *Cainodactylus* part), or:

2/ less than 39.5 mm SV length in adults; 7-10 chin scales; 5 circumnasal scales; 1-5 scales between supranasals; 9-12 supralabials; 8-11 infralabials; 16-18 dorsal scale rows; 8-10 ventral scale rows; lamellar formula on forefoot 4-4-4-4; lamellar formula on hindfoot 4-5-5-5; femoral pores absent in both sexes, 9 precloacal pores in males; 1 or 2 cloacal spurs on each side present in both sexes; dark postorbital stripe; no anteriorly projecting arms of postsacral mark, (subgenus *Cainodactylus* part), or:

3/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black; adult females with no or fewer than five secreting precloacal pores; adult size seldom greater than 38 mm SVL; usually two U-shaped digital lamellae under the fourth digit of forefoot; dorsal trunk pattern is bold, transverse dark blotches, longitudinal series of white dorsolateral spots and postsacral mark of dark brown and orange, (subgenus *Maculacruscalotes* subgen. nov.) the preceding being diagnostic for the subgenus *Maculacruscalotes* subgen. nov.. *Maculacruscalotes* subgen. nov. is treated herein as monotypic for *M. aurantiacus* (Beddome, 1870). However there are number of unnamed species currently identified as the single taxon which await formal scientific description.

The genus *Cassandracampbelllea* gen. nov. type species *Lepidodactylus harterti* Werner, 1900, is separated from the other three genera by the following suite of characters: Chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, rarely higher; adults of moderate size, usually less than 42 mm SVL; postsacral mark without anterior arms; trunk usually with a distinct dark dorsolateral stripe; precloacal and femoral pore series continuous with 44-45 pores in males and a single cloacal spur.

The genus *Malayacolotes* gen. nov. type species *Gehyra larutensis* Boulenger, 1900 is separated from the other three genera by one or other of the following suites of characters:

1/ Chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, rarely higher; adults of moderate size, usually less than 42 mm SVL; postsacral mark without anterior arms; trunk usually with a distinct dark dorsolateral stripe; precloacal and femoral pore series continuous with 2-36 pores in males and two to three cloacal spurs (subgenus *Malayacolotes* gen. nov.), or:

2/ Adults large, usually more than 45 mm SVL; chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous usually more than 22 (17-39) pores; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, hindfoot digital lamellar formula is usually 4-4-5-5 or 4-5-5-5; postsacral mark with anterior arms (subgenus *Titiwangsacolotes* subgen. nov.).

Distribution: India (mainly western Ghats) and one or more locations in the Himalayan foothills and nearby ranges to the east, generally at high elevation localities.

Etymology: In Latin *Maculacruscalotes* means spotted legged gecko.

Content: *Maculacruscalotes aurantiacus* (Beddome, 1870) (type species) (species complex).

GENUS CASSANDRACAMPBELLEA GEN. NOV.

LSID urn:lsid:zoobank.org:act:2D47E3D4-7344-482C-B6BF-EEAE45DE201

Type species: *Lepidodactylus harterti* Werner, 1900.

Diagnosis: The genus *Hemiphyllodactylus* Bleeker, 1860 *sensu lato*, as defined to date is separated from other Asian gecko genera by the following suite of characters: Numerous adhesive lamellae on widened digits; tail is not lobulate; no skin fringe on the side of the body; terminal joints of digits are not united with the widened lamellae, subdigital lamellae are always divided; inner digit is vestigial, without free terminal joint; the claw is minute and often concealed.

