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The Affinities of the Rat-kangaroos (Marsupialia) as revealed by a comparative study of the Female Urogenital System.

BY

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1. INTRODUCTION

According to the accepted view the family Macropodidae is divided into three sub-families, the Hypsiprymnodontinae, the Potoroinae, and the Macropodinae. The members of the first two are collectively known as the rat-kangaroos and the third sub-family comprises the true kangaroos and wallabies.

The present paper is concerned mainly with the rat-kangaroos, which consist of five genera, as follows:—

Sub-family HYPSIPRYMNODONTINAE

(1) *Hypsiprymnodon* Ramsay, 1876

Contains a single little-known species recorded from Queensland. This genus is the only form in which the hallux is present. Mainly for this reason it is regarded as the most primitive rat-kangaroo and is usually placed in a separate sub-family from the rest.

Sub-family POTOROINAE

(2) *Potoroüs* Desmarest, 1805

Three species have been recorded of which probably only one, *P. tridactylus* (Kerr, 1792), can now be obtained.

(3) *Bettongia* Gray, 1837

There are four species, all of which are rare or extinct, with the exception of the Tasmanian form, *B. cuniculus* (Ogilby, 1838).

(4) *Aepyprymnus* Garrod, 1875

Contains only one species, *Ae. rufescens* (Gray, 1837), which is extremely rare. Nothing is known of its internal anatomy.

(5) *Caloprymnus* O. Thomas, 1888

A single species, *C. campestris* (Gould, 1843), which was re-discovered fifteen years ago after a lapse of ninety years.

The female urogenital system of only two of these genera is known, viz., *Bettongia* (Owen, 1834; Brass, 1880; Pearson, 1944, 1945) and *Potoroüs* (Pearson, 1944, 1945). In the present paper descriptions of the female urogenital system of *Caloprymnus* and *Hypsiprymnodon* are given. Nothing is known of the internal anatomy of *Aepyprymnus*.

2. The Female Urogenital System of Caloprymnus campestris

(Figs 1-3)

Caloprymnus campestris was first described by Gould in 1843 as *Bettongia campestris* from three specimens obtained by Sir George Gray. After a lapse of nearly ninety years a single specimen was obtained by Mr. Reese from the north-eastern part of South Australia, and this important re-discovery led to a special expedition being sent out in 1931, with the result that Mr. Finlayson, Honorary Curator of Mammals, South Australian Museum, secured several specimens of this rare species and made important observations on its habits, external structure, and probable affinities (Finlayson, 1932). Through the good offices of the Director of the National Museum, Melbourne, an opportunity has now been presented of reporting upon its female urogenital system, thereby extending our knowledge of the comparative anatomy of this important group of marsupials. This help so readily afforded is gratefully acknowledged.

The following description of the female urogenital system of *Caloprymnus* is based upon an examination of spirit specimen No. R. 13609 from the collections of the National Museum, Melbourne. The parts described have been dissected but have not been detached from the carcass, and should be available, therefore, for future examination in Melbourne.

The external measurements of the spirit specimen are as follows:—

Length of head and body	34 cm.
Length of tail	33 cm.
Length of ear	3·7 cm.
Length of pes	11·2 cm.

The specimen examined is a mature female. The left uterus is considerably enlarged and contains a foetus which, though recognizable, is not sufficiently well preserved to enable the details of its structure to be made out. However, the urogenital system in general is in a satisfactory state of preservation and no difficulty has been experienced in making out the details which are given below.

A general inspection of the female urogenital system shows that it resembles that of *Potoroüs* to a marked degree, though the anterior vaginal expansion is relatively much larger and bears out the suggestion made in previous papers (Pearson, 1944, 1945) that this portion of the vagina is, in fact, an incipient caecum such as is seen in full development in *Bettongia.*

Uteri (l.ut., r.ut.)

The two uteri would, in normal circumstances, have a somewhat similar appearance to those of *Potoroüs* as described by Pearson (1945), but, as mentioned above, the left uterus of this specimen is considerably enlarged owing to the presence of a foetus, and has a length of 47 mm. (body and neck) and a maximum width of 22 mm. The normal right uterus is 28 mm. long and 12 mm. wide.

