Taxonomic Resolution to the Problem of Polyphyly in the New Caledonian Scincid Lizard Genus *Lioscincus* (Squamata: Scincidae)

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Abstract. Recent genetic studies have identified the New Caledonian scincid genus *Lioscincus* to be polyphyletic, comprising four distinct evolutionary lineages which we recognize at the generic level. The revised concept of *Lioscincus s.s.* now includes only the type species *Lioscincus steindachneri* Bocage, 1873 and the recently described *Lioscincus vivae* Sadlier, Bauer, Whitaker & Smith, 2004. The three remaining lineages identified are: *Leiolopisma tillieri* Ineich & Sadlier, 1991 and *Lioscincus maruia* Sadlier, Whitaker & Bauer, 1998 for which the genus *Phasmasaurus* gen. nov. is proposed; *Lygosoma* (*Mocoa*) *nigrofasciolatus* Peters, 1869 and *Leiolopisma greeri* Böhme, 1979 for which the genus *Epibator* gen. nov. is proposed; and *Lygosoma* (*Leiolopisma*) *novaecaledoniae* Parker, 1926 for which the genus *Caesoris* gen. nov. is proposed. Each of these genera is diagnosed by a suite of morphological apomorphies which in combination is unique within the *Eugongylus* group of skinks of which each is a member. The revised taxonomy presented here, which recognises an additional three new genera, brings the number of endemic skink genera present in New Caledonia to 17, representing approximately 40% of the generic diversity within the Australian/Pacific region *Eugongylus* group of skinks as currently recognised. Although we are reluctant to erect new genera to accommodate one or two species, the data at hand suggest this as the most accurate reflection of the available genetic and morphological data.

Keywords. Taxonomy; scincid; new genera; *Lioscincus*; New Caledonia.

The discovery and description of the New Caledonian scincid lizard fauna covers a period of just over 150 years. The first century of investigation in the period 1869–1970 saw contributions by five workers (Bavay, 1869; Peters, 1869, 1879; Günther, 1872; Bocage, 1873; Brocchi, 1876) describing 17 species in the nineteenth century, and six workers (Andersson, 1908; Werner, 1909; Roux, 1913; Parker, 1926; Mertens, 1928; Loveridge, 1941) describing nine species or subspecies in the early twentieth century. Twenty of these 26 taxa remain valid today. The most significant contributions were the *Catalogue des reptiles de la Nouvelle-Calédonie et description d'espèces nouvelles* of

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Bavay published in 1869 and the monograph *Les reptiles de la Nouvelle-Calédonie et des Îles Loyalty* of Roux published in 1913. Bavay's work described seven of the species recognized today, while Roux provided a synthesis of his own discoveries and observations with the contributions of the previous 40 years. The majority of New Caledonian species recognized by Roux were included within four of the 11 subgenera that resided under an expansive *Lygosoma*, at that time one of the most diverse genera in terms of number of species and worldwide distribution.

During this first century of research, generic conservatism in skink systematics was a consistent theme. The recognition of increasingly finer subgeneric units by Smith (1937) and Mittleman (1952) began the process of recognizing groups of species that later formed the basis of many of the skink genera recognized today. However, as classifications that reflected natural groupings, particularly with regard to the New Caledonian species, these were only a marginal improvement over earlier taxonomies. As such, the systematic status of the lineages of "lygosomid" skinks, the group in which the majority of New Caledonian skink fauna was placed, remained largely unresolved for over 100 years, with the consequence that the generic diversity of the island's skink fauna was grossly under-appreciated (Bauer, 1989; Bauer & Sadlier, 2000), as was that of other regional skink faunas belonging to this group.

In the latter part of the twentieth century, Allen Greer began a 35 year refinement of scincid systematics which re-defined the subfamily Lygosominae (Greer, 1970), identified major subgroups within this subfamily (Greer, 1974, 1979, 1989), and extensively reviewed lygosomine genera and their relationships, identifying and refining characters for diagnosing natural groups in the process. The contributions of Greer had a major impact on understanding the relationships of the Australian and Pacific region skink fauna, including the establishment over time of a systematic framework within which the intra- and inter-generic relationships of this fauna could be assessed (see below for a more detailed account of Greer's contributions, and the implications of his work on defining lineages of New Caledonian skinks and the relationships of these lineages to other skinks).

It is within the context of this framework that investigations into the diversity and relationships of the New Caledonian skink fauna have been conducted over much of the past 30 years, considerably changing previous concepts of the species richness and generic diversity for this regional fauna. During this period the recognition and definition of monophyletic groups within the New Caledonian skinks has largely been undertaken within the phylogenetic framework for the *Eugongylus* group established by Greer (1974, 1979, 1989), and utilized similar operational principles in identifying suites of morphological synapomorphies to define natural or monophyletic genera (Sadlier, 1987; Sadlier & Bauer, 1997, 1999b, 2000, 2002a; Sadlier *et al.*, 1997, 2004b, 2006b), and intrageneric groupings (Sadlier, 1990; Sadlier *et al.*, 2002b).

Later studies, the more recent of which have utilized morphological data in combination with genetic information derived from DNA sequence data, have further identified and defined supraspecific groups of New Caledonian skink taxa as distinct evolutionary lineages (Smith *et al.*, 2007; Ineich *et al.*, 2014), in some cases drawing extensively from the genetic data for support for monophyly of the constituent species (Sadlier *et al.*, 2004a), and as support for taxa with limited morphological apomorphies as discrete evolutionary entities (Sadlier *et al.*, 2014b). As a result the diversity in terms of the number of skink genera strictly endemic to New Caledonia has nearly doubled, with the recognition of an additional six genera since 1987. Contributing to this increased island generic endemism has been the transfer of the New Caledonian species previously retained in *Leiolopisma* to *Lioscincus* (Bauer & Sadlier, 1993), a redefined *Nannoscincus* that includes only New Caledonian taxa (Sadlier *et al.*, 2006a) and five newly erected genera (*Lacertoides* Sadlier, Shea & Bauer; *Simiscincus* Sadlier & Bauer; *Kanakysaurus* Sadlier, Smith, Bauer & Whitaker; *Celatiscincus* Sadlier, Smith & Bauer; *Phaeoscincus* Sadlier, Bauer, Smith, Shea & Whitaker) to accommodate new taxa. With these additions there are currently 16 genera of skinks in New Caledonia, of which 14 are either strictly endemic, or nearly so, to the region, with more than 60 described constituent species, over half of which have been discovered and described in the past quarter of a century.

These earlier studies that defined natural groups on morphological characters provided the platform for a comprehensive genetic analysis of the intra and intergeneric relationships of the New Caledonian taxa, and of these with other members of the *Eugongylus* group of skinks (Smith *et al.*, 2007). This study identified the endemic New Caledonian genera, together with the New Zealand skink radiation, as a monophyletic lineage restricted to the Gondwanan Tasman continental block. It also recognized a number of suprageneric groups within the New Caledonian radiation, and identified the taxa within *Lioscincus* as belonging to four independent unrelated lineages, which are the focus of the investigation presented here. A later genetic study concentrating on the endemic New Zealand skink fauna (Chapple *et al.*, 2009), but using a larger number of genes, confirmed the endemic New Caledonian and New Zealand skink genera as a monophyletic lineage with the New Caledonian and New Zealand skink fauna as discreet sister lineages, and also the polyphyly of *Lioscincus*. Further contributions highlighting the polyphyly of *Lioscincus* were apparent in the molecular phylogenies of Caut *et al.* (2013) and Ineich *et al.* (2014) in investigating the relationships of the giant New Caledonian skink *Phoboscincus bocourti* (Brocchi). It is the purpose of this paper to diagnose the evolutionary lineages currently included under *Lioscincus* and to erect new genera for those taxa no longer included in that genus.

Leiolopisma and its role in New Caledonian skink systematics

Greer's early work on lygosomine skinks identified the "greatest single taxonomic problem with the Lygosominae" as the "delimitation and relationships of genera" (Greer, 1970, p. 171), and in particular the relationships within "*Leiolopisma*" "as a major unresolved problem in skink systematics" (Greer, 1970, p. 179). Generic concepts were refined by Greer (1974), who diagnosed a number of monophyletic genera from Malcolm Smith's (1937) Section *Leiolopisma*, and allocated these and related genera to three major groups based on a suite of osteological and scalation characters. Within this scheme of relationships, the New Caledonian skink species known at the time all resided in

genera placed in a large group of taxa, later formally referred to as the "*Eugongylus* Group" (Greer, 1979). The majority of the New Caledonian species were retained within a redefined *Leiolopisma*, which also included species from New Zealand, Australia (including Lord Howe Island), and Mauritius in the Indian Ocean. Greer (1974, p. 17) seems to have regarded *Leiolopisma* as a (monophyletic) lineage. However, the genus was weakly diagnosed, with exceptions amongst the included species for almost every diagnostic character presented. The significance of Greer's early contributions to the systematics of the New Caledonian skinks lies with being the first worker to assess relationships and diagnose natural groups among related lygosomine skinks in a contemporary phylogenetic context, and in doing so provided a considerably more robust framework within which to investigate interspecific and intergeneric relationships of the New Caledonian taxa. The major groups of genera identified by Greer within the Lygosominae have proven remarkably robust, and subsequent studies (Austin & Arnold, 2006; Brandley *et al.*, 2005; Honda *et al.*, 2000, 2003; Pyron *et al.*, 2013; Rabosky *et al.*, 2007; Skinner *et al.*, 2011; Whiting *et al.*, 2003) have largely supported these groupings.

Field studies initiated in 1978 were the basis of a monograph of the scincid lizards by Sadlier (1987), the first review in over 70 years, which recognized a doubling in the number of endemic species to 24 and a similar increase in the number of genera from 4 to 10, of which 7 were strictly endemic. Sadlier (1987) proposed several putatively monophyletic genera (*Caledoniscincus*, *Marmorosphax* and *Sigaloseps*, and a resurrected *Tropidoscincus* Bocage, 1873) to accommodate most of the New Caledonian species formerly assigned to *Leiolopisma*. All were defined by suites of apomorphic morphological character states, the polarity of which was determined within the context of Greer's (1979) *Eugongylus* group of skinks. However, four species with relatively plesiomorphic morphology (*nigrofasciolatus* Peters, *greeri* Böhme, *steindachneri* Bocage and *novaecaledoniae* Parker) were retained within the "cosmopolitan" *Leiolopisma*, though two of these (*nigrofasciolatus* and *greeri*) were recognized at the time as probable sister taxa in a putative sublineage. Subsequently three more New Caledonian species were added to the genus, *Leiolopisma tillieri* Ineich & Sadlier in 1990, *maruia* Sadlier, Whitaker & Bauer in 1998 (by which time the New Caledonian *Leiolopisma* had been moved to *Lioscincus*, see below), and *vivae* Sadlier, Bauer, Whitaker & Smith (as *Lioscincus*) in 2004.