Hemiphyllodactylus has now been divided into four genera, two named for the first time and while all conform to the preceding diagnosis, can be separated from one another by the following additional character suites:

Hemiphyllodactylus Bleeker, 1860 type species *H. typus*, as defined herein is separated from the other three genera by one or other of the following five suites of characters:

1/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black; adult females with actively secreting precloacal and femoral pores; unisexual species, all individuals are females; adult size often more than 36 mm SVL, (subgenus *Hemiphyllodactylus* part), or:

2/ Six chin scales; no enlarged postmentals; five circumnasal scales; three or four scales between the supranasals; 12 supralabials; 24 or 25 dorsal scales; 14 ventral scales; a lamellar forefoot formula of 4-5-5-4, 5-5-5-4 or 4-4-5-4; a contiguous femoroprecloacal pore series of 42; five cloacal

spurs in males; no enlarged subcaudal scales; no dark postorbital stripes or striping on body; small dark blotches on the upper body; a yellowish postsacral mark bearing anteriorly projecting arms; and a pigmented caecum and gonads (subgenus *Hemiphyllodactylus* part), or:

3/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black, adult females with no or fewer than five secreting precloacal pores; adult size seldom greater than 38 mm SVL; three or four U-shaped digital lamellae under fourth digit of forefoot; dorsal trunk pattern muted, faded and small dark blotches or widely separated dark spots; postsacral mark with U- or V-shaped outer edge of yellow or red; dorsolateral spots yellow or red, (subgenus *Hemiphyllodactylus* part) or:

4/ Chin scales bordering mental scale posteriorly distinctly enlarged, appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series separate; females commonly with precloacal pores; forefoot digital lamellar formula usually 4-4-4-4, (subgenus *Ferehemiphyllodactylus* subgen. nov. part), or:

5/ Chin scales bordering mental scale posteriorly distinctly enlarged appear as a pair of scales usually labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4; adults moderate size, usually less than 42 mm SVL; hindfoot digital lamellar formula usually 3-4-4-4, occasionally higher; postsacral mark without anterior arms; trunk usually without dark dorsolateral stripe; precloacal and femoral pore series continuous usually with less than 23 pores; precloacal and femoral pore series usually more than 18 pores (subgenus *Ferehemiphyllodactylus* subgen. nov. part).

The genera *Cainodactylus* Barbour, 1924, *Cassandracampbelllea* gen. nov. and *Malayacolotes* gen. nov. are each separated from *Hemiphyllodactylus* and *Ferehemiphyllodactylus* subgen. nov. as defined below (next page):

The genus *Cainodactylus* Barbour, 1924, type species *Cainodactylus yunnanensis* Barbour, 1924 is separated from the other three genera by one or other of the following three suites of characters:

1/ Chin scales bordering mental scale posteriorly distinctly enlarged appear as a pair of scales usually labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4; adults moderate size, usually less than 42 mm SVL; hindfoot digital lamellar formula usually 3-4-4-4, occasionally higher; postsacral mark without anterior arms; trunk usually without dark dorsolateral stripe; precloacal and femoral pore series continuous usually with less than 26 pores; precloacal and femoral pore series usually more than 23 pores; postsacral mark of anterior dark blotch and posterior larger light bar or alternatively this marking may be absent (subgenus *Cainodactylus* part), or:

2/ less than 39.5 mm SV length in adults; 7-10 chin scales; 5 circumnasal scales; 1-5 scales between supranasals; 9-12 supralabials; 8-11 infralabials; 16-18 dorsal scale rows; 8-10 ventral scale rows; lamellar formula on forefoot 4-4-4-4; lamellar formula on hindfoot 4-5-5-5; femoral pores absent in both sexes, 9 precloacal pores in males; 1 or 2 cloacal spurs on each side present in both sexes; dark postorbital stripe; no anteriorly projecting arms of postsacral mark, (subgenus *Cainodactylus* part), or:

3/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black; adult females with no or fewer than five secreting precloacal pores; adult size seldom greater than 38 mm SVL; usually two U-shaped digital lamellae under the fourth digit of forefoot; dorsal trunk pattern is bold, transverse dark blotches, longitudinal series of white dorsolateral spots and postsacral mark of dark brown and orange, (subgenus *Maculacruscalotes* subgen. nov.).

Maculacruscalotes subgen. nov. is treated herein as monotypic for *M. aurantiacus* (Beddome, 1870). However there are number of unnamed species currently identified as the single taxon which await formal scientific description.