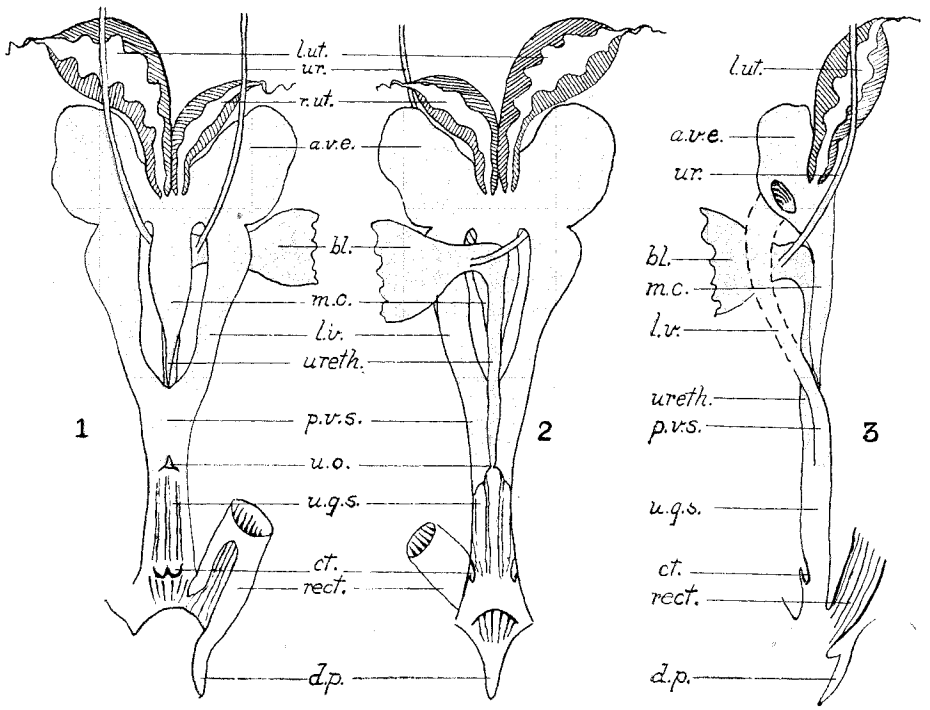
Median vaginal cul-de-sac (m.c.)

This has an extreme length of about 26 mm. and the first (anterior) quarter forms part of the anterior vaginal expansion. The cul-de-sac is about 5 mm. wide in its second quarter and tapers gradually as it passes caudally. It ends blindly immediately anterior to the junction of the two lateral vaginae.

Anterior vaginal expansion (a.v.e.)

This is a commodious, winged chamber formed by the hypertrophy of the anterior portion of the vaginal system. It occupies much the same position as the comparable structure in *Potoroüs*, but differs from it in being larger and possessing two well-defined spheroidal wings which are somewhat flattened dorso-ventrally. The outlines

of these wings are somewhat irregular, which may be due, in part, to the effects of the preservative. This anterior vaginal expansion has a single continuous cavity, the medial portion of which may be regarded as the anterior part of the vaginal cul-de-sac already described. The lumen of each wing opens freely into this central cavity and also communicates posteriorly with the lumen of the contiguous lateral vagina.



(Figs 1-3)

Caloprymnus campestris

Diagrams of the female urogenital system.

FIG. 1.—Horizontal section, Dorsal view x $1\frac{1}{5}$.

FIG. 2.—Horizontal section, Ventral view x $1\frac{1}{5}$.

FIG. 3.—Paramedial section x $1\frac{1}{4}$.

NOTE.—In all figures *pink* represents the vaginal system; *blue* represents the urinary system.

a.v.e.—Anterior vaginal expansion
bl.—Urinary bladder
ct.—Clitoris
d.p.—Digital process projecting from the postero-dorsal lip of the cloaca.
l.l.v.—Left lateral vagina
l.ur.—Left ureter
l.ut.—Left uterus, considerably swollen and containing a foetus.
l.v.—Lateral vagina.
m.c.—Median vaginal cul-de-sac (becoming a true median vagina in fig. 7)
p.v.s.—Posterior vaginal sinus
rect.—Rectum
r.ut.—Right uterus (normal size)
u.g.s.—Urogenital sinus
u.o.—Opening of urethra into urogenital sinus
ur.—Ureter
ureth.—Urethra
ut.—Uterus
v.c.—Vaginal caecum.

The extreme width of the anterior vaginal expansion is about 27 mm. Each wing has an antero-posterior length of about 15 mm. and a width of about 11 mm. As in the case of *Potoroüs* the uterine necks project from the roof of the median portion of the chamber on papillae which are not so well developed as in *Potoroüs*. As in that genus each papilla is perforated near its tip by the os uteri.

Although there can be little doubt that the vaginal system is completely separated into right and left elements in early development, the septum separating the two halves completely disappears in the mature female.

Lateral vaginae (l.v.) and posterior vaginal sinus (p.v.s.)

Each lateral vagina arises from the postero-lateral wall of the corresponding wing of the anterior vaginal expansion and has a length of about 21 mm. The right and left lateral vaginae have a straight course as they pass caudally and gradually converge to meet behind the blind extremity of the median cul-de-sac. They are widest near their anterior end, where they have a width of about 5 mm. and gradually narrow to a width of 3 mm. or less. The two coalesce to form the posterior vaginal sinus, which, as in the case of both *Potoroüs* and *Bettongia*, is a median tube lying immediately dorsal to the posterior section of the urethra. Both the posterior vaginal sinus and urethra open together into the urogenital sinus. The posterior vaginal sinus is 8 mm. long and about 5 mm. wide. It is shorter than the comparable structure in *Potoroüs*, but slightly longer than that of *Bettongia*.

Urinary bladder (bl.) and urethra (ureth.)

As in *Potoroüs* and *Bettongia* the urinary bladder has an extreme anterior attachment situated immediately behind the anterior vaginal expansion (or caecum). The urethra runs ventral to the median cul-de-sac and posterior vaginal sinus, and together with the latter, opens into the urogenital sinus. The urethra has a total length of about 26 mm. It is about 3 mm. wide anteriorly and narrows somewhat towards its posterior end.

Urogenital sinus (u.g.s.)

This is about 14 mm. long and about 5 mm. wide. There is a well-developed clitoris attached to the ventral wall near the posterior extremity.

3. Female Urogenital System of Hypsiprymnodon moschatus

(Figs 4, 5.)

After the present paper had been completed in its original form an unpublished account by Miss F. R. Heighway of the anatomy of this species was brought to the writer's notice through the good offices of Professor Abbie of the Anatomy Department, University of Adelaide. Later Professor Burkitt of the Anatomy Department, University of Sydney, in whose laboratory Miss Heighway's work was carried out, was kind enough to allow the writer to examine a dissection of the female urogenital system of this species which had been made by Miss Heighway in the course of her work. It is desired to express the deepest appreciation of the facilities thus offered. The information obtained in this way has filled an important gap in the known comparative anatomy of this group and has enabled the writer to discuss with greater confidence the affinities and associated problems of these interesting marsupials.

A brief statement of the salient features of the female urogenital system of *Hypsiprymnodon* is given below. This account and the figures which accompany it (figs 4 and 5) are drawn up from the writer's own examination of the material placed at his disposal.

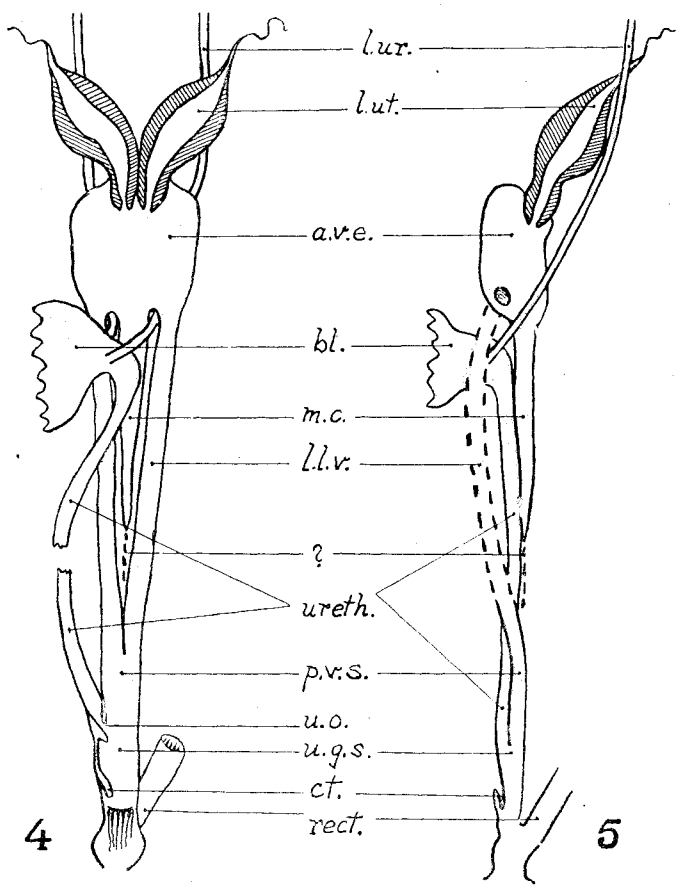
This species falls into line with the other members of the group in so far as the general topography of the urogenital organs is concerned.

Uteri (l.ut.)

These call for no special comment as they closely resemble the comparable structures in all other rat-kangaroos. The two uterine necks are in contact with each other in the middle line.

Median vaginal cul-de-sac (m.c.)

As in the three other genera of the group, this portion of the vaginal system is intimately connected with the anterior vaginal expansion, so much so that the median portion of the latter is for all intents and purposes the anterior portion of the median cul-de-sac. Caudally the cul-de-sac tapers considerably. In the dissected specimen upon which the present description is based the cul-de-sac has been



(Figs 4 and 5)

Hypsiprymnodon moschatus

Diagrams of the female urogenital system.

FIG. 4.—Horizontal section, ventral view. The urethra is displaced from its median position, turned to the right side, and cut about the middle of its course. The ventral wall of the urogenital sinus is shown deflected to the right side so that the clitoris is displaced from its median ventral position. x 1½.

FIG. 5.—Paramedial section. The left lateral vagina which is out of the plane of the section is shown by broken lines. x 1½.

separated from the underlying urethra and would appear to terminate blindly some distance anterior to the point of junction of the converging lateral vaginae. If this is actually so it would mark a difference between *Hypsiprymnodon* and the other genera in this respect. But in the other three genera the cul-de-sac and the urethra are so intimately bound together that the separation of one from the other requires very delicate manipulation. In the other three genera the lumen of the cul-de-sac has actually been traced as far as the level of the junction of the two lateral vaginae, and this has been confirmed in the case of *Potoroüs* by the inspection of serial sections. In the case of an extremely immature specimen the cul-de-sac might be found to be very short, but the specimen examined appears to be from a mature animal. In figs 4 and 5 the possible existence of a posterior extension of the cul-de-sac is indicated by a dotted line (marked ?).

Anterior vaginal expansion (a.v.e.)

This would appear to be the most variable part of the vaginal system in the group. In *Hypsiprymnodon* the condition is reminiscent of that already described in *Potoroüs* (Pearson, 1945). In the specimen examined the outline of this thin-walled chamber is not symmetrical. This may be due to the pressure exerted by surrounding organs after the carcass was placed in preservative.

Length 11 mm. Greatest width 12 mm.

As in the other forms the uterine necks project from the roof of this chamber on two well-defined papillae, lying side by side. Each papilla is perforated by the os uteri.

Lateral vaginae (l.l.v.) and posterior vaginal sinus (p.v.s.)

The lateral vaginae pass straight back from the postero-lateral corners of the anterior vaginal expansion. As they proceed caudally, lying on either side of the median cul-de-sac, they gradually converge and ultimately coalesce to form a common chamber, the posterior vaginal sinus, which, as in the other three forms, lies dorsal to the posterior portion of the urethra. Each lateral vagina is about 27 mm. long and the posterior vaginal sinus is about 9 mm. long.

Urinary bladder (bl.) and urethra (ureth.)

As is seen in figs 4 and 5, the attachment of the bladder lies nearly as far forward as the posterior extremity of the anterior vaginal expansion. This conforms to the arrangement found in the other three genera. The urethra has a total length of about 30 mm. and opens near the base of a well-defined papilla.

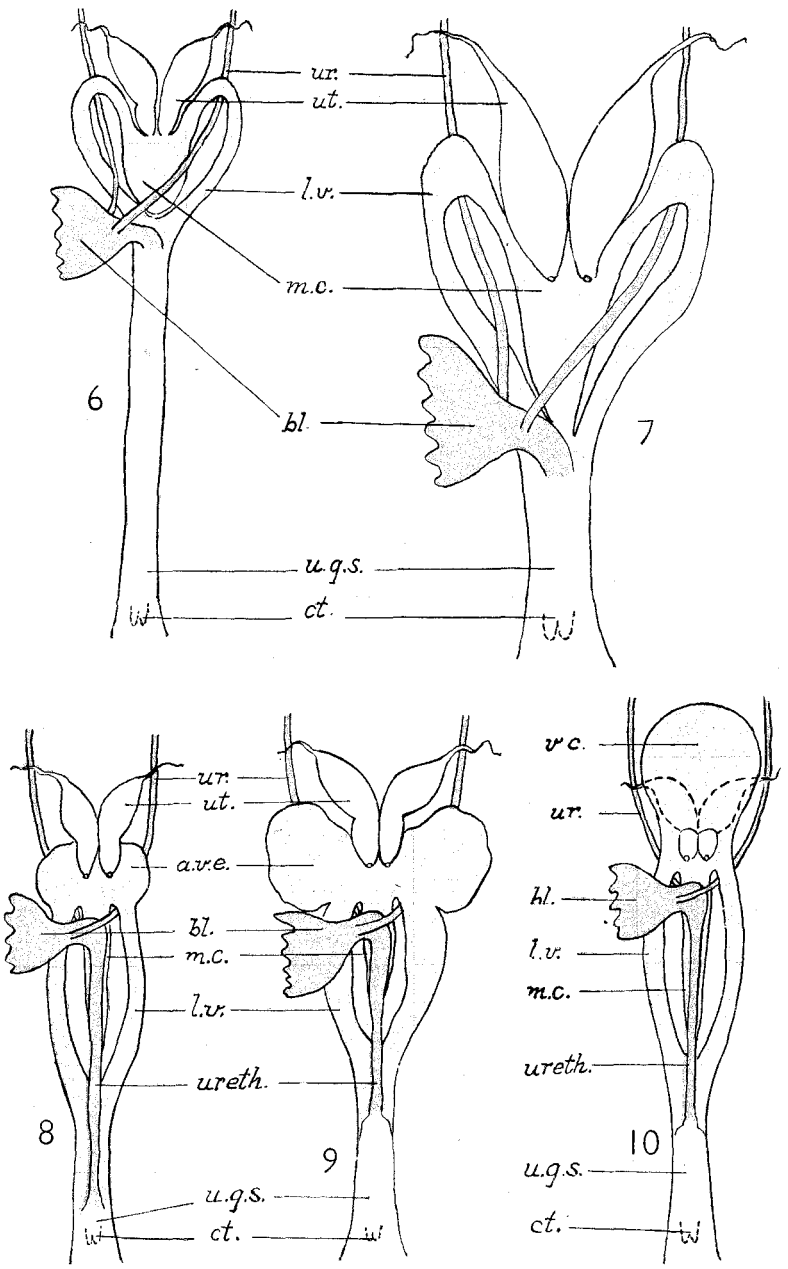
Urogenital sinus (u.g.s.)

This is extremely short and is about 6 mm. in length to the level of the clitoris.

4. The Inter-relationships of the Rat-kangaroos

(Figs 1-10)

A comparison of the female urogenital systems of *Bettongia*, *Potoroüs*, *Caloprymnus*, and *Hypsiprymnodon* (figs 1-5, 8-10) makes it clear that they follow the same common design and differ from the phalangers and kangaroos (figs 6, 7) in at least three important respects, viz., the presence of an anterior vaginal expansion, or its homologue the vaginal caecum; the anterior attachment of the urinary bladder with an extremely long urethra; and the presence of a posterior vaginal sinus.



Diagrammatic horizontal sections of the female urogenital system, seen from the ventral side.

FIG. 6.—*Petaurus breviceps* (Phalangeridæ) x 3.
FIG. 7.—*Thylogale billardierii* (Macropodidae) x 1.
FIG. 8.—*Potoroüs tridactylus.*
FIG. 9.—*Caloprymnus campestris.* } (Potoroidae) x 1.
FIG. 10.—*Bettongia cuniculus.*

The following table gives a statement of the relative size of each part of the female urogenital system in these four genera based in all cases upon measurements taken from specimens preserved in spirit or formalin:—

	Bettongia	*Potoroïs*	*Caloprymnus*	*Hypsiprymnodon*
Total length of urogenital system from anterior end of uteri to clitoris	58 mm.	55 mm.	60 mm.	63 mm.
Percentages of total lengths.				
Extreme length of median cul-de-sac (including median portion of anterior vaginal expansion)	55%	64%	45%	?
Length of lateral vaginae	46%	54%	35%	47%
Length of posterior vaginal sinus	10%	27%	13%	12%
Length of urogenital sinus as far back as the clitoris	24%	11%	23%	9%
Length of urethra	52%	75%	43%	50%

Since the first genus, *Potoroïs*, was established by Desmarest in 1804 the classification of this group of marsupials has been based upon external characters alone and principally upon foot-structure and dentition. It is surprising to find that taxonomists, who are vitally concerned with phyletic problems, should be satisfied with the evidence of external characters only and should ignore, more often than not, the study of comparative anatomy for their purpose. It is a fitting commentary upon the evaluation of the basic characters which should serve as a guide to phylogeny that until a year ago our knowledge of the internal morphology of the rat-kangaroos was confined to the genus *Bettongia*. Based upon external characters alone it is difficult to assess the precise relationships of the various genera within the group, and the evidence from foot-structure and dentition is confusing and contradictory. For instance, *Caloprymnus* resembles *Bettongia* in at least three points, the character of the pes, the appearance of the rhinarium, and the presence of a characteristic finger-shaped process on the postero-dorsal margin of the cloaca. On the other hand, it approaches closely to *Potoroïs* in its dentition. Again *Hypsiprymnodon* possesses a well-developed hallux, a primitive character which distinguishes it from the rest of the rat-kangaroos. *Potoroïs* resembles it more closely in foot-structure than *Bettongia* or any of the other genera which have highly specialized feet reminiscent of the condition found in the true kangaroos (see fig. 11). But *Hypsiprymnodon* has a similar type of dentition to *Bettongia*. Bensley (1903) drew attention to this contradictory evidence and came to the conclusion that ' the correct plan of division is according to dentition '.

It has been stated above (p. 13) that the accepted classification of the rat-kangaroos separates *Hypsiprymnodon* from the others because of the possession of the hallux. But this in itself can hardly be regarded as sufficient reason for establishing a separate sub-family. Both the dasyures and peramelids, for example, show variability in this character. Neither is there sufficient justification for Bensley's classification based upon tooth-structure which, though still recognizing two sub-families, places what is here regarded as the most primitive genus, *Hypsiprymnodon*, in the same sub-family as the most highly specialized form, *Bettongia*. Bensley considered the rat-kangaroos to be diphyletic in origin and grouped *Potoroïs* and *Caloprymnus* together in the sub-family Potoroinae as

having arisen from some primitive phalanger by a different line from the other three genera which he placed in the sub-family Bettongiinae (see fig. 12). It has been shown in a previous communication (Pearson, 1945) and in the present paper that the homogeneous plan upon which the female urogenital system of the rat-kangaroos is built indicates clearly not only community of origin of all members of this group but also fundamental differences from all other diprotodonts.

Bensley attempted to reconcile the contradictions which result from the study of foot-structure and dentition by postulating that the phalangerine stocks from which the rat-kangaroos have sprung were homogeneous in foot-structure, though diversified in dentition. This assumption is neither convincing nor satisfactory and the impression is created that these two sets of characters, taken either singly or collectively, give no reliable indication of the true affinities of the various genera of rat-kangaroos. Gregory (1910) in his classic monograph on the Mammalia sounded a warning against attaching too much importance to either of these characters, both of which are liable to be affected by external influences. In his opinion structures should be sought which are relatively stable and less susceptible to changes in external conditions. He instanced the urogenital system, the brain and skull as presenting more reliable evidence of phyletic relationship.

In the rat-kangaroos foot-structure and tooth-character, particularly the former, have been affected by the widely diverse conditions under which the different genera have been evolved. On the other hand, the evidence collected in the present paper and in a previous communication (Pearson, 1945) serves to emphasize the stability of the female urogenital system which follows a common design throughout the group. The only striking deviation from this plan is seen in the degree of development of the anterior vaginal expansion, but it has been shown (Pearson, 1945) that the small size of this structure in *Potoroüs* is merely an early stage in the development of the large caecum of *Bettongia*. This difference could hardly be attributed to the effects of environmental changes. The present writer therefore agrees with Gregory that the comparative morphology of the female urogenital system provides a reliable guide to the phylogeny of a group.

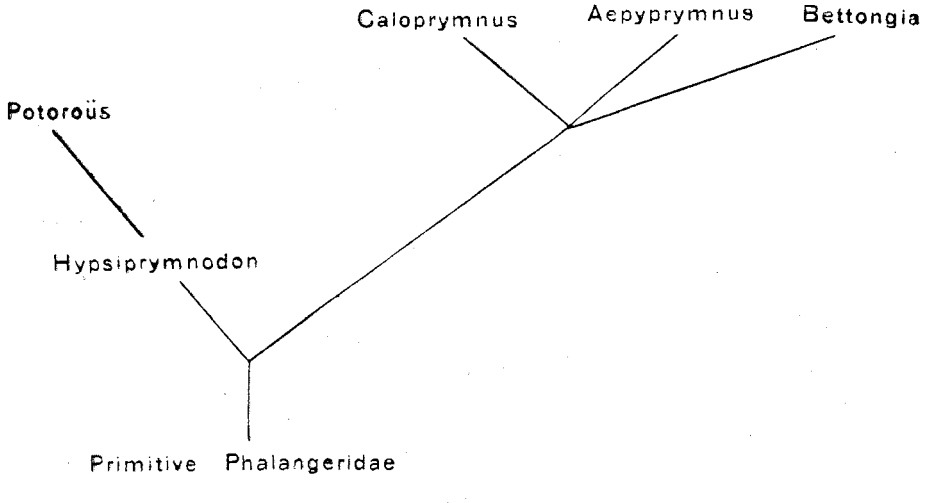


FIG. 11.—Probable inter-relationships of the rat-kangaroos based upon foot-structure.

The genera *Hypsiprymnodon, Potoroïs, Caloprymnus,* and *Bettongia*(1) agree on the following important points in the female urogenital system:—

(1) There is a gradual elaboration of the anterior portion of the vaginal system from a small, though well-defined, enlargement (anterior vaginal expansion) in *Hypsiprymnodon* and *Potoroïs*; through *Caloprymnus* in which this expansion assumes greater proportions; and culminating in the condition found in *Bettongia* where the large vaginal caecum is an obvious further development of the condition found in *Caloprymnus*. In other words, the relatively insignificant anterior vaginal expansion of *Potoroïs* and *Hypsiprymnodon* may be regarded as the precursor of the large caecum found in *Bettongia*. The presence of this cæcum, either in the incipient stages or in its full development, must be regarded as a departure from the prototypal condition.

(2) Unlike the usual marsupial arrangement the urinary bladder is attached a considerable distance anterior to the urogenital sinus and consequently there is an extremely long urethra opening into a relatively short urogenital sinus. As already pointed out (Pearson, 1945) this is a highly specialized condition found nowhere else in the Marsupialia except in the Peramelidae.

(3) The two lateral vaginae do not open directly into the urogenital sinus but coalesce to form a median sinus, the posterior vaginal sinus, lying dorsal to the urethra. This is a substantial structure varying in length between 10% to 27% of the total extent of the urogenital system. So far as is known this arrangement is not found elsewhere in the marsupials and must be regarded as a specialized development (see Pearson, 1945).

(4) The lateral vaginae commence at the postero-lateral corners of the anterior vaginal expansion (or its homologue the vaginal caecum) and then follow a straight course in a caudal direction on each side of the median cul-de-sac. In this respect the rat-kangaroos differ from most other marsupials

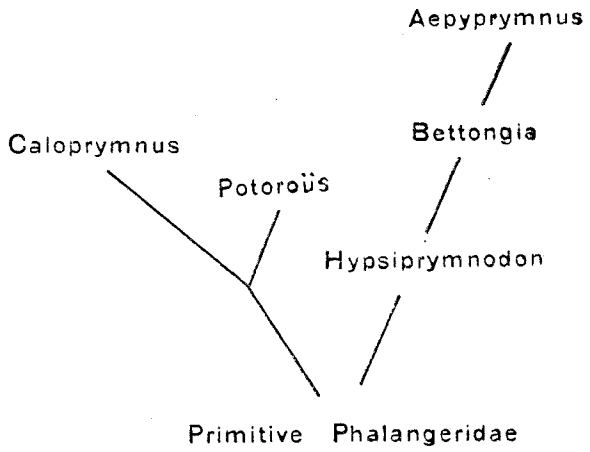


FIG. 12.—Probable inter-relationships of the rat-kangaroos based upon dentition. (After Bensley.)

(1) Nothing is known of the female urogenital system of *Aepyprymnus*.

in which the lateral vaginae follow a devious course and have a shape like the handles of a vase (figs 6 and 7). The Peramelidae are an exception to this. The straight course which these canals take in the rat-kangaroos is probably correlated with the special type of parturition (see No. 5 below).

(5) It is known that in at least one genus (*Potoroüs*) parturition takes place through the lateral vaginae (Flynn, 1923; Pearson, 1945). This is probably true also of *Bettongia*. In the specimen of *Caloprymnus* described in the present paper an intra-uterine foetus was present and the lateral vaginae were swollen so as to suggest that they were being prepared for parturition. It is not unlikely that in all the genera of this group parturition takes place through the lateral vaginae. This, however, is not a primitive condition but a secondary return to it(1).

The plan of the urogenital system is extraordinarily uniform throughout the group, though, as stated above, the condition of the anterior vaginal expansion is variable.

The following conclusions may be drawn from this comparative study of the rat-kangaroos:—

(1) Foot characters and dentition often provide conflicting evidence. Taken separately or together they do not give a satisfactory picture of true relationships. On the other hand, the female urogenital system offers a reliable criterion of phyletic affinities.

(2) The female urogenital system of the rat-kangaroos shows uniformity of design combined with a high degree of specialization.

(3) The peculiarly specialized nature of the female urogenital system of the rat-kangaroos indicates (*a*) that they form a small homogeneous group of genera with close affinities and (*b*) that they differ from all other marsupials.

(4) The rat-kangaroos are a natural group of cursorial and saltatorial marsupials which live under diverse conditions. These conditions have produced variability in foot-structure and dentition but have not affected materially the homogeneous nature of the female urogenital system.

(5) Contrary to the opinion expressed by Bensley, the rat-kangaroos are a monophyletic group and there would appear to be no justification for his division of the group into two sub-families indicative of a dual origin from primitive phalangers.

(6) Neither is there any justification for the generally accepted classification of the group in which *Hypsiprymnodon* is placed in a separate sub-family from the others. The presence of a hallux in this genus is not in itself sufficient reason for separating it from the other genera in which the first toe is absent.

(7) The variability of the anterior vaginal expansion provides a means of assessing the inter-relationships of the genera within the group. The most primitive form is *Hypsiprymnodon* (possession of hallux and the rudiment of the vaginal caecum). At the other end of the series is the specialized *Bettongia* in which the caecum attains its fullest development. The complete sequence is *Hypsiprymnodon, Potoroüs, Caloprymnus, Bettongia.*

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(1) In addition to these five characters, the rat-kangaroos possess an important diagnostic character in the skull. The squamosal makes a wide contact with the frontal, a characteristic of all rat-kangaroos and bandicoots, as pointed out by Finlayson (1932). In all other marsupials the parietal makes contact with the alisphenoid, thus separating the frontal and squamosal.

(8) It would appear, therefore, that the rat-kangaroos are a highly specialized, but homogeneous, group which have arisen from some primitive phalanger and the affinities of the various genera are indicated in fig. 13.

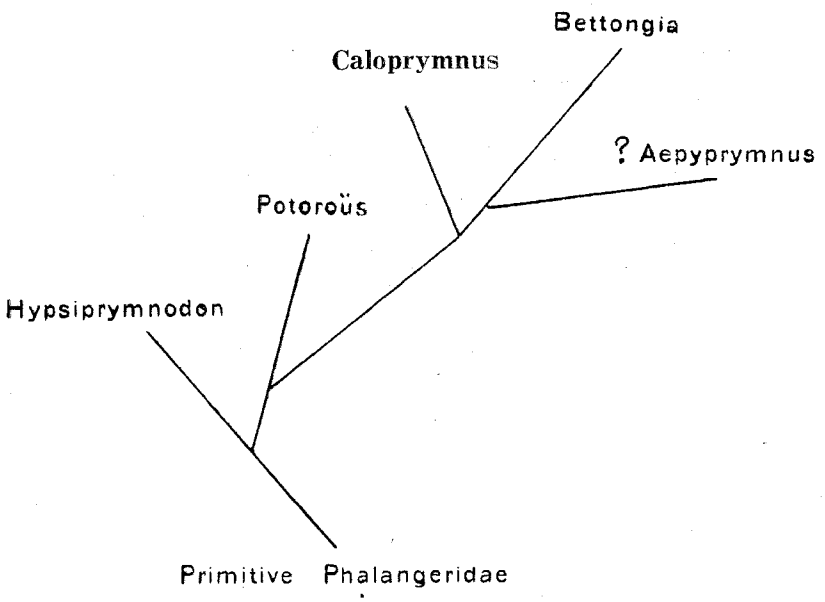

FIG. 13.—Probable inter-relationships of the rat-kangaroos based upon the female urogenital system.

This figure agrees closely with fig. 11 based upon foot-structure and does not fall into line with Bensley's conclusions based upon dentition as given in fig. 12. The presentation of the comparative features of the female urogenital system given in the present paper shows how inconceivable it is that the rat-kangaroos can be regarded as a diphyletic group or that *Hypsiprymnodon* is more closely related to *Bettongia* than it is to *Potoroüs*, as Bensley claims.

5. THE RELATIONSHIP OF THE RAT-KANGAROOS TO THE TRUE KANGAROOS

It has been shown in a previous paper (Pearson, 1945) that a logical serial evolution of the female urogenital system in the Marsupialia can be traced from the primitive American Didelphidae at one end of the series to the specialized Macropodidae at the other end, with intermediate links being provided by the Australian polyprotodonts and the Phalangeridae. Neither the bandicoots nor the rat-kangaroos find a place in this sequence. The members of the former group, though possessing a primitive type of dentition, have a specialized pes and a female urogenital system which is a curious mixture of primitive and highly specialized features. In the rat-kangaroos this system shows a high degree of specialization, and, though homogeneous throughout the group, it is fundamentally different from that of either the phalangers or true kangaroos (see figs 6-10). If the rat-kangaroos are an off-shoot of some primitive phalangerine stock, as may well be the case, they have departed from the Phalangeridae-Macropodidae line of evolution.

Bensley's conclusions based upon an exhaustive and critical examination of foot-structure and dentition support the view, commonly accepted by all systematists, that the rat-kangaroos belong to the family Macropodidae. He regarded the rat-kangaroos as being more primitive than the true kangaroos and thought it possible that either the latter arose from the *Potoroïs-Caloprymnus* stock, or that both groups arose from a common primitive *Dromicia*-like phalanger. But it has been shown in the present paper that the rat-kangaroos are not a primitive group. On the contrary, their female urogenital system is a considerable departure from the simple general marsupial plan in which the lateral vaginae are convoluted, a vaginal caecum is not developed, and the urinary bladder is attached by a very short urethra to the anterior end of the urogenital sinus.

On the evidence which has been brought together in the present paper, it is impossible to conceive that the rat-kangaroos have given rise to the true kangaroos or have such general affinities with that group as to warrant their being placed in the same family. It is proposed, therefore, to remove the five genera of rat-kangaroos from the family Macropodidae and to establish a new family, the Potoroidae, for their reception, and the genus *Potoroïs* Desmarest, 1804, is named as the type-genus.

6. Summary

Systematists are agreed that the rat-kangaroos should be included in the family Macropodidae. This conclusion is based upon the consideration of external characters only, such as foot-structure and dentition, but it is doubtful whether such features, which are readily susceptible to environmental influences can have much phyletic value. It is claimed that the female urogenital system of the marsupials provides a more reliable guide to phylogeny. An account of this system in *Caloprymnus campestris* and *Hypsiprymnodon moschatus* is given in the present paper and it is further shown that the female urogenital system of the four genera *Hypsiprymnodon, Potoroïs, Caloprymnus*, and *Bettongia* is based upon a common plan which differs in several fundamental respects from that of the true kangaroos and all other marsupials. It is contended that (1) the rat-kangaroos are a monophyletic group and that Bensley's view that the rat-kangaroos arose from two separate primitive phalangerine stocks cannot be sustained, (2) the rat-kangaroos are a highly specialized offshoot from primitive phalangers and cannot be regarded as being closely related to the true kangaroos, as the accepted classification would indicate. It is considered, therefore, that the rat-kangaroos should be placed in a separate family, the Potoroidae.

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