The members of "*Leiolopisma*" at the time of Sadlier's monograph (1987) also included all New Zealand skinks (20 species), a group of Australian skinks (13 species that now represent *Bassiana*, *Pseudemoia* in part, and *Niveoscincus* in part), the Lord Howe/ Norfolk Island species *lichenigera*, a single Fijian species (*alazon* Zug), and the type species for the genus, *Leiolopisma telfairii* from Mauritius. The diagnosis for "*Leiolopisma*" given by Greer (1970) contained both "primitive" and "derived" character traits with both states present for some characters (frontoparietal scales), but was later modified by Sadlier (1987) to include only the single most unifying apomorphy to define the genus, lack of supranasal scales in most species. Further, limited knowledge of morphological variation for some characters and the simplistic assumption that some states, such as the presence of supranasal scales and presence of a scaled lower

eyelid (both considered plesiomorphic) were homologous across genera, would ultimately prove to be misleading, and clouded interpretations of relationships within this group of species well into the future. In effect "*Leiolopisma*" at this time remained (as before) a genus of convenience rather than one reflecting defined evolutionary relationships, and the New Caledonian taxa retained within it (Sadlier, 1987) were the residual species lacking a distinct supranasal scale that could not be otherwise accommodated within any of the existing putatively monophyletic genera within the *Eugongylus* group.

A decade after Greer defined the *Eugongylus* group, two not entirely concordant works were published which were to influence generic concepts of this group of skinks in the years following, and in particular the dynamics of taxa formerly included in the all-encompassing "*Leiolopisma*" of earlier studies. In one Greer (1989) diagnosed a *Pseudemoia* subgroup within the *Eugongylus* group on the basis of a single apomorphy not observed in other major groups of skinks, fusion of the elements of the atlantal vertebra, for a group of Australian taxa (covering 12 genera), but also stated as including taxa from New Guinea and New Caledonia (though these were not specifically listed). The *Pseudemoia* group as conceived by Greer comprised an extensive suite of taxa centred on the Coral and western Tasman Seas, but explicitly excluded part of the New Caledonian skink fauna, and in doing so argued for non-monophyly of the group of endemic New Caledonian skink lineages. Concurrently Hutchinson *et al.* (1990) reviewed the Australian species previously assigned to *Leiolopisma* using primarily genetic criteria. This study further promoted the dismembering of the large, still polyphyletic "*Leiolopisma*" as it existed at the time, by transferring the Australian species formerly in the genus to five (four newly erected) putatively monophyletic (endemic) genera, and suggesting *Leiolopisma* be restricted to the type species *telfairii*. The genera proposed by Hutchinson *et al.* (1990) were identified by micro-complement fixation comparisons, and supported by a suite of putative morphological apomorphies consistent with these genetic groupings. In the process, genetic comparisons were made with a very limited suite of extralimital taxa that included two species from New Caledonia, two from New Zealand, and the type species for *Leiolopisma*, *Scincus telfairii* Desjardin 1831, from Mauritius.

The results of the genetic study by Hutchinson *et al.* (1990) had two implications for New Caledonian skink systematics. Firstly the New Caledonian and New Zealand species of *Leiolopisma* were identified as not being congeneric with, or particularly close to, the Australian taxa, and neither was the type species *telfairii*. Secondly, while the condition of the elements of the atlantal arch was invariant for the taxa in most of the genera proposed by Hutchinson *et al.*, it was variable between the species in one of the genera proposed. *Niveoscincus*, with eight species from Tasmania and adjacent south-east Australia, included one species with the apomorphic condition of having the atlantal arches of the first cervical vertebrae fused to the intercentrum (*palfreymani*), while the remaining species in the genus had the plesiomorphic condition in which all elements are separate, in effect suggesting the possibility of multiple evolutionary events for this character state, which had been the sole evidence for monophyly of Greer's *Pseudemoia* group.

The actions of Hutchinson *et al*. (1990) in restricting *Leiolopisma* to the type species *telfairii* prompted the transfer of the residual New Caledonian "*Leiolopisma*" to *Lioscincus* (type species *Lioscincus steindachneri* Bocage, 1873) by Bauer & Sadlier (1993), the only available generic name among the constituent species. The lack of apomorphies defining *Lioscincus* and its probable polyphyly were explicitly acknowledged at that time, the action being a nomenclatural necessity rather than an inference of intra-generic cohesiveness. For the same reason the New Zealand "*Leiolopisma*" were transferred to *Oligosoma* by Patterson and Daugherty (1995). These actions have resulted in the concept of a significantly redefined *Leiolopisma* restricted to a single extant taxon, the type species *telfairii*, and the fossil species *mauritianus* from the Mascarene Islands (Arnold, 1980), and the fossil species *ceciliae* from Réunion (Arnold & Bour, 2008). However, one species, described as *Leiolopisma alazon* Zug in 1985, has not been considered in these recent studies. The species occurs on the outer islands of Fiji, and until recently was only known from the type series, and no tissue samples have been available for genetic studies. It currently resides within the Lygosominae (Zug, 2013), but otherwise its affinities remain obscure.

Taxonomy

A revised taxonomy for "*Lioscincus*"

Recent investigation of intergeneric relationships among the members of the *Eugongylus* group of skinks has been through the use of mitochondrial and nuclear DNA sequence data. The scheme of relationships (Fig. 1) resulting from the study by Smith *et al*. (2007) strongly supported monophyly of all the morphologically based New Caledonian genera previously recognized (Sadlier, 1987; Sadlier & Bauer, 1997; Sadlier *et al*., 1997, 2004b, 2006b) exclusive of "*Lioscincus*", and identified four independent and unrelated genetic lineages within "*Lioscincus*":

- *Leiolopisma tillieri* Ineich & Sadlier, 1991 + *Lioscincus maruia* Sadlier, Whitaker & Bauer, 1998.
- *Lygosoma* (*Leiolopisma*) *novaecaledoniae* Parker, 1926.
- *Lygosoma* (*Mocoa*) *nigrofasciolatus* Peters, 1869.
- *Lioscincus steindachneri* Bocage, 1873 + *Lioscincus vivae* Sadlier, Bauer, Whitaker & Smith, 2004.

The lineage "*Lioscincus*" *maruia* + "*Lioscincus*" *tillieri*, and the species "*Lioscincus*" *novaecaledoniae*, were each found to have no obvious affinities to other New Caledonian skink genera or to each other. Within a well-supported group that included all other New Caledonian taxa, a sister group relationship between *Lioscincus steindachneri* + *Lioscincus vivae* (= *Lioscincus s.s.*) and *Celatiscincus* was identified, while "*Lioscincus" nigrofasciolatus* was nested within a poorly supported group that also included *Phoboscincus* (as represented by *garnieri*), and *Lacertoides*.

Genetic analyses presented subsequently by Chapple *et al*. (2009), Caut *et al*. (2013) and Ineich *et al*. (2014), while either involving less thorough sampling of New Caledonian genera, or fewer genes, have similarly found no evidence for monophyly of any combination of these four *Lioscincus* groups.

"*Lioscincus" novaecaledoniae* was found to be the outgroup to the lineage of all other New Caledonian genera

plus the New Zealand *Oligosoma* by Ineich *et al*. (2014). The position of "*Lioscincus*" *tillieri* + "*Lioscincus*" *maruia* (Smith *et al*., 2007; Ineich *et al*. 2014) has varied in different studies, but it has never been recovered as sister to other *Lioscincus* alone nor *tillieri* when included without its sister species (Chapple *et al*., 2009). The study by Ineich *et al*. (2014), using only two of the genes used by Smith *et al*. (2007), similarly found this group to be closer to the New Zealand *Oligosoma* than to the New Caledonian radiation, but with low support. In contrast, Chapple *et al*. (2009), using five mitochondrial genes and one nuclear gene, but with just four New Caledonian genera represented, found *tillieri* to nest deeply among the other New Caledonian genera, as sister to *Caledoniscincus*. Caut *et al*. (2013), using two mitochondrial genes, neither used by Smith *et al*. (2007), similarly found *tillieri* to nest among the New Caledonian genera, but as sister to *Phoboscincus* + *nigrofasciolatus*, with *Caledoniscincus* outside this (Caut *et al*., 2013). "*Lioscincus" nigrofasciolatus* was recovered as sister to *Phoboscincus* by Caut *et al*. (2013), but with low support, and *Lioscincus steindachneri* has consistently been recovered as sister to *Celatiscincus* (Ineich *et al*., 2014).

Similarities in aspects of morphology and behaviour between "*Lioscincus*" *tillieri* and "*Lioscincus*" *maruia*, and by inference a sister species relationship, had previously been suggested (Sadlier *et al*., 1998; Bauer & Sadlier, 2000). However, the suite of morphological apomorphies shared by these two species was at that time not considered sufficiently compelling alone to diagnose them as a monophyletic lineage exclusive of other "*Lioscincus*" taxa.

The distinctiveness of "*Lioscincus*" *novaecaledoniae* had long been recognized, as had the problematic nature of its relationships with regard to other New Caledonian skinks. Its blue mouth colour (Sadlier, 1987), a feature not present in any other New Caledonian skink, was not considered sufficient by itself to identify the species as a lineage warranting generic recognition. Subsequent morphological studies (Sadlier, 2010) have identified a broader suite of apomorphies that further diagnose the species, and which in combination with a high level of genetic differentiation indicate the species warrants recognition as a separate genus but with no clear indication as to its relationships.

A sister taxon relationship between "*Lioscincus*" *nigrofasciolatus* and "*Lioscincus*" *greeri* has also long been recognized and diagnosed on morphological criteria (Sadlier, 1987; Bauer & Sadlier, 2000). The latter species is known only from the original specimen(s) collected (Böhme, 1979; Meier, 1979) and no tissue samples were available for the study by Smith *et al*. (2007). Recognition of these taxa as a lineage warranting generic rank had been tempered by uncertainty regarding its affinities with a morphologically similar subset of species in the Pacific region—genus *Emoia* (the *samoensis* group, Greer pers. comm.)—a problem that no longer exists with the recognition of a monophyletic New Caledonian skink radiation inclusive of "*Lioscincus*" *nigrofasciolatus* but exclusive of the *Emoia samoensis* group (as represented by *Emoia loyaltiensis*, Smith *et al*., 2007).