The genus *Cassandracampbellae* gen. nov. type species *Lepidodactylus harterti* Werner, 1900, is separated from the other three genera by the following suite of characters and diagnosis: Chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, rarely higher; adults of moderate size, usually less than 42 mm SVL; postsacral mark without anterior arms; trunk usually with a distinct dark dorsolateral stripe; precloacal and femoral pore series continuous with 44-45 pores in males and a single cloacal spur.

The genus *Malayacolotes* gen. nov. type species *Gehyra larutensis* Boulenger, 1900 is separated from the other three genera by one or other of the following suites of characters:

1/ Chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, rarely higher; adults of moderate size, usually less than 42 mm SVL; postsacral mark without anterior arms; trunk usually with a distinct dark dorsolateral stripe; precloacal and femoral pore series continuous with 2-36 pores in males and two to three cloacal spurs (subgenus *Malayacolotes* gen. nov.), or:

2/ Adults large, usually more than 45 mm SVL; chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous usually more than 22 (17-39) pores; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, hindfoot digital lamellar formula is usually 4-4-5-5 or 4-5-5-5;

postsacral mark with anterior arms (subgenus *Titivangsacolotes* subgen. nov.).

Distribution: Restricted to West Malaysia.

Etymology: Named in honour of Cassandra Campbell, of Bexley, NSW, Australia, a lawyer working with Alex Tees (also a lawyer from Sydney, NSW), for services to wildlife conservation spanning some decades.

Content: *Cassandracampbellae harterti* (Werner, 1900) (type species); *C. bintik* (Grismer, Wood, Anuar, Quah, Muin, Onn, Sumarli and Lored, 2015); *C. cicak* (Cobos, Grismer, Wood, Quah, Anuar and Muin, 2016).

GENUS MALAYOCOLOTES GEN. NOV.

LSID urn:lsid:zoobank.org:act:5034000B-77C0-49FC-B436-133563B3D80A

Type species: *Gehyra larutensis* Boulenger, 1900.

Diagnosis: The genus *Hemiphyllodactylus* Bleeker, 1860 *sensu lato*, as defined to date is separated from other Asian gecko genera by the following suite of characters: Numerous adhesive lamellae on widened digits; tail is not lobulate; no skin fringe on the side of the body; terminal joints of digits are not united with the widened lamellae, subdigital lamellae are always divided; inner digit is vestigial, without free terminal joint; the claw is minute and often concealed.

Hemiphyllodactylus has now been divided into four genera, two named for the first time and while all conform to the preceding diagnosis, can be separated from one another by the following additional character suites:

Hemiphyllodactylus Bleeker, 1860 type species *H. typus*, as defined herein is separated from the other three genera by one or other of the following five suites of characters:

1/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black; adult females with actively secreting precloacal and femoral pores; unisexual species, all individuals are females; adult size often more than 36 mm SVL, (subgenus *Hemiphyllodactylus* part), or:

2/ Six chin scales; no enlarged postmentals; five circumnasal scales; three or four scales between the supranasals; 12 supralabials; 24 or 25 dorsal scales; 14 ventral scales; a lamellar forefoot formula of 4-5-5-4, 5-5-5-4 or 4-4-5-4; a contiguous femoroprecloacal pore series of 42; five cloacal

spurs in males; no enlarged subcaudal scales; no dark postorbital stripes or striping on body; small dark blotches on the upper body; a yellowish postsacral mark bearing anteriorly projecting arms; and a pigmented caecum and gonads (subgenus *Hemiphyllodactylus* part), or:

3/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black, adult females with no or fewer than five secreting precloacal pores; adult size seldom greater than 38 mm SVL; three or four U-shaped digital lamellae under fourth digit of forefoot; dorsal trunk pattern muted, faded and small dark blotches or widely separated dark spots; postsacral mark with U- or V-shaped outer edge of yellow or red; dorsolateral spots yellow or red, (subgenus *Hemiphyllodactylus* part) or:

