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The Relationships of the Potoroidae to the Macropodidae (Marsupialia) (1)

By

JOSEPH PEARSON
Tasmanian Museum

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WITH 21 TEXT FIGURES

INTRODUCTION

There is perhaps no group of mammals to which so much attention has been directed as the Marsupialia and the interests of investigators have been particularly concerned with the relationships and phylogeny of the Order. But in spite of a very considerable literature dealing with speculations on these problems we are still in doubt as to which classification would give the best picture of the phylogenetic relationships of the group. Owen's division of the marsupials into Polyprotodontia and Diprotodontia(2), though having much to commend it, is hardly more satisfactory than the division into Diadactyla and Syndactyla which was first suggested by de Blainville in 1834. Both break down hopelessly before the paradox of the Perameloidea and the enigma of the Caenolestoidea. Owing to the imperfections of the geological record the palaeontology of Australian marsupials has little to offer as a contribution to the main problems. Thus we are thrown back upon the study of the comparative anatomy and embryology of recent forms.

In the present paper we are not concerned with one of these major phylogenetic problems. The question to be discussed is whether the true kangaroos and rat-kangaroos possess sufficient fundamental characters in common to justify their being placed in the same family, as is almost universally held by systematists at the present day. This matter has already been discussed at some length (Pearson, 1946, 1947) and I then submitted new evidence to show that the rat-kangaroos (sub-families Hypsiprymnodontinae and Potoroinae) possess in common certain highly specialized structures which, in my opinion, clearly indicate close basic relationship between the two sub-families and cardinal differences from the Macropodinae. I have therefore suggested that the family Macropodidae, using the term in its older and wider sense, should be split into two families, the kangaroos (fam. Macropodidae, *s.nov.*) and the rat-kangaroos (fam. Potoroidae). A comparison of the old and new systems of classification is as follows:—

Old Classification		*New Classification*	
Family	*Sub-families*	*Families*	*Sub-families*
Macropodidae	Macropodinae	Macropodidae	
	Hypsiprymnodontinae	Potoroidae	Hypsiprymnodontinae
	Potoroinae		Potoroinae

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(1) The investigations dealt with in this paper have been assisted by a grant provided equally by the Trustees of the Commonwealth Science and Industry Endowment Fund and the Tasmanian State Government.

(2) This grouping had been anticipated fifty years earlier by de Blainville in 1816.

It may be contended that the older classification satisfies all the requirements of the systematist in its insistence on the separation of the family into three groups, each of which has certain distinctive characters and that such an arrangement differs in no material way from the new classification. A further point could be made that family and sub-family rank are to some extent arbitrary terms and are often vague and unimportant. I suggest with some diffidence that many mammalogists pin their faith almost entirely upon evidence which may be obtained from skulls, dentition and external characteristics. Without wishing to detract from the value of such evidence, I feel that more use should be made of the evidence which may be obtained from the comparative study of the internal organs. Particularly in the case we are now considering, I feel that such an examination would place our knowledge of the relationships of the true kangaroos and the rat-kangraoos in an entirely different light.

There appears to be a vital principle involved in the proposed change from the old to the new system of classification. In the former we have a separation of the family Macropodidae into three sub-families. It is thereby implied that the three sub-families hold equal rank and differ from each other in certain fundamental respects, no two of them having common characteristics of outstanding importance which separate them from the third. This implication gives an entirely false impression of the set-up of the group. It will be shown later that in at least two fundamental respects in which the influence of environmental changes could not possibly have had any effect the two sub-families of rat-kangaroos agree with each other and differ jointly from the true kangaroos. I refer to the female urogenital system and the arrangement of certain bones of the temporal region of the skull. It is on this evidence that I rest my case. In the course of the present series of investigations attention has been concentrated upon the female urogenital system of the Marsupialia. A very careful and comprehensive survey of representative genera of all three Australian super-families has been made on a scale not attempted hitherto. Unique experience has been gained in the comparative anatomy of the female urogenital system of the marsupials and with this experience it is possible to say that the plan upon which this system is built in the Potoroidae constitutes an important departure from the generalized arrangement seen in nearly all marsupials, including the Macropodidae.