The close genetic relationship of the species *Lioscincus steindachneri* and *Lioscincus vivae* indicated by genetic analysis (Smith *et al*., 2007) was unexpected. The two species are dissimilar in their biology and overall appearance, but share a limited suite of morphological apomorphies (Sadlier *et al*., 2004a) that supported the relationship retrieved in the
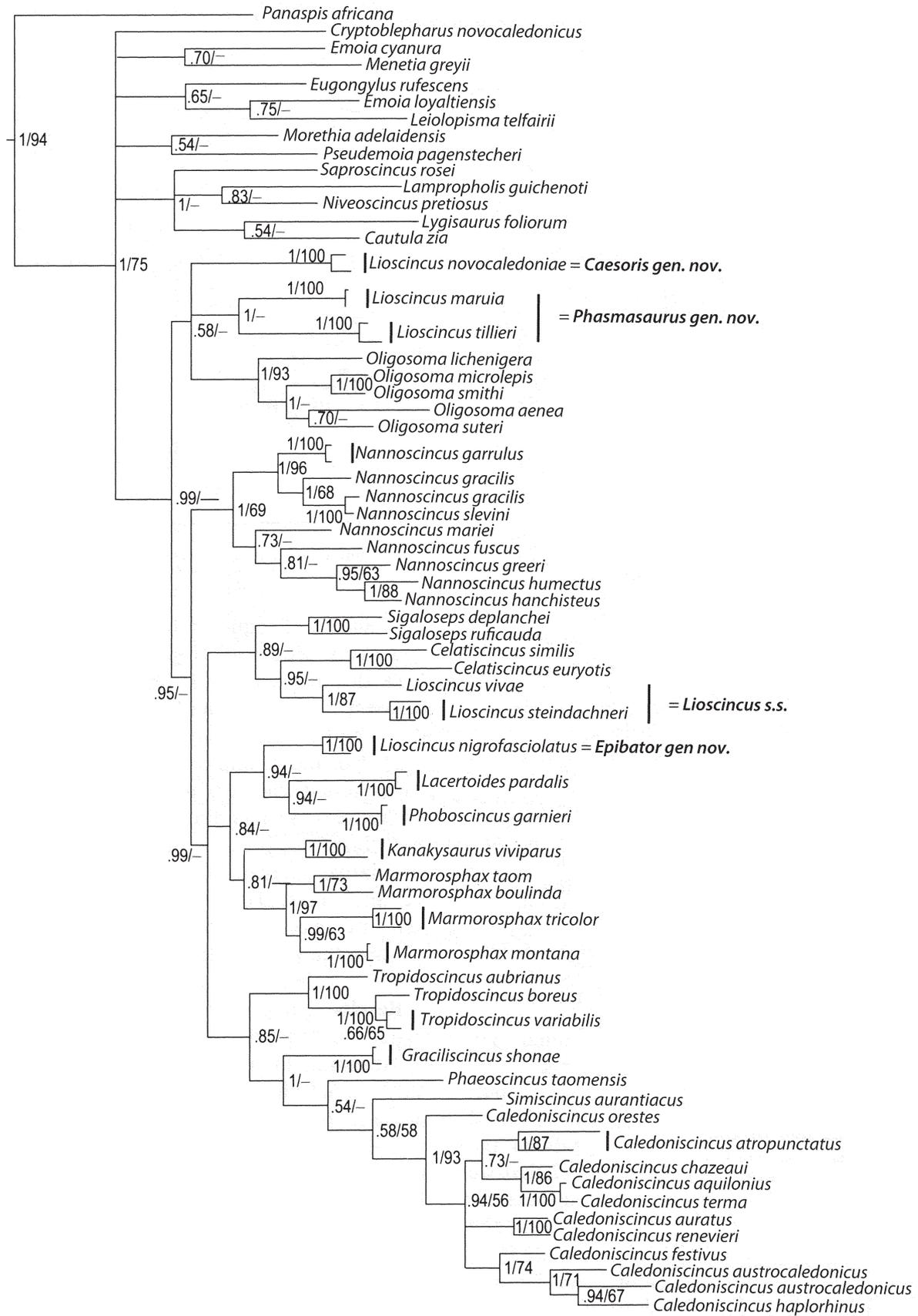
Figure 1. Phylogenetic relationships of the New Caledonian skinks within the *Eugongylus* group of skinks as determined by DNA sequence data (after Smith *et al.*, 2007) based on combined partitioned Bayesian analysis of one mitochondrial (ND2) and two nuclear genes (c-*mos* & Rag-1) with the polyphyly of "*Lioscincus*" highlighted. Support values are Bayesian posterior probability/bootstrap values, support less than $P_p 0.50$ or bootstrap 50% not shown.

molecular study. The placing of *Lioscincus steindachneri* + *Lioscincus vivae* (= *Lioscincus s.s.*). by the genetic data in a well-supported sister relationship with *Celatiscincus* is supported by these taxa sharing a morphological apomorphy, divided nuchal scales, not commonly seen in other *Eugongylus* group taxa, and further reinforces the distinctiveness and relationships of this revised and more limited *Lioscincus* from the other taxa formerly included in *Lioscincus*.

It is also worth noting here that in the study by Smith *et al.* (2007), *Phoboscincus* was represented by only a single species, *P. garnieri*, and monophyly of the genus inclusive of that species was called into question by Ineich (2009), based primarily on morphological criteria. Subsequent inclusion of the recently rediscovered *P. bocourti* into the Smith *et al.* (2007) tree supported monophyly of the genus inclusive of both taxa (Ineich *et al.* 2014).

The redefinition and restriction of *Lioscincus* and erection of three new genera proposed here to accommodate the genetic lineages identified by Smith *et al.* (2007) for the species *nigrofasciolatus*, *tillieri* + *maruia*, and *novaecaledoniae* (see Fig. 2 for representatives of these lineages) draw substantially from genetic data to support these each being distinctive evolutionary entities. Although we are reluctant to erect new genera to accommodate one or two species, the data at hand suggest this as the most prudent course of action. As noted above, *Lioscincus* as presently conceived, is demonstrably non-monophyletic and to retain this name for the current constituent species would be misleading. Affinities of three of the lineages of "*Lioscincus*" are obscure or poorly supported, suggesting that the initial radiation of the New Caledonian skinks was rapid and to date neither the addition of more taxa or more genes has clarified these relationships. To link these clades with any other genus or with one another through the use of a shared generic name would be baseless, and even in the case of *Lioscincus s.s.* + *Celatiscincus*, where affinities are well-supported, deep genetic divergence and contrasting sets of apomorphies are more consistent with generic level differences typical in the *Eugongylus* group. Diagnoses for these generic arrangements are derived from an expanded suite of morphological characters (Sadlier, 2010: appendix 1), and are here applied to these newly recognized lineages identified by the genetic studies. In this respect the morphological data does not in itself provide an independent test for monophyly of these genetic lineages, but rather serves to provide further support for the genetic lineages being natural groups of species on independent evolutionary trajectories. Similar approaches to the use of morphology were made by Hutchinson *et al.* (1990) in providing characters to diagnose evolutionary units identified by genetic studies within the Australian *Eugongylus* group skinks, within the Australian skink genus *Egernia* (Gardner *et al.*, 2008) and more recently within the *Sphenomorphus* group skink genus *Eulamprus* (Skinner *et al.*, 2013), to which generic names were assigned in each case.

An asterisk indicates the apomorphic character state for the genus within the context of the *Eugongylus* group skinks as determined by Sadlier (2010) in the following generic diagnoses.

Genus *Lioscincus* Bocage

Lioscincus Bocage, 1873: 228.

Type species. *Lioscincus steindachneri* Bocage, 1873: 228.

Diagnosis. The species of *Lioscincus s.s.* are moderately large in size (maximum snout vent length [SVL]: *L. vivae* 55 mm; *L. steindachneri* 88.5 mm) with a stout body, moderately well-developed limbs and digits, and a relatively long tail (maximum tail length: *L. steindachneri* 180% SVL; *L. vivae* 210% SVL). The ear opening is large and lacks obviously enlarged lobules around the anterior edge.

Scalation (Fig. 3): *distinct supranasal scales absent; nasal scale lacking a postnasal suture (a crease is sometimes present in *steindachneri*); frontonasal broader than long; prefrontals large and narrowly to moderately separated; frontal elongate, longer than broad; supraoculars four; *frontoparietals fused to form a single scale; interparietal distinct; *nuchal scales divided so that the parietals are each bordered by three scales comprising a divided nuchal (two similar sized scales) and the upper secondary temporal scale; primary temporal single; lower secondary temporal single; tertiary temporals two; postlabials two; *anterior loreal reduced to a semilunar scale positioned on the anterodorsal margin of the nasal and either failing to, or only narrowly contacting, the labials; supraciliaries usually seven; upper labials seven with the fifth subocular and either contacting the lower eyelid (*steindachneri*) or separated by a complete row of subocular scales (*vivae*); postmental contacting first and second lower labial; transversely enlarged chinshields three, first pair in broad contact, second pair separated by one scale, third pair separated by three scales, all chinshields contacting the lower labials; dorsal scales of body smooth.

Osteology: premaxillary teeth 11; atlantal arches and intercentrum of first cervical vertebrae present as three separate units but showing some degree of partial (*vivae*) or superficial (*steindachneri*) fusion; presacral vertebrae usually 29; phalangeal formula for the manus 2.3.4.5.3 and for the pes 2.3.4.5.4; two pairs of mesosternal ribs.

The suite of apomorphic character states identified above will distinguish a redefined *Lioscincus* from all other genera in the *Eugongylus* group of skinks, including the new genera described here. In particular the combination of fused frontoparietal scales and division of the nuchal scale (such that three scales border each of the parietal scales) serves to distinguish *Lioscincus* from all genera outside the endemic New Caledonian skink radiation. Within the endemic New Caledonian skink radiation only *Celatiscincus*, *Kanakysaurus* and *Phoboscincus bocourti* also share this pair of scalation apomorphies (Sadlier, 2010), although division of the nuchal scale occurs variably in *Simiscincus*. The nuchal scale division in *Kanakysaurus* is regular but part of a more extensive pattern of fragmentation of scales in the temporal and nuchal region, and fragmentation of the nuchal and temporal scales in *Phoboscincus bocourti* is extreme and irregular and also part of a pattern of fragmentation of scales in the temporal and nuchal region. By contrast division of the nuchal scale in *Lioscincus* and *Celatiscincus* is regular and not associated with a more extensive pattern of head shield fragmentation. As such, division of the nuchal scales to varying degrees has likely evolved independently in several

Figure 2. Species now included in *Lioscincus s.s.*, *(a) L. steindachneri* and *(b) L. vivae*; and representatives of species included in the genera: *Phasmasaurus*, *(c) P. tillieri* and *(d) P. maruia*; *Epibator*, *(e) E. nigrofasciolatus*, and *Caesoris*, *(f) Caesoris novaecaledoniae*.

of the major groups of endemic New Caledonian skinks, with its presence in *Lioscincus* and *Celatiscincus* a putative synapomorphy for a sister relationship between these genera. *Celatiscincus* has two morphological apomorphies not shared with *Lioscincus*, an elevated number of premaxillary teeth (13 vs 11) and the body scales with weak keels (*vs* smooth).