4/ Chin scales bordering mental scale posteriorly distinctly enlarged, appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series separate; females commonly with precloacal pores; forefoot digital lamellar formula usually 4-4-4-4, (subgenus *Ferehemiphyllodactylus* subgen. nov. part), or:

5/ Chin scales bordering mental scale posteriorly distinctly enlarged appear as a pair of scales usually labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4; adults moderate size, usually less than 42 mm SVL; hindfoot digital lamellar formula usually 3-4-4-4, occasionally higher;

postsacral mark without anterior arms; trunk usually without dark dorsolateral stripe; precloacal and femoral pore series continuous usually with less than 23 pores; precloacal and femoral pore series usually more than 18 pores (subgenus *Ferehemiphyllodactylus* subgen. nov. part).

The genera *Cainodactylus* Barbour, 1924, *Cassandrampbellaea* gen. nov. and *Malayacolotes* gen. nov. are each separated from *Hemiphyllodactylus* and *Ferehemiphyllodactylus* subgen. nov. as defined below,

The genus *Cainodactylus* Barbour, 1924, type species *Cainodactylus yunnanensis* Barbour, 1924 is separated from the other three genera by one or other of the following three suites of characters:

1/ Chin scales bordering mental scale posteriorly distinctly enlarged appear as a pair of scales usually labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4; adults moderate size, usually less than 42 mm SVL; hindfoot digital lamellar formula usually 3-4-4-4, occasionally higher; postsacral mark without anterior arms; trunk usually without dark dorsolateral stripe; precloacal and femoral pore series continuous usually with less than 26 pores; precloacal and femoral pore series usually more than 23 pores; postsacral mark of anterior dark blotch and posterior larger light bar or alternatively this marking may be absent (subgenus *Cainodactylus* part), or:

2/ less than 39.5 mm SV length in adults; 7-10 chin scales; 5 circumnasal scales; 1-5 scales between supranasals; 9-12 supralabials; 8-11 infralabials; 16-18 dorsal scale rows; 8-10 ventral scale rows; lamellar formula on forefoot 4-4-4-4; lamellar formula on hindfoot 4-5-5-5; femoral pores absent in both sexes, 9 precloacal pores in males; 1 or 2 cloacal spurs on each side present in both sexes; dark postorbital stripe; no anteriorly projecting arms of postsacral mark, (subgenus *Cainodactylus* part), or:

3/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black; adult females with no or fewer than five secreting precloacal pores; adult size seldom greater than 38 mm SVL; usually two U-shaped digital lamellae under the fourth digit of forefoot; dorsal trunk pattern is bold, transverse dark blotches, longitudinal series of white dorsolateral spots and postsacral mark of dark brown and orange, (subgenus *Maculacruscalotes* subgen. nov.). *Maculacruscalotes* subgen. nov. is treated herein as monotypic for *M. aurantiacus* (Beddome, 1870). However there are number of unnamed species currently identified as the single taxon which await formal scientific description.

The genus *Cassandrampbellaea* gen. nov. type species *Lepidodactylus harterti* Werner, 1900, is separated from the other three genera by the following suite of characters: Chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, rarely higher; adults of moderate size, usually less than 42 mm SVL; postsacral mark without anterior arms; trunk usually with a distinct dark dorsolateral stripe; precloacal and femoral pore series continuous with 44-45 pores in males and a single cloacal spur.

The genus *Malayacolotes* gen. nov. type species *Gehyra larutensis* Boulenger, 1900 is separated from the other three genera by way of diagnosis by one or other of the following suites of characters:

1/ Chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, rarely higher; adults of moderate size, usually less than 42 mm SVL; postsacral mark without anterior arms; trunk usually with a distinct dark dorsolateral stripe; precloacal and femoral pore series

continuous with 2-36 pores in males and two to three cloacal spurs (subgenus *Malayacolotes* gen. nov.), or:

2/ Adults large, usually more than 45 mm SVL; chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous usually more than 22 (17-39) pores; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, hindfoot digital lamellar formula is usually 4-4-5-5 or 4-5-5-5; postsacral mark with anterior arms (subgenus *Titiwangsaacolotes* subgen. nov.).