An attempt is made in the present paper to indicate the probable course of evolution of the families Macropodidae and Potoroidae and to show that the new classification presents a more logical and satisfactory picture of the precise relationship of one family to the other. It also provides a reasonable explanation of their line of common descent from prototypal phalangerine stock.

A system of classification is more convincing if it is based upon evidence taken from many differerent sources and particularly if due recognition is given to characters which have a high phylogenetic value. By this test the commonly accepted grouping of the true kangaroos and the rat-kangaroos into a single family lacks conviction as it is based almost entirely upon dentition and foot structure, which are highly susceptible to environmental changes.

The classic survey of the dentition and foot-structure of Australian marsupials made by Bensley (1903) did not, in my opinion, provide a satisfactory solution to the problem he set out to solve. In fact, his conclusions about the inter-relationships of the genera of the rat-kangaroos, based upon the evidence of these two characteristics were confused and contradictory (Pearson, 1946, 1947). Bensley's careful analysis made it clear that we must widen the field considerably so as to make use of characters less susceptible to changes in habitat. It is incumbent, therefore, upon the systematist to seek more permanent and deep-seated characters which might be less susceptible to the influences of environment and which might act as valuable pointers to the phylogeny of these two families.

A careful study of the internal comparative anatomy of members of the two families has been made for the first time in the course of the present investigations. This has revealed the highly specialized nature of the female urogenital system of the rat-kangaroos and thus places the question of the relationship of the Macropodidae and the Potoroidae in an entirely new light. This ground has already been covered (Pearson, 1946, 1947) but is now presented from a somewhat different angle. Evidence will also be submitted regarding the important relationship of four bones in the temporal region of the skull, viz., the frontals, parietals, alisphenoids, and squamosals, to which attention has been directed by Finlayson (1932). No doubt, other evidence may be forthcoming in due course and it is necessary to stress once again the importance of bringing together such further evidence, particularly from those elements of the mammalian structure which are least affected by changes in external conditions of living. In my opinion, the two systems I propose to deal with come within this category.

FEMALE UROGENITAL SYSTEM

The comparative anatomy of the female urogenital system in the Marsupialia has been discussed at some length in previous papers (Pearson, 1945, 1946, 1947). Fig. 1 (dorsal aspect) and fig. 2 (lateral aspect) show the simplest type of adult development of the Müllerian ducts, which may be found in most members of the Didelphoidea and Dasyuroidea. Each Müllerian duct is S-shaped in both dorsal and lateral aspects.

The first arm of the S runs caudally and is composed of the Fallopian tube and the uterus. At the elbow joining the first and second arms is the vaginal cul-de-sac, which is the most proximal region of the vagina. From this arises the second arm known as the anterior vaginal canal. This passes forward and is connected with the third arm or lateral vagina which runs caudally and opens dorso-laterally into the urogenital sinus along with the lateral vagina of the other side. The urethra enters the sinus ventrally at the same level.

As a preliminary to the discussion which follows, it will be useful to enumerate the elements of the female urogenital system which, in their unspecialized condition, are to be found in the most primitive of recent marsupials. There primitive characters are:—

1. The two Müllerian ducts remain separate throughout life.
2. The two culs-de-sac are short and remain separate in the adult condition.
3. The antero-posterior length of the vaginal complex is relatively very short.
4. The vaginal complex is clearly divided into culs-de-sac, anterior vaginal canals and lateral vaginae.
5. The two lateral vaginae open into the urogenital sinus immediately after joining.
6. The urogenital sinus is relatively very long.
7. The urethra is short in relation to the total length of the urogenital system.

