THE GENERA *RHOPTROPUS* AND *PHELSUMA* (REPTILIA: GEKKONIDAE) IN SOUTHERN AFRICA: A CASE OF CONVERGENCE AND A RECONSIDERATION OF THE BIOGEOGRAPHY OF *PHELSUMA*.

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ABSTRACT

The genus *Rhoptropella* Hewitt, 1937 is shown to be a junior synonym of *Phelsuma* Gray, 1825 and the genera *Phelsuma* and *Rhoptropus* Peters, 1869 are compared. It is pointed out that *Phelsuma ocellata* shows a great deal of convergence with *Rhoptropus* but that both of these forms exhibit their own distinctive derived character combinations. The distribution pattern of *Phelsuma* on the mainland of Africa and on Madagascar is reviewed in the light of current theories of biogeography and past continental relationships. It is suggested that the distribution of *Phelsuma* may represent a track which is also occupied by other reptilian genera.

DEDICATION

I would like to dedicate this paper to the memory of Karl Patterson Schmidt who first erected the combination *Phelsuma ocellata* and in so doing pointed out the true relationships of this southern African species. His conclusions were denied acceptance due to the lack of supporting biogeographic evidence and the absence of an acceptable system for the construction of phylogenies.

INTRODUCTION

It has recently been pointed out (Russell 1976) that although a great deal of work has been carried out over a number of years on various aspects of the biology of geckos, little is known of the interrelationships between many of the genera. It is the object of this paper to point out how such interrelationships may be investigated and how true interrelationships have been obscured in the past by a reliance on geographic rather than phylogenetic evidence.

The gekkonid genus *Rhoptropella* Hewitt, 1937 has, since its inception, been regarded as monotypic and represented by the sole species *Rhoptropella ocellata* (Boulenger, 1885). The relationships of this form, however, have proved to be problematical. Although this

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matter provoked a good deal of discussion during the first half of this century the problem has not been reappraised since recent advances in phylogenetic systematics, biogeography and plate tectonics have become widely known. There is now a greater body of information available to enable us to firstly construct phylogenies and then to attempt to assess where these theories leave us with respect to ideas about past earth history.

I have chosen here to discuss the genus "*Rhoptropella*" as its true interrelationships appear to be of particular interest from the point of view of biogeography and because it shows an extreme degree of convergence with those forms with which it was previously supposed to be related. The structure and relationships of many of the genera of Southern African geckos have recently been reviewed by Haacke (1976), but as this work dealt only with burrowing forms the genus "*Rhoptropella*" was not included in the main body of the discussion. It appears that "*Rhoptropella*" has its affinities outside of the area in which it is found and mainly for this reason have its true relationships been obscured.

MATERIALS AND METHODS

Specimens of the genera *Rhoptropus, Rhoptropella* and *Phelsuma* were examined and, in some cases, dissected in order to obtain sufficient data for a correct phylogenetic analysis. Drawings were made using a Wild M5 dissecting microscope with camera lucida attachment.

The specimens were not examined in isolation but instead with the benefit of a complete analysis of foot structure in the family Gekkonidae (Russell 1972). It has thus been possible to place the phylogenetic conclusions reached in this study in perspective with respect to the entire family, and to distinguish significant consistencies in structure from superficial similarities due to convergence. In excess of 230 specimens were examined and these are listed in the appendix to this paper.

DISCUSSION

Past ideas concerning the interrelationships of Rhoptropella *Hewitt, 1937*

When originally described, *Rhoptropella ocellata* was placed within the genus *Rhoptropus* (Peters 1869), a genus with which most authors have assumed it to be closely related. Hewitt (1937) stated that its affinities lay with *Rhoptropus* but erected the genus *Rhoptropella* because of certain consistent differences between the two. Because, however, Hewitt compared *Rhoptropella* chiefly with other southern African genera he had already made a subjective decision that it must be related most closely to southern African forms, and *Rhoptropus* came closest. Thus, by inferring that geographic position must determine relationships the true affinities of *Rhoptropella* have been obscured for the past 40 years.

The classic work on African geckos (Loveridge 1947) sealed the fate of obscuring the relationships of *Rhoptropella* as it reaffirmed the conclusions reached by Hewitt (1937).

Again other possible relationships were denied chiefly on the grounds of distribution and habits. This decision by Loveridge (1947) seems all the more strange when it is considered that he revised the genus *Phelsuma* only five years earlier (Loveridge 1942).

Before the work of Hewitt (1937) or Loveridge (1942, 1947), however, the status of *Rhoptropella ocellata* had already been questioned. After examining this species (at the time known as *Rhoptropus ocellatus)* and comparing it with *Phelsuma*, Roux (1907) was forced to ask, "Is *Rhoptropus* a synonym of *Phelsuma?*" Only a tentative suggestion of the placement of *Rhoptropus* into synonymy with *Phelsuma* was made, however, and it was left to Schmidt (1934) to formally change the status of *Rhoptropella ocellata*. He proposed the new combination of *Phelsuma ocellata* (Boulenger, 1885). In so doing he was careful to clearly distinguish *ocellata* from all other species of the genus *Rhoptropus*, and stated that although the above-mentioned taxonomic change was necessary it did not affect the validity of the latter genus.

It appears, therefore, that Schmidt's (1934) contribution was largely overlooked due to the insistence of Hewitt (1937) and Loveridge (1947). The possibility of relationship with *Phelsuma* was dismissed by Hewitt (1937) because he did not believe that forms separated by such great distances could be congeneric, and because his comparison with members of the genus *Phelsuma* was based upon an unfortunate examination of the segment of that genus least like *Rhoptropella* in both habits and morphology (see below). It is now evident that *Phelsuma* is not as uniform a genus as has previously been assumed. Hewitt thus concluded, after a brief discussion of largely superficial and primitive features, that "*Rhoptropella* may perhaps be regarded as representing the earliest *Rhoptropus* condition more or less unchanged" (Hewitt 1937: 203).

Loveridge reiterated Hewitt's (1937) conclusions and presented a table of comparisons illustrating why relationship with *Phelsuma* was untenable (Loveridge 1947:203). This table was based upon differences and no attempt was made to compile similarities between *Rhoptropella* and *Phelsuma*. Again the species of *Phelsuma* compared with *Rhoptropella* were from that part of the former genus which bears least resemblance to the latter (see below). Although concurring in his general opinions with those of Hewitt (1937) concerning the relationships of *Rhoptropella*, Loveridge reversed the apparent phylogeny, without giving any reasons for doing so, by stating that "*Rhoptropella* appears to be immediately descended from *Rhoptropus*" (Loveridge 1947:294). Fitzsimons (1943) does not contribute anything of substance to help settle this argument.

It is my contention that, after a thorough re-examination of the genera *Rhoptropus*, *Rhoptropella* and *Phelsuma*, Schmidt (1934) was correct in placing *Rhoptropella* (*Rhoptropus ocellatus* at the time) into synonymy with *Phelsuma* and I am therefore resurrecting the combination *Phelsuma ocellata* (Boulenger, 1885). *Rhoptropella* Hewitt, 1937 thus becomes a junior synonym of *Phelsuma* Gray, 1825. This, obviously, extends the range of *Phelsuma* considerably and I would thus also like to put forward some views about why such a distribution is now tenable and acceptable; information which Schmidt did not have available to him.

A reassessment of the interrelationships of Rhoptropella Hewitt, 1937

In Loveridge's (1947) summary of the information then available concerning the relationships of *Rhoptropella* he stated that the generic diagnosis of this genus was almost identical to that of *Phelsuma,* but that it differed in a number of minor characters. Repeated reference was made, however, to *Phelsuma mutabilis* and *Phelsuma breviceps* which did not fit the "usual" characters of *Phelsuma.* It was apparent, then, that *Rhoptropella* did not differ markedly from all members of the genus *Phelsuma,* but only from some of them. These similarities, however, seemed not to impress Loveridge.

Hewitt (1937), like Loveridge after him, also presented morphological evidence in an attempt to illustrate that the affinity of *Phelsuma* and *Rhoptropella* was not very close. As has been pointed out (see above) his choice of species for comparison was unfortunate. Some of his points were that *Phelsuma* always has a greater number of subdigital lamellae (scansors) than *Rhoptropella;* that the dorsal aspect of the digital expansion is much more numerously scaled in *Phelsuma;* the relative size of the rostral scale differed between the two and the size of the snout also differed. Such characters, especially the last two, are difficult to judge and hazardous to discuss unless the full range of variation within the genus is known. In certain features there also appear to be inconsistencies of interpretation between Hewitt (1937) and Loveridge (1942). For example, with respect to the former, it was stated that *Phelsuma* showed no indication of an upper *eyelid* (italics mine), while the latter stated that the *eyelid* was distinct all around the eye (italics mine).

In considering the similarities between *Phelsuma* and *Rhoptropella* Hewitt (1937) dismissed them and stated that their taxonomic value was doubtful. Such features as the scaling of the mental and gular regions, scaling of the ventral abdominal surface, the number and position of pre-anofemoral pores, the reduction of the inner digits and the undivided nature of the distalmost scansor on each digit were all stated to be phylogenetically unimportant and to be the result of convergence. The reason, for example, for considering the reduction of the inner digit to be unimportant was that the same feature occurs in *Lygodactylus* Gray, 1864, which Hewitt assumed to be not closely related to either *Phelsuma* or *Rhoptropella.* Subsequent studies have shown, however, that *Lygodactylus* is indeed closely allied to *Phelsuma* (Pasteur 1964; Russell 1972).

I have carried out a complete recomparison of the three genera in question and have come to the conclusion that not only is *Rhoptropella* more closely related to *Phelsuma* than to *Rhoptropus* but that it is, indeed, similar enough to be considered as congeneric with the former (see above). The following is an account of the major features considered in this comparison and the reasons why they are deemed to be of particular importance.

The number of scansors (lamellae) is always a difficult feature to assess and has probably led to a good deal of confusion in the description and comparison of pad-bearing gecko species. This is chiefly due to the fact that there is usually no sharp break between the functional scansors and other enlarged subdigital scales, but instead a continuous gradation all the way back to the sole of the foot. Deciding what is and what is not a scansor has therefore been somewhat of an arbitrary decision. It has been shown, however, that the scansors are functional in the adhesive process and that they are subject to special control mechanisms which enable them to be adequately deployed and protected (Russell 1975). It is suggested, therefore, that in recording the number of scansors only the functionally significant structures, that is, only the scansors which lie beneath the hyperextensible portion of the digit, should be counted. This will then give an accurate assessment and will provide a standardized method of comparison between species (for an explanation of the hyperextension process see Russell 1975, 1976). In this study only the functional scansors have been counted and compared (Figure 1). The divided nature of the terminal scansor in *Phelsuma* is a constant difference when compared to *Rhoptropus* and is also considered to be a phylogenetically significant feature.

The presence of claws on the digits seems variable in both *Phelsuma* and *Rhoptropus*. In both genera if claws are present they are minute and cannot function in locomotion. Their presence or absence seems to vary even between individuals of the same species, but it appears that the members of the section of the genus *Phelsuma* to which *P. ocellata* belongs (see below) exhibit a constant lack of claws.

Several features of scalation pattern appear to show constant differences between *Phelsuma* and *Rhoptropus* and these are best exemplified by means of illustration. Differences occur in such areas as the dorsal aspects of the digital expansions (Figure 2), the scales surrounding the external nares (Figure 3) and the pattern of the chin-shields (Figure 4).

The arrangement and number of pre-anofemoral pores also shows a series of constant

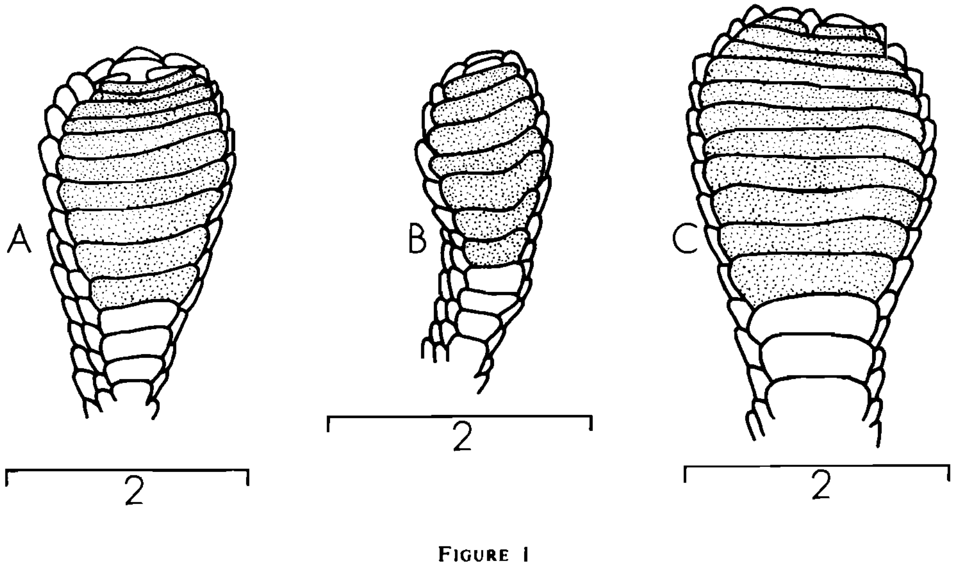

FIGURE 1

Ventral aspects of the digits of A: *Phelsuma barbouri* (digit III, left pes: registered number TM 35640); B: *Rhoptropella ocellata* (digit IV, left pes: registered number TM 34299); C: *Rhoptropus boultoni* (digit III, left pes: registered number TM 41270). The functional scansors (lamellae) are stippled. Note the divided terminal scansor of *Rhoptropus*. All scales are in millimetres.

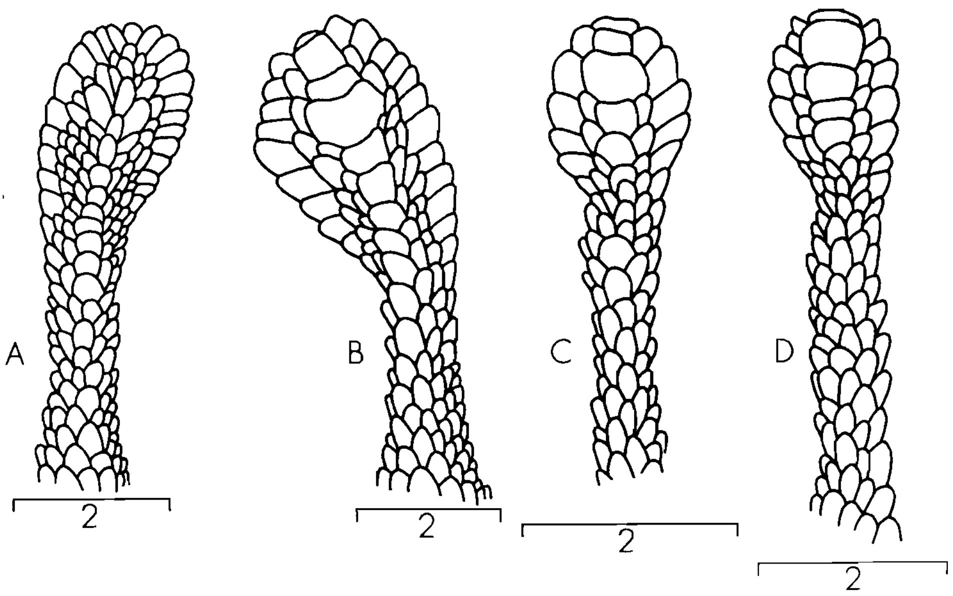

FIGURE 2

The dorsal digital scalation of A: *Phelsuma abbotti longinsulae* (member of *Phelsuma*, Group I; digit IV, right pes: registered number BMNH 1956. 1. 13. 9); B: *Phelsuma breviceps* (member of *Phelsuma*, Group II; digit IV, right pes: registered number BMNH 96. 12. 7. 1); C: *Rhoptropella ocellata* (digit IV, right pes: registered number BMNH 1946. 8. 25. 14); D: *Rhoptropus afer* (digit IV, right pes: registered number BMNH 1937. 12. 3. 55). All scales are in millimetres and all digits are drawn to approximately the same size for ease of comparison. Note particularly the difference in scalation between *Phelsuma*, Group I and II.

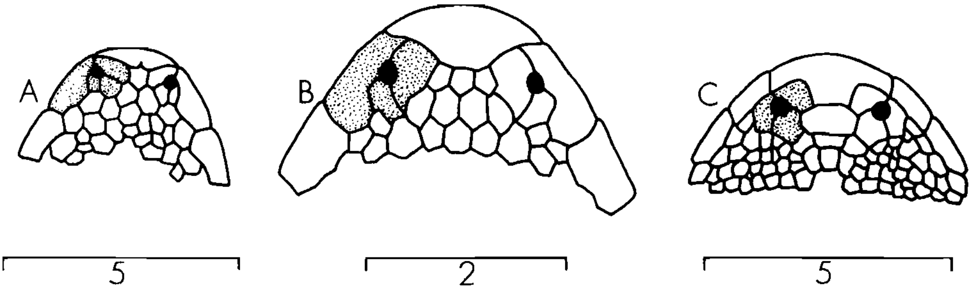

FIGURE 3

Arrangement of scales surrounding the external nares in A: *Phelsuma mutabilis* (registered number TM 4066); B: *Rhoptropella ocellata* (registered number TM 32499); C: *Rhoptropus boultoni* (registered number TM 41270). Scales actually bordering the naris are stippled on the left side. All scales are in millimetres.

differences between the two genera. It appears that such pores are present only in males in both genera. In *Rhoptropus*, when present, the pores are few in number and are only pre-anal in position whilst in *Phelsuma* they are much more numerous and occur on the ventral femoral aspects of the limbs as well as in the pre-anal region and form an unbroken series.

Perhaps the most important set of differences between the two genera, and the ones on which most phylogenetic inference can be placed, are those concerned with the structure and arrangement of the phalanges. The phalangeal formula of *Pachydactylus* Wiegmann, 1834 and its allies, including *Rhoptropus*, is unique amongst the Gekkonidae (Russell 1976). Here an extra phalanx is present in the first digit of both manus and pes (Fig. 5). Such a feature is important because the addition of elements in phylogeny is much more difficult (from an evolutionary viewpoint) than is their loss (Russell 1976; Haacke 1976) and hence hyperphalangy may be considered to be an important phylogenetic indicator. *Phelsuma*,

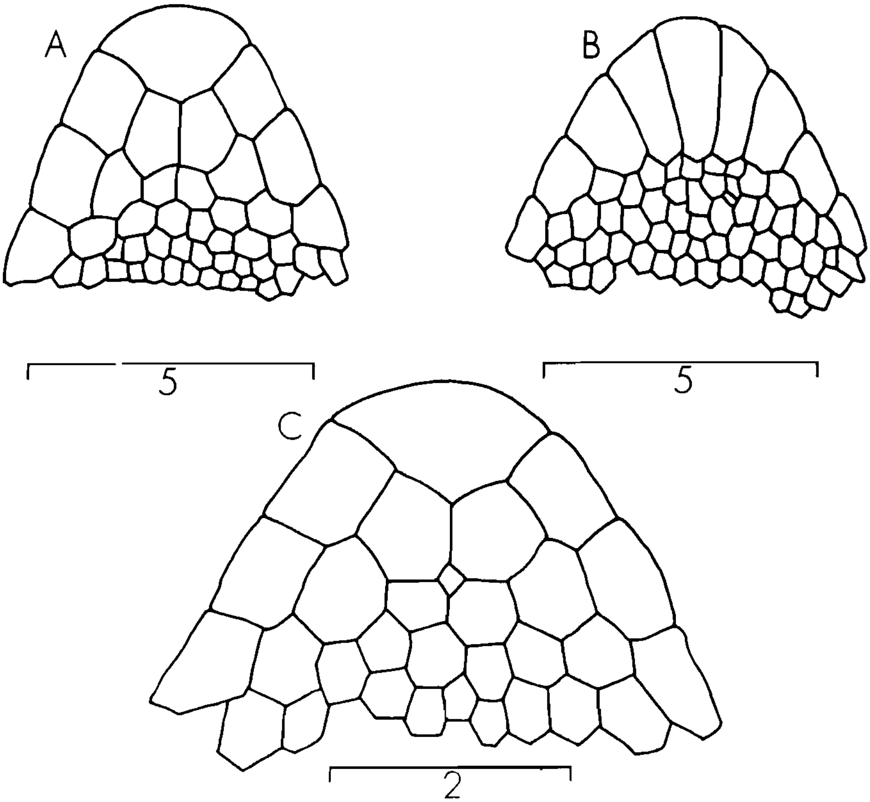

FIGURE 4

Arrangement of the scales of the chin in A: *Phelsuma mutabilis* (registered number TM 4066); B: *Rhoptropus afer* (registered number TM 17413); C: *Rhoptropella ocellata* (registered number TM 34299). All scales are in millimetres.

including *P. ocellata*, does not exhibit a modified phalangeal formula (Russell 1972; Haacke 1976) but it does exhibit its own phalangeal modifications which it bears in common only with other members of the *Phelsuma*-like group of gekkonine geckos (Russell 1972). Here the basal portions of the digits are extremely elongate (except for the reduced first digit) and this is reflected in the enormous elongation of the first phalanx in these digits

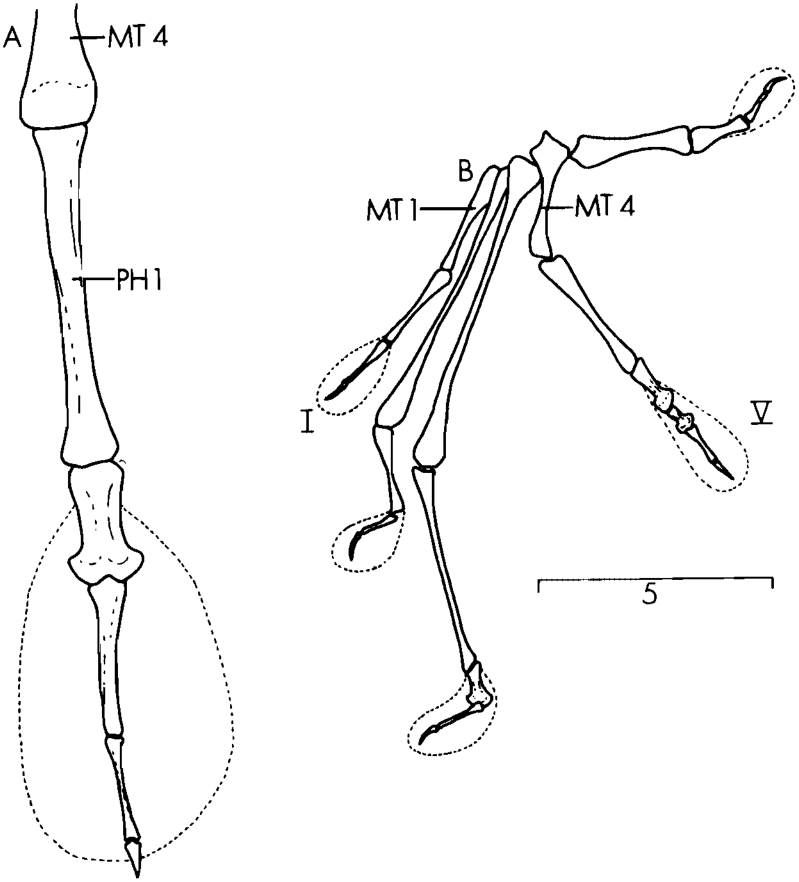

FIGURE 5

Phalangeal arrangement in *Phelsuma* and *Rhoptropus*. A: *Phelsuma abbotti longinsulae* (dorsal aspect, digit IV, right pes: registered number BMNH 1956. 1. 13. 51); B: *Rhoptropus afer* (dorsal aspect of the left pes, drawn from an alizarin transparency). Note that in *Phelsuma* the penultimate phalanx is shorter than the antepenultimate, and in *Rhoptropus* hyperphalangy is evident in the first digit. In B the fifth metatarsal has been omitted. Dashed lines represent the extremity of the digital pads. All scales are in millimetres. Key: MT 1 = metatarsal of the first digit; MT 4 = metatarsal of the fourth digit; PH 1 = first phalanx of digit four; I = digit one; V = digit five.

(Figure 5). The distal phalanges also show considerable modification (Figure 5) and the penultimate phalanx is extremely short. This is unlike the primitive condition for pad-bearing geckos in which the penultimate phalanx is longer than the antepenultimate (Russell 1975, 1976). These derived features serve to unite all of the *Phelsuma*-like forms (*sensu* Russell 1972), including *P. ocellata*.

A comparison of the main features considered in this study is presented in tabular form (Table 1) so that the similarities between "*Rhoptropella*" and *Phelsuma* may be more easily seen. Those features expressed in numerical form are given as averages where more than one specimen was available for examination.

TABLE 1

A comparison of *Rhoptropus*, *Rhoptropella* and *Phelsuma* Group II.
(*Taken from Loveridge (1947)—no counts available from specimens examined by me.)

FEATURE ↓	*Rhoptropus*					*Phelsuma*		
	bradfieldi	*afer*	*barnardi*	*boultoni*	*taeniostictus*	'*Rhoptropella*' ocellata	*barbouri*	*mutabilis*
Scansors: Manus R	9-9-9-9-10	5-6-6-6-6	5-6-6-7-6	9-9-9-10-10	6-7-8-8-7	0-5-5-7-5	0-8-10-9-9	0-7-8-9-8
L	10-8-9-9-9	5-6-6-6-6	5-6-7-7-6	9-9-10-10-10	6-7-7-8-7	0-5-6-7-6	0-8-9-9-9	0-7-8-8-8
Scansors: Pes R	9-9-9-9-9	6-6-7-7-7-	6-6-7-7-7	9-9-10-10-10	6-7-8-8-8	0-6-6-7-6	0-8-11-10-10	0-7-8-9-8
L	8-9-9-9-9	6-6-7-6-6	6-6-7-7-7	8-9-10-11-9	6-7-8-8-7	0-6-6-7-6	0-9-11-11-11	0-7-8-9-8
Terminal scansor divided	Yes	Yes	Yes	Yes	Yes	No	No	No
Longest digit: Manus	3	3	3	3	3	4	4	4
Pes	3	3	3	3	3	4	4	4
Claws: Manus	—	—	—	—	—	—	—	—
Pes	—	I & V	—	I & V	I & II	—	—	—
Phalangeal formula: Manus	3-3-4-5-3	3-3-4-5-3	3-3-4-5-3	3-3-4-5-3	3-3-4-5-3	2-3-4-5-3	2-3-4-5-3	2-3-4-5-3
Pes	3-3-4-5-4	3-3-4-5-4	3-3-4-5-4	3-3-4-5-4	3-3-4-5-4	2-3-4-5-4	2-3-4-5-4	2-3-4-5-4
Penultimate phalanx digit IV reduced	No	No	No	No	No	Yes	Yes	Yes
First digit, manus and pes, markedly reduced	No	No	No	No	No	Yes	Yes	Yes
Naris surrounded by	3 nasals	3 nasals	2 nasals	3 nasals	3 nasals	1st upper lab. + 2 nasals	1st upper lab. + 3 nasals	1st upper lab. + 2 nasals
Upper labials R	11	10	10	10	10	8	8	7
L	11	9	9	11	10	7	8	7
Lower labials R	8	9	7	7	8	7	6	6
L	9	9	7	7	8	7	6	6
Pre-anofemoral pores	0	0	5*	5–8*	0	24–32*	28	30
Nasals on swollen prominence	Yes	Yes	Yes	Yes	Yes	No	No	No
Pupil shape in life	Crenate	Crenate	Crenate	Crenate	Crenate	Round	Round	Round

Considerations of ecology and biogeography

Once it has been established that *ocellata* is part of the genus *Phelsuma* the problem of its isolated distribution becomes more intriguing. No longer can it conveniently be derived from other local genera and so we must examine more fully the biogeographical history of the area in which the genus is found.

The genus *Phelsuma* is quite variable in both structure and habits and, as has been pointed out before (see above), previous comparisons involving *ocellata* were made with species of *Phelsuma* which differed considerably in minor details from it. Russell (1972), however, pointed out that within the genus *Phelsuma* two groups (I and II) were recognizable. The first (I) consists of the larger forms which are chiefly arboreal in their habits whilst the second (II) contains smaller forms (*P. barbouri; P. breviceps; P. dubia; P. mutabilis; P. standingi* and *P. guttata*) which have, in general, different features and, to some extent, different habits. Loveridge (1947) stated that *Phelsuma* was largely, if not entirely, arboreal while "*Rhoptropella*" *ocellata* was rupicolous. This, then, was another reason for denying relationship. These categorizations are not, however, entirely accurate or as clear-cut as they might at first seem. While *P. ocellata* has often been taken on rocks (Hewitt 1937; Fitzsimons 1956) it has also been taken on vegetation (thick stem of a *Cyphostemma* plant) (Haacke 1970). On the other hand too little is known of many of the species of *Phelsuma* to make a statement that all species are exclusively arboreal. Indeed Stoliczka (1873) says of *Phelsuma andamanense* Blyth, 1860 that it generally hides beneath the bark of trees but also often feeds upon the ground, whilst Loveridge himself (1942) in quoting from Pike (1873) states that *Phelsuma guentheri* Boulenger, 1885 is found "in the steep rocks on the mountainside".

The six features used by Loveridge (1947) to distinguish *Rhoptropella* from *Phelsuma* lose their impact when *Phelsuma* Group II is examined and, indeed, Loveridge had made reference himself to the problems posed by *Phelsuma mutabilis* and *P. breviceps.*

The distribution of *Phelsuma* (Groups I and II) on Madagascar (data largely from Loveridge 1942) and of *P. ocellata* in southern Africa (data largely from Loveridge 1947; Haacke 1970; Huey pers. comm.) is illustrated (Figure 6). The floristic regions into which these areas are divided are those given by Moreau (1952) for southern Africa and Croizat (1962) for Madagascar. Both Croizat (1962) and Fitzsimons (1956) divide southern Africa into three floristic regions (excluding the "Mediterranean" of Moreau 1952) but it is evident that the central region of these two authors is included in the "South West Arid" of Moreau (1952). Fitzsimons (1956) states that the central region is faunistically most closely allied to the western regions.

Cracraft (1973) has indicated how studies of phylogeny and biogeography may be more closely integrated. It is evident here that the problem of the disjunct distribution of *Phelsuma* only becomes apparent once the affinities of *P. ocellata* have been established. It is necessary to tailor our knowledge of biogeography to fit the phylogenetic facts.

The geckos are, at least in part, part of the Gondwana faunistic element (Cracraft 1974) and are also an extremely ancient group (Hoffstetter 1964; Kluge 1967). Estes (1970) has reported geckos from the Palaeocene of Brazil which are very similar to forms living today.

Such antiquity and distribution indicates that the geckos have been a widespread and successful group for a long time and that their structure has shown a good deal of inherent stability.

The position of the several components of Gondwanaland prior to break-up is still a matter of discussion, and perhaps the most enigmatic part of this puzzle is the association of Madagascar with the African mainland. Keast (1973) has expressed the opinion that southern Africa separated from the Gondwana land mass ahead of the other components and proposes that this may be a reason why the southern temperate biota of Africa is so distinct. Because contemporary distribution patterns are, in part, a consequence of past connections (Keast 1973) it seems pertinent to examine here how the distribution of *Phelsuma* fits into such a framework. Due to the fact that geckos are such an old and variable group, however, it is not possible to make generalizations about interconnections

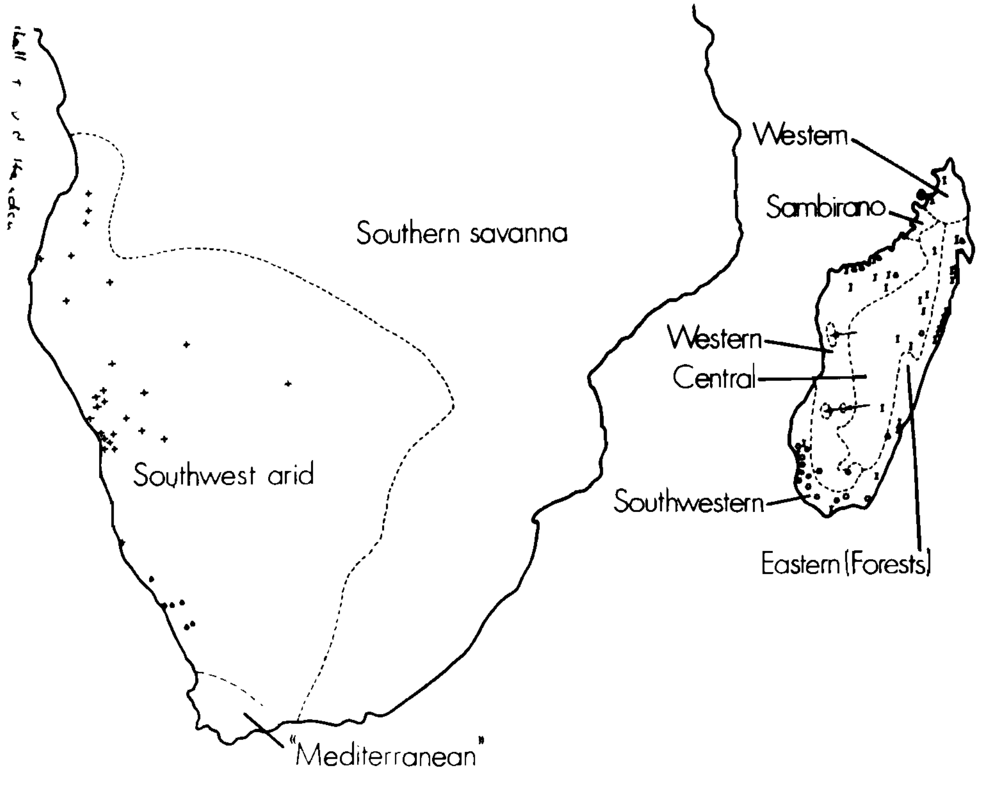

FIGURE 6

The distribution of *Phelsuma* and *Rhoptropus*. The floristic areas of mainland Africa are after Moreau (1952) and of Madagascar are after Croizat (1962). The distribution of *Rhoptropus* is presented by crosses (+); *Phelsuma*, Group I, by the Roman numeral I (I); *Phelsuma*, Group II, by open circles (o) and *Phelsuma ocellata* (= *Rhoptropella ocellata*) by solid circles (•). Distributional data chiefly Haacke (1965, 1970); Huey (pers. comm) and Loveridge (1942, 1947).

and dispersal patterns for the entire family and each case must be taken on its own merits and analyzed independently. For example, although *Phelsuma ocellata* appears to have associations with forms on Madagascar, the *Pachydactylus* group, to which *Rhoptropus* belongs, appears to have invaded southern Africa from the north (Russell 1976).

Cracraft (1975) has indicated that the southern continents maintained interconnections well into the Cretaceous, thus allowing land dispersal over these areas during this time. The Gekkonidae were at that time well established (Hoffstetter 1964). The hypothetical palaeopositions of Madagascar have been discussed by many authors and the theories resulting may be placed into one of three categories (Förster 1975). The first contention is that the two were connected in the region of the southern Moçambique coast (Figure 7) and that Madagascar subsequently moved north and east (Wegener 1929; Tarling 1972). The second is that Madagascar bordered the coast of Tanzania and Kenya from whence it moved southeast (Smith *et al.* 1973). The third is that Madagascar has remained in its present position at least since the Carboniferous and perhaps since the Precambrian (Dixey 1956). In support of this last idea Förster (1975) has presented evidence amassed from geological history, stratigraphy, palaeogeography and drilling in the Moçambique channel to suggest that the Moçambique channel is geosynclinal. Seas gradually infiltrated the area between the present day Madagascar and African coastlines as the channel sunk and it is proposed that the last land-bridge between the two areas disappeared in the early Miocene, cutting off migration between them. Whatever the contention it is apparent that Madagascar has had a close association with the African mainland which has only relatively recently been broken.

Croizat (1962) has analyzed the faunistic and floristic similarities between southern Africa and Madagascar. He divided the latter into five botanical domains (Figure 6) and indicated that the south and south-west region of Madagascar is markedly arid and rich in xerophytes. It is in this region that the greatest concentration of *Phelsuma* Group II occurs (Figure 6). This region has a good deal in common with the Karroo region of southern Africa and Croizat (1962) indicates that early colonizations involved South Africa and Madagascar as one and that only at a later time did massive geographic and topographic alterations occur which were responsible for the interdigitations of different floristic elements.

We should not be surprised, therefore, to find *Phelsuma* on the African mainland, given the age and stability of the family to which it belongs, the historical biogeography of the area and the overall similarity in floras with respect to generalized tracks (Croizat 1962). Indeed the area in which *P. ocellata* is found is quite similar to the area of Madagascar in which its closest congeners are found. Other distribution patterns of reptiles also support this contention. Fitzsimons (1962) states that two species of *Typhlops* from the Cape Province show no relationship to other South African forms but instead show affinity with those of Madagascar. Also another gekkonid lizard, *Phyllodactylus porphyreus*, of the Cape Province appears to be most closely related to *Phyllodactylus brevipes* of Madagascar. At one time both were included under the same specific designation (*P. porphyreus)* but *P. brevipes* has recently been utilized again (Dixon & Kroll 1974).

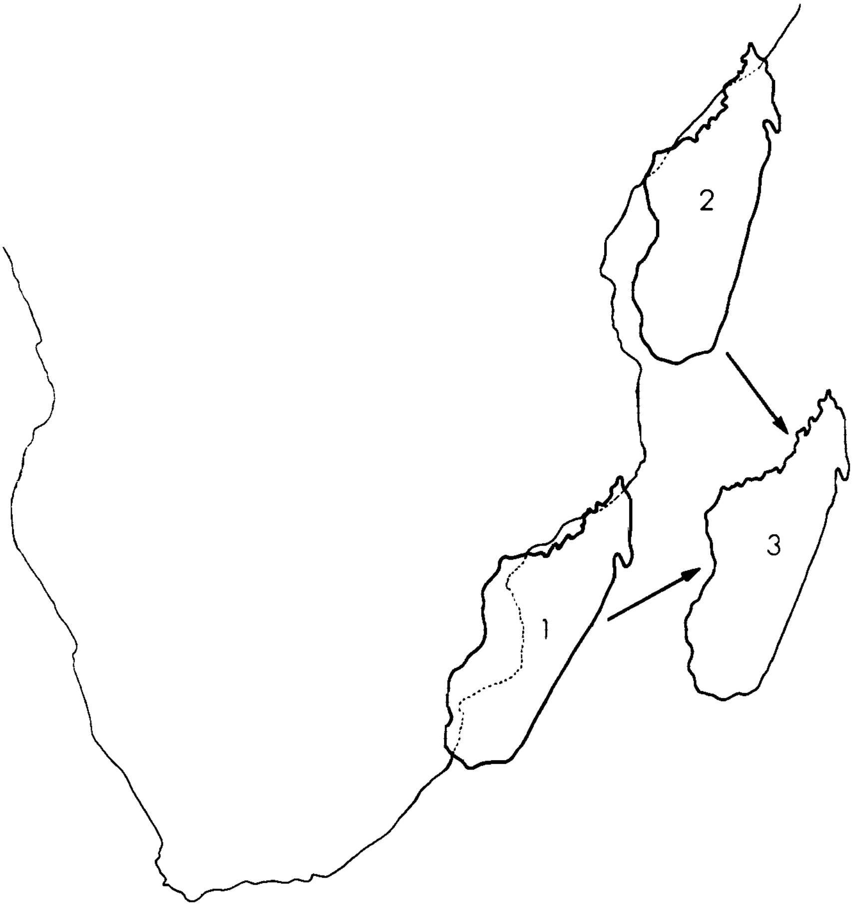

FIGURE 7

The hypothetical palaeopositions of Madagascar. 1. Connection with Africa in the region of southern Moçambique (Wegener 1929; Tarling 1972). 2. Connection with Africa in the region of Tanzania and Kenya (Smith *et. al.* 1973). 3. Maintenance of its present position with respect to Africa at least since the Carboniferous - the Moçambique channel being a geosyncline (Dixey 1956, Förster 1975).

CONCLUSIONS

From the foregoing study it is evident that the genus *Rhoptropella* Hewitt, 1937 has no basis for further recognition and should be regarded as a junior synonym of *Phelsuma* Gray, 1825. The combination first suggested by Schmidt (1934) of *Phelsuma ocellata* should be reinstated for the sole African mainland form. Inclusion of this species in the genus *Phelsuma* is based upon the common possession of a number of derived character states, and geographical proximity of other genera is shown to be a misleading factor in the assessment of relationships.

Once true relationships for *Phelsuma ocellata* had been established it was possible to reassess the ecological and biogeographic implications of its newly proposed status. It is found that the categorical characterization of the habits and habitat preferences of *Phelsuma* are not as rigid as suggested by Loveridge (1947), and that overlap does exist between the African form and those from Madagascar. Recent biogeographic evidence and floristic and faunistic analyses of the regions in question also support the inclusion of *Phelsuma ocellata* in the primarily Madagascan genus.

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REFERENCES

CRACRAFT, J 1973. Vertebrate evolution and biogeography in the Old World tropics: implications of continental drift and paleoclimatology. In *Implications of continental drift to the earth sciences,* ed. D H Tarling & S K Runcorn, 1: 373-393. NATO Advanced Study Institute, New York: Academic Press.

CRACRAFT, J 1974. Continental drift and vertebrate distribution. *A. Rev. Ecol. Syst.* 5: 215-261.

CRACRAFT, J 1975. Mesozoic dispersal of terrestrial faunas around the southern end of the world. *Mém. Mus. natn. Hist. nat. Paris.* (A) 88: 29-54.

CROIZAT, L 1962. *Space, time, form: the biological synthesis.* Caracas, Venezuela: published by the author.

DIXEY, F 1956. The East African rift system. *Bull. colon. Geol. Miner. Resour.* Suppl. 1: 1-71.

DIXON, J R & KROLL, J C 1974. Resurrection of the generic name *Paroedura* for the phyllodactyline geckos of Madagascar, and a description of a new species. *Copeia*, 1974 (1): 24-30.

ESTES, R 1970. Origin of the recent North American lower vertebrate fauna; an inquiry into the fossil record. *Forma Functio*, 3: 139-163.

FITZSIMONS, V F M 1943. The lizards of South Africa. *Mem. Transv. Mus.* 1: 1-528.

FITZSIMONS, V F M 1956. Reptilia (Serpentes and Sauria). In *South African Animal Life.* Results of the Lund University Expedition in 1950-51, ed. B. Hanström, P Brinck & G Rudbeck: 385-405. Stockholm: Almquist & Wiskell.

FITZSIMONS, V F M 1962. *Snakes of southern Africa.* Cape Town: Macdonald.

FÖRSTER, R 1975. The geological history of the sedimentary basin of southern Mozambique, and some aspects of the origin of the Mozambique Channel. *Palaeogeogr. Palaeoclimat. Palaeoecol.* 17: 267-287.

HAACKE, W D 1965. Additional notes on the herpetology of South West Africa with descriptions of two new subspecies of geckos. *Cimbebasia*, 11: 1-40.

HAACKE, W D 1970. New herpetological records from South West Africa. *Ann. Transv. Mus.* 26: 277-283.

HAACKE, W D 1976. The burrowing geckos of southern Africa, 5 (Reptilia: Gekkonidae). *Ann. Transv. Mus.* 30: 71-89.

HEWITT, J 1937. Descriptions of South African lizards. *Ann. Natal Mus.* 8: 199-209.

HOFFSTETTER, R 1964. Les Sauria du Jurassique supérieur et spécialement les Gekkota de Baviere et de Mandchourie. *Senckenberg. biol.* 45: 281-324.

KEAST, A 1973. Contemporary biotas and the separation sequence of the southern continents. In *Implications of continental drift to the earth sciences*, ed. D H Tarling & S K Runcorn, 1: 309-343. NATO Advanced Study Institute, April 1972. New York: Academic Press.

KLUGE, A G 1967. Higher taxonomic categories of gekkonid lizards and their evolution. *Bull. Am. Mus. nat. Hist.* 135: 1-59.

LOVERIDGE, A 1942. Revision of the Afro-Oriental geckos of the genus *Phelsuma*. *Bull. Mus. comp. Zool. Harv.* 89: 437-482.

LOVERIDGE, A 1947. Revision of the African lizards of the family Gekkonidae. *Bull. Mus. comp. Zool. Harv.* 98: 1-469.

MOREAU, R E 1952. Africa since the Mesozoic: with particular reference to certain biological problems. *Proc. zool. Soc. Lond.* 121: 869-913.

PASTEUR, G 1964. Recherches sur l'évolution des lygodactyles, lézards Afro-Malagaches actuels. *Trav. Inst. scient. chérif.* (Zool.) 29: 1-132.

PETERS, W K H 1869. Uber neue Gattungen und Arten von Eidechsen. *Mber. dt. Akad. Wiss. Berl.* 1869: 57-66.

PIKE, N 1873. *Sub-tropical rambles in the land of the Aphanapteryx.* New York: Harper Bros.

ROUX, J 1907. Beiträge zur Kenntnis der Fauna von Süd-Afrika. Ergebnisse einer Reise von Prof. Max Weber im Jahre 1894. VII. Lacertilia (Eidechsen). *Zool. Jb.* (Syst.) 25: 403-444.

RUSSELL, A P 1972. The foot of gekkonid lizards: a study in comparative and functional anatomy. Ph.D. Thesis, Univ. London, England.

RUSSELL, A P 1975. A contribution to the functional analysis of the foot of the tokay, *Gekko gecko* (Reptilia: Gekkonidae). *J. Zool., Lond.* 176: 437-476.

RUSSELL, A P 1976. Some comments concerning interrelationships amongst gekkonine geckos. In *Morphology and biology of reptiles*, ed. A d'A Bellairs & CB Cox: 217-244. London: Academic Press.

SCHMIDT, K P 1934. *The reptiles of the Pulitzer Angola expedition. Ann. Carneg. Mus.* 22: 1-15.

SMITH, A G, BRIDEN, J C & DREWRY, G E 1973. Phanerozoic world maps. *Palaeontol. Assoc. Lond.* Spec. Pap. 12: 1-42.

STOLICZKA, F 1873. Notes on some Andamanese and Nicobarese reptiles, with the descriptions of three new species of lizards. *J. Asiat. Soc. Beng.* 42: 162-169.

TARLING, D H 1972. Another Gondwanaland. *Nature, Lond.* 238: 92-93.

WEGENER, A 1929. *The origin of continents and oceans*, ed. 4 (1966 English translation). London: Methuen.

APPENDIX

List of the specimens examined during this study. [BM(NH) = British Museum (Natural History); TM = Transvaal Museum]. [† signifies type specimen].

Phelsuma abbotti abbotti: BM(NH) 1905.4.25.2-3; 1907.10.15.49-50; 1910.3.18.19-25; 1938.8.3.26. *Phelsuma abbotti longinsulae:* BM(NH) 1956.1.13.48-56. *Phelsuma andamanense:* BM(NH) 98.10.27.24-47; 1962.213-219. *Phelsuma astriata:* BM(NH) 1937.7.24.17. *Phelsuma barbouri:* TM 35640. *Phelsuma breviceps:* BM (NH) 96.12.7.1-6; 97.7.16.1-2. *Phelsuma cepediana:* BM(NH) 51.7.17.10; 58.10.28.1; 62.1.15.7; 70.11.30.10; 1933.8.1.1-2; 1964.34-36. *Phelsuma dubia:* BM(NH) 93.11.1.5-9; 1947.1.1.31-36. *Phelsuma edwardnewtonii:* BM(NH) 87.8.25.38; 1946.8.13.44; 1946.8.14.75; *Phelsuma guentheri:* BM(NH) 1935.5.5.5; 1964.40. *Phelsuma laticauda:* BM(NH) 77.8.9.11-17; 83.4.14.7-8; 1907.10.15.51-52; 1930.7.11.114-115. *Phelsuma lineata:* BM(NH) 51.7.19.38; 71.6.28.7-10; 85.6.8.5-10; 95.10.29.7; 1936.3.3.54-79; 1946.8.26.31†. *Phelsuma madagascariensis:* BM(NH) 69.5.14.55-56; 70.3.10.16-19; 85.6.8.3; 1910.3.18.14-15; 1930.7.1.116-117; 1946.8.26.33-34†. *Phelsuma mutabilis:* BM(NH) 1930.7.1.101-113; TM 4058; TM 4060; TM 4066; TM 4073. *Phelsuma ornata:* BM(NH) 1946.8.30.82; 1964.37-39. *Phelsuma parkeri:* BM(NH) 1947.1.2.22-27; 1950.1.5.7-8. *Phelsuma trilineata:* BM(NH) 55.12.26.323; 1946.8.26.32†; 1948.1.7.65. *Rhoptropella ocellata:* BM(NH) 1946.8.28.4†; TM 34299. *Rhoptropus afer:* BM(NH) 88.6.25.4; 1937.12.3.49-60; TM 17413. *Rhoptropus barnardi:* BM(NH) 1905.1.27.8; 1931.10.12.3; 1936.8.1.278-281; 1936.8.1.285; TM 32574. *Rhoptropus boultoni:* BM(NH) 1906.8.24.3-7; 1936.8.1.286; TM 41270. *Rhoptropus bradfieldi:* BM(NH) 1937.12.3.39-46; TM 43093. *Rhoptropus taeniostictus:* TM 41120.