Etymology. Bocage (1873) does not give the origin of the name *Lioscincus*, but it is presumably derived from the Greek *leios* (smooth), and in allusion to the unkeeled scalation of the type species *steindachneri*.

Intergeneric relationships. The sister group relationship between *Lioscincus s.s.* and *Celatiscincus* inferred by the genetic data (Smith *et al.*, 2007) is supported by these taxa sharing the apomorphic condition for three scalation characters, the combination of which is unique within the *Eugongylus* group of skinks: fusion of the frontoparietal scales; parietals each bordered by at least three scales, two of which are a divided nuchal scale and one the upper secondary temporal; and a narrowing of the anterior loreal basally to the point where it can be occluded from contact with the
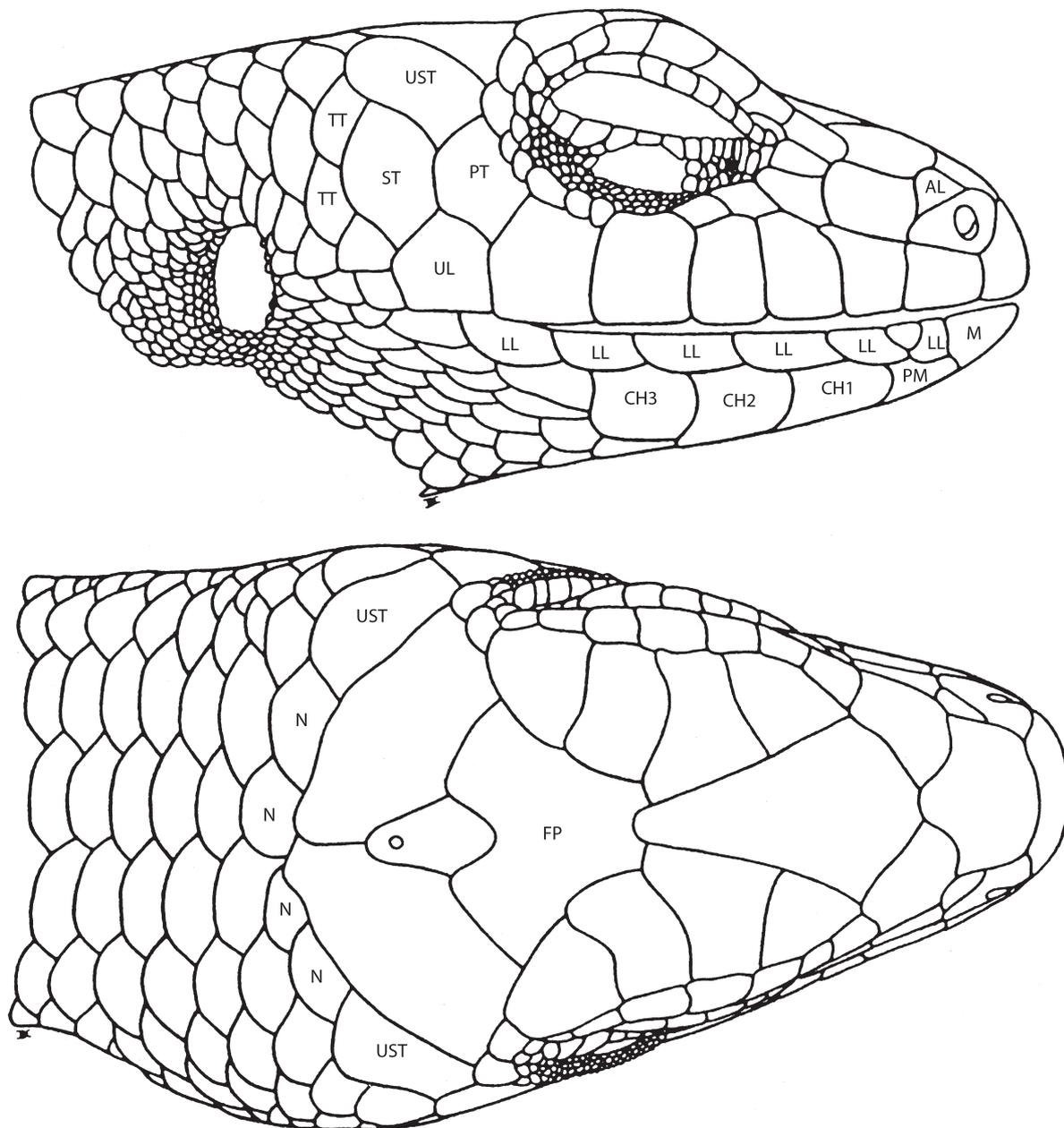
Figure 3. Head scalation of *Lioscincus s.s.* as seen in *L. steindachneri* (adapted from Sadlier, 1987) showing some of the primary diagnostic features for the genus including fused frontoparietal scales *(FP)*, a narrow-based and semilunar anterior loreal scale *(AL)* which contacts the upper labial scales narrowly or not at all, and divided nuchal scales *(N)*, compared to the plesiomorphic condition of a broad-based anterior loreal and single transversely elongate nuchal either side of the neck as seen in *Epibator* (Fig. 4), *Phasmasaurus* (Fig. 5) and *Caesoris novaecaledoniae* (Fig. 7), and paired frontoparietals seen in *Epibator* (Fig. 4).

labials. *Celatiscincus* is distinguished from *Lioscincus s.s.* in having an elevated number of premaxillary teeth (13 *vs* 11). The relationships of *Geoscincus*, an unusual monotypic genus of skink known only from the two type specimens collected in 1975 (Böhme, 1976), are not available from any of the genetic analyses and its relationships to other *Eugongylus* group skink remain obscure. Regardless, *Geoscincus* is readily distinguished from *Lioscincus s.s.* in

having highly fragmented posterior head shields, including division of the upper secondary temporal scale, a greatly reduced number of premaxillary teeth (6–9 *vs* 11), and in having the plesiomorphic condition of divided (*vs* fused) frontoparietal scales.

Recognized species. Two, *Lioscincus steindachneri* Bocage and *Lioscincus vivae* Sadlier, Bauer, Whitaker & Smith.

Lioscincus steindachneri Bocage, 1873: 228

Distribution. Panié Range in the far north-east, and central metamorphic ranges as far south as Mé Adéo.

Comments. Recorded only from humid forest habitat.

Lioscincus vivae Sadlier, Bauer, Whitaker & Smith, 2004: 211

Distribution. The central-west ultramafic massifs of Kopéto and Paéoua.

Comments. Recorded from the edge of high elevation closed forest and throughout maquis shrubland to as low as 500m elevation (Whitaker, 2006).

Intrageneric relationships. There is a high level of support for *L. steindachneri* and *L. vivae* as sister taxa (BPP 0.95) in the combined mitochondrial ND2 and nuclear RAG1 + c-*mos* molecular phylogeny (Smith *et al.*, 2007), but with substantial nucleotide sequence divergence between these taxa for the mitochondrial ND2 gene of around 12.5% (a similar level of sequence divergence was found between the two species of the sister-genus *Celatiscincus*). Ineich *et al*. (2014) similarly found a high level of support (BPP 1.0) for the sister-species relationship. The high level of genetic differentiation between the two taxa is complemented by the differences in morphology previously identified, and clearly supports their recognition as divergent and independent evolutionary entities. The differences in morphology are substantial, such that their sister relationship was not immediately obvious. The two species differ markedly in overall appearance, most notably in the absence of sexual dichromatism in *L. steindachneri*, whereas adult male *L. vivae* have a different coloration to adult females and juveniles of that species. They also differ significantly in distribution and habitat preferences. *Lioscincus steindachneri* is restricted to moist habitat in humid forests on non-ultramafic soils of the north-east and east-central ranges, whereas *Lioscincus vivae* occurs primarily in maquis shrubland on the west coast ultramafic ranges of Massif de Kopéto and Paéoua (Whitaker *et al*., 2004).

Epibator gen. nov.

Type species. *Lygosoma* (*Mocoa*) *nigrofasciolatum* Peters, 1869: 435 designated hereby.

Diagnosis. The species are moderately large to large in size (maximum SVL range 61 mm for *greeri* and 112 mm for *nigrofasciolatus*) with a moderately elongate body, long limbs and digits, and a moderately long tail (maximum tail length 145 and 180% of SVL, respectively).

Scalation: *no distinct supranasal; nasal scale with a prominent postnasal suture or crease; frontonasal as broad as long; prefrontals large and narrowly separated or in narrow contact; frontal longer than broad; supraoculars four; frontoparietals paired; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal scale; *primary temporals usually two; lower secondary temporal single; tertiary temporals two; loreals two, each contacting the labials broadly; supraciliaries 7 (*greeri*) or 8 (*nigrofasciolatus*); *upper labials 8 or more with the sixth subocular and contacting the lower eyelid, and the *last divided by an oblique suture into an upper and lower scale (Fig. 4); postmental contacting first and second lower labial; *enlarged chinshields 4–5, first pair in broad contact medially, second pair in moderate contact, first pair usually in partial contact with lower labials but *remaining chinshields separated from lower labials by 1–2 rows of smaller scales (Fig. 4); body scales smooth and moderately small (34–42 longitudinal rows at midbody); *basal dorsal scales of the toes divided.

Osteology: premaxillary teeth 11; atlantal arches of first cervical vertebrae and intercentrum present as three separate units; 29 presacral vertebrae; a phalangeal formula of 2.3.4.5.3 for the manus and 2.3.4.5.4 for the pes; two pairs of mesosternal ribs.

The suite of apomorphic character states identified above will distinguish *Epibator* gen. nov. from all other genera in the *Eugongylus* group of skinks, including the new genera described here. Within the endemic New Caledonian skink radiation the presence of 8 or more upper labials with the last divided by an oblique suture and the separation of the chinshields from the lower labial scales by 1–2 rows of small intervening scales will distinguish *Epibator* gen. nov. from all other genera except *Phoboscincus*. *Epibator* gen. nov. is distinguished from *Phoboscincus* in having no distinct supranasal scale whereas the nasal scale of *Phoboscincus* is distinctly divided into three separate elements, the plesiomorphic condition. Further, *Phoboscincus* has two apomorphic character states not present in *Epibator* gen. nov., fused (*vs* paired) frontoparietal scales and enlarged fang-like (*vs* peg-like) anterior teeth.

Etymology. From the Greek for climber (*epi*, upon + *bates*, one that walks or haunts), alluding to the arboreal habits of the type species. The gender is masculine (Brown, 1956).