The Macropodidae conform to the primitive condition in the last four characters, but the Potoroidae possess none of these seven primitive characters, except that in *Hypsiprymnodon* the cul-de-sac, a single chamber formed by the fusion of the primitive right and left culs-de-sac, is short and does not reach as far as the posterior vaginal sinus (Pearson, 1946, 1950). This character serves to strengthen the evidence in support of the view that *Hypsiprymnodon* is the most primitive member of the Potoroidae.

There are four respects in which the female urogenital system of the Potoroidae show considerable specialization. These are:—

(1) The enlargement of the anterior region of the vaginal complex to form the anterior vaginal expansion which acts as a receptaculum seminis.
(2) The fusion of the posterior parts of the two lateral vaginae to form a median dorsal tube, the posterior vaginal sinus, which opens into the urogenital sinus.
(3) The relatively small length of the urogenital sinus.
(4) The extreme anterior attachment of the urinary bladder with the consequence that the urethra is inordinately long.

In these four specialized characters the Potoroidae depart from the generalized macropod condition. An analysis of the outstanding features of the female urogenital system of the Potoroidae is given below, and differences between the two families are indicated.

1. The Anterior Vaginal Expansion (figs 4-16, *a.v.e.*)

Throughout the recent Marsupialia the lateral vaginae are not normally used for parturition but serve as ducts for the reception of the spermatozoa. These spermatazoa are usually stored in the lateral vaginae and anterior vaginal canals until their purpose has been served. In some cases, however, even in the primitive didelphoids, as pointed out by Hill and Fraser (1925) and others, the junction of each anterior vaginal canal and lateral vagina may be greatly distended by the presence of a fluid containing spermatazoa. This conversion of the anterior part of the anterior vaginal canal into a distended receptaculum seminis is also manifested in the Macropodidae. Fig. 4 illustrated the anoestrous phase in a kangaroo, a condition which differs in no fundamental respect from the phalangerid plan, and fig. 5 shows the state in the same animal in the oestrous phase when two swollen receptacula seminis are present in the anterior vaginal canals.

The condition of the anterior vaginal canals and lateral vaginae in the Macropodidae conforms to the standard marsupial pattern in which there are two receptacula seminis, right and left. The vaginal complex of the Potoroidae does not follow this pattern. Instead, the anterior vaginal region consists of a single chamber which acts as common receptaculum seminis for both sides. This

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FIG. 1 (opposite page).—Condition in primitive marsupial; also early stage in marsupials generally. Dorsal view.

FIG. 2.—Same as fig. 1. Lateral view.

FIG. 3.—Condition in certain adult marsupials in which the septum between r. and l. culs-de-sac has broken down.

FIG. 4.—Condition in phalanger and kangaroo (anoestrous phase).