Distribution: Peninsular Malaysia.

Etymology: *Malayacolotes* in Latin means gecko from Malaya.

Content: *Malayacolotes larutensis* (Boulenger, 1900) (type species); *M. cassandrampbellaea* sp. nov.; *M. tehtarik* (Grismer, Wood Jnr., Anuar, Muin, Quah, McGuire, Brown, Tri and Thai, 2013); *M. titiawangsaensis* (Zug, 2010)

SUBGENUS TITIWANGSACOLOTES SUBGEN. NOV.

LSID urn:lsid:zoobank.org:act:ED618285-C7A5-4F26-8CBF-4F21D7AB9297

Type species: *Hemiphyllodactylus titiawangsaensis* Zug, 2010.

Diagnosis: The genus *Hemiphyllodactylus* Bleeker, 1860 *sensu lato*, as defined to date is separated from other Asian gecko genera by the following suite of characters: Numerous adhesive lamellae on widened digits; tail is not lobulate; no skin fringe on the side of the body; terminal joints of digits are not united with the widened lamellae, subdigital lamellae are always divided; inner digit is vestigial, without free terminal joint; the claw is minute and often concealed.

Hemiphyllodactylus has now been divided into four genera, two named for the first time and while all conform to the preceding diagnosis, can be separated from one another by the following additional character suites:

Hemiphyllodactylus Bleeker, 1860 type species *H. typus*, as defined herein is separated from the other three genera by one or other of the following five suites of characters:

1/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black; adult females with actively secreting precloacal and femoral pores; unisexual species, all individuals are females; adult size often more than 36 mm SVL, (subgenus *Hemiphyllodactylus* part), or:

2/ Six chin scales; no enlarged postmentals; five circumnasal scales; three or four scales between the supranasals; 12 supralabials; 24 or 25 dorsal scales; 14 ventral scales; a lamellar forefoot formula of 4-5-5-4, 5-5-5-4 or 4-4-5-4; a contiguous femoroprecloacal pore series of 42; five cloacal

spurs in males; no enlarged subcaudal scales; no dark postorbital stripes or striping on body; small dark blotches on the upper body; a yellowish postsacral mark bearing anteriorly projecting arms; and a pigmented caecum and gonads (subgenus *Hemiphyllodactylus* part), or:

3/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black, adult females with no or fewer than five secreting precloacal pores; adult size seldom greater than 38 mm SVL; three or four U-shaped digital lamellae under fourth digit of forefoot; dorsal trunk pattern muted, faded and small dark blotches or widely separated dark spots; postsacral mark with U- or V-shaped outer edge of yellow or red; dorsolateral spots yellow or red, (subgenus *Hemiphyllodactylus* part) or:

4/ Chin scales bordering mental scale posteriorly distinctly enlarged, appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series separate; females commonly with precloacal pores; forefoot digital lamellar formula usually 4-4-4-4, (subgenus *Ferehemiphyllodactylus* subgen. nov. part), or:

5/ Chin scales bordering mental scale posteriorly distinctly

enlarged appear as a pair of scales usually labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4; adults moderate size, usually less than 42 mm SVL; hindfoot digital lamellar formula usually 3-4-4-4, occasionally higher; postsacral mark without anterior arms; trunk usually without dark dorsolateral stripe; precloacal and femoral pore series continuous usually with less than 23 pores; precloacal and femoral pore series usually more than 18 pores (subgenus *Ferehemiphyllodactylus* subgen. nov. part).

The genera *Cainodactylus* Barbour, 1924, *Cassandraccampbellae* gen. nov. and *Malayacolotes* gen. nov. are each separated from *Hemiphyllodactylus* and *Ferehemiphyllodactylus* subgen. nov. as defined below.

The genus *Cainodactylus* Barbour, 1924, type species *Cainodactylus yunnanensis* Barbour, 1924 is separated from the other three genera by one or other of the following three suites of characters:

1/ Chin scales bordering mental scale posteriorly distinctly enlarged appear as a pair of scales usually labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4; adults moderate size, usually less than 42 mm SVL; hindfoot digital lamellar formula usually 3-4-4-4, occasionally higher; postsacral mark without anterior arms; trunk usually without dark dorsolateral stripe; precloacal and femoral pore series continuous usually with less than 26 pores; precloacal and femoral pore series usually more than 23 pores; postsacral mark of anterior dark blotch and posterior larger light bar or alternatively this marking may be absent (subgenus *Cainodactylus* part), or:

2/ less than 39.5 mm SV length in adults; 7-10 chin scales; 5 circumnasal scales; 1-5 scales between supranasals; 9-12 supralabials; 8-11 infralabials; 16-18 dorsal scale rows; 8-10 ventral scale rows; lamellar formula on forefoot 4-4-4-4; lamellar formula on hindfoot 4-5-5-5; femoral pores absent in both sexes, 9 precloacal pores in males; 1 or 2 cloacal spurs on each side present in both sexes; dark postorbital stripe; no anteriorly projecting arms of postsacral mark, (subgenus *Cainodactylus* part), or:

3/ Chin scales bordering mental scale posteriorly slightly or not enlarged, their size nearly same as more medial chin scales; caecum and gonadal-duct peritoneum pigmentation usually black; adult females with no or fewer than five secreting precloacal pores; adult size seldom greater than 38 mm SVL; usually two U-shaped digital lamellae under the fourth digit of forefoot; dorsal trunk pattern is bold, transverse dark blotches, longitudinal series of white dorsolateral spots and postsacral mark of dark brown and orange, (subgenus *Maculacruscalotes* subgen. nov.).

Maculacruscalotes subgen. nov. is treated herein as monotypic for *M. aurantiacus* (Beddome, 1870). However there are number of unnamed species currently identified as the single taxon which await formal scientific description.

The genus *Cassandraccampbellae* gen. nov. type species *Lepidodactylus harterti* Werner, 1900, is separated from the other three genera by the following suite of characters: Chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, rarely higher; adults of moderate size, usually less than 42 mm SVL; postsacral mark without anterior arms; trunk usually with a distinct dark dorsolateral stripe; precloacal and femoral pore series continuous with 44-45 pores in males and a single cloacal spur.

The genus *Malayacolotes* gen. nov. type species *Gehyra larutensis* Boulenger, 1900 is separated from the other three genera by one or other of the following suites of characters, which diagnose each subgenus:

1/ Chin scales bordering mental scale posteriorly distinctly

enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, rarely higher; adults of moderate size, usually less than 42 mm SVL; postsacral mark without anterior arms; trunk usually with a distinct dark dorsolateral stripe; precloacal and femoral pore series continuous with 2-36 pores in males and two to three cloacal spurs (subgenus *Malayacolotes* gen. nov.), or:

2/ Adults large, usually more than 45 mm SVL; chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous usually more than 22 (17-39) pores; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, hindfoot digital lamellar formula is usually 4-4-5-5 or 4-5-5-5; postsacral mark with anterior arms (subgenus *Titiwangsaacolotes* subgen. nov.), this being diagnostic for the subgenus *Titiwangsaacolotes* subgen. nov..

Etymology: *Titiwangsaacolotes* in Latin means gecko from Titiwangsa.

Distribution: Peninsular Malaysia in the vicinity of Titiwangsa.

Content: *Malayacolotes* (*Titiwangsaacolotes*) *titiwangsaensis* (Zug, 2010) (type species); *Malayacolotes* (*Titiwangsaacolotes*) *cassandraccampbellae* sp. nov..

MALAYACOLOTES CASSANDRACAMPBELLAE SP. NOV.

