

DO NOT CIRCULATE

MUS. COMP. ZOOLOGICAL
LIBRARY

B R E V I O R A MAY 13 1970

Museum of Comparative Zoology HARVARD UNIVERSITY

CAMBRIDGE, MASS.

15 MAY 1970

NUMBER 348

THE RELATIONSHIPS OF THE SKINKS REFERRED TO
THE GENUS *DASIA*

Allen E. Greer

ABSTRACT. The time honored lygosomine genus *Dasia* is divided into three genera (*Dasia*, *Lamprolepis* and *Apterygodon*) primarily on the basis of differences in skull osteology and external morphology. *Dasia* (6 species) and *Lamprolepis* (3 species) seem to have evolved independently from a primitive *Mabuya*-like ancestor, whereas *Apterygodon* (1 species) seems to have evolved from a basically *Dasia*-like stock. All three taxa appear to have had southeast Asia as their area of origin.

When Boulenger (1887) published his third volume of the Catalogue of the Lizards in the British Museum, he placed three species in the subgenus *Keneuxia*. In the two major revisions of lygosomine skinks since Boulenger (M. A. Smith, 1937; Mittleman, 1952), these three species plus other more recently described species have been grouped together in the genus *Dasia*. Yet in spite of the long historical precedent of treating these species as a generic entity, there are no characters that will serve to unite the species in a common genus, distinct from other skink genera. On the contrary, there are several characters by which the species can be assigned to three distinct genera, viz.: *Dasia* (6 species), *Apterygodon* (1 species), and *Lamprolepis* (3 species).¹ Curiously enough, the type species of the three genera are the three species that comprised Boulenger's (1887) subgenus *Keneuxia*.

In Table 1 I have listed, roughly in order of what seems to me to be their taxonomic importance, the characters that readily serve to distinguish the three genera.

¹ The names of the two genera beside *Dasia* are available from the primary synonymy of *Dasia*.

TABLE 1

A summary of the diagnostic characters of the three genera of skinks previously grouped together in the genus *Dasia*.

<i>Dasia</i> (6 species)	<i>Apterygodon</i> (1 species)	<i>Lamprolepis</i> (3 species)
Palatal rami of pterygoids meet medially (Fig. 1).	Palatal rami of pterygoids meet medially (Fig. 3).	Palatal rami of pterygoids separated medially; medial processes from palatines project posteriorly into interpterygoid vacuity (Fig. 1).
Pterygoid teeth present (Fig. 1).	Pterygoid teeth absent (Fig. 3).	Pterygoid teeth absent (Fig. 1).
No ectopterygoid process to palatine; palatal ramus of pterygoid borders infraorbital vacuity (Fig. 1).	Ectopterygoid process to palatine excludes much of palatal ramus of pterygoid from a position on the infraorbital vacuity (Fig. 3).	No ectopterygoid process to palatine; palatal ramus of pterygoid borders infraorbital vacuity (Fig. 1).
Young with sharply delineated light and dark crossbands which may or may not persist into adulthood (Fig. 2).	Adults with five white stripes on the very dark anterior part of the body; no crossbands. Young unknown.	Young and adults more or less uniformly colored and patterned. Any patterning tends to run longitudinally; no cross bars or stripes at any stage in life.
Gait slow.	Gait not slow.	Gait not slow.
Keeled body scales.	Keeled body scales.	Smooth body scales.
Postorbital bone present or absent.	Postorbital bone present.	Postorbital bone absent.
A pair of nuchal scales.	No, or rarely 1, pair of nuchal scales.	One or more pairs of nuchal scales.
Interparietal completely separates parietals except in some <i>haliana</i> .	Interparietal completely separates parietals.	Parietals meet behind interparietal.

Dasia Gray

Dasia Gray, 1839, Ann. Mag. Nat. Hist., vol. 2, p. 335 (Type species: *Dasia olivacea* Gray, 1839, by monotypy).

Liotropis Fitzinger, 1843, Systema Reptilium, p. 22 (Type species: *Euprepes ernestii* Duméril and Bibron, 1839 = *Dasia olivacea* Gray, 1839, by monotypy).

Theconyx Annandale, 1906, Spolia Zeylanica, vol. 3, p. 191 (Type species: *Euprepes haliana* Haly and Nevill, 1887, by monotypy; not *Theconyx* Gray, 1845).

Diagnosis. Of all the skinks with supranasal scales (*Apterygodon*, *Dasia*, *Emoia*, *Eugongylus*, *Eumecia*, *Lamprolepis*, *Mabuya*, *Macroscincus*, "Otosaurus," and *Riopa*) only *Dasia*, *Eumecia*, *Mabuya* (17 of 30 species examined), and *Riopa* (3¹ of 13 species examined) have pterygoid teeth. *Eumecia* is a genus encompassing one or two species with greatly reduced appendages and digits and is easily distinguishable from the strong-limbed, pentadactyl *Dasia*. *Dasia* differs from *Riopa* and *Mabuya* in palatal characters: in *Dasia* the palatal rami of the pterygoids meet medially, whereas they are separated by an interpterygoid vacuity in *Mabuya* and by posteriorly projecting medial processes from the palatines in *Riopa* (Fig. 1).

Referred species. *Griffini* Taylor, 1915; *haliana* Haly and Nevill, 1887; *moultoni* Barbour and Noble, 1916; *olivacea* Gray, 1839; *semicineta* Peters, 1867; *subcaerulea* Boulenger, 1891.

There may be more species of *Dasia* than those listed here, for Taylor (1963) believes that "more than a single species" has been confused under the name *olivacea*.

Distribution. Extreme southwestern India (*subcaerulea*); Ceylon (*haliana*); southern Thailand, Cambodia, Laos and Vietnam south of 15° N Lat., Con Son, the Andaman and Nicobar Islands, Borneo and Java (*olivacea*); Palawan Islands (*griffini*); Philippines (*semicineta*). *Moultoni* occurs on Borneo with *olivacea* in the only known case of sympatry between any two species in the genus. The distribution is disjunct; there are no species between southern India and Ceylon and southeast Asia.²

¹ In an earlier paper (Greer, 1967b) I said that only 1 (*bowringi*) of these 13 species had pterygoid teeth. This is not correct, for a re-examination of this material shows two additional species (*afer* and *punctata*) with pterygoid teeth.

² This particular disjunct distribution is relatively well known in other reptiles and vertebrates. See the symposium on the zoogeography of this distribution in the Proc. Nat. Inst. Sci. India, vol. 15, no. 8, 1949.

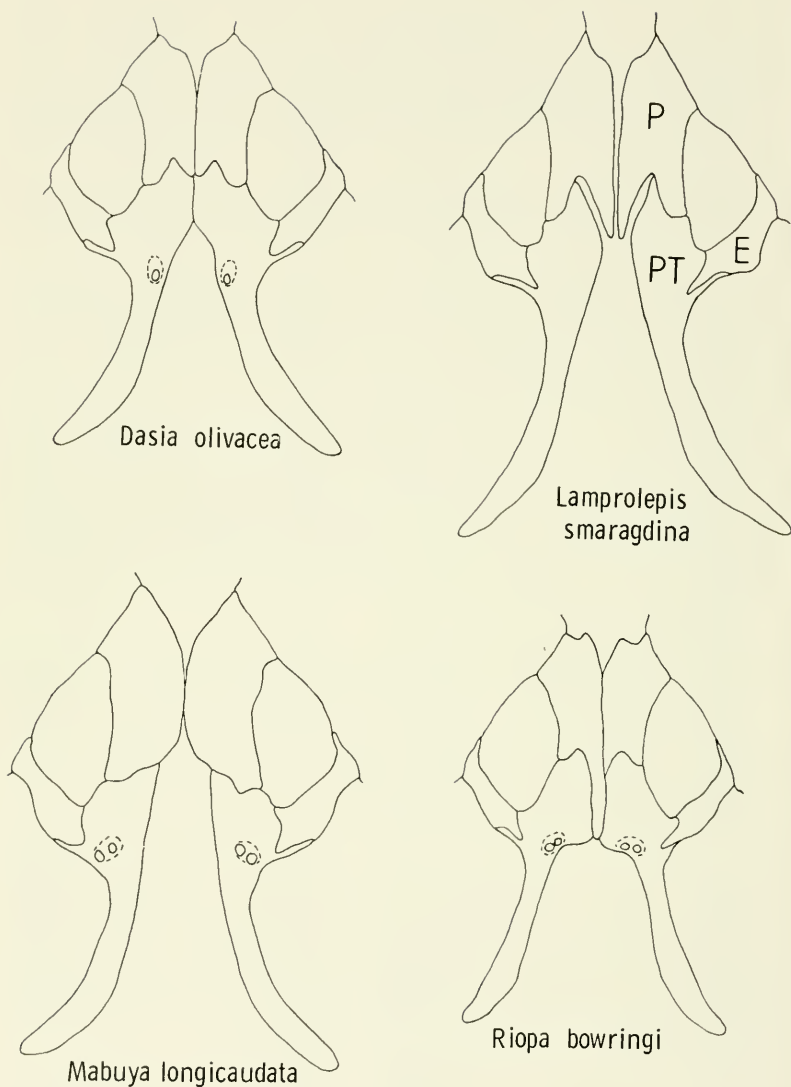


FIGURE 1. Ventral view of the secondary palate in *Mabuya longicaudata*, a primitive lygosomine, and representatives of three genera—*Dasia*, *Lamprolepis* and *Riopa*—thought to have evolved independently from an ancestor much like this primitive lygosomine. Not drawn to scale. Abbreviations: E, ectopterygoid; P, palatine; PT, pterygoid.

Although it is evident from the distribution outlined above, I should perhaps emphasize that *Dasia*, although quite widespread in southeast Asia and the western end of the Indo-Australian Archipelago, is an almost classic example of a taxon whose easternmost distributional limits extend to, and thereby help to define, Wallace's Line.

Species taxonomy. Several factors make it difficult to know where the species boundaries should be drawn in this genus. First, with the exception of *moultoni* and *olivacea* on Borneo, all the species are allopatric. Second, with the exception of the Ceylonese *haliana*, the species are very similar in several classically important scale counts, and third, two of the species (*moultoni* and *subcaerulea*) are only known from single specimens. In view of these difficulties it may be worthwhile for me to express my opinions of the species taxonomy of *Dasia*.

Taylor (1922) proposed that *griffini* (Palawan) and *semicineta* (Philippines) be reduced to the rank of subspecies of the widespread *olivacea* of southeast Asia. Although the three forms are similar in several important scale counts, the following features serve to separate them and, to me, suggest specific status for each.

<i>olivacea</i>	<i>griffini</i>	<i>semicineta</i>
Supranasals separated	Supranasals meet	Supranasals meet
Black bands broader than light bands in young	Black bands about equal to light bands in young	Black bands broader than light bands in young (Fig. 2)
Postorbital bone present	?	Postorbital bone absent

I have been able to examine only a single skull of two of the species, but as I have never found the presence or absence of the postorbital to vary intraspecifically in skinks, I do not hesitate to accept it as a reflection of specific difference until more material is available to prove otherwise. Unfortunately I have not been able to see a skull of *griffini*.

The type and only known specimen of *moultoni* is a young individual that differs from the only other *Dasia* occurring with it on Borneo, i.e., *olivacea*, in having the supranasals meeting medially instead of being separated and in having the black bands narrower, instead of broader, than the light bands. *Moultoni* is most similar to *griffini* on Palawan, which has the black bands equal in width

to the light bands and which shows, as a variation, 3 of the 4 supraoculars in contact with the frontal, as is the case in the type of *moultoni*. Other *Dasia* and some *griffini* have but 2 of the 4 supraoculars in contact with the frontal.

Only two specimens of the south Indian *subcaerulea* are known, and the similarity between this species and the southeast Asian *olivacea* is reputed to be remarkable (M. A. Smith, 1935, 1949). Apparently the most noticeable difference between the two species is the presence of two black streaks on the neck of *subcaerulea* that are never present in *olivacea*. The great geographic distance between the two species is no assurance that other, as yet undiscovered, difference might exist between the two species, for as mentioned above (see footnote on page 3), the relationships between many vertebrates in the two separate areas of southern India-Ceylon and southeast Asia are surprisingly close. There are, however, only a few examples of conspecific relationship between nonflying animals in the two areas, and this fact, along with the slight differences that do exist between the two forms, tend to make me retain *subcaerulea* and *olivacea* as distinct species.

The Ceylonese *haliana* is readily distinguished from other *Dasia* on the basis of a lower number of longitudinal scale rows at mid-body (24 instead of 26-30) and in the persistence of the juvenile banding into adulthood.

Reproduction. Information on the mode of reproduction is available for only two of the six species of *Dasia* and both are oviparous. M. A. Smith (1935) says that *olivacea* is oviparous and lays "six eggs at a time," but Cantor (1847) found 11 eggs in one female. Deraniyagala (1953) reports that a captive *haliana* laid "two soft-shelled eggs."

Field notes. As far as is known all the species of *Dasia* are arboreal to semiarboreal.

According to M. A. Smith (1935) and Taylor (1922), *olivacea* is arboreal and subarboreal in its habits and, in addition, shows "a preference for small islands" (M. A. Smith, 1935). Hendrickson (1966) found that on Palau Tioman, *olivacea* occurred mainly on the coastal plain where it replaced the upland *Mabuya multifasciata*, but it was not as common in its lowland habitat as was *M. multifasciata* in the upland forest.

Mr. James P. Bacon, Jr., who has observed *olivacea* from platforms in the forests of Sarawak, informs me (letter of 15 July 1968) that he and his group saw ten specimens, all of which were above 50 feet from the forest floor, and with respect to sites and

types of activity were similar to *Apterygodon vittatus* (see below). There was, however, one major difference between these two arboreal skinks: "In comparison to *vittatus*, which scampers around like a terrestrial *Mabuya* or *Sphenomorphus*, *olivacea* moves with almost painful deliberateness."

Taylor (1915, 1922) has the following comments on *Dasia semicineta*, a close relative of *olivacea*: "Specimens of this species were collected from the tops of large felled trees. It is a retiring species and is never observed on the ground," and "it is retiring and is seldom observed. It is arboreal in habit, feeding for the most part in the trees. Usually the animals inhabit trees which are densely covered with vines."

W. C. Brown (letter of 20 June 1968) has very kindly summarized for me his observations on *Dasia griffini*, a close relative of both *olivacea* and *semicineta*: "The specimens of *griffini* were collected in dipterocarp forest between 200 and 1000 feet elevation in the Thumb Peak area of Palawan. Most were taken in bark crevices or beneath loose bark on both living and dead trees. Two [were] collected on rocks on the river bank. . . . This is not an abundant species."

All we know of the ecology of *subcaerulea* is that the type and second known specimen were collected at 1100 and 5900 feet altitude respectively. M. A. Smith (1949) thought that the subdigital lamellae of the species indicated that it had "arboreal habits."

Dasia haliana is considered by Deraniyagala (1953) to be a "rare arboreal species restricted to the low country" of Ceylon. The same author mentions two individuals being captured from a hole and a cavity of a tree, respectively, and "according to Haly it lives on the tops of high trees" (Smith, 1935).

Deraniyagala (1953) provides another important clue to the behavior of *haliana* in his comment, "the gait of this arboreal species is much slower than in other Ceylon skinks even when climbing a tree." This comment calls to mind Bacon's statement of the "almost painful deliberateness" with which *olivacea* moves about the trees. One wonders if the slow movements of these two species may not be characteristic of all the species of *Dasia* in contrast to the more usual, quicker motions of the species of the other two genera recognized here.

Juvenile color patterns. As far as is known, all juvenile *Dasia* are strikingly marked with light and dark crossbands. The bands persist in adult *haliana* but disappear with age in the other species for which information is available.

Taylor's (1922) account of a juvenile *semicineta* is the most vivid available for any species in the genus: "The body above is glossy coal black with a series of brilliant orange yellow bars from the tip of the snout to the end of the tail. . . . The legs and digits [are] barred with canary yellow; the regenerated tail is brick red; below, on [the] body the bars widen and lose themselves in the immaculate canary yellow of the abdomen." There is a total of eight to nine yellow bars on the neck and body of this specimen described by Taylor. Another juvenile with ten light crossbands on the neck and body is shown in Figure 2.



FIGURE 2. Dorsal view of a juvenile (snout-vent length = 57 mm) and adult (snout-vent length = 117 mm) *Dasia semicineta* from the Philippine Islands showing the light and dark crossbands in the juvenile and their absence in the adult.

According to M. A. Smith (1935), "young [*olivacea*] are black above, with narrow silvery or yellowish, rather irregular transverse crossbars, from 11 to 14 in number, on the neck and body."

A late juvenile or subadult *griffini* (snout-vent length = 67 mm) in the Museum of Comparative Zoology (MCZ) may indicate something of the juvenile coloration for this species. This specimen is light brownish above with 14 dark brown crossbars, encompassing 13 light interspaces, from the nape to the base of the tail.

The type and only known specimen of *moultoni* is in the MCZ. It is clearly a juvenile (snout-vent length = 45 mm) and is predominately yellowish brown with 14 narrow dark brown crossbands, separated by 13 wider light interspaces, from the nape to the base of the tail. The crossbands extend laterally to, but not across, the venter.

In *haliana* "the number of black crossbands [in both juveniles and adults] varies from five to six from the shoulders to above [the] hips. . . . The width of the black bands alters with age. In the young they are equal to or only slightly narrower than the light interspaces. . . ." (Deraniyagala, 1953). Annandale (1906) figures a juvenile *haliana* in which there are seven dark crossbands, encompassing six light interspaces, from the nape to the base of the tail. According to Deraniyagala (1953) the "young [are] pink with black crossbands."

The two known specimens of *subcaerulea* are 57 and 70 mm in snout-vent length, but both lack any trace of crossbarring. It would seem, therefore, that either this species has no crossbanded pattern in the juvenile or the only known specimens are too old to display them.

The most interesting question about these crossbanded patterns is, of course, their function. Their function, however, is almost surely related to the ecology and behavior of their bearer, and as we know precious little of these matters in the adults and nothing in juveniles, we have very few facts with which to work.

Striking crossbanded patterns such as those seen in *Dasia* are really quite unusual in skinks, whether adult or juvenile. In fact, there are only about six other species among the approximately 800+ species of skinks that have an even closely comparable pattern, *viz.*: the scincines *Scincopus fasciatus*, *Scincus scincus* (some individuals), and *Scelotes splendidus*, and the lygosomines *Sphenomorphus fasciolatus*, *Tiliqua occipitalis* (some individuals), and *T. gerrardi* (especially pronounced in juveniles).

Other morphological evidence argues against a common ancestry for *Dasia* and any of these other species with crossbanded patterns, so their similarity in this regard is truly convergent.

The species of this list do share one ecological similarity, i.e., they are all ground dwellers that occasionally penetrate the loose substrate, but this is not a particularly unique ecological situation for skinks and it carries no ready explanation of the adaptiveness of the crossbanded pattern in such a situation.

Perhaps the juvenile color patterns are mimetic, taking advantage of either a specific but as yet unknown aposematic model or a general abstract model recognizable to predators gaining their experience with several different specific models. It could also be that the young occupy the same general habitat as the parents, and the juvenile color pattern acts as a signal to inhibit feeding attacks by the adult.

Relationships with other genera. In any group of skinks it is reasonable to assume that pterygoid teeth and supranasal scales are primitive features which may be lost in more advanced species. In possessing these two characters, therefore, *Dasia* is a primitive genus. On the basis of the secondary palate, however, *Dasia* is advanced, for the close medial apposition of the palatal rami of the pterygoids may be reasonably thought of as the extreme development of the uniquely scincid secondary palate (Greer, 1970).

The only living lygosomines that are like *Dasia* in retaining both supranasals and pterygoid teeth are *Riopa*, *Mabuya*, and *Eumecia*. Of these three genera, *Mabuya* is the best candidate for the closest ancestral relative of *Dasia*.

Eumecia is an African genus with one or two species. The taxon is very similar to *Mabuya* in its skull morphology and is distinguishable from this genus solely by its attenuate body form and reduced appendages and digits. *Eumecia* is clearly derived from *Mabuya* (Greer, 1967b), and its diagnostic specializations make it an unlikely ancestor for any other living skink.

If one combines all the primitive features of the various species of *Riopa* (exclusive of *Eugongylus*), the similarities with *Dasia* are impressive; supranasal scales, scaly lower eyelid, pterygoid teeth and oviparity. There is, however, an important difference in the relationships of the bones of the secondary palate, for in *Riopa* the pterygoids are separated by close-fitting, posteriorly-projecting medial processes from the palatines (Fig. 1), whereas in *Dasia* the

pterygoids meet medially and are not separated by palatine processes. In both genera the secondary palate, initiated by the medial apposition of the palatine bones, is extended further posteriorly by the partial (*Riopa*) or complete (*Dasia*) incorporation of the pterygoids. A posterior extension of the secondary palate is undoubtedly an advanced condition in lygosomines, but there is only a functional similarity between *Riopa* and *Dasia* in this regard, for the way in which the complete secondary palate is extended posteriorly, is fundamentally different in both taxa.

In addition to the palatal differences between *Riopa* and *Dasia* which preclude any close phylogenetic relationship, there are other important differences between the two groups. *Riopa*, for instance, lacks the crossbanded patterns in the young that are characteristic of *Dasia*, and it is also an essentially terrestrial taxon in contrast to the arboreal *Dasia*.

Mabuya is quite unlike both *Dasia* and *Riopa* in that the palatal rami of the pterygoids are widely separated with their medial edges smoothly diverging posteriorly (Fig. 1). This palate is primitive for lygosomines in the sense that the pterygoids are in an "uncommitted" state and could theoretically be incorporated into the secondary palate in a number of ways. In fact, it is this primitive palatal condition, along with the presence of supranasal scales, scaly eyelids, pterygoid teeth, well-developed pentadactyl limbs, a full complement of distinct head scales, and oviparity that makes *Mabuya* (especially the southeast Asian species in which all these characters occur) a very likely candidate for the ultimate ancestor of any lygosomine skink. In this light, it is easy to regard *Dasia* as being derived from a primitive *Mabuya*-like ancestor by the medial apposition and ultimate meeting of the palatal rami of the pterygoids along the midline.¹

Dasia is similar to *Mabuya* in regards other than the sharing of the primitive lygosomine characters mentioned above. The body scales of *Dasia* (primarily the posterior body scales in adults) are keeled, as are the body scales of all the species of *Mabuya* except those eight or nine species (exclusive of *M. atlantica*) inhabiting the New World; these have smooth scales. Also, unlike *Riopa* and *Eumecia*, which are largely terrestrial and cryptic in their habits,

¹ Similarly, one can conceive of the evolution of *Riopa* from a primitive *Mabuya* through the medial apposition of the palatal rami of the pterygoids concurrently with the posterior extension of medial palatine processes (Fig. 1).

many species of *Mabuya* are partly arboreal in their habits. Such a propensity for arboreality could have provided the behavioral background on which to build the morphological adaptations to arboreality in *Dasia*.

To summarize this section we may outline the changes that occurred in the evolution of *Dasia* from a primitive *Mabuya*-like ancestor (also see Fig. 6).

1. The apposition of the palatal rami of the pterygoids along the midline of the secondary palate until they met and formed a posterior extension to the secondary palate.
2. The evolution of a striking crossbanded pattern in the young.
3. The evolution of a greater degree of arboreality.
4. The development of a slower gait.

Zoogeography. It is interesting to note that *Dasia* occupies the same general southeast Asian area occupied by the species that seem to be its closest ancestral relatives, i.e., the primitive species of *Mabuya*. In fact, like *Dasia*, *Mabuya* is, with only one or two exceptions, also confined to the area west of Wallace's Line. It looks, therefore, as if the evolution of *Dasia* from a *Mabuya*-like ancestor, and perhaps even the early evolution of *Mabuya* itself, is a phenomenon of the tropical parts of the southeastern Oriental Region and has had little or nothing to do with the area east of Wallace's Line, i.e., Wallacea and the Australian Region.

Apterygodon Edeling

Apterygodon Edeling, 1864, Nedel. Tijdschr. Dierk., vol. 2, p. 201 (Type species: *Apterygodon vittatum* Edeling, 1864, by monotypy).

Diagnosis. Along with *Dasia*, *Apterygodon* differs from all other skinks with supranasal scales in having the palatal rami of the pterygoids meeting medially along the midline of the palate. *Apterygodon*, however, differs from *Dasia* in lacking pterygoid teeth and in having a small fingerlike process of the ectopterygoid bone that projects anteriorly toward the palatine and partially excludes the palatal ramus of the pterygoid from a position on the infra-orbital vacuity (Fig. 3).

Referred species. Only the type species is placed in the genus.

Distribution. Borneo. There is also a single specimen in the British Museum (Natural History) which is questionably from Ceram. This locality is almost certainly in error, however, for, with the exception of the Ceram record, the species has never been recorded from anywhere other than Borneo.

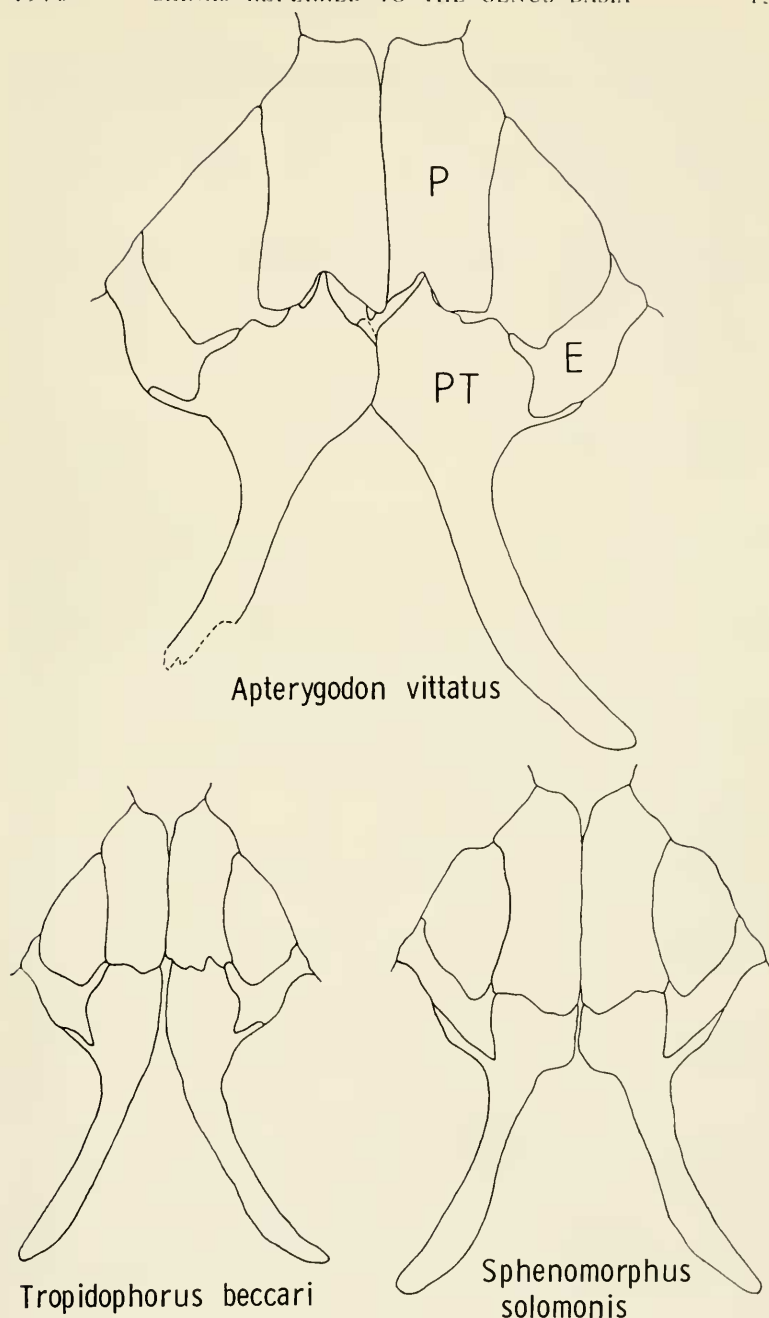


FIGURE 3. Ventral view of the secondary palate in *Apterygodon* and representatives of two other genera, *Sphenomorphus* and *Tropidophorus*, with species displaying similar palates. The ectopterygoid process has probably evolved independently in each of these three groups. The palatal bones of *Apterygodon* are partially disarticulated. Not drawn to scale. Abbreviations as in Figure 1.

Mode of reproduction. A female with a snout-vent length of 71 mm, collected in the Baram District of Sarawak, contains two eggs in the right oviduct and one in the left oviduct. The three eggs are surrounded by a fairly thick shell which indicates that the species is probably oviparous.

Field notes. By letter, Mr. James P. Bacon, Jr. has very generously summarized for me his observations on *vittatus* which were made in the course of platform observations on the altitudinal stratification of the reptiles in the Sarawak forest. Below, I have paraphrased the information on this species contained in Mr. Bacon's letter of 15 July 1968.

In one year of platform work from 36 to 110 feet above the forest floor there were 169 observations of *vittatus*. On the basis of number of observations, *vittatus* was the most frequently encountered lizard; a *Draco* was the second most frequently encountered species with 32 observations. *Vittatus* occurs between 0-120+ feet. The majority of the observations were made between 40 and 120 feet, although this range may reflect platform distribution more than it does lizard distribution. The observations made so far indicate that *vittatus* is the dominant canopy lizard in Sarawak, at least in the upper canopy (A and B strata).

Vittatus is a sunloving skink and moves about on trunks and branches of all kinds during the day. It spends its time exploring bark crevices and the interiors of epiphytes and in basking. The lizards are capable of short (half a foot or less) jumps between adjacent branches and vines.

Dr. Robert Inger has also given me his brief but valuable impressions about *vittatus* in the field. He says in a letter of 28 June 1968 that "*vittatus* is a sun lover. On rare occasions *vittatus* will descend to the ground, but only at the base of large trees."

Variation. Undoubtedly because of its canopy-dwelling habits (see "Field notes" section for the genus), *Apterygodon vittatus* is a little known skink. The Museum of Comparative Zoology is fortunate in having 15 specimens, and it is worthwhile to record the variation in several taxonomically useful characters for these specimens. All the specimens are from Sarawak.

The prefrontal scales are separated in all specimens, but two individuals have the scales of the snout broken up into a number of small, asymmetrical scales. Nuchal scales are lacking except in two individuals, which each have a single pair. There are always 4 supraoculars with 2 (in 18 of the 30 possible cases) or 3 (in the remaining 12 cases) supraoculars in contact with the

frontal. The fifth supraocular is beneath the eye except in one of the 30 possible cases where it is the fourth. There are 28-30 longitudinal scale rows at midbody, and 16-22 (avg. = 18.2) subdigital lamellae beneath the fourth toe. All 15 specimens are adults, and the largest two are each 72 mm in snout-vent length.

Relationships with other genera. Except for the absence of pterygoid teeth and the presence of an ectopterygoid process, *Apterygodon* and *Dasia* are very similar in several important skull characters. In both taxa there is a small postorbital bone, the palatal rami of the pterygoids are similar in shape in both taxa and meet medially, and there are 9 teeth on the premaxillae. The skull differences between the two genera do not really preclude the idea of the close relationship, for, as will be shown below, an ectopterygoid process has probably evolved numerous times in lygosomines, and the loss of pterygoid teeth is a familiar feature of lygosomine evolution.

Two aspects of the external morphology of the two genera make the idea of their close relationships even more compelling. The more remarkable of these is the numerous fine, approximately longitudinal striations on the dorsal and lateral body scales and the scales of the appendages. These striations were first noted by M. A. Smith (1935) in *Mabuya longicaudata* and were later rediscovered by Taylor and Elbel (1958) in *Dasia olivacea* and *Mabuya longicaudata*. An extensive examination of other lygosomines has revealed the striations only in *Dasia semicineta*, *D. griffini*, *D. moultoni* (the only species of *Dasia* available for examination), *Apterygodon*, and *Mabuya tyleri*. The striations, therefore, seem to be confined to *Dasia*, *Apterygodon*, and two species of southeast Asian *Mabuya*, i.e., those *Mabuya* which are most similar to the probable ancestor of *Dasia*. It appears then that the striations are another indication of the close relationships within this group of skinks. Unfortunately, the function of these striations is completely unknown.

The second external character that aligns *Dasia* and *Apterygodon* is a pair of enlarged "heel scales" on the rear foot in the males of both taxa. These scales in males are not only considerably larger than the surrounding scales, but they also seem to have an inner texture (viewed through the semitransparent epidermis) which distinguishes them from nearby scales and which belies a glandular function. In females this pair of scales is only slightly larger than the surrounding scales, and they appear to lack the textural differences that distinguish the scales from their fellows in

males. Paired enlarged heel scales are also evident in some *Mabuya*, but only in a few species (most notably *M. longicaudata*) are they larger (and then only slightly) in males than in females, and they are never differentiated as in male *Dasia* and *Apterygodon* (Fig. 4). The heel scales of *Mabuya* are probably homologous with those of *Dasia* and *Apterygodon*, but only in this latter group have they become greatly differentiated (to serve a glandular function?) in males.

Because we know nothing about the juvenile color patterns of *Apterygodon*, we have no idea how the genus compares with *Dasia* in this important regard. It seems unlikely, however, that a skink with an adult color pattern of anterior light longitudinal stripes on a dark ground color would have a juvenile color pattern consisting of light and dark crossbands, but admittedly my feeling on this may stem more from a sense of "taste" than from biological logic.

Aside from the differences in adult and possibly juvenile color pattern, the only other nonskeletal difference of any significance between *Apterygodon* and *Dasia* is in the gait, for, as mentioned above (see "Field notes" section under *Dasia*), *Apterygodon* has a faster, more commonly "skink-like" gait than does *Dasia*.

In summary, the differences between the two taxa are important but do not override the similarities on which the idea of their close relationship rests. I think, however, the differences do serve to justify the generic separation of the two taxa. In attempting to interpret these similarities and differences phylogenetically, we can hypothesize that *Apterygodon* and *Dasia* once shared a common ancestor that was decidedly *Dasia*-like except for the slower gait (and cross-banded juvenile color pattern?), and from this ancestor, *Apterygodon* evolved on the one hand through the loss of the pterygoid teeth and the independent evolution of an ectopterygoid process, and *Dasia* evolved on the other hand through a line that subsequently acquired a slower gait (Fig. 6).

Since this view of the phylogeny of *Apterygodon* and *Dasia* implies that the ectopterygoid process in *Apterygodon* has evolved independently of its evolution in other lygosomines, perhaps a word should be said about the significance of this process in lygosomines in general. It is true that the process, especially when it is well developed to the point of forming a firm articulation with the palatine bone, correlates well with other characters, which, taken together, serve to delimit large natural groups (Greer, 1967a). That this process, however, is not indicative of one and

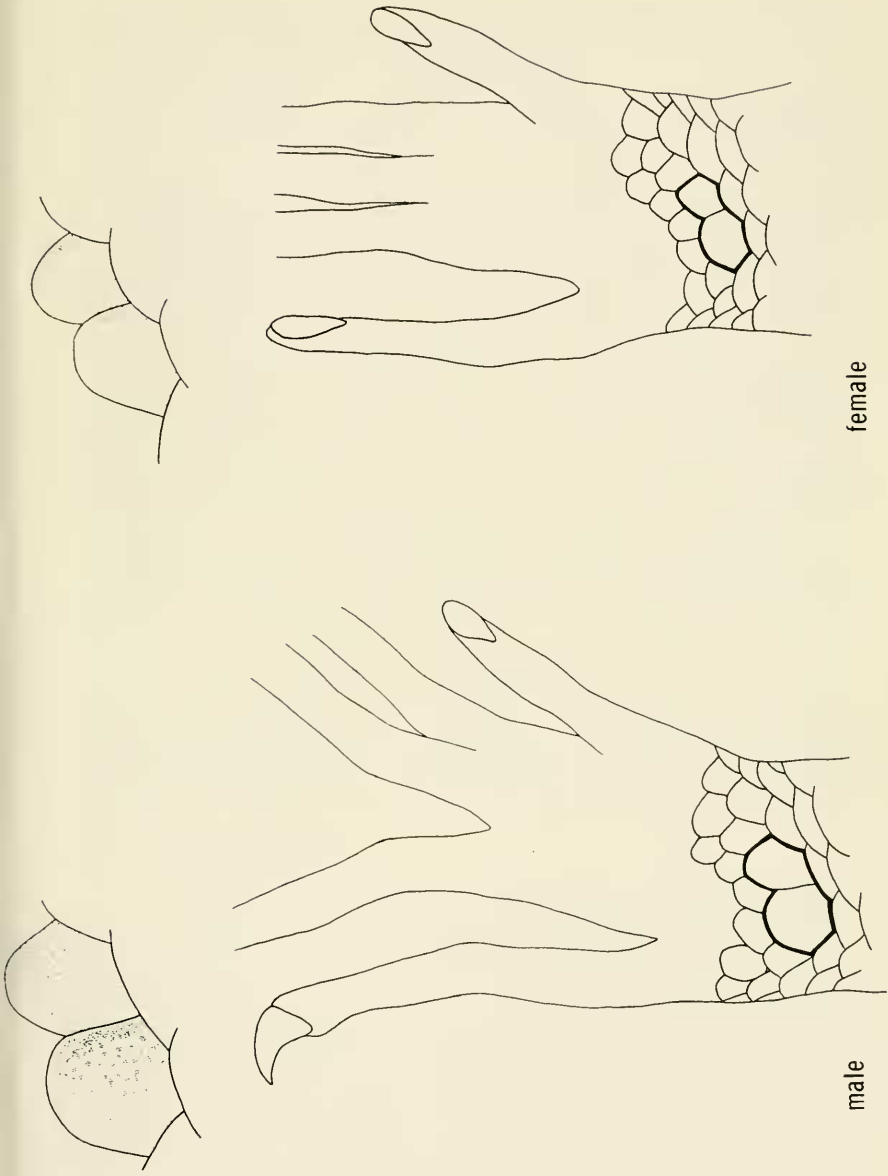


FIGURE 4. A comparison of the "heel" scales of a male (snout-vent length = 69 mm) and female (snout-vent length = 64 mm) *Apterygodon vittatus* from the Baram District, Sarawak.

only one major line of lygosomine evolution, i.e., that it has evolved more than once, is suggested by two lines of evidence. First, the process is variably developed in its anterior extent in species that are clearly closely related, e.g., *Hemiergus* and the Australian alpha *Leiolopisma*, and second, even those major groups which show a consistently strongly developed process articulating with the palatine often have very little else in common and, in some cases, are quite distantly separated geographically (Table 2). Thus not only has the process evolved independently in *Apterygodon*, but it has also done so in several other lygosomine lines as well. Again, like so many other skull characters that seem to have some taxonomic importance, we have no information about the function of the ectopterygoid process in these skinks. Presumably it may have something to do with skull kinetics, which in turn may have something to do with feeding habits. In any event, once the function of the process is known, its evolutionary significance and, therefore, its taxonomic significance should become clearer.

Zoogeography. The Bornean distribution of *Apterygodon* fits with the hypothesis of the close relationship of *Apterygodon* and *Dasia*, for Borneo is in that area of the Oriental Region where *Dasia* seems to have had much of its evolutionary history.

TABLE 2

Lygosomine taxa which are apparently only distantly related but which as groups show strongly developed ectopterygoid processes.

<i>Group</i>	<i>Area of Evolution</i>
1.) <i>Ctenous</i> , <i>Egernia</i> (most species), <i>Tiliqua</i> , <i>Corucia</i> , <i>Tribolonotus</i>	Australian Region
2.) <i>Leiolopisma virens</i> , <i>L. flavipes</i> , <i>L. prehensicauda</i> , <i>L. semoni</i>	Australian Region
3.) <i>Tropidophorus</i> (some species)	Southeast Asia, Philippines
4.) <i>Solomonis</i> subgroup of <i>Sphenomorphus</i> (see Greer, 1967a)	Australian Region
5.) <i>Macrosцинus</i> (see Hoffstetter, 1949)	Cape Verde Islands

Lamprolepis Fitzinger

Lamprolepis Fitzinger, 1843, *Systema Reptilium*, p. 22 (Type species: *Scincus smaragdina* Lesson, 1830, by monotypy).

Keneuxia Gray, 1845, *Catalogue of the Specimens of Lizards in the Collection of the British Museum*, p. 79 (Type species: *Scincus smaragdina* Lesson, 1830, by monotypy).

Diagnosis. On the basis of its palatal characters (Fig. 1) and the single large pair of nuchal scales bordering the parietals, *Lamprolepis* is an alpha skink (Greer and Parker, 1968). Most alphas, however, have either 11 premaxillary teeth (e.g., *Anotis*, *Emoia*, *Eugongylus*, most Australian and Pacific *Leiopisma* and "*Sphenomorphus*" *bignelli*, "*S.*" *minutus* and "*S.*" *pseudornatus*), or a spectacle in a movable lower eyelid, or permanent brille (e.g., all alpha *Leiopisma* and *Ablepharus*). They can thus be distinguished from *Lamprolepis*, which has but 9 premaxillary teeth and a scaly lower eyelid. In these two characters *Lamprolepis* is similar to the primitive alpha genus *Mabuia*; in fact, the only way *Lamprolepis* can be readily distinguished from all *Mabuia*, except the most geographically distant species in tropical America (exclusive of *M. atlantica*), is by the absence of keels on the body scales.

The only other alpha taxon not mentioned above is the African *Eumecia*. This genus encompasses one or two attenuate species with a reduced number of digits and is easily distinguished from the more robust, pentadactyl *Lamprolepis*.

Referred species. *nieuwenhuisi* Lidth de Jeude, 1905; *smaragdina* Lesson, 1830; *vyneri* Shelford, 1905.

Distribution. Two of the three species, *nieuwenhuisi* and *vyneri*, are confined to Borneo, whereas *smaragdina* is very widespread. This species occurs from Formosa, the Philippines, Palawan and the Sulu Archipelago, the Celebes and Lombok (but not Bali or west) south and east through Micronesia (Palau Islands and the Carolines east to the Marshalls), the Indo-Australian Archipelago, New Guinea and Cape York (Australia) to the Solomon Islands

and the Santa Cruz Islands.¹ In the Indo-Australian Archipelago south of the Philippines, the western limit of *smaragdina's* distribution follows Wallace's Line exactly (see fig. 7 on page 167 in Mertens, 1930).

Reproduction. *L. smaragdina* is the only species in the genus for which information about reproduction is available, and from all accounts (Hediger, 1934; Alcalá, 1966; and Fred Parker, personal observation) as well as my own observations, it is clear that the species consistently lays but two eggs in a clutch.

The eggs are laid inside the rotten wood and rubbish in hollow branches and trunks (Fred Parker, personal observation), in the "moist humus collected in rotting parts of tree trunks, exposed roots, and points of intersection of main tree trunks . . . in nesting sites . . . very close to or several meters above the ground" (Alcalá, 1966) or, probably less frequently, on the ground under logs or stones (Hediger, 1934).

Brown and Reyes (1956) found that the maximum incubation period for *smaragdina* in the Philippines was 54 days, while Parker reports that "an egg laid on 1 October . . . hatched on 27 November," indicating an incubation time of approximately 58 days.

Field notes. *L. smaragdina* is one of the best known lizards in the Pacific. This notoriety is undoubtedly due to the species' great abundance, its medium-large size and beautiful coloration, and its propensity for the more or less bare parts of tree trunks. In an effort to incorporate the best known aspects of the lizard's ecology and behavior, I have chosen for presentation below the accounts of four people, each of whom has seen *smaragdina* in the field in a different part of its range.

¹ Reports of *L. smaragdina* from Java and Borneo (de Rooij, 1915) are probably in error. Mertens (1929) says that the species is certainly absent from Java and attributes its inclusion in the Javanese fauna to a kind of thoughtless recording of locality that was apparently fairly usual in regard to species actually native to more eastern islands in the Indo-Australian Archipelago.

The single specimen on which the Bornean locality is based is not *L. smaragdina* but *L. nieuwenhuisi* (Mertens, 1929; Brongersma, 1933), a species which is endemic to Borneo. Furthermore, Dr. Robert Inger, who has been involved in recent studies on the herpetology of Borneo, writes (letter of 17 July 1968): "So far as I know, *Dasia smaragdina* does not occur on Borneo. I have never seen any specimens in any museum here or in Europe with a Bornean locality."

According to Hediger (1934), who worked primarily in the Bismarck Archipelago and in northern New Guinea, *smaragdina* lives primarily in isolated trees, small groups of trees, and on the forest edge. It is most usually found on tree trunks and resorts to the tree branches only for protection from the rain and on cloudy days. The lizard is extremely arboreal in its activities and apparently descends to the ground only for an occasional insect and sometimes to lay its eggs. When approached by an intruder, these skinks characteristically scurry around to the other side of the tree trunk just as squirrels often do. Although primarily insectivorous, some individuals examined by Hediger had masses of leaves and flowers in their stomachs.

In the Philippines *smaragdina* "has been found in dipterocarp, freshwater swamps, and mangrove forests, wooded grasslands, and coconut groves. It prefers areas with big trees that are exposed to the sun, irrespective of the amount of ground cover. Its altitudinal distribution is from sea level to about 600 meters" (Alcala, 1966).

Fred Parker, speaking of *smaragdina* on Bougainville and its neighboring islands in the Solomons, says that it is "mainly an arboreal species but during the day some can be found feeding on the ground in undergrowth. When they are disturbed they run to the nearest tree trunk. The preferred trees are those without thick creeper growth, such as coconut palms and breadfruit trees. The species is more common in open cleared areas, on trees still standing in gardens, and in small coconut plantings. In thick primary forest they are rarely seen. Found all over the lowlands and into the mountains but not very common over 2000 feet, except perhaps in the Guava area."

Marshall (1951) had the opportunity of observing *smaragdina* on the extreme northeastern periphery of its range on the islets of Arno Atoll in the Marshall Islands. He noted that here "this strictly arboreal skink is the diurnal counterpart of the Big Tree Gecko [*Gehyra oceanica*], and one or two can be seen on almost every coconut trunk during their hours of activity from about 7:30 a.m. to 5 p.m. (if sunny). They may remain motionless for long periods, pressed against the clear trunk, with the head held out at an angle. On uninhabited islands where there is denser vegetation, they will come lower in the leafy understory of vines and shrubs but are rarely found on the ground. They occur on just about all the islets of the atoll; though . . . none [were found] on Autore, one was seen on tiny Rakijer, much smaller than Autore, and containing only 3 or 4 coconut palms. A little

islet next to Rakijer, which had only a growth of *Scaevola*, lacked any lizards of any kind. . . . [*Smaragdina*] sleeps at night on the trunk, wherever they happen to be at the end of the day, as evidenced by the fact that individuals will seldom be roosting at the same spot on successive nights."

In contrast to this vast amount of information for *smaragdina*, we know virtually nothing about *nieuwenhuisi* or *vyneri*. According to M. A. Smith (1931), two *nieuwenhuisi* were collected at 3000 feet on Mt. Kinabalu, North Borneo, and a *vyneri* in the Field Museum was collected 8 feet up a tree in forest.

Relationships within the genus. The two Bornean species of *Lamprolepis*, *nieuwenhuisi* and *vyneri*, are extremely closely related, perhaps even conspecific, and both are seemingly more primitive than *smaragdina*. Both *nieuwenhuisi* and *vyneri*, for example, have retained supranasal scales, whereas *smaragdina* has lost them; *nieuwenhuisi* and *vyneri* also lack the single enlarged heel scales characteristic of male *smaragdina* (Gandolfi, 1907, and Fig. 5, this paper), and in this lack the two species may also be primitive.¹

Within *smaragdina* itself Mertens (1929) has suggested that the Moluccas "subspecies," *moluccarum*, is the most primitive living population. This argument was based on two lines of reasoning: first, this population is more or less centrally located in regard to the other named populations of *smaragdina* and can therefore be looked upon as occupying a central area from which the species could have dispersed evenly in all directions, and second, the light grey to greyish brown ground color of *moluccarum*—in contrast to the unusual (for skinks) green color in most other named forms

¹ Although the single enlarged heel scale of male *Lamprolepis smaragdina* is very similar to the paired enlarged heel scales of *Dasia* and *Apterygodon*, even to the point of having a glandlike appearance, the scales have probably differentiated independently in each group. The best evidence for this lies in the fact that the nearest living relatives of the two groups' common ancestor, i.e., the primitive southeast Asian *Mabuya* (see below), lack such highly differentiated heel scales. An histological examination of the scales' morphology and perhaps a chemical analysis of the cell products (if the scales are glandular) would make an interesting extension of the comparison of these heel scales.

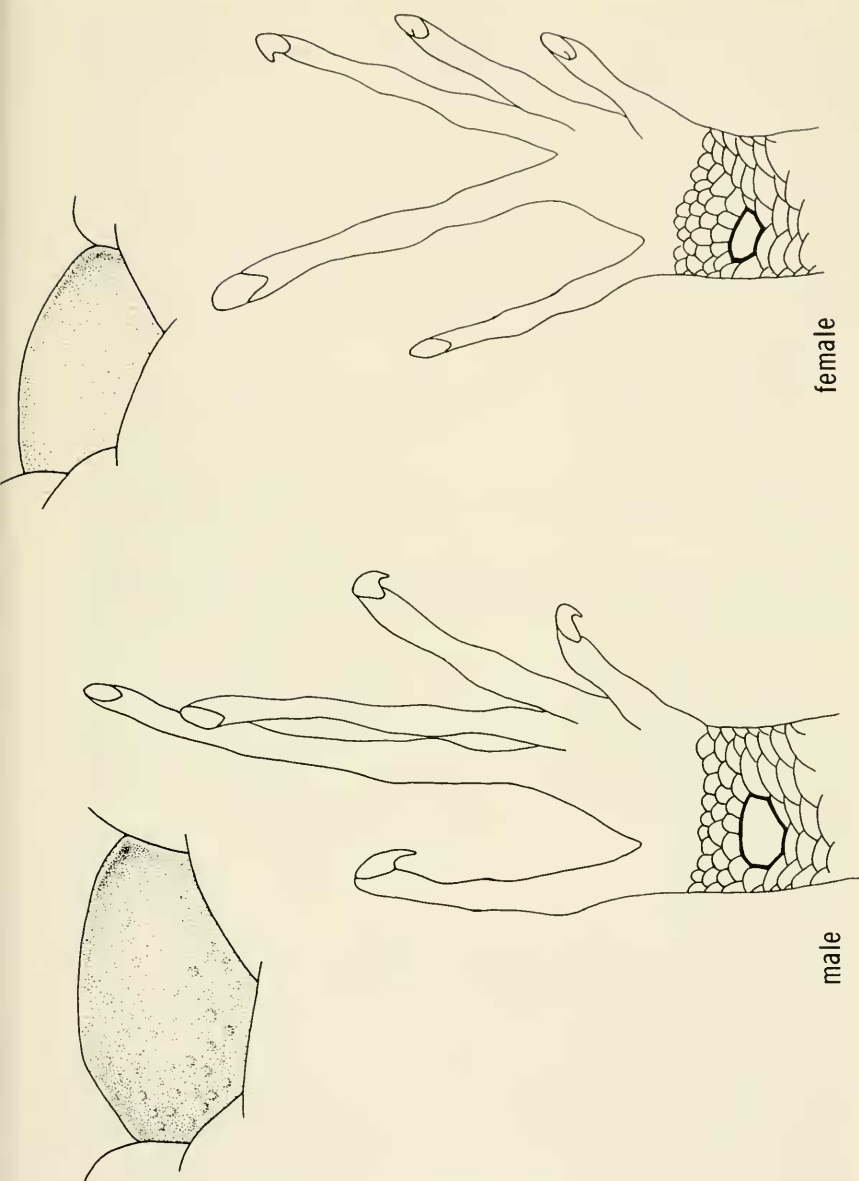


FIGURE 5. A comparison of the "heel" scales of a male (snout-vent length = 86 mm) and female (snout-vent length = 83 mm) *Lauprolepis snaragdina* from Bougainville, Solomon Islands.

of *smaragdina*¹—is probably most similar to the drab ground color of most other ground inhabiting skinks that are presumably most similar to the ancestor of *smaragdina*.

As they stand, Mertens' arguments are overdrawn, but they do point the way; thus, while it is naive to place too much emphasis in pinpointing the geographically central area of a species as the center of its dispersal, I do think that the origin and early distribution of *smaragdina* is more likely to have occurred in the western part of its range, in an area close to its nearest relatives and well known as a source area, than in the remote Pacific island chains where *smaragdina* reaches its easternmost limits. And while it is probably true that a drab color pattern is more likely ancestral to a bright green one than vice versa, it is unnecessary to imply that the amount of green in a color pattern is strongly correlated with evolutionary age. In this more diffuse argument the two lines of evidence mesh as they were supposed to in Mertens' argument, for the subdued, more achromatic (primitive) color patterns are characteristic of the populations in the western part of the range, where, as I said, *smaragdina* probably first arose and from whence it dispersed, whereas the predominately green (advanced) color patterns are characteristic of the populations in the eastern part of

¹ All the attempts to name subspecies of *smaragdina* (Barbour, 1912 and 1921; de Rooij, 1915; Mertens, 1929) have relied heavily on differences in color pattern. This method, however, has several shortcomings. First, the taxonomically important greens and yellows are lost in preservation so that the remaining structural and melanistic color patterns are very unlike, and generally not correlated with, the patterns in life, and second, there is often a good deal more continuous variation, or possibly in some cases, discrete polymorphism, in single breeding populations than those who ascribe to the current subspecies concept of *smaragdina* would like to admit (some of this pattern variation in single breeding populations is described by Taylor, 1922; Hediger, 1934; Marshall, 1951; and Brown and Marshall, 1953).

This is not to say, however, that differences between populations of *smaragdina* do not exist. There are clear differences in color pattern between populations, but they are of a statistical nature and not absolute; also, judging from preliminary observation, there are discernible proportional differences between populations. Whether these differences can be worked out to the point of establishing a new subspecies concept for *smaragdina* is problematical, for the basic data-gathering task will be Herculean. In the meantime, however, and by way of taking a step toward unraveling this larger problem, there is a real need to understand the genetic and ecologic aspects of color pattern variation in populations of *smaragdina*.

the range, i.e., in the Pacific island chains, which are more likely to receive colonists than to send them.

I can add one additional piece of color pattern data to the argument that the western populations of *smaragdina* are generally more primitive than the eastern populations. This is the fact that in western *smaragdina* there is often a whitish, "paint brush" streak extending from the flank onto the base of the tail which passes directly over the back leg. This streak is also present in the Bornean *vyneri* and *nieuwenhuisi*, i.e., the closest living relatives of primitive western *smaragdina*, but it is absent in the *smaragdina* from the eastern part of the species range, i.e., in those populations derived from the more primitive western *smaragdina*. Presumably, therefore, the white flank stripe of *vyneri*, *nieuwenhuisi*, and primitive western *smaragdina* has been lost in the evolution of the advanced eastern *smaragdina*.

Relationships with other genera. *Lamprolepis* is most similar to *Mabuya* and differs from all the Old World species of this genus only in having smooth instead of keeled body scales. The New World species of *Mabuya* (except *atlantica*) also have smooth body scales but the great geographical distance between the smooth-scaled *Lamprolepis* and the smooth-scaled *Mabuya* argues for the independent evolution of this condition in both groups.

If one assumes that the most geographically proximate species of *Mabuya* are probably most like the ancestors of *Lamprolepis*, then the loss of pterygoid teeth has been another feature in the evolution of *Lamprolepis* from *Mabuya*. All southeast Asian *Mabuya* have pterygoid teeth, whereas the palatal teeth have been lost in all the New World species and in about half the African species, but in only one of the south Asian species (*bibroni*) examined to date. It looks, therefore, as if the pterygoid teeth, like keeled body scales, may have been lost independently in both *Lamprolepis* and the advanced species of *Mabuya*.

It thus seems that both *Dasia* (*sensu stricto*) and *Lamprolepis* are independently derived from a *Mabuya*-like ancestor, and they might, in fact, have shared the same ancestor. Since this time, however, the two taxa have diverged to a great extent. *Dasia* evolved a more extensive secondary palate (by incorporating the pterygoid bones), a slower gait, and an unusual juvenile color pattern but retained, as a primitive feature from its *Mabuya*-like ancestry, pterygoid teeth and keeled body scales. *Lamprolepis*, on the other hand, retained a basically *Mabuya*-like palate, gait, and color pattern (except in the greenish eastern populations of

smaragdina) but lost the pterygoid teeth and keeled body scales (and later the supranasal scales in *smaragdina*) of their *Mabuya* ancestry (Fig. 6).

Zoogeography. The significance of Wallace's Line to the zoogeography of *Lamprolepis* probably lies in its coincidence with the eastern edge of the Sunda Shelf, i.e., the eastern limit of the Asian land mass that would result with normal Pleistocene lowering of sea levels. With such lowering of sea levels, Borneo, the island harboring the two primitive species of *Lamprolepis*, would be connected to the Asian mainland along with Sumatra and Java, while the area to the east of this land mass, i.e., the area inhabited by the advanced species of *Lamprolepis*, would still be an archipelago, albeit with an increased average island size.

The dynamics of this distribution might have been somewhat as follows: The ancestor of *vyneri* and *nieuwenhuisi* probably arose from a primitive *Mabuya*-like skink on the land mass of the Sunda Shelf when this area was a dry extension of the southeast Asian mainland. This *vyneri-nieuwenhuisi* ancestor reached the island archipelago to the east of the Sunda Shelf and here gave rise to *smaragdina*, which then spread east with great success but which could not spread west back onto the dry land regions of the Sunda Shelf. The inability of *smaragdina* to spread westward onto the land of the Sunda Shelf was certainly not the result of an inability to cross water gaps, as its success in the east proves, but was probably due instead to an inability to penetrate the complex, basically mainland continental fauna of the Sunda Shelf land mass.

ACKNOWLEDGMENTS

I would like to thank first and foremost Mr. James P. Bacon, Jr., Dr. Walter C. Brown, Dr. Robert F. Inger, and Mr. Fred Parker for relating to me their field experiences with some of the animals discussed in this paper. Dr. Inger also very generously permitted me to examine two specimens of *Lamprolepis vyneri* in the Field Museum of Natural History. In addition, I have benefitted greatly from discussions with Mr. Ross Kiester about *Lamprolepis smaragdina* in Micronesia.

Dr. Ernest E. Williams of the Museum of Comparative Zoology has read the manuscript in several drafts and has offered many useful criticisms.

Mr. Ian T. Riddell took the photograph for Figure 2 and Mr. Laszlo Meszoly did the drawing for Figures 4 and 5.

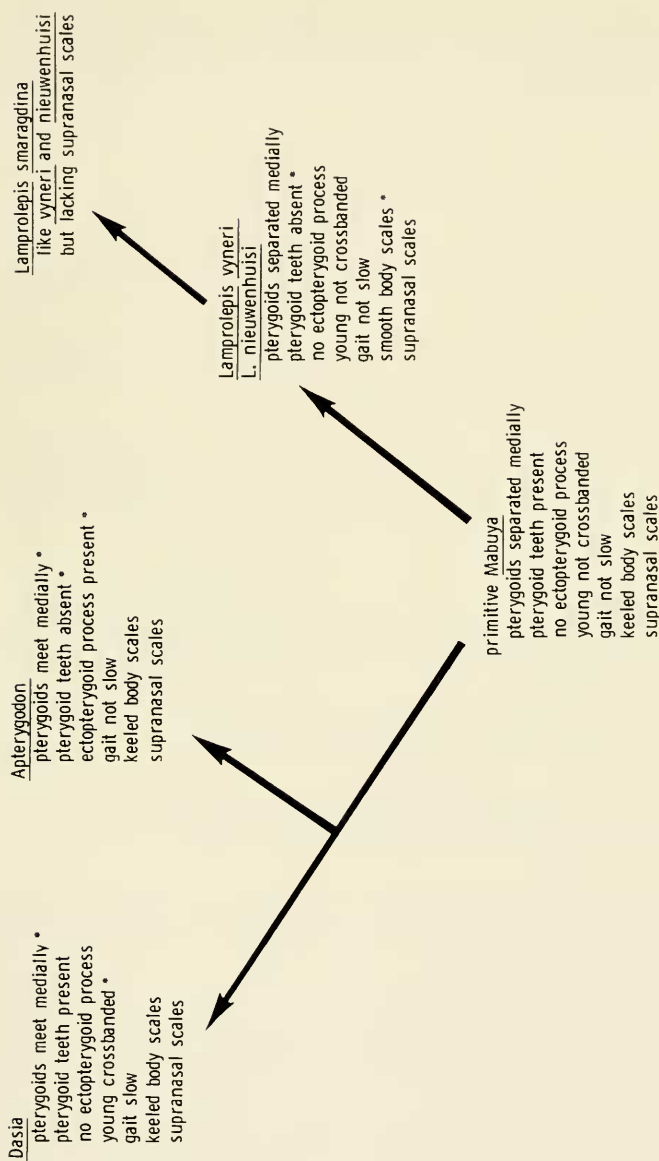


FIGURE 6. A hypothetical phylogeny of *Apterygodon*, *Dasia* and *Lamprolepis*. An asterisk (*) indicates a change in the character state of the derived taxon from that of the ancestral taxon. The young of *Apterygodon* being unknown, there is no information on their color pattern.

Work for this paper was carried out while I was first a National Science Foundation predoctoral and then later a postdoctoral fellow. An NSF grant to Dr. Williams (GB 6944) also provided funds for the completion of the paper.

LITERATURE CITED

- ALCALA, A. C.
1966. Populations of three tropical lizards on Negros Island, Philippines. Unpublished Ph.D. thesis, Stanford University; 269 pp.
- ANNANDALE, N.
1906. New and interesting lizards in Colombo Museum. *Spolia Zeylanica* 3(11): 189-192.
- BARBOUR, T.
1912. A contribution to the zoögeography of the East Indian Islands. *Mem. Mus. Comp. Zool.* 44(1): 1-203.
1921. Reptiles and amphibians from the British Solomon Islands. *Proc. New England Zoöl. Club* 11: 91-112.
- BOULENGER, G. A.
1887. Catalogue of the Lizards in the British Museum (Natural History). Vol. 3, 2nd ed. London, British Museum: vii + 575 pp.
- BRONGERSMA, L. D.
1933. Herpetological notes. 1. *Lygosoma nieuwenhuisii* van Lidth de Jeude. *Zool. Meded. Leiden* 16: 1-2.
- BROWN, W. C., AND J. T. MARSHALL, JR.
1953. New scincoid lizards from the Marshall Islands, with notes on their distribution. *Copeia* 1953(4): 201-207.
- BROWN, W. C., AND A. Y. REYES
1956. Philippine lizards. Observations on the incubation period and on hatchlings of several oviparous species. *Silliman J.* 3(2): 139-143.
- CANTOR, T.
1847. Catalogue of Reptiles Inhabiting the Malayan Peninsula and Islands. Calcutta: Baptist Mission Press, 157 pp.
- DERANIYAGALA, P. E. P.
1931. Some Ceylon lizards. *Spolia Zeylanica* 16(2): 139-180.
1953. A Colored Atlas of Some Vertebrates from Ceylon. Volume Two. Tetrapod Reptilia. Ceylon Nat'l. Mus. Publ., Ceylon Gov't. Press; vii + 101 pp.

GANDOLFI, H.

1907. Ein sekundärer Geschlechtsunterschied bei *Lygosoma smaragdinum* (Less). Zool. Anzeig. **32**(7): 186-188.

GREER, A. E.

- 1967a. A new generic arrangement for some Australian scincid lizards. Breviora **267**: 1-19.
- 1967b. The generic relationships of the African scincid genus *Eumecia*. Breviora **276**: 1-9.
1970. A subfamilial classification of scincid lizards. Bull. Mus. Comp. Zool. **139**(3): 151-183.

GREER, A. E., AND F. PARKER

1968. *Geomyersia glabra*, a new genus and species of scincid lizard from Bougainville, Solomon Islands, with comments on the relationships of some lygosomine genera. Breviora **302**: 1-17.

HEDIGER, H.

1934. Beitrag zur Herpetologie und Zoogeographie Neu Britanniens und einiger umliegender Gebiete. Zool. Jahrb. (Syst.) **65**(5-6): 441-582.

HENDRICKSON, J. R.

1966. Observations on the fauna of Palau Tioman and Palau Tulai. 5. The reptiles. Bull. Nat'l. Mus. Rep. Singapore **34**: 53-71.

HOFFSTETTER, R.

1949. Les reptiles subfossiles de l'île Maurice. I.-Les Scincidae. Ann. Paleontologie **35**: 45-72.

MARSHALL, J. T., JR.

1951. Vertebrate ecology of Arno Atoll, Marshall Islands. Atoll Res. Bull. No. 3: ii + 38 pp.

MERTENS, R.

1929. Die Rassen des Smaragdskinke. *Dasia smaragdinum* Lesson. Zool. Anzeig. **84**(9-10): 209-220.
1930. Die Amphibien und Reptilien der Inseln Bali, Lombok, Sumbawa und Flores. Abh. senckenberg. naturf. Ges. **42**(3): 115-344.

MITTLEMAN, M. B.

1952. A generic synopsis of the lizards of the subfamily Lygosominae. Smithsonian Misc. Coll., **117**(17): 1-35.

DE ROOIJ, N.

1915. The Reptiles of the Indo-Australian Archipelago. I. Lacertilia, Chelonia, Emydosauria. Leiden: E. J. Brill, Ltd., xiv + 384 pp.

SMITH, M. A.

1931. The herpetology of Mt. Kinabalu, North Borneo, 13,455 ft. Bull. Raffles Mus. **5**: 3-32.
1935. The Fauna of British India, Including Ceylon and Burma. Reptilia and Amphibia. Vol. II—Sauria. London: Taylor and Francis, xiii + 440 pp.
1937. A review of the genus *Lygosoma* (Scincidae: Reptilia) and its allies. Rec. Indian Mus., **39**(3): 213-234.
1949. Notes on a second specimen of the skink *Dasia subcaerulea* from southern India. J. Bombay Nat. Hist. Soc. **48**(3): 596-597.

TAYLOR, E. H.

1915. New species of Philippine lizards. Philippine J. Sci., Sec. D. **10**(2): 89-109.
1922. The Lizards of the Philippine Islands. Gov't. Philippine Islands, Dept. Agricult. Nat. Res. Bureau of Sci. Publ. No. **17**: 1-269.
1963. The lizards of Thailand. Univ. Kansas Sci. Bull. **44**(14): 687-1077.

TAYLOR, E. H., AND R. E. ELBEL

1958. Contribution to the herpetology of Thailand. Univ. Kansas Sci. Bull. **38**(13): 1033-1189.

(Received 11 December 1969.)