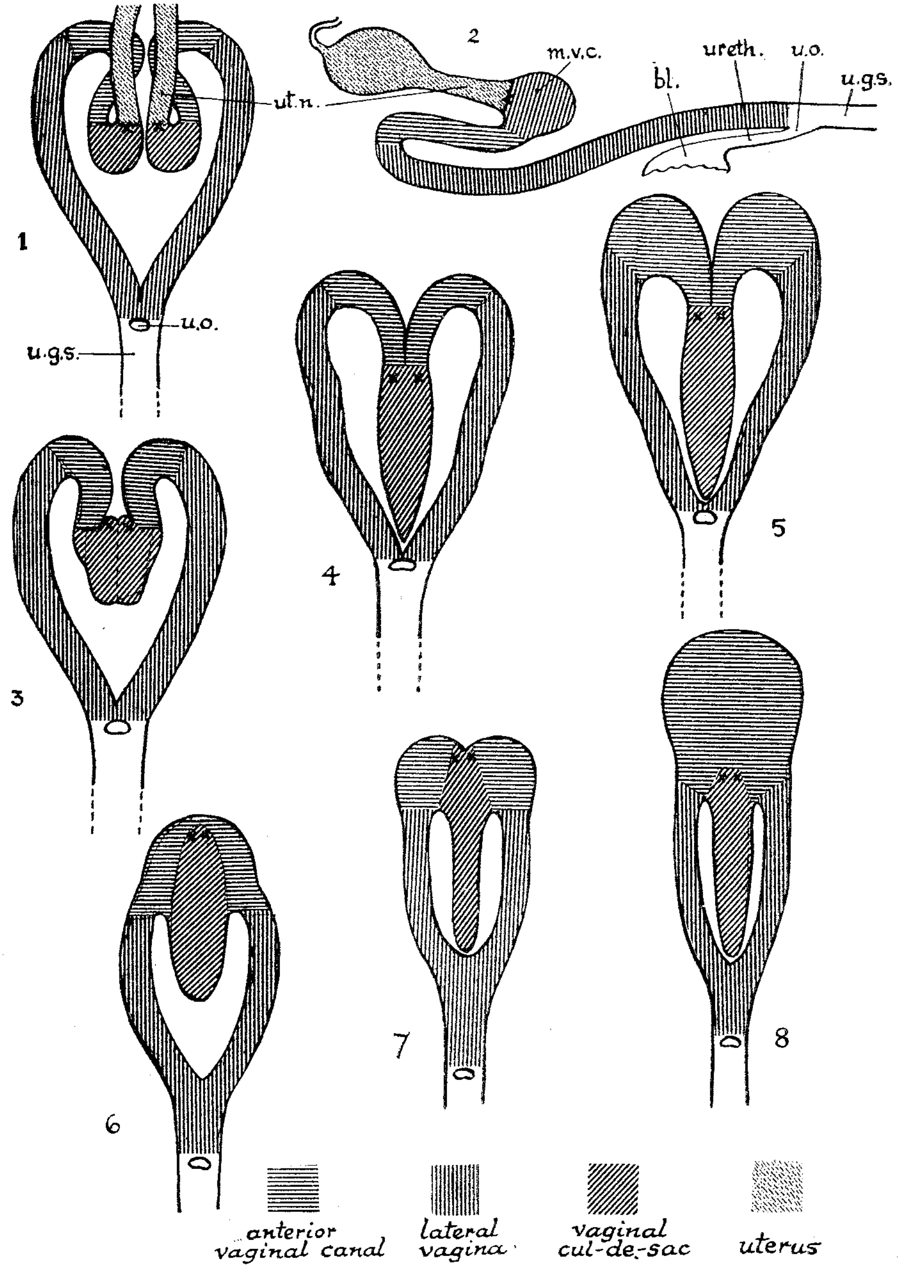
FIG. 5.—Condition in pro-oestrous and oestrous stages of kangaroo *(Protemnodon)* showing the swollen receptacula seminis.

FIG. 6.—*Hypsiprymnodon* showing single anterior vaginal expansion and abbreviated cul-de-sac.

FIG. 7.—*Potoroüs* showing elongated cul-de-sac.

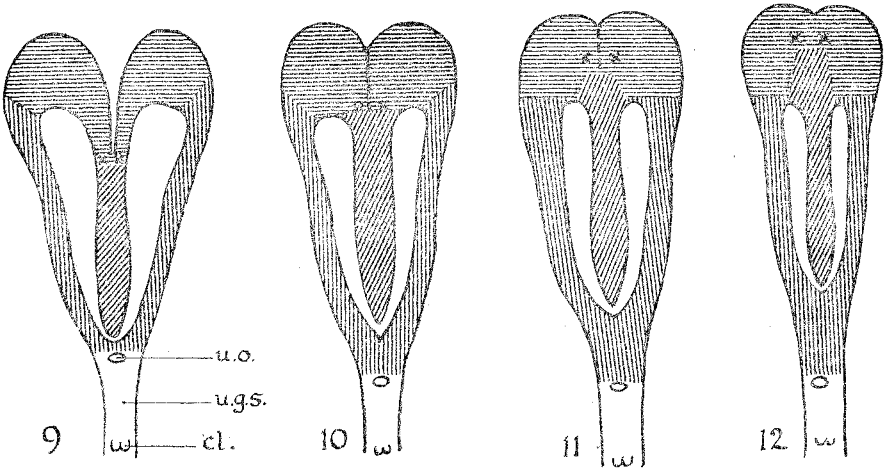
FIG. 8.—*Bettongia* showing vaginal caecum (modified anterior vaginal expansion).