LSID urn:lsid:zoobank.org:act:CF5D0651-B779-4171-9A2E-BFB8777FD55A

Holotype: A preserved specimen at the University of Texas at El Paso Biodiversity Collections, specimen number: UTEP Herps H-11708, erroneously identified as "*Hemiphyllodactylus typus*", collected at Bukit Fraser (= Fraser's Hill) at between 4000 to 4200 feet, Pahang Province, Malaysia, Latitude: 3.71 N., Longitude 101.7 E. The University of Texas at El Paso Biodiversity Collections allows access to its holdings.

Paratypes: Two preserved specimens at the University of Texas at El Paso Biodiversity Collections, specimen number: UTEP Herps H-11709 and UTEP Herps H-11707 of the same taxon collected at the same location as the holotype.

Diagnosis: The species *Malayacolotes cassandraccampbellae* sp. nov. is morphologically similar to *M. titiwangsaensis* (Zug, 2010), as defined by Zug (2010) and both are separated from all other species formerly included within *Hemiphyllodactylus* Bleeker, 1860 on the basis of the diagnosis for "*Hemiphyllodactylus titiwangsaensis*" on pages 48-50 of Zug (2010).

Malayacolotes cassandraccampbellae sp. nov. is most readily separated from the other species (*M. titiwangsaensis*) on the basis of markings on original tails.

M. cassandraccampbellae sp. nov. have obvious black spots on the flanks of the tail, whereas these are not present in *M. titiwangsaensis*. Furthermore markings on the tail of *M. cassandraccampbellae* sp. nov. are not tending towards cross bars as seen in *M. titiwangsaensis*.

Both species *M. cassandraccampbellae* sp. nov. and *M. titiwangsaensis*, forming the entirety of the subgenus *Titiwangsaacolotes* subgen. nov. are separated from all other species formerly included in the genus *Hemiphyllodactylus* (now within four genera) by the following unique character combination: Adults large, usually more than 45 mm SVL; chin scales bordering mental scale posteriorly distinctly enlarged and appear as a pair of scales labelled postmentals in other geckos; caecum and gonadal peritoneum white; precloacal and femoral pore series continuous usually more than 22 (17-39) pores; females usually lack precloacal pores; forefoot digital lamellar formula 3-3-3-3 or 3-4-4-4, hindfoot digital lamellar formula is usually 4-4-5-5 or 4-5-5-5; postsacral mark with anterior arms. Photos of *M. cassandraccampbellae* sp. nov. in life, that conform to the preceding diagnosis, being depicted as *M. titiwangsaensis* can be found at: <https://www.ecologyasia.com/verts/lizards/titiwangsa-slender-gecko.htm> (Baker, 2018).

Distribution: Restricted to the immediate vicinity of Fraser's Hill, Pahang Province, Peninsular Malaysia.

Etymology: Named in honour of Cassandra Campbell, of Bexley, NSW, Australia, a lawyer working with Alex Tees (also a lawyer from Sydney, NSW), for services to wildlife conservation spanning some decades.

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CONFLICT OF INTEREST

There are no conflicts of interest in terms of this paper and author.

GENUS AND SPECIES LIST FOR CURRENTLY RECOGNIZED TAXA WITHIN *HEMIPHYLLODACTYLUS SENSU LATO*.

Note: This list underestimates actual species diversity.

GENUS *HEMIPHYLLODACTYLUS* BLEEKER, 1860

Subgenus *Hemiphyllodactylus* Bleeker, 1860

Hemiphyllodactylus (*Hemiphyllodactylus*) *typus* Bleeker, 1860 (type species)

Hemiphyllodactylus (*Hemiphyllodactylus*) *engganensis* Grismer, Riyanto, Iskander and McGuire, 2014

Hemiphyllodactylus (*Hemiphyllodactylus*) *ganoklonis* Zug, 2010

Hemiphyllodactylus (*Hemiphyllodactylus*) *insularis* Taylor, 1918

Hemiphyllodactylus (*Hemiphyllodactylus*) *margarethae* Brongersma, 1931

Subgenus *Ferehemiphyllodactylus* subgen. nov.

Hemiphyllodactylus (*Ferehemiphyllodactylus*) *jinpingensis* (Zhou and Liu, 1981) (type species)

Hemiphyllodactylus (*Ferehemiphyllodactylus*) *changningensis* Guo, Zhou, Yan and Li, 2015

Hemiphyllodactylus (*Ferehemiphyllodactylus*) *chiangmaiensis* Grismer, Wood and Cota, 2014

Hemiphyllodactylus (*Ferehemiphyllodactylus*) *khlonglanensis* Sukprasert, Sutthiwiwes, Lauhachinda and Taksintum, 2018

Hemiphyllodactylus (*Ferehemiphyllodactylus*) *linnwayensis* Grismer, Wood, Thura, Zin, Quah, Murdoch, Grismer, Li, Kyaw and Lwin, 2017

Hemiphyllodactylus (*Ferehemiphyllodactylus*) *longlingensis* (Zhou and Liu, 1981)

Hemiphyllodactylus (*Ferehemiphyllodactylus*) *montawaensis* Grismer, Wood, Thura, Zin, Quah, Murdoch, Grismer, Li, Kyaw and Lwin, 2017

Hemiphyllodactylus (*Ferehemiphyllodactylus*) *tonywhitteni* Grismer, Wood, Thura, Zin, Quah, Murdoch, Grismer, Li, Kyaw and Lwin, 2017

GENUS *CAINODACTYLUS* BARBOUR, 1924

Subgenus *Cainodactylus* Barbour, 1924

Cainodactylus (*Cainodactylus*) *yunnanensis* (Boulenger, 1903) (type species)

Cainodactylus (*Cainodactylus*) *banaensis* (Tri, Grismer, Thai and Wood, 2014)

Cainodactylus (*Cainodactylus*) *dushanensis* (Zhou and Liu, 1981)

Cainodactylus (*Cainodactylus*) *flaviventris* (Sukprasert, Sutthiwiwes, Lauhachinda and Taksintum, 2018)

Cainodactylus (*Cainodactylus*) *hongkongensis* (Sung, Lee, Ng, Zhang and Yang, 2018)

Cainodactylus (*Cainodactylus*) *huishuiensis* (Yan, Lin, Guo, Li and Zhou, 2016)

Cainodactylus (*Cainodactylus*) *kiziriani* (Nguyen, Boto, Le Duc, Nophaseud, Bonkowski and Zeigler, 2014)

Cainodactylus (*Cainodactylus*) *zugii* (Nguyen, Lehmann, Le Duc, Duong, Bonkowski and Ziegler, 2013)

Subgenus *Maculacruscalotes* subgen. nov.

Cainodactylus (*Maculacruscalotes*) *aurantiacus* (Beddome, 1870) (type species) (species complex)

GENUS *CASSANDRACAMPBELLEA* GEN. NOV.

Cassandrampellea *harterti* (Werner, 1900) (type species)

Cassandrampellea *bintik* (Grismer, Wood, Anuar, Quah, Muin, Onn, Sumarli and Lored, 2015)

Cassandrampellea *cicak* (Cobos, Grismer, Wood, Quah, Anuar and Muin, 2016)

GENUS *MALAYACOLOTES* GEN. NOV.

Subgenus *Malayacolotes* subgen. nov.

Malayacolotes *larutensis* (Boulenger, 1900) (type species)

Malayacolotes *tehtarik* (Grismer, Wood Jnr., Anuar, Muin, Quah, McGuire, Brown, Tri and Thai, 2013)

Subgenus *Titiwangsacolotes* subgen. nov.

Malayacolotes (*Titiwangsacolotes*) *titiwangsensis* (Zug, 2010) (type species)

Malayacolotes (*Titiwangsacolotes*) *cassandrampelleae* sp. nov. (this paper).