

AUSTRALIAN MUSEUM SCIENTIFIC PUBLICATIONS

Woodruff, D. S., 1975. Morphological and geographic variation of *Pseudophryne corroboree* (Anura: Leptodactylidae). *Records of the Australian Museum* 30(4): 99–113. [20 November 1975].

doi:10.3853/j.0067-1975.30.1975.400

ISSN 0067-1975

Published by the Australian Museum, Sydney

nature culture **discover**

Australian Museum science is freely accessible online at
www.australianmuseum.net.au/publications/
6 College Street, Sydney NSW 2010, Australia



MORPHOLOGICAL AND GEOGRAPHIC VARIATION OF
PSEUDOPHRYNE CORROBOREE
(ANURA: LEPTODACTYLIDAE)

DAVID S. WOODRUFF *

The Biological Laboratories, Harvard University, Cambridge,
Massachusetts 02138 U.S.A.

SUMMARY

The toadlet *Pseudophryne corroboree* is confined to the mountains of southeastern New South Wales and the Australian Capital Territory. The first detailed distribution map is presented. The species ranges from Mt Kosciusco in the south to the Brindabella Range near Canberra in the north. The Brindabella Range populations are isolated from those in the south. The species has not been found below 1,040 m. Its range may, in part, be limited by competitive interactions with the closely related *P. dendyi*.

P. corroboree has only a single phalanx in the first toe. In this it differs from all other Australian leptodactylids except *P. guentheri* in which the condition probably evolved independently.

Geographic variation in coloration is briefly described. The adaptive significance of this variation is not clear.

Univariate analysis of morphometric variation (ten characters, four populations) shows that Brindabella Range individuals are larger bodied than those from the Snowy Mountains area. Furthermore, there are indications of clinal (altitudinal) trends in some variables. Discriminant function and Q-mode multiple factor analyses elucidate and confirm these patterns and separate altitudinal and ontogenetic components of variation within and between populations. Large body size in specimens from the Brindabellas may be an adaptation to the size of sympatric *P. dendyi* rather than a response to ecogeographic factors.

INTRODUCTION

The toadlet, *Pseudophryne corroboree*, with its striking pattern of black and yellow dorsal stripes, occurs only in the mountains of southeastern New South Wales and the Australian Capital Territory. First described by Moore (1953), the type specimen, R13103 is in the Australian Museum. Colefax (1956), Jacobson (1963),

*Present address: Department of Biological Sciences, Purdue University, West Lafayette, Indiana 47907 U.S.A.

Martin (1967), and Watson and Martin (1973) discussed aspects of the adult and larval morphology, habits, and development of this species. Pengilley (1971 a, b) described the reproductive behaviour and feeding habits of a single population in detail. In this paper, I report a previously unobserved morphological feature of this species, provide the first detailed distribution map, and describe and discuss the nature of geographic variation in size and coloration in the samples examined.

METHODS

Descriptions of adult morphology are based on the study of live and preserved material in the collections of the Australian Museum, the National Museum of Victoria, and the Department of Zoology, University of Melbourne. Ninety-five adults were examined. Morphometric measurements (to 0.1 mm) were taken on males (known to have been collected from breeding aggregations) preserved in 70 per cent alcohol, using vernier calipers and an ocular micrometer. Ten measurements were taken on each specimen: the lengths of the body, head, tibia, foot, and each toe, and the width of the head. Body length is the snout-vent distance. Tibia length is the distance from the centre of the knee to the centre of the heel, measured with the leg flexed. Foot length is the distance from the tip of the fourth toe to the near edge of the outer metatarsal tubercle. Head length is the distance from the corner of the mouth to the tip of the snout, measured ventrally. Head width is measured ventrally at the level of the corners of the mouth. Toe length is the distance from the tip of the toe to the midpoint of the proximal end, viewed dorsally. Skeletal features were investigated by X-radiography using Nippon Softex apparatus.

Morphometric data were processed at the computer centres of the University of Melbourne and Harvard University. The stepwise discriminant analysis was performed with the BMD07M health services computing facility (U.C.L.A.) programme. The Q-mode multiple factor analysis was performed with the Columbia-Alberta factor analysis (CABFAC) programme written by J. Imbrie and E. Klován.

DISTRIBUTION

Pseudophryne corroboree has been found at 17 localities in southeastern N.S.W. and the Australian Capital Territory (figure 1). The Australian Museum has specimens from the Brindabella Range; Alpine Hut, Mt Kosciusco; Round Mountain; Smiggin Holes; and Happy Jacks Plain. The National Museum of Victoria has a sample from Pretty Plain. Melbourne University has specimens from Smiggin Holes and six localities in the Brindabella Range: 9.6 and 1.6 km S. of Bulls Head; Lees Spring; 1.6 km SE. of Mt Franklin Chalet; Ginini Flat; and Snowy Flat on Mt Gingera. There are five literature records: Coree Flat, 3.2 km N. Smiggin Holes, and 2 km SE. Yarrangobilly (Pengilley 1971a, 1973); between Island Bend and Smiggin Holes, and at Fifteen Mile, about 8 km N. of Round Mountain (Colefax 1956).

The geographic range is somewhat linear in shape extending about 160 km in a north-south direction. The range appears to be divided into two parts. The northern populations in the Brindabella and Fiery Ranges appear to be isolated from those further south. For convenience these southern populations will be referred to in this paper as from the Snowy Mountains area. The intervening country is of difficult access, and exploration between Kiandra, Youak, and Gudgenby may lead to the discovery of intermediate populations.

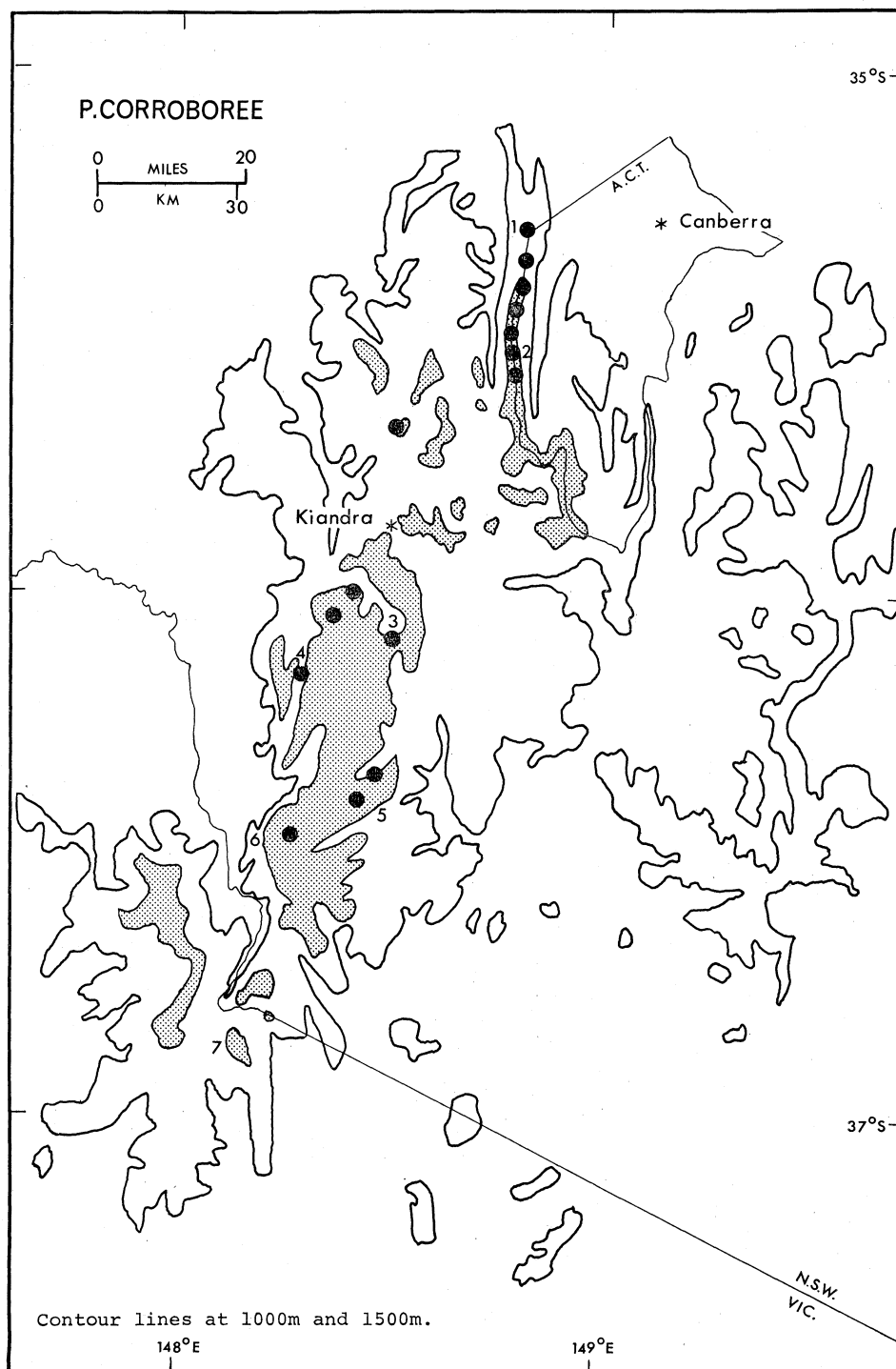


Figure 1. Distribution of *P. corroboree*. The following localities of special interest are shown: (1) Coree Flat, Brindabella Range; (2) Ginini Flat, Brindabella Range; (3) Happy Jacks Plain; (4) Pretty Plain; (5) Smiggin Holes; (6) Mt Kosciusco; (7) Mt Cobberas, Victoria.

The range of *P. corroboree* is circumscribed by that of a related species, *P. dendyi*, from which it differs strikingly in coloration and morphology (Woodruff 1972). The possibility that the distributional limits of *P. corroboree* may be determined, in part, by its interactions with *P. dendyi* is discussed below.

The southern limit of *P. corroboree* is Mt Kosciusco. *P. dendyi* occupies the Murray River valley further south and west: specimens have been taken at Tom Groggin and Cowombat. Despite occasional reports to the contrary (e.g. Fleay 1963: 407) *P. corroboree* has not yet been found in Victoria. In the subalpine bogs on Mt Cobberas, about 32 km south of Mt Kosciusco (and perhaps the most likely place to find this species if it occurred in Victoria), I found breeding choruses of *P. dendyi* during January, 1967. Searches for *P. corroboree* have also been made further west on the Bogong High Plains, the Dargo High Plains, the Mt Buffalo Plateau, and in the Mt Wellington area, but no *P. corroboree* have been found there (Woodruff 1959; Littlejohn 1965).

The northern limit of this species is near Mt Coree in the Brindabella Range. *P. corroboree* has not been found below 1,040 m at Coree Flat. In view of its apparent preference for alpine and subalpine habitats it is unlikely to occur further north. *P. dendyi* also occurs in the Brindabella Range and the two species are sympatric at Coree Flat and Lees Spring, the two northernmost localities shown in figure 1. Thus, both environmental and biotic factors may affect the position of the species border in this area.

MORPHOLOGY

X-radiography of six adults from the Brindabella Range and one from Smiggin Holes in the Snowy Mountains revealed that *P. corroboree* has only a single phalanx in the first toe (figure 2). In this feature it resembles *P. guentheri* from Western Australia but differs from all other *Pseudophryne*. I found that *P. australis*, *P. bibroni*, *P. coriacea*, *P. dendyi*, *P. occidentalis*, and *P. semimarmorata* all possess two phalanges in the first toe, as do *P. douglasi* (Main 1964) and *P.* (previously *Metacrinia*) *nichollsi* (Blake 1973).