NOTE.—The position of each os uteri is represented by a small cross.



Diagrammatic comparison of the vaginal system of various marsupials (see footnote on opposite page).

is a distinct advance on the macropod condition and is found nowhere else in the Marsupialia. This chamber, which is known as the anterior vaginal expansion (Pearson, 1945), occupies the whole of the anterior portion of the vaginal complex of the Potoroidae and is a characteristic feature of the family. All genera of the family*, including the more primitive *Hypsiprymnodon*, have this character in common and differ in this respect from the Macropodidae. In my original description of the anterior vaginal expansion I defined it as an extension of the anterior portion of the vaginal culs-de-sac and the lateral vaginae. In defining it thus, I had in mind that each lateral vagina, consisting of a proximal and distal loop, might be regarded as that part of the vaginal complex which linked the cul-de-sac with the urogenital sinus. Perhaps, however, it would be more correct to recognize Hill's definition of the proximal limb as the anterior vaginal canal (Hill, 1899), so that the anterior vaginal expansion may more strictly be regarded as the homologue of the right and left anterior vaginal canals together with the anterior portion of the cul-de-sac. The precise difference between the receptacula seminis in the Macropodidae and the receptaculum seminis (anterior vaginal expansion) in the Potoroidae can best be understood by referring to figs 5 and 7 which represent the oestrous stage of the Macropodidae and the normal condition found in *Potorous* respectively.



Transition from vaginal condition in Macropodidae to that in Potoroidae.

FIG. 9.—Oestrous condition in kangaroo (*Protemnodon*).
FIGS 10, 11.—Hypothetical intermediate stages linking figs 9 and 12.
FIG. 12.—Potoroüs.

Figs 9-12 show how the Macropod condition of the anterior vaginal canals (figs 5 and 9) may have become converted into the typical Potoroid condition in which the right and left anterior vaginal canals have coalesced to form a single chamber, the anterior vaginal expansion (figs 7 and 12). Figs 10 and 11 are hypothetical intermediate stages in this sequence. Further complications are seen when we pass from the simple condition seen in *Hypsiprymnodon* (fig. 6) and *Potoroüs* (figs 7 and 12) to a more complicated arrangement in *Caloprymnus*

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* The condition in *Aepyprymnus* is at present unknown though it can be forecast with certainty that its urogenital system will agree substantially with the condition found in other members of the family.

in which the right and left portions of the chamber are expanded into wings (Pearson, 1946, p. 15). From this condition it is not difficult to conceive how the most specialized arrangement, seen in *Bettongia*, is reached (fig. 8). Here we have a large vaginal caecum which is homologous in every respect with the anterior vaginal expansion. It is interesting to note in passing that a specialization similar to that of *Bettongia* is also found in the perameloids where, however, a septum is present completely separating the right and left halves of the vaginal caecum.*

If we refer for a moment to the phylogenetic tree given in fig. 21 it may be stated without question that throughout the macropod line of evolution represented by stems A, D, E, and F the general plan of the vaginal complex conforms to the typical marsupial condition found in the prototypal phalangerines. The diversion at E leads to the Potoroidae and, presumably, it was somewhere along stem E that the right and left anterior vaginal canals became merged into a single chamber which we know as the anterior vaginal expansion.