Intergeneric relationships. The molecular data presented by Smith *et al*. (2007) retrieved a phylogeny which placed *Epibator* gen. nov. (as represented by *nigrofasciolatus*) within a subgroup containing *Epibator* gen. nov. as the sister to *Lacertoides* + *Phoboscincus*. This grouping received a moderate to low level of support (BPP 0.94; bootstrap values <50%), and the species *Phoboscincus bocourti* and *Epibator greeri* were missing from the analysis. However, there are no obvious shared apomorphies in morphology between these genera, though there is a tendency towards extreme fragmentation of the scales in the temporal region in all genera. However, this trait is also seen in a number of other members of the *Eugongylus* group, particularly larger taxa e.g. *Eugongylus* species and *Oligosoma grande* (Sadlier, 2010), and it is possible its occurrence in the subgroup that includes *Phoboscincus*, *Epibator* gen. nov. and *Lacertoides*, could be independently derived.

The genetic grouping of *Phoboscincus*, *Lacertoides*, and *Epibator* gen. nov., or an inference of relationship between any of these genera, has not previously been suggested. Limited support for this grouping comes from the three genera sharing two scalation characters which could be considered as putative apomorphies to define the subgroup: an elevated number of 8 or more upper labial scales; and division of the basal dorsal toe scales, a derived trait that has evolved independently in several groups of endemic New Caledonian skinks (see Sadlier, 2010: appendix 1). Species in all three genera also share an additional apomorphy in having two (rather than a single) primary temporal scales, though this trait is also present in *Kanakysaurus* and a range
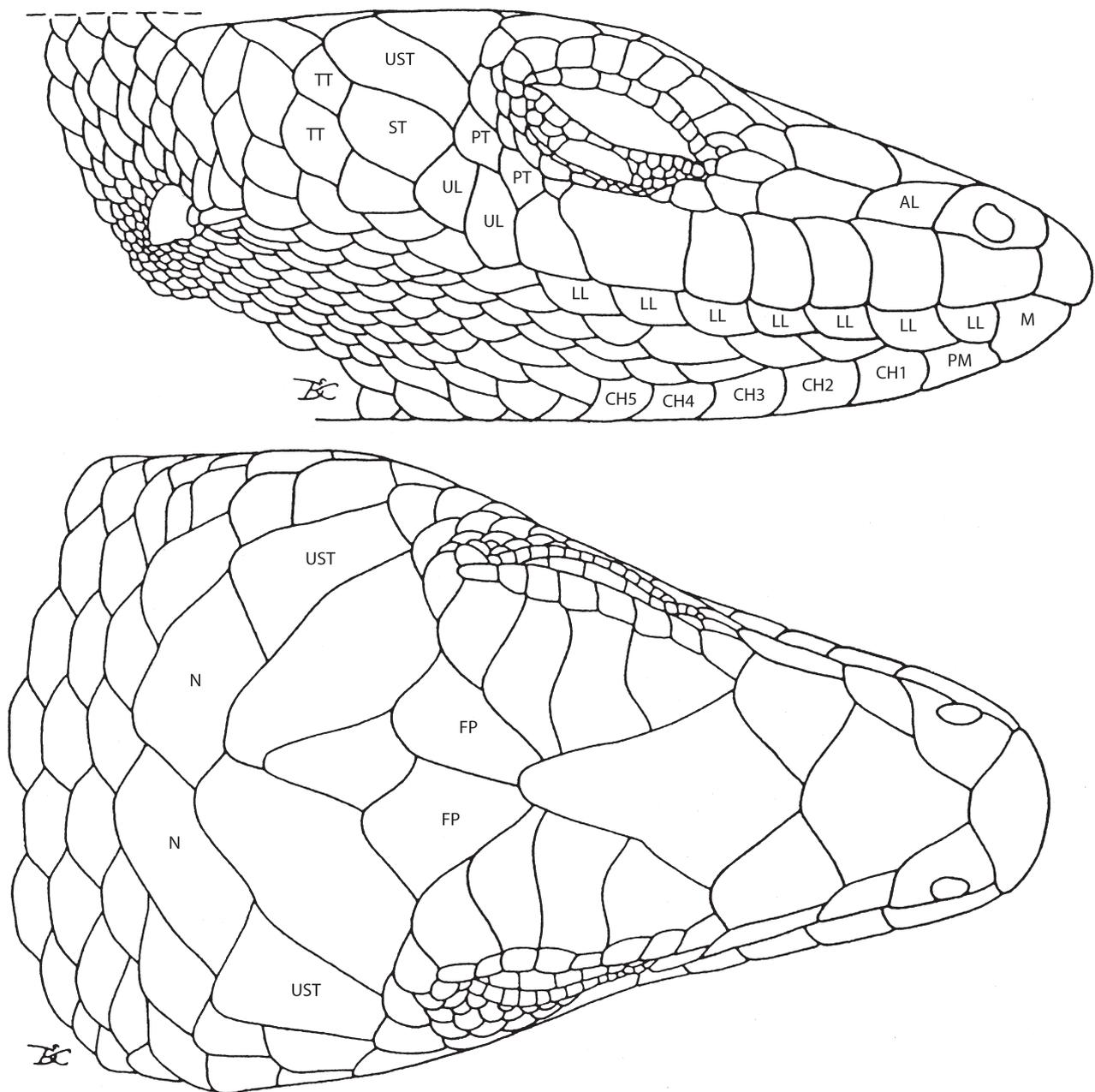
Figure 4. Head scalation of *Epibator* as seen in *E. nigrofasciolatus* (adapted from Sadlier, 1987) showing some of the primary diagnostic features for the genus including a divided primary temporal scale *(PT)* and the majority of chinshields *(CH)* separated from lower labials by 1–2 rows of smaller scales, compared to the plesiomorphic condition of a single enlarged primary temporal scale and the enlarged chinshields contacting the lower labials as seen in *Epibator* (Fig. 4), *Phasmasaurus* (Fig. 5) and *Caesoris novaecaledoniae* (Fig. 7).

of other more distant taxa in the *Eugongylus* group. A more recent genetic study (Ineich *et al.*, 2014) that included both *Phoboscincus bocourti* and *Phoboscincus garnieri* also recovered a relationship of *E. nigrofasciolatus* with *Phoboscincus*, although that study used one less nuclear gene, had lower support values for the relationship of these two taxa (BPP 0.53, bootstrap values <50%), and *Lacertoides* was not identified as part of this lineage. Rather, the genetic study of Ineich *et al.* retrieved a relationship for *Lacertoides* with *Kanakysaurus* and *Marmorosphax*, but with no support for relationships between these genera and only low support for the three genera as a subgroup (BPP 0.53, bootstrap values <50%).

Epibator gen. nov. and *Phoboscincus* share two morphological apomorphies, separation of the chinshields from the lower labial scales by 1–2 rows of small intervening scales and division of the last upper labial obliquely, that argue for a sister taxon relationship between these genera, contrary to the genetic evidence of Smith *et al.* (2007) which retrieves *Lacertoides* as the sister to *Phoboscincus*, but in accordance with the genetic evidence of Ineich *et al.* (2014). Separation of the chinshields from the lower labials by an intervening row of scales is variable within *Phoboscincus*, with the chinshields of *bocourti* completely separated from the lower labials, but only partially (third chinshield only) in *garnieri*. These traits have only otherwise been

recorded from the monotypic *Geoscincus* (Sadlier, 1987), a genus whose phylogenetic affinities are obscure and for which genetic data are unavailable. *Geoscincus* is readily distinguished from *Epibator* gen. nov. in having a highly reduced number of premaxillary teeth (6–9 *vs* 11), and a "scaled" lower eyelid, the homology of which is unclear and is otherwise only seen in the New Caledonian skink radiation in *Phoboscincus bocourti*. By comparison, *Lacertoides* has the plesiomorphic condition of all three chinshields fully in contact with the lower labials and an undivided last upper labial.

Recognized species. Two, *Epibator nigrofasciolatus* (Peters) and *Epibator greeri* (Böhme).

Epibator nigrofasciolatus (Peters)

Synonyms. *Lygosoma* (*Mocoa*) *nigrofasciolatum* Peters, 1869: 435. *Lygosoma arborum* Bavay, 1869: 19. *Lygosoma deplanchei* Bocage, 1873: 229 (non *Lygosoma deplanchei* Bavay, 1869 = *Sigaloseps deplanchei*).

Distribution. Widespread throughout New Caledonia, including large and small offshore islands, and the Loyalty Islands.

Comments. Recorded from a wide range of habitats at all elevations.

Epibator greeri (Böhme)

Synonym. *Leiolopisma greeri* Böhme, 1979: 140.

Distribution. Koumac region in the north-west of Grande Terre.

Comments. Böhme described the species from a single individual collected in forest. It has not been seen with certainty since, although live individuals similar in colouration to the type of *Epibator greeri* have been photographed (by one of us, RS) from southern Grande Terre.

Genus *Phasmasaurus* gen. nov.

Type species. *Leiolopisma tillieri* Ineich & Sadlier, 1991 designated hereby.

Diagnosis. Moderately large in size, maximum SVL 61 mm (*maruia*) and 64 mm (*tillieri*), with a moderately elongate body, well developed limbs and digits, and very long tail* (maximum tail length range c. 250–300% of SVL respectively).

Scalation (Fig. 5): distinct supranasal absent*; nasal scale lacking a prominent postnasal suture; frontonasal broader than long; prefrontals large; frontal longer than broad; supraoculars four; *frontoparietals fused; interparietal distinct; parietals each bordered by a single nuchal and one (*maruia*) or two (*tillieri*) upper secondary temporal scales; primary temporal single; lower secondary temporal single; tertiary temporals usually two; nasals widely separated; supraciliaries usually seven (*maruia*) or fewer (*tillieri*), reduction through fusion; upper labials usually seven with the fifth subocular and contacting the lower eyelid; postmental contacting first and second lower labial; chinshields three, first pair in broad contact, all in contact laterally with the lower labial scales; *body scales keeled (*maruia* three weak keels; *tillieri* two strong keels).

Osteology: premaxillary teeth 9 (*tillieri*) or 11 (*maruia*); atlantal arches and intercentrum of first cervical vertebrae present as three separate units; 29 presacral vertebrae; *postsacral vertebrae c. 60+; phalangeal formula for the manus of 2.3.4.5.3 and for the pes of 2.3.4.5.4; two pairs of mesosternal ribs.

Reproduction mode: variable within the genus with one species oviparous (egg laying: *maruia*) and one viviparous (live-bearing: *tillieri*).

The suite of apomorphic character states identified above is modest, but will distinguish *Phasmasaurus* gen. nov. from all other genera in the *Eugongylus* group of skinks, including the new genera described here. The key morphological apomorphy uniting *tillieri* and *maruia* as sister taxa, and which serves to distinguish them from as a distinct evolutionary entity from most *Eugongylus* group genera is the exceptionally long tail of the species of *Phasmasaurus*, characterized by a high postsacral vertebrae number of 60 or more. This character state is otherwise only seen within the *Eugongylus* group in some *Emoia* (species in the *samoensis* group), which are outside the endemic New Caledonian skink radiation. *Phasmasaurus* gen. nov. can be distinguished from these *Emoia* in having fused (*vs* paired) frontoparietals, keeled (*vs* smooth) body scales, and fused (*vs* distinct) supranasal scales, although the evolution of supranasal scales within the *Eugongylus* group, and the polarity of their presence are open to question (Sadlier, 2010).

Etymology. From the Greek *Phasma*, a spectre, in the sense of the insect genus *Phasma* Lichtenstein, type genus for the family Phasmatidae, and for the order Phasmatodea in general, alluding to the phasmid-like appearance and behaviour of species in the group. Gender of the generic name based on the Greek *sauros* (masculine).

Intergeneric relationships. Support for the two species included in *Phasmasaurus* as a genetic lineage in the study by Smith *et al.* (2007) based on one mitochondrial (ND2) and two nuclear (c-*mos* & RAG-1) genes was high (BPP 1 but with Bootstrap support <50%), and a similar, but slightly lower level of support (BPP 0.95%, bootstrap 71%) was recovered by Ineich *et al.* (2014). The two species in *Phasmasaurus* share only a modest suite of morphological apomorphies that serve to define it, including fused frontoparietal scales, keeled body scales, a windowed lower eyelid and a very long tail, all character states that can be found in some other taxa in the *Eugongylus* group. Additional support for monophyly of the two species as a lineage (outside of the genetic data) comes from unusual shared attributes in habitat preference and behaviour. The strict habitat preference of both species to maquis shrubland and shared unusual aspects of behaviour (Sadlier *et al.*, 1998) in combination, lend further support to the genetic data for these taxa comprising an independent evolutionary lineage highly divergent from others in the *Eugongylus* group of skinks.

The scheme of relationships for the *Eugongylus* group skinks presented by Smith *et al.* (2007) placed the species here included in *Phasmasaurus* (and the New Caledonian species here recognized as *Caesoris novaecaledoniae*), outside the well-supported lineage that included nearly all other endemic New Caledonian skinks, and within a cluster that included the New Zealand genera inclusive of the Norfolk/Lord Howe Island *Oligosoma lichenigera*,
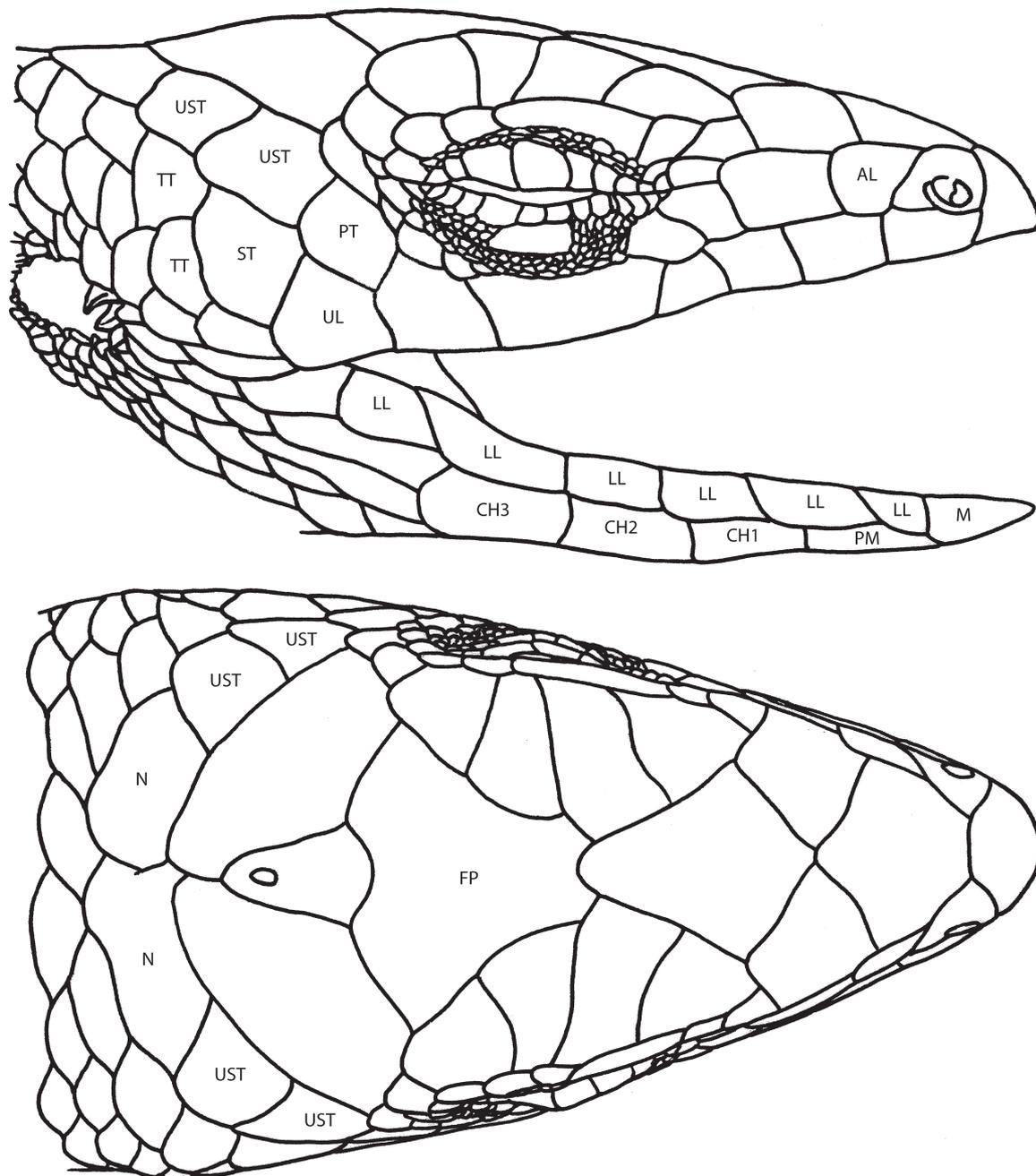
Figure 5. Head scalation of *Phasmasaurus* as seen in *P. tillieri* showing the relatively plesiomorphic configuration of the majority of head scales except for the fused frontoparietal scales *(FP)*. Note the divided upper secondary temporal *(UST)* an apomorphy for *P. tillieri* not shared with *P. maruia*.

although this latter group received no support as a lineage in its own right. A more recent molecular phylogeny of Chapple *et al*. (2009) which sampled extensively the New Zealand *Eugongylus* group skinks, and which also included representative taxa from the New Caledonian skink fauna for out-group comparison, retrieved a monophyletic New Caledonian skink group represented by the taxa *Caledoniscincus austrocaledonicus*, *Nannoscincus mariei*, *Marmorosphax tricolor*, and "*Lioscincus*" *tillieri* that was the sister group to the New Zealand + Lord Howe/Norfolk Island *O. lichenigera*, and with *tillieri* now nested within the (albeit reduced) New Caledonian group. The most

recent molecular phylogeny of Ineich *et al*. (2009), which concentrated primarily on the endemic New Caledonian skink radiation and the genetic relationships of the recently discovered *Phoboscincus bocourti*, but which also included a range of other *Eugonglus* group genera in the outgroup, placed the species here included in *Phasmasaurus* as the sister to all the endemic New Zealand skinks (also including *Oligosoma lichenigera*), but with no support.

Recognized species. Two, *Phasmasaurus tillieri* (Ineich & Sadlier) and *Phasmasaurus maruia* (Sadlier, Whitaker & Bauer).

Phasmasaurus tillieri (Ineich & Sadlier)

Synonym. *Leiolopisma tillieri* Ineich & Sadlier, 1991: 344.

Distribution. Restricted to the southern ultramafic ranges of New Caledonia.

Comments. Endemic to maquis shrubland habitats.

Phasmasaurus maruia (Sadlier, Whitaker & Bauer)

Synonym. *Lioscincus maruia* Sadlier, Whitaker & Bauer, 1998; 335.

Distribution. East-central region ultramafic ranges and the west-central ultramafic ranges as far north as Plateau de Tia and Massif de Kopéto.

Comments. Restricted to maquis shrubland habitats.

Intrageneric relationships. Two genetic-based studies (Smith *et al.*, 2007; Ineich *et al.*, 2014) retrieve *P. tillieri* and *P. maruia* as highly supported (BPP 1.0) sister taxa. However, there is also substantial genetic and morphological differentiation between the two taxa. Nucleotide sequence divergence between *P. tillieri* and *P. maruia* for the mitochondrial gene ND2 was around 20.0%, approaching the level of genetic distance found between some genera of New Caledonian skinks (Sadlier & Bauer, unpublished). The high level of genetic differentiation between the two taxa is complemented by a number of differences in morphology and clearly supports their recognition as independent evolutionary entities. While the two species are similar in overall body form in both having long legs, a long tail and an angular head, there are substantial differences in scalation. In particular, the degree of morphological differentiation seen in *tillieri*, as expressed in the number of species-specific apomorphies, is exceptional in comparison to most other New Caledonian skinks. In particular the strongly bicarinate scales with the keel interrupting the posterior free edge is a trait unique to the species within the context of the Tasmantis group skinks (Fig. 6a). By comparison *maruia* is plesiomorphic in its head scalation and the weakly tricarinate body scales (Fig. 6b) of this species likely represent the more plesiomorphic form of this character for the genus (see Sadlier, 2010: appendix 1). The two species also differ markedly in reproductive mode, with *P. tillieri* giving birth to live young while *P. maruia* has retained the plesiomorphic egg-laying condition. This is the only genus in the *Eugongylus* group where both modes of reproduction occur. The extent of genetic and morphological differentiation between *P. tillieri* and *P. maruia* raises the question of recognising each as a distinct monophyletic genus. While a convincing stand-alone diagnosis could be made for *tillieri*, the morphological diagnosis for *maruia* as a lone entity would be weak and lacking in unique apomorphies to further differentiate it from *tillieri*. For these reasons this action has not been proposed at this time and their inclusion as sister taxa under *Phasmasaurus* rests primarily on the implications of the phylogenetic relationships retrieved so far from molecular studies.

In overall ecology the two species share traits in behaviour and a strict habitat preference only rarely seen in other endemic New Caledonian skink genera (Sadlier *et al.*, 1998). Both are restricted solely to maquis shrubland (*Lacertoides* is the only other taxon of skink reliant on this habitat type), with *tillieri* widespread across the southern ultramafic region and *maruia* on the adjacent central-west ultramafic ranges. As such, the two species are broadly parapatric, and they act as ecological analogues within their respective regions.
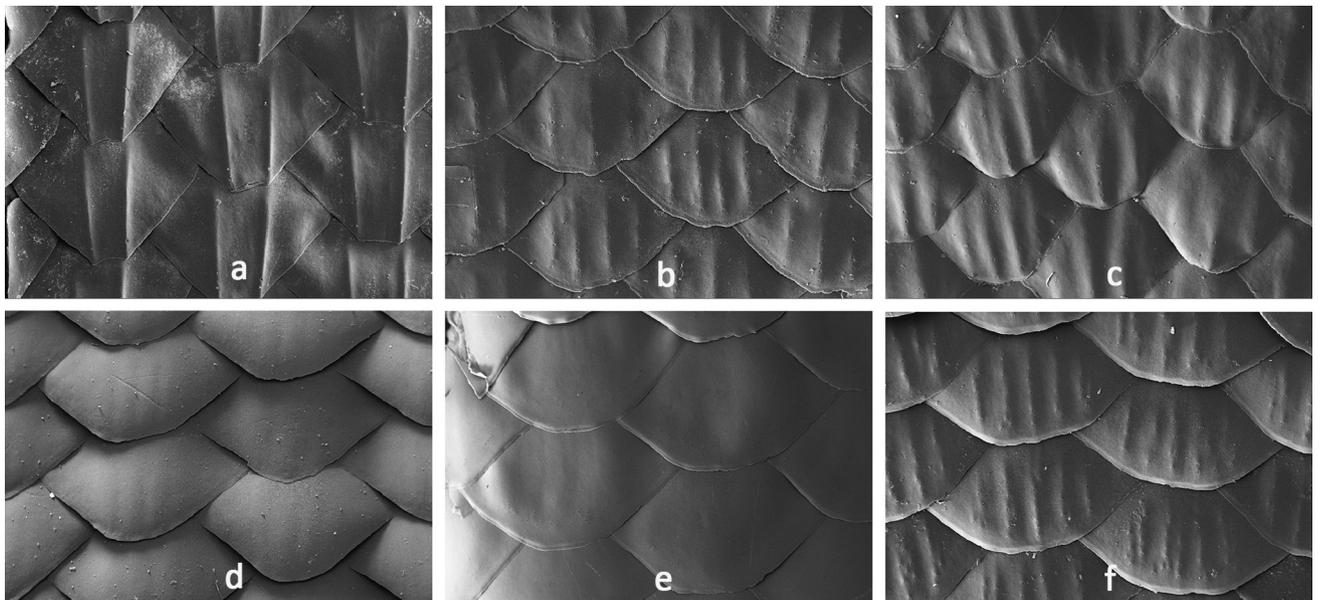

Figure 6. SEM image of markedly bicarinate body scales seen in *(a) Phasmasaurus tillieri* compared to weakly tri-quadricarinate body scales seen in *(b) Phasmasaurus maruia*, and compared to the tricarinate body scales seen in *(c) Caesoris novaecaledoniae*, the plesiomorphic condition of smooth body scales seen in *(d) Epibator nigrofasciolatus* and in *(e) Lioscincus steindachneri*, and the multicarinate body scales seen in *(f) Lioscincus vivae*.
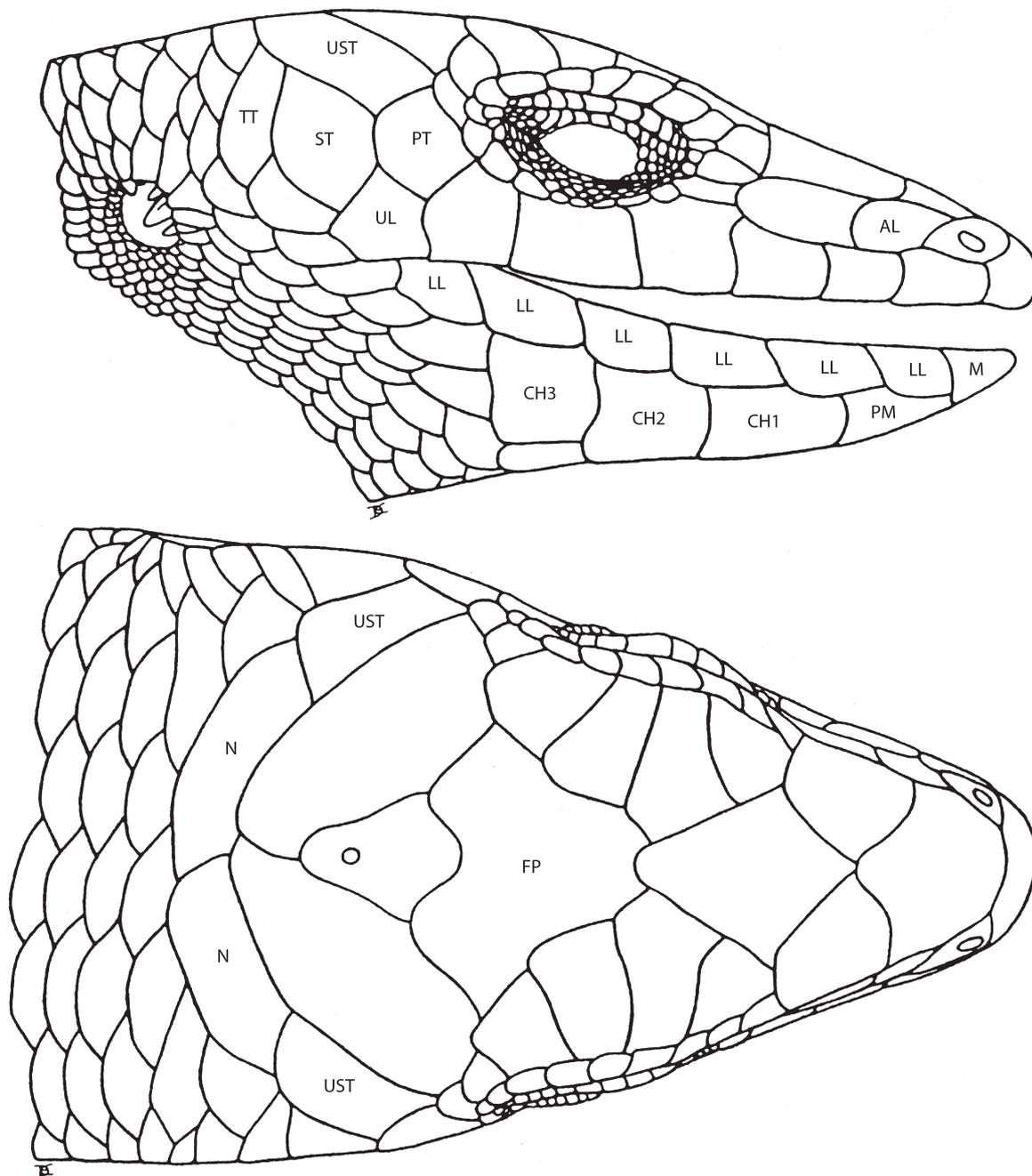
Figure 7. Head scalation for *Caesoris novaecaledoniae* (adapted from Sadlier, 1987) showing the relatively plesiomorphic configuration of the majority of head scales except for the fused frontoparietal scales *(FP)* and single enlarged tertiary temporal scale *(TT)*, compared to the plesiomorphic condition of paired frontoparietals seen in *Epibator* (Fig. 4) and two tertiary temporal scales seen in *Epibator* (see figure 4), *Phasmasaurus* (see figure 5) and *Caesoris novaecaledoniae* (Fig. 6).

Genus *Caesoris* gen. nov.

Type species. *Lygosoma (Leiolopisma) novaecaledoniae* Parker, 1926, designated hereby.

Diagnosis. Maximum SVL 68 mm with a moderately elongate body, well developed limbs and digits, and relatively long tail (maximum tail length c. 200% of SVL).

Scalation (Fig. 7): *no distinct supranasal; nasal scale lacking a prominent postnasal suture; frontonasal slightly broader than long; prefrontals large; frontal longer than broad; supraoculars four; *frontoparietals fused; interparietal distinct; parietals each bordered by a single nuchal and upper secondary temporal scale; primary temporal single; lower secondary temporal single; *tertiary temporals fused to form a single scale; nasals widely separated; supraciliaries usually seven; upper labials usually seven with the fifth subocular and contacting the lower eyelid; postmental contacting first and second lower labial; chinshields three, first pair in broad contact, all in contact laterally with the lower labial scales; *body scales with three moderately strong keels dorsally.

Osteology: premaxillary teeth 11; *atlantal arches of first cervical vertebrae fused to intercentrum; 29 presacral vertebrae; phalangeal formula for the manus of 2.3.4.5.3 and for the pes of 2.3.4.5.4; two pairs of mesosternal ribs.

Reproductive mode: egg laying.

Mouth lining and tongue colour: *deep blue.

The suite of apomorphic character states identified above will distinguish *Caesoris* gen. nov. from all other genera in the *Eugongylus* group of skinks, including the new genera described here. In particular, the exceptionally bright blue mouth colour of *Caesoris* is unique within the endemic New Caledonian skink radiation. The presence of a single large tertiary temporal scale will also serve to distinguish *Caesoris* from most other New Caledonian skink genera which have two tertiary temporal scales, except for *Phasmasaurus* (a single enlarged tertiary temporal scale occurs in most *P. maruia*) and *Lioscincus* (a single enlarged tertiary temporal scale occurs in c. 50% of *L. vivae*). The species also has an unusual toe morphology in the context of the *Eugongylus* group of skinks in which the basal lamellae of each toe are broadened laterally compared to those on the distal part of the toe (Fig. 8), resembling the condition seen in some of the arboreal geckos in the genus *Cyrtodactylus*.

Etymology. Derived from the Latin for blue (*caesius*) and mouth (*oris*), in reference to the unique blue mouth colour of the type species. Gender of name based on "oris", neuter (see Brown, 1956).

Intergeneric relationships. The study by Smith *et al*. (2007) was unable to identify any close relationship of the single species in *Caesoris* to any other genus within the Tasmantis group of skinks. In this scheme of relationships the *Caesoris* lineage lies outside a well-supported clade of most other endemic New Caledonian skink genera (*Nannoscincus* (*Lioscincus* group + *Phoboscincus* group + *Caledoniscincus* group), as does the New Caledonian *Phasmasaurus* lineage and the lineage that includes the New Zealand and Norfolk/Lord Howe Island genus *Oligosoma*. The most recent molecular phylogeny of Ineich *et al*. (2014) placed *Caesoris* as the sister to all other taxa in the Tasmantis Clade (= the endemic New Caledonian and New Zealand skinks combined), but with no support for this placement.

Among the morphological apomorphies that diagnose *Caesoris*, a single broad tertiary temporal scale and blue mouth lining and tongue are unique to the genus within the context of the taxa included in the endemic New Caledonian skink fauna. These two characters, in combination with a broader suite of apomorphies, serve to diagnose *Caesoris* from all other genera of skinks in the Tasmantis group, and support its recognition as a distinct evolutionary lineage as indicated by the genetic data.

Recognized species. One, *Caesoris novaecaledoniae* (Parker).

Caesoris novaecaledoniae (Parker)

Synonym. *Lygosoma (Leiolopisma) novae-caledoniae* Parker, 1926: 493.

Distribution. Widespread (albeit sparsely) across the central and northern regions of New Caledonia, with photographs of live individuals indicating it also occurs in southern Grande Terre.

Comments. Recorded from a wide range of habitats including low-mid elevation humid forest and coastal scrub (Sadlier, 1987), and *Acacia* scrubland bordering mesophyll dry forest (Whitaker *et al*., 2005).
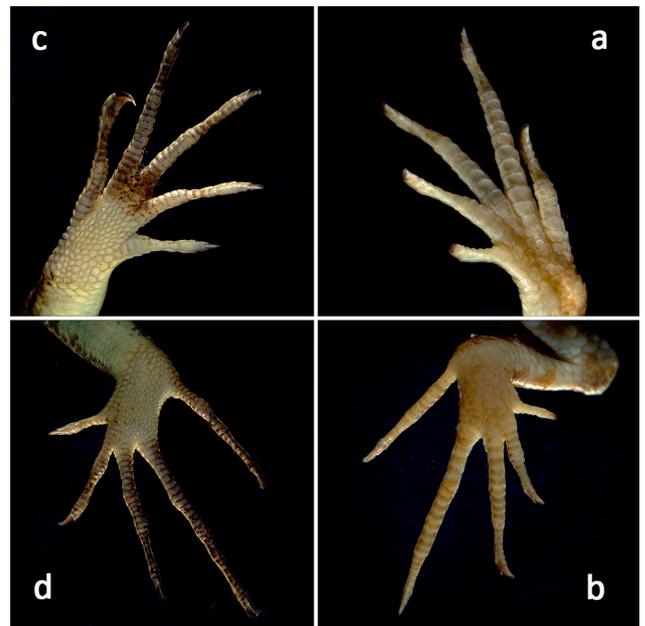

Figure 8. Underside of the *(a)* manus and *(b)* pes of *Caesoris novaecaledoniae* (AMS R.90454 SVL 61 mm) showing the broad basal lamellae of all digits and markedly narrower terminal on the distal-most part of each digit, extending to approximately the junction of the 3rd and 4th plalange on the 4th toe of the pes, compared to the lamellae of the *(c)* manus and *(d)* pes of *Epibator nigrofasciolatus* (AMS R.177492 SVL 64 mm), also an arboreal species, which are only moderately broad basally and only extend to approximately the junction of the 1st and 2nd plalange on the 4th toe of the pes.

Generic diversity in the endemic New Caledonian skink fauna

The *Eugongylus* group of skinks has a primarily Australian/Pacific region distribution, but with taxa from the sub-Saharan African region also included (Greer, 1974; Schmitz *et al*., 2005; Pyron *et al*., 2013). The group is currently undergoing an extensive molecular-based survey of relationships (Shea *et al*., unpublished data). It currently stands at 41 recognized genera, although some (*Emoia*) are clearly composite, while the affinities of others (*Geoscincus*, *Tachygyia*) are still unclear or under debate (Ineich *et al*., 2014).

The description of the three new genera presented here brings the number of endemic skink genera present in New Caledonia to 17 (Table 1). This represents approximately 40% of the generic diversity within the Australian/Pacific region *Eugongylus* group of skinks as currently recognised, and is equivalent to the number of genera in the group endemic to Australia (c. 14) and New Zealand (1) combined.

The number of endemic Australian genera in the *Eugongylus* group of skinks is likely to undergo further refinement, and their content likely to change, but not substantially. Regardless, the paradigm of the exceedingly high level of generic diversity for the endemic New Caledonian skink fauna when adjusted for area (19,103 km^2) compared to other islands in the Pacific region remains exceptional, particularly when compared to New Zealand (268,704 km^2) which is 14 times its size.

The extent of generic diversity in the endemic New Caledonian skink fauna reflects the extent of morphological and behavioural diversity found, which in turn is a reflection

Table 1. The currently recognized endemic New Caledonian skink genera in order of description.

Year	Genus	Author
1872	*Nannoscincus*	Günther
1873	*Lioscincus*	Bocage
1873	*Tropidoscincus*	Bocage
1974	*Phoboscincus*	Greer
1987	*Geoscincus*	Sadlier
1987	*Graciliscincus*	Sadlier
1987	*Marmorosphax*	Sadlier
1987	*Caledoniscincus*	Sadlier
1987	*Sigaloseps*	Sadlier
1997	*Lacertoides*	Sadlier, Shea & Bauer
1997	*Simiscincus*	Sadlier & Bauer
2004	*Kanakysaurus*	Sadlier, Smith, Bauer & Whitaker
2006	*Celatiscincus*	Sadlier, Smith & Bauer
2014	*Phaeoscincus*	Sadlier, Smith & Bauer
2015	*Epibator* gen. nov.	Sadlier, Bauer, Shea & Smith
2015	*Phasmasaurus* gen. nov.	Sadlier, Bauer, Shea & Smith
2015	*Caesoris* gen. nov.	Sadlier, Bauer, Shea & Smith

of the extent of niche diversity on the New Caledonian terrain, the end product of which is expressed as an array of highly divergent lineages, each characterized by a unique suite of adaptive characteristics.

The initial reallocation of New Caledonian skink taxa by Sadlier in 1987 to putatively monophyletic genera resulted in the recognition an additional four genera (*Caledoniscincus*, *Marmorosphax* and *Sigaloseps*, and a resurrected *Tropidoscincus* Bocage, 1873) to accommodate most of the New Caledonian species formerly assigned to *Leiolopisma*. These genera were each defined by a suite of apomorphic morphological character states, the combination of which was unique within the *Eugongylus* group of skinks. Similarly the monotypic genera *Geoscincus* (Sadlier, 1987), *Graciliscincus* (Sadlier, 1987), *Lacertoides* (Sadlier *et al.*, 1997), *Simiscincus* (Sadlier & Bauer, 1997) and *Kanakysaurus* (Sadlier *et al.*, 2004) were recognized and defined on morphological criteria (although *Kanakysaurus* had supporting genetic data). The single species included in each genus had an array of unusual and highly derived morphological character states, only a few of which were shared with taxa in existing genera. Similarly, the reassessment of *Nannoscincus* as a strictly endemic New Caledonian taxon (Sadlier *et al.*, 2002, 2006), rather than one shared with Australia, was based on morphological criteria and monophyly of the genus later supported by genetic data (Smith *et al.*, 2007). Recognition of "*Lygosoma*" *euryotis* as warranting its own genus (Bauer & Sadlier, 2000) was more complex. Although initially recognized as unique on a combination of morphological and biological criteria, the erection of *Celatiscincus* (Sadlier *et al.*, 2006) for the species *euryotis* (and its newly described sister taxon *C. similis*) ultimately drew heavily on genetic data for recognition as a distinct evolutionary entity. By contrast, the recently proposed *Phaeoscincus* Sadlier, Smith & Bauer was initially recognized as a highly divergent evolutionary

lineage on genetic criteria (Sadlier *et al.*, 2014b). The type species for the genus (*P. taomensis*) is known from a single specimen and is markedly similar in morphology to taxa in *Caledoniscincus* to which it is the sister, but from which it is diagnosed by a limited suite of apomorphic characters.

More recently the rediscovery of the enigmatic giant New Caledonian skink *Eumeces bocourti* Brocchi, the type species for the genus *Phoboscincus* Greer, has permitted a genetic analysis of the relationships between this species and its putative congener *P. garnieri* (Bavay). *Phoboscincus* was erected on morphological criteria, and the genetic study by Ineich *et al.* (2014) confirms the relationship between *bocourti* and *garnieri* exclusive of all other New Caledonian taxa, but could not explore a relationship between *bocourti* and the giant Tongan species *Tachygyia microlepis* suggested earlier by Greer (1974) and later Ineich (2009), as no recent tissue samples for *microlepis* were available for analysis. However, if such a close relationship exists, it would mean that *Tachygyia* is also a member of the New Caledonian skink radiation, implying overwater colonization from New Caledonia to Tonga.

In summary, most of the endemic skink genera exclusive of those described here were originally recognized and defined primarily on morphological criteria, and the monophyly of these genera (Smith *et al.*, 2007) and the content of their constituent taxa have since been supported by an array of genetic studies (Sadlier *et al.*, 2009, 2014a). The initial recognition of these genera on attributes of morphology, the validity of which has been independently verified by genetic studies, is testimony to the breadth of diversity in form and structure within the endemic New Caledonian skink radiation.

The historical retention of the species *nigrofasciolatus* Peters, *greeri* Böhme, *steindachneri* Bocage; and *novaecaledoniae* Parker within a "cosmopolitan" *Leiolopisma* (Sadlier, 1987), assignment of *tillieri* Ineich & Sadlier (Ineich & Sadlier, 1991) to that genus, and the subsequent assignment of these taxa to *Lioscincus* Bocage (Bauer & Sadlier, 1993), reflected more the conundrum of not being able to assign these taxa to existing genera without compromising (and weakening) the integrity of the generic diagnoses of established taxa. In the case of *steindachneri*, *novaecaledoniae* and *tillieri* this situation was exacerbated in the past by a lack of confidence in the (sometimes limited) individual suite of unique character states (autapomorphies) for each taxon as sufficient to diagnose them as distinct lineages on morphological criteria alone. The discovery of new (sister) taxa for *tillieri* with the description of *Lioscincus maruia* Sadlier, Whitaker & Bauer (Sadlier *et al.*, 1998) and more recently for *steindachneri* with the description of *Lioscincus vivae* Sadlier, Bauer, Whitaker & Smith (Sadlier *et al.*, 2004a) provided evidence that each of these species was now part of a putative multi-species lineage. As such, the discovery of new taxa related to the species included in "*Lioscincus*", in combination with the acquisition of extensive genetic data over the past 15 years in particular, have considerably advanced our understanding of the affinities of the these species to each other, and to other New Caledonian skinks, and in doing so realized the true and extraordinary extent of generic diversity within the endemic New Caledonian skink fauna.

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