Moore's (1961) account of morphology and coloration may be supplemented with the following observations. As in most other members of the genus, post-femoral and inguinal glands are present. In *P. corroboree* they are inconspicuous. The dorsal pattern of coloration is more variable than Moore observed in his smaller sample. The central dorsal stripe may be either black or yellow. In some specimens the stripes (particularly the lateral ones) are broken. The top of the head may bear a single large yellow patch, or it may be mottled with smaller yellow patches. In some individuals the pale patches on the ventral surfaces may be a yellow or blue colour in life. The latter colour fades in alcohol.

Comparison of live specimens from the Snowy Mountains area with those from the Brindabella Range indicates that there are regional differences in coloration. There is a decrease in the amount of yellow pigmentation in the northern populations: individuals from the Brindabella Range have less yellow on the dorsal and ventral surfaces than specimens from around Smiggin Holes. There is usually a light patch on the back of the hand; invariably yellow in the specimens from the Snowy Mountains area but usually white in those from the Brindabella Range.



Figure 2. *Pseudophryne corroboree*. X-radiograph of the right foot of a male (Melbourne University Zoology Department No. 182/64) from Ginini Flat, Brindabella Range. The first (shortest) toe has only one phalange.

Small samples of adult males from four localities (Snowy Mountains: Smiggin Holes, Happy Jacks Plain, and Pretty Plain; Brindabella Range: Ginini Flat) were measured. The variation in the ten characters studied is summarized in figure 3. Preliminary univariate analyses indicated that the three samples from the Snowy Mountains were not significantly different from one another (at the $P > 0.05$ per cent level) with respect to each of the variables. The pooled samples from the Snowy Mountains area were significantly different, however, from the Brindabella Range sample with respect to two variables; the northern sample had significantly longer bodies and shorter tibias. Variation in these two characters was non-overlapping and the magnitude of this difference is strikingly brought out in the tibia length/body length ratio:

Snowy Mountains area (N = 27)	0.29-0.34 (mean: 0.31)
Brindabella Range (N = 7)	0.22-0.24 (mean: 0.23)

The differences in the means of the northern and southern samples are not significantly different with respect to the other eight variables. There are, however, some most interesting trends in interpopulation variation which emerge when the data are examined for variation along an altitudinal gradient. The samples are arranged in such an order in figure 3: Smiggin Holes (1,650 m), Ginini Flat (1,585 m), Happy Jacks Plain (1,460 m), and Pretty Plain (1,300 m). Mean values for body length, head width, and the lengths of toes 1-4 all increase slightly with increased altitude. Mean values for head length and the length of the fifth toe, on the other hand, decrease slightly with increasing altitude. These trends are clearer if one considers just the three samples from the Snowy Mountains area.

These patterns of variation are not satisfactorily established on the basis of these univariate analyses. Multivariate analyses were therefore performed to investigate the overall pattern of intraspecific variation in size and shape and to determine the morphometric affinities of the four samples.

The results of the stepwise discriminant function analysis are shown graphically in figure 4. The group centroids and the thirty-four individual specimens are plotted against the first two canonical axes. The first canonical variate accounts for 81 per cent of the total variation, the second variate takes up an additional 16 per cent. Together these two axes account for fully 97 per cent of the total variation in the pooled data. The individual specimens are seen to be clustered around the group centroids and only a single specimen is misclassified by formal group classification based on the computed discriminants. The first canonical axis is interpreted as a general size axis. It clearly separates the large males from the Brindabella Range from the smaller Snowy Mountains area animals. Furthermore the centroids of the three Snowy Mountains area samples also separate out in order of decreasing size. More interesting is the pattern developed by the second canonical variate which apparently reflects altitudinal variation. The position of the Happy Jacks Plain sample between the Smiggin Holes and Pretty Plain samples corresponds closely to its altitude relative to the other two. The overall pattern also indicates that the Brindabella Range population has diverged morphometrically from those of the Snowy Mountains area. The close relationship between the Happy Jacks Plain and Pretty Plain samples is probably a reflection of their geographic proximity. Overlap between members of the four samples is minimal, and occurs only in the case of the Happy Jacks and Pretty Plain samples. I conclude that both geographic and altitudinal components of variation are present but confirmation requires the measurement of additional samples from the Brindabella Range.

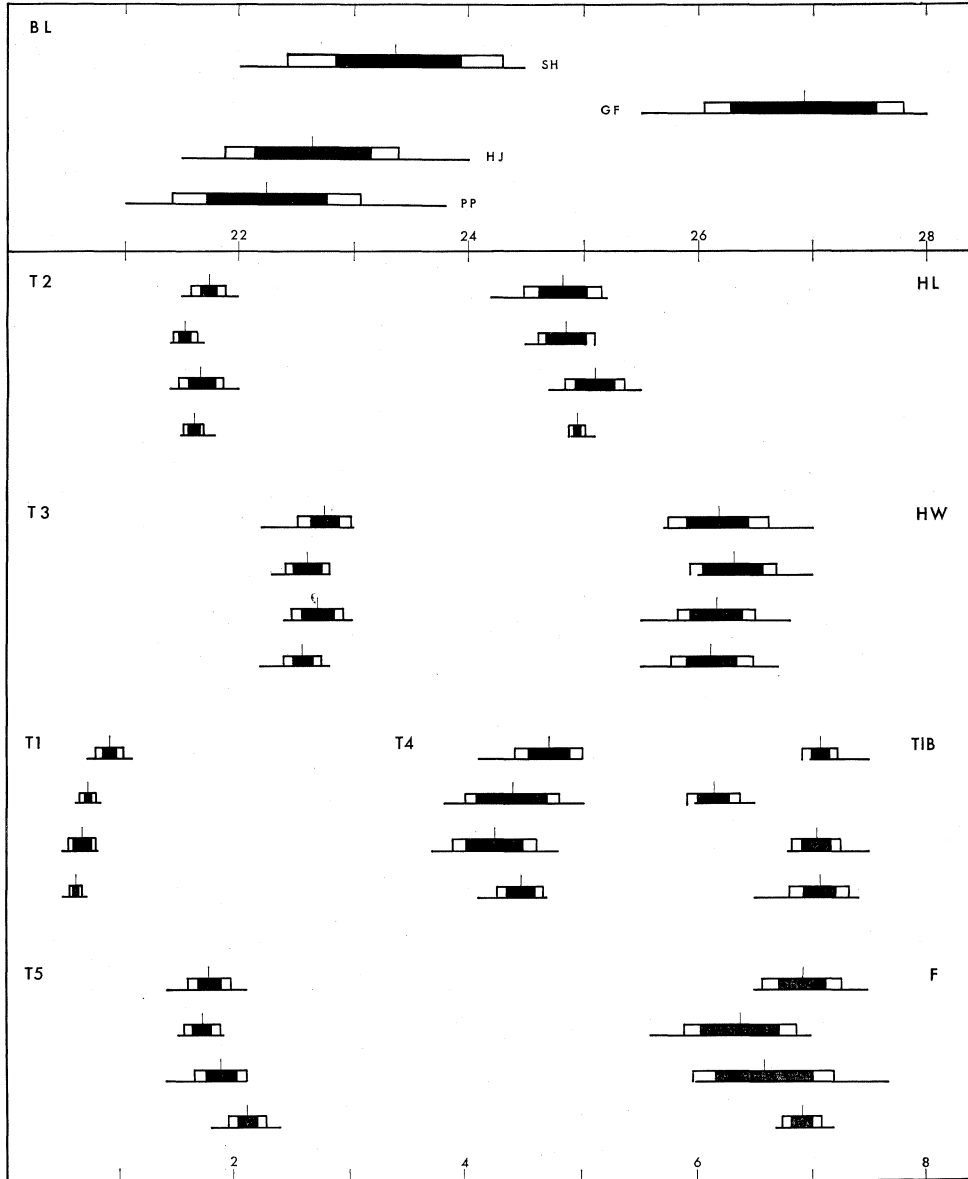


Figure 3. Geographical variation in size of four populations of *P. corroboree*. The data are for adult males and the samples are arranged in order of decreasing altitude: (SH) Smiggin Holes, N = 10; (GF) Ginini Flat, N = 7; (HJ) Happy Jacks Plain, N = 8; (PP) Pretty Plain, N = 9. The samples are compared with respect to ten morphometric variables: (BL) body length; (T1)–(T5) length of toes 1–5; (HL) head length; (HW) head width; (TIB) tibia length; and (F) foot length. Measurements are in mm. The method of graphical display employed is described by Hubbs and Hubbs (1953). For each sample the range is shown by the lower horizontal line; the mean by the vertical line; the solid rectangle encloses two standard errors of the mean on either side; and the open rectangle plus half the solid rectangle indicates one standard deviation on either side of the mean.

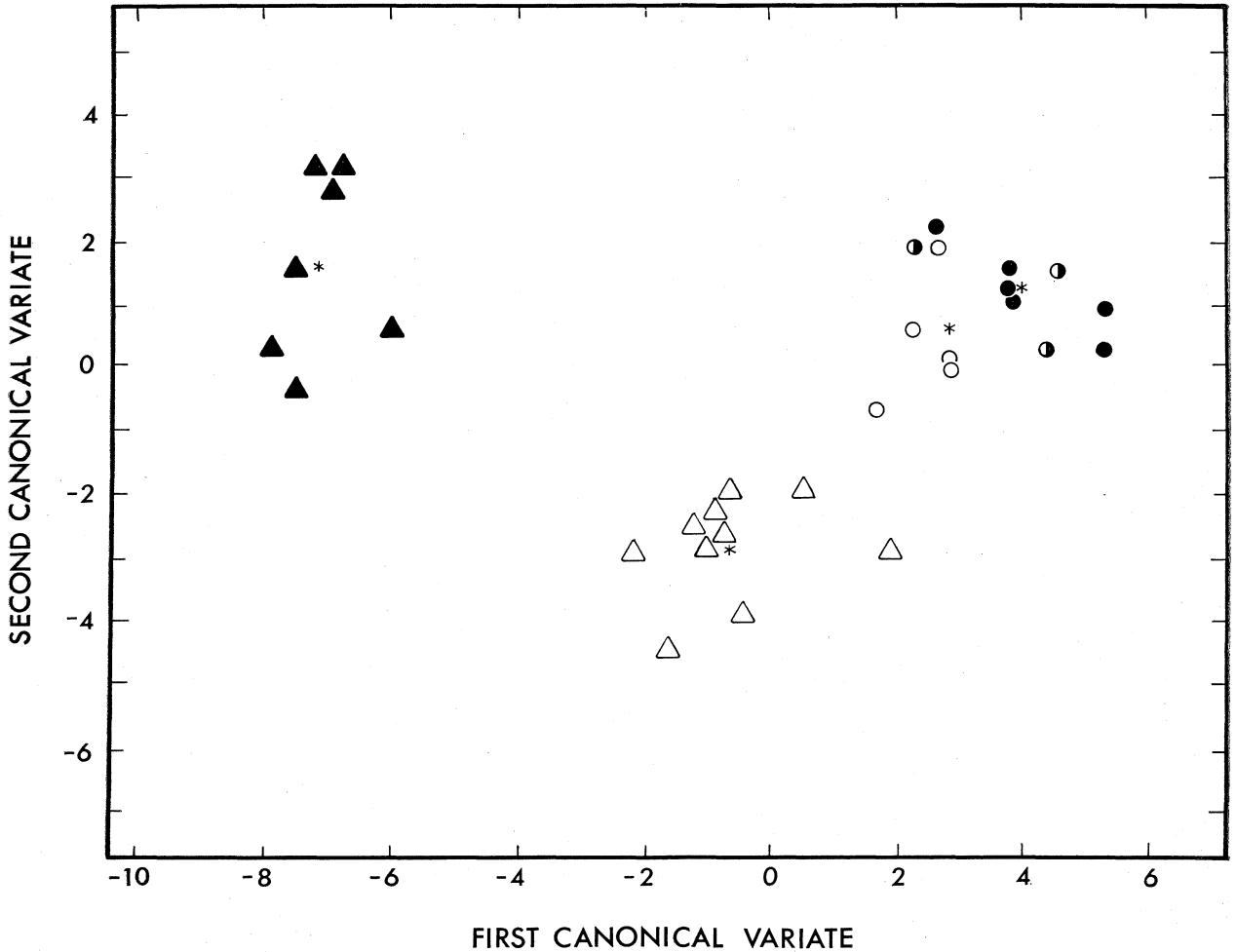


Figure 4. Canonical variate chart for the four samples of male *P. corroboree* described in figure 3. The asterisks indicate sample centroids. The symbols indicate the positions of individual specimens. Open triangles represent specimens from Smiggin Holes; closed triangles, Ginini Flat; open circles, Happy Jacks Plain; closed circles, Pretty Plain. Three cases of overlap between Happy Jacks and Pretty Plain individuals are indicated by half closed circles.

In the Q-mode multiple factor analysis the four samples are pooled. The data for each of the ten variables are first transformed to per cent range and then normalized. In this procedure, which has been described by Imbrie and Van Andel (1964), each variable receives "0" for the lowest value, "100" for the highest value, and the remaining values are expressed on the same scale. Q-mode varimax factor matrices are then calculated. It was found that the first two axes account for nearly 89 per cent of the total variation. A factor score matrix indicates the contribution of each original variable to variation along these axes (table 1). Factor loadings are then determined for each specimen and the results are shown graphically in figures 5 and 6. Instead of using the two varimax factors as the axes of a single graph (as in Gould, 1967) I have plotted the variation against each axis separately. This allows me to impose an order on the original samples. In each figure, I have arranged the samples in order of decreasing altitude, and within each sample the specimens are arranged in order of decreasing body length. The CABFAC programme can plot these results automatically.

TABLE 1. Factor Score Matrix

Body length	-0.220	0.717
Tibia length	0.628	-0.235
Head width	0.052	0.420
Head length..	0.275	0.240
Toe 1 length	0.092	0.281
Toe 2 length	0.271	0.046
Toe 3 length	0.259	0.251
Toe 4 length	0.310	0.201
Toe 5 length	0.329	0.066
Foot length	0.355	0.085

Variation along the first varimax factor axis (figure 5) is due primarily to the length of the hind limb, as measured by the length of the tibia, foot, and toes 2-5. The Brindabella Range sample has relatively shorter limbs than the samples from the Snowy Mountains area. Within each of the Snowy Mountains area samples it is clear that larger individuals have relatively shorter hind limbs. This raises the important point that this form of multiple factor analysis elucidates the ontogenetic component of variation. This pattern is confused in the Brindabella Range sample by the inclusion of specimen 17. (The anomalous position of specimen 17 results from the fact that this individual has unusually short tibia, foot, and second toe. Its short body relative to the other specimens from this locality (Ginini Flat) suggests that despite its collection from a breeding chorus it may be subadult.)

Variation along the second varimax factor axis (figure 6) is due primarily to variation in body length and head width. Again we see the striking ontogenetic trend within each sample, and a clear separation of the Brindabella Range sample from the others. The northern specimens have much longer bodies than could be anticipated on the basis of the established altitudinal variation within the Snowy Mountains area. Finally the altitudinal trend demonstrated above is also discernable on the second axis.

Studies of this type are subject to errors of three kinds (Sneath and Sokal 1973: 376-380). First we must expect sampling error due to the natural variation at each locality. Second, errors of measurement may be introduced and may become highly significant when sample sizes are small. Finally, the study of a particular suite of localities may not accurately represent the overall pattern of geographic variation in the species. While considerable care has been taken to reduce errors of measurement, the samples available were lamentably small and may have included individuals of different ages. Inadequacies in geographic representation could also be quite significant in a species with a patchy distribution like *P. corroboree*. Only

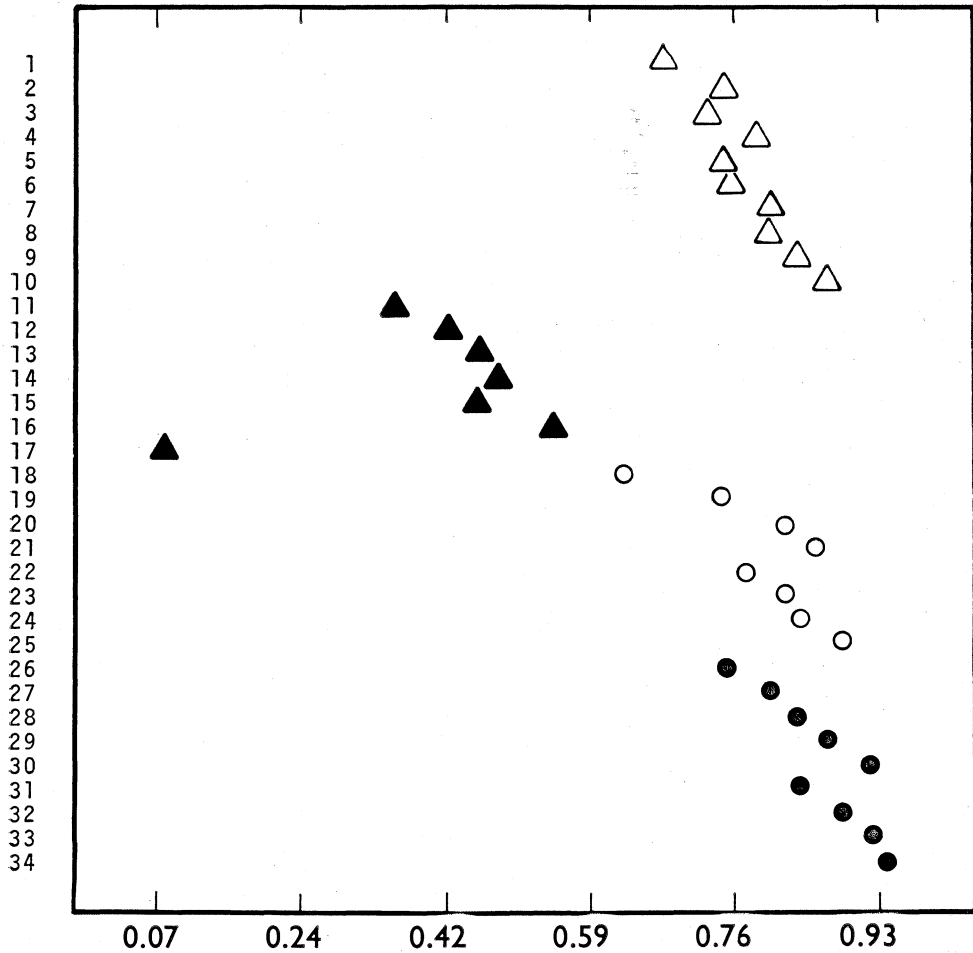


Figure 5. Variation of individual *P. corroboree* against the first varimax factor axis derived by Q-mode multiple factor analysis of the data presented in figure 3. Symbols are the same as those used in figure 4. Specimens 1-10 are from Smiggin Holes, specimens 11-17 are from Ginini Flat, specimens 18-25 are from Happy Jacks Plain; the remaining specimens are from Pretty Plain.

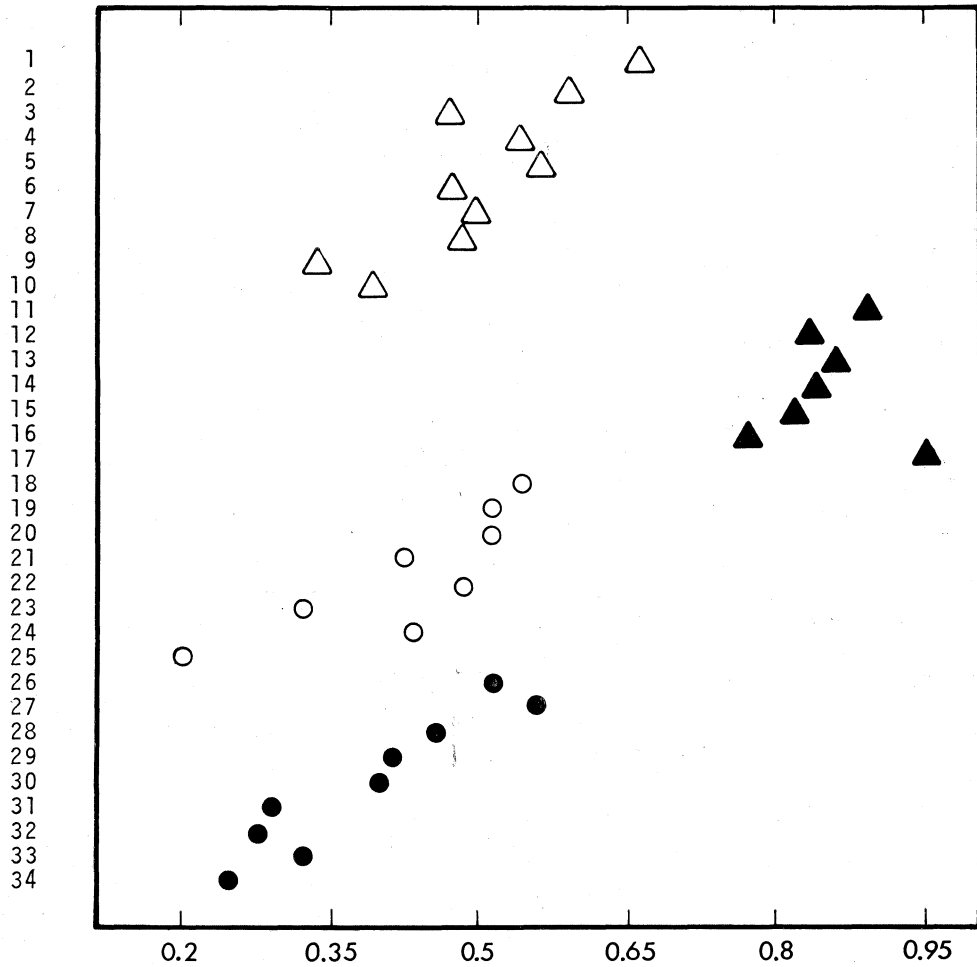


Figure 6. Variation of individual *P. corroboree* against the second varimax factor axis. Arrangement of the specimens is the same as in figure 5.

the study of larger samples from a larger number of sites will determine the significance of such errors in the present study. The preliminary results are certainly biologically meaningful and the situation warrants closer examination.

DISCUSSION

The loss of the terminal phalanx in the first toe of *P. corroboree* is surprising. The primitive phalangeal formulae of the anuran foot is apparently 2-2-3-4-3 (Lynch 1971, 1973). Phalangeal reduction has been reported in only four of the 16 families of modern anurans (rhinophrynids, certain bufonids and microhylids, and one leptodactylid: *P. guentheri* from Western Australia) (Parker 1940, Lynch 1973). A consideration of variation within the genus *Pseudophryne* as a whole (Woodruff 1972) supports the hypothesis that toe phalanx loss occurred independently in these two species.

Since I completed this study, Pengilley (1973) has published additional data on variation in "snout-urostyle" length in *P. corroboree*. Unfortunately our results are difficult to compare as different localities were sampled. Furthermore, Pengilley makes no allowance for the effects of growth on the single variable he measured. His results are consistent, however, with my finding of altitudinally dependent variation, and show that it occurs in the Brindabella Range as well as the Snowy Mountains.

The adaptive significance of the intraspecific variation in size and shape is not immediately clear. The altitudinal clines in body size and hind limb length may be tied to ecogeographic temperature factors. Alternatively, geographic differences in body size may be related to the sizes of competitors or prey species as suggested by Cody (1969) and Schoener (1969). With respect to this latter possibility the interaction between *P. corroboree* and *P. dendyi* in the northern Brindabella Range is particularly interesting. Pengilley (1971a) observed *P. dendyi* males moving into *P. corroboree* breeding sites at Coree Flat after the peak of the *P. corroboree* breeding season. He noted that when a male *P. dendyi* entered a burrow occupied by a male *P. corroboree* "... aggressive behaviour is always displayed by the male *P. corroboree* and often this can last for 3 or 4 hours before the male *P. dendyi* moves out of the burrow" (Pengilley 1971a: 87-88). There is no evidence that the two species hybridize and Pengilley suggests that differences in breeding season serve as the prime premating isolating mechanisms. Yet, it is known now that *P. dendyi* begins breeding activity as early as January at comparable altitudes in the Mt Cobberas area. Similarly, Pengilley (1973) noted males of *P. dendyi* commencing breeding activity at two localities south of Smiggin Holes (where no *P. corroboree* were present) as early as the end of January. These observations suggest that in the areas of sympatry *P. corroboree* may be physically delaying the breeding of *P. dendyi*. If this is the case then the relative size of the two species in the northern Brindabellas bears scrutiny. I was able to measure a sample of eight male *P. dendyi* from the Brindabella Range in the Australian Museum collection and the two species are compared morphometrically in table 2.

P. corroboree is smaller than *P. dendyi* with respect to nine of the ten variables measured, but *P. corroboree* has a longer body than *P. dendyi*. I suggest that direct interspecific competition in this area of sympatry may account for the selection of large body size in *P. corroboree*. This hypothesis would explain why the Brindabella Range sample is so different from the Snowy Mountains area populations and why this difference is restricted primarily to only one component of size and shape. This hypothesis can be tested by examining variation on a microgeographic level. Pengilley's (1973) data for several populations of the two species are unfortunately inadequate for this purpose.

TABLE 2. Comparison of two samples from the Brindabella Range. In each couplet the *P. corroboree* males (N = 7) precede the *P. dendyi* males (N = 8). Data are in mm.

Character	Mean	Range	Standard Deviation
Body length	26.93 24.24	(25.5-28.0) (22.0-26.7)	0.89 1.44
Tibia length	6.14 7.28	(6.0- 6.5) (7.0- 7.8)	0.24 0.31
Head width	6.31 7.26	(6.0- 7.0) (7.0- 7.6)	0.38 0.23
Head length	4.86 5.64	(4.5- 5.0) (5.3- 6.1)	0.24 0.27
Foot length	6.39 7.29	(5.6- 7.0) (6.9- 8.0)	0.49 0.36
Toe 1 length	0.71 1.28	(0.6- 0.8) (1.1- 1.4)	0.07 0.14
Toe 2 length	1.53 1.84	(1.4- 1.7) (1.6- 2.0)	0.11 0.16
Toe 3 length	2.61 2.95	(2.3- 2.8) (2.7- 3.2)	0.20 0.17
Toe 4 length	4.40 4.94	(3.8- 5.0) (4.5- 5.6)	0.41 0.35
Toe 5 length	1.71 1.76	(1.5- 1.9) (1.5- 2.2)	0.16 0.21

The observation of competition for breeding sites between *P. corroboree* and *P. dendyi*, and the possible effect of such competition on the size of *P. corroboree*, raise the question of the extent and significance of such interaction in the past. The fragmented distribution pattern of *P. corroboree* today suggests that this species has been more widely distributed. Whether range fragmentation is a result of climatic change or of interspecific competition cannot be established. The occurrence of *P. dendyi* on Mt Cobberas, in the Bago Range (northwest of Round Mountain), and near Kiandra (5.6 km SW. of Kiandra at 1,460 m), suggests that this species may have replaced *P. corroboree* in some areas. On the other hand, dramatic climatic changes have characterized *P. corroboree*'s habitat during the late Cenozoic and undoubtedly have had a significant effect on its distribution. Many of this species breeding sites are less than 9000 years old. The Ginini Flat bog, one of the largest sphagnum peat bogs in southeastern Australia, is only about 3000 years old (Costin 1972).

The possibility of intense interspecific competition in the northern Brindabella Range raises another difficult question. In connection with Pengilley's (1971a) detailed analysis of the behaviour of the Coree Flats population it remains uncertain whether the behaviour of *P. corroboree* in this area is markedly affected by the presence of *P. dendyi*. Behavioural convergence and divergence are likely to evolve in this situation (Cody 1969; Grant 1972) and we should not regard the Coree Flats population as typical of the species until the possible effects of these phenomena have been examined.

Finally, the geographic variation in coloration of *P. corroboree* deserves attention. Marked differences in the amount of black and yellow pigmentation have been noted between the Brindabella Range and Snowy Mountains area samples. The overall pattern is probably not aposematic. It is clearly disruptive, blending closely with the sphagnum moss of the animal's normal habitat. Although biochemical analyses have not been undertaken my observations of developing *Pseudophryne* embryos (Woodruff 1972) suggest that three cell types are responsible for

this pattern: melanophores (containing melanin), xanthophores (containing yellow carotenoids), and guanophores (containing white platelets of guanine or related purines). In terms of chromatophores we must explain why there has been selection for more melanophores in the Brindabella Range populations and more xanthophores in the Snowy Mountains area. While I could speculate about the relative role of these changes in thermoregulation, fat storage, protection from predators or parasites, and competitive interactions with *P. dendyi*, such a discussion would be premature.

ACKNOWLEDGMENTS

H. G. Cogger (Australian Museum), J. Dixon (National Museum of Victoria), and M. J. Littlejohn (University of Melbourne) permitted me to examine specimens in their care. R. S. Frankenberg and J. Sepkoski assisted me with the X-radiography and computer programming respectively. I am indebted to S. J. Gould for the CABFAC programme, advice on the interpretation of the multivariate analysis, and for his critical reading of the manuscript.* While working on this problem I received support from a Commonwealth of Australia Postgraduate Award and a Research Fellowship at the Museum of Comparative Zoology, Harvard University.

REFERENCES

- Blake, A. J. D., 1973. Taxonomy and relationships of myobatrachine frogs (Leptodactylidae): a numerical approach. *Aust. J. Zool.* 21: 119-149; with 3 Appendices issued separately.
- Cody, M. L., 1969. Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. *Condor* 71: 222-239.
- Colefax, A. N., 1956. New information on the corroboree frog (*Pseudophryne corroboree* Moore). *Proc. Linn. Soc. N.S.W.* 80: 258-266.
- Costin, A. B., 1972. Carbon-14 dates from the Snowy Mountains area, southeastern Australia, and their interpretation. *Quaternary Res.* 2: 579-590.
- Fleay, D., 1963. Strange animals of Australia. *National Geographic Mag.* 124: 388-411.
- Gould, S. J., 1967. Evolutionary patterns in pelycosaurian reptiles: a factor analytic study. *Evolution* 21: 385-401.
- Grant, P. R., 1972. Convergent and divergent character displacement. *Biol. J. Linn. Soc.* 4: 39-68.
- Hubbs, C. L., and C. Hubbs, 1953. An improved graphical analysis and comparison of series of samples. *Syst. Zool.* 2: 49-56, 92.
- Imbrie, J. and T. H. van Andel, 1964. Vector analysis of heavy mineral data. *Bull. Geol. Soc. Amer.* 75: 1131-1156.
- Jacobson, C. M., 1963. Observations on distribution, behaviour and development in the Australian toad genus *Pseudophryne* Fitzinger. *Proc. Linn. Soc. N.S.W.* 88: 41-46.
- Littlejohn, M. J., 1962. Zoology of the High Plains: Part I. Ichthyology and herpetology. *Proc. R. Soc. Vict.* 75: 311-313.
- , 1967. Patterns of zoogeography and speciation in south-eastern Australian Amphibia. Chapter 6 in Weatherley, A. H. (ed.) *Australian Inland Waters and Their Fauna: Eleven Studies*. A.N.U. Press, Canberra.

* Anonymous reviewers also made significant contributions to the clarity of the manuscript.

- Lynch, J. D., 1971. Evolutionary relationships, osteology, and zoogeography of leptodactylid frogs. *Misc. Publ. Univ. Kans. Mus. Nat. Hist.* pp. 53.
- , 1973. The transition from archaic to advanced frogs. Chapter 3 in Vial, J. L. (ed.) *Evolutionary Biology of the Anurans*. Univ. Missouri Press, Columbia.
- Main, A. R., 1964. A new species of *Pseudophryne* (Anura: Leptodactylidae) from north-western Australia. *West. Aust. Nat.* 9: 66–72.
- Martin, A. A., 1967. Australian anuran life histories: some evolutionary and ecological aspects. Chapter 7 in Weatherley, A. H. (ed.) *Australian Inland Waters and Their Fauna: Eleven Studies*. A.N.U. Press, Canberra.
- Moore, J. A., 1953. A new species of *Pseudophryne* from Victoria, *Proc. Linn. Soc. N.S.W.* 78: 179–180.
- , 1961. Frogs of eastern New South Wales. *Bull. Amer. Mus. Nat. Hist.* 121: 149–386.
- Parker, H. W., 1940. The Australasian frogs of the family Leptodactylidae. *Novitates Zool.* 42: 1–106.
- Pengilley, R., 1971a. Calling and associated behaviour of some species of *Pseudophryne* (Anura: Leptodactylidae). *J. Zool., Lond.* 163: 73–92.
- , 1971b. The food of some Australian anurans (Amphibia). *J. Zool. Lond.* 163: 93–103.
- , 1973. Breeding biology of some species of *Pseudophryne* (Anura: Leptodactylidae) of the Southern Highlands, New South Wales. *Aust. Zool.* 18: 15–30.
- Schoener, T. W., 1969. Models of optimal size for solitary predators. *Amer. Natur.* 103: 277–313.
- Sneath, P. H. A., and R. R. Sokal, 1973. *Numerical Taxonomy*. W. H. Freeman, San Francisco.
- Watson, G. F., and A. A. Martin, 1973. Life history, larval morphology and relationships of Australian leptodactylid frogs. *Trans. Roy. Soc. S. Aust.* 97: 33–45.
- Woodruff, D. S., 1959. Amphibians and reptiles of the Bogong High Plains. *Vict. Nat.* 76: 214.
- , 1972. The Evolutionary Significance of Hybrid Zones in *Pseudophryne* (Anura: Leptodactylidae). Ph.D. Thesis. University of Melbourne.