2. Median Vaginal Cul-de-sac (figs 13-16, *m.v.c.*)

As we have seen *Hypsiprymnodon* is the only living representative of the two families we are now discussing in which the fused right and left culs-de-sac remain in the primitive abbreviated condition in parous adults. It may be taken for granted, therefore, that the primitive stock from which all rat-kangaroos have been derived (stem G, fig. 21) was characterized by the possession of a short cul-de-sac which may have retained the primitive double condition in parous adults. It would follow, too, that stem D had this primitive characteristic. A good deal has been written (Brass, 1880, Lister and Fletcher, 1881, and others) about the advanced development of the cul-de-sac in some of the recent Macropodidae which is said to culminate in the establishment of a permanent connexion between the cul-de-sac and the urogenital sinus to form a 'median vagina' after the first parturition in some species. Brass (1880) went so far as to state that in Bennett's Wallaby a permanent median vagina was produced in non-parous specimens. All these earlier observations were based upon ordinary dissections. In an earlier paper (Pearson, 1945) I was prepared to accept without question the conclusions of these pioneer workers. In the course of the present investigations, however, detailed examinations of serial sections have proved that in some cases at least non-parous specimens of Bennett's Wallaby do not possess a connexion between the cul-de-sac and urogenital sinus. It would, I think, be a fairer statement of the case to say that a permanent median vagina lined with continuous epithelium may be present in some individuals of a species and not in others. Beyond such a general statement it would be dangerous to go, but further evidence is being collected on this question. The above statement need not affect, however, the general discussion and conclusions on this point already given in earlier papers (Pearson, 1945, 1947). In the matter of parturition, it is clear that the Potoroidae have not developed a permanent median vagina and the inadequate evidence available shows that, in some cases at any rate, parturition takes place through the lateral vaginae (Pearson, 1945, p. 83). The only two recorded instances of observed parturition in the Potoroidae were through the lateral vagina, so that I ventured to state that it was *probable* that this type of parturition was characteristic of the family. Professor J. P. Hill *(in litt.)* did not agree with this conclusion. As my opinion was qualified, I am prepared to abide by it pending further evidence.

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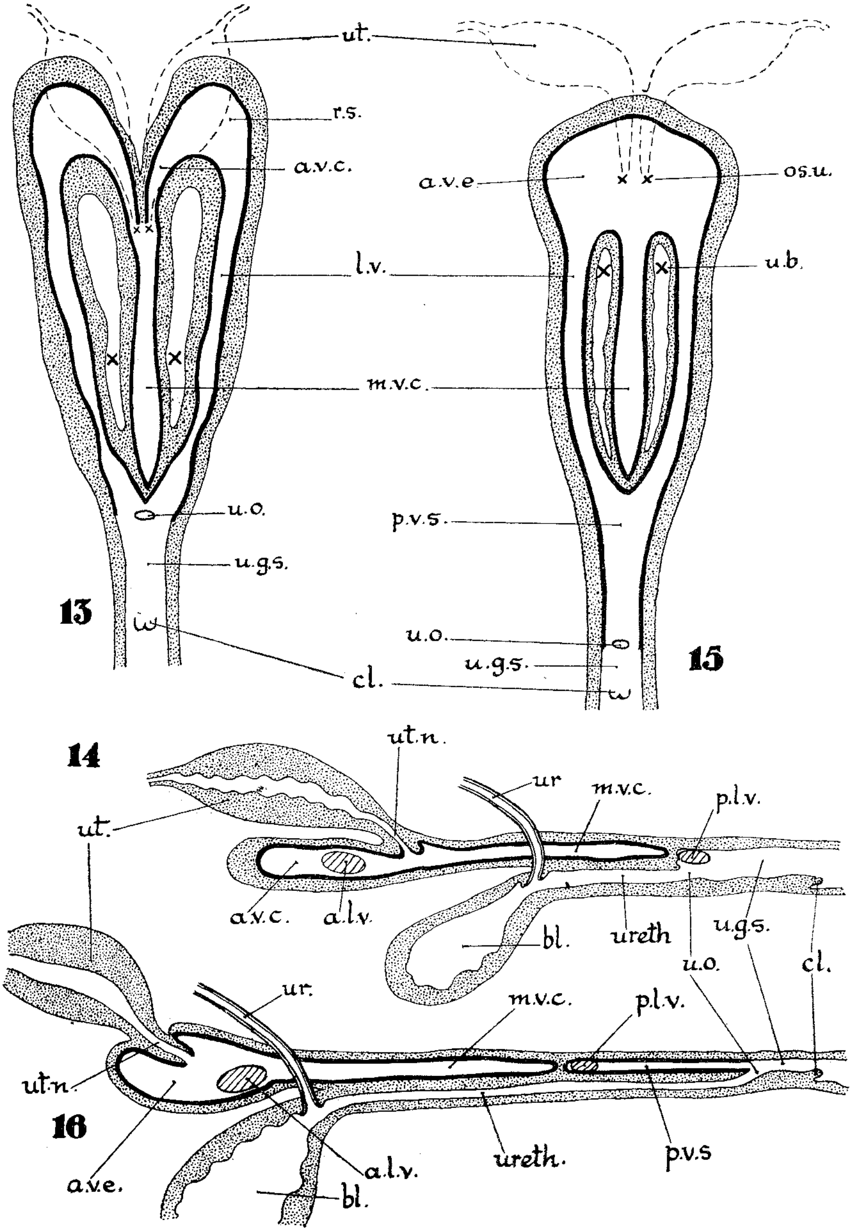
* The right and left Müllerian ducts do not, however, remain completely separate in the Perameloidea as the septum between the right and left culs-de-sac breaks down in parous specimens.



Comparison of urogenital system in the Macropodidae and Potoroidae (see footnote on opposite page).

The vaginal complex of the Macropodidae (figs 4, 5, 9, and 13) is so constructed as to offer two alternative paths for parturition after the foetus leaves the os uteri, first, to continue in a direct line in a caudal direction through the cul-de-sac and thus take the line of least resistance. The alternative route to reach the urogenital sinus would be to double back along the hair-pin bend of the anterior vaginal canal and lateral vagina, a devious path which would offer insuperable difficulties. This double vaginal kink is characteristic of most marsupials, including the more primitive groups (Hill, 1899, &c.), and has resulted in pseudovaginal parturition in a caudal direction along the median line. In the case of the potoroids, however, the formation of the anterior vaginal expansion has caused its connexion with each lateral vagina to be placed in the posterior wall of the sinus (figs 6 and 7) caudal to the ora uterorum. In such cases the foetus after emerging from the os uteri has three courses open to it, along the cul-de-sac or along the lateral vaginae. The median path is not much more accessible than the lateral paths and parturition by the lateral vaginae in the Potoroidae may be common if not almost universal. The prototypal marsupials probably used the lateral vaginae for parturition, but this habit in the Potoroidae is not primitive but is a secondary return to the primitive and is therefore specialized.

It follows that the type of parturition established in the Macropodidae is a direct development of the pseudovaginal parturition which is found in all recent marsupials. The only method of parturition so far observed in the Potoroidae is a secondary return to the prototypal marsupial condition brought about by the specialization of the anterior part of the vaginal complex.

3. **The Posterior Vaginal Sinus** (figs 15, 16, *p.v.s.*)

The urogenital sinus, as its name denotes, is formed by the confluence of the posterior extremities of the lateral vaginae on the dorso-lateral side, and the urethra on the ventral side. Before entering the sinus the lateral vaginae fuse to form a common chamber, the posterior vaginal sinus, which is of infinitesimal length in most marsupials including the Macropodidae. The Potoroidae, however, are exceptional in this respect as the posterior vaginal sinus is of considerable size. This common vaginal tube runs dorsal to the urethra for a considerable distance before emptying into the urogenital sinus. In this respect the Potoroidae are widely different from all other marsupials, including the members of the Macropodidae. This is obviously a specialization and in this respect the Macropodidae are simpler and more generalized than the Potoroidae. It is suggested that the posterior vaginal sinus is formed by the fusion of the embryonic sinus horns of the right and left sides, though material to prove this point has not yet been obtained.

4. **The Urogenital Sinus** (figs 13-16, *u.g.s.*)

In the Didelphoidea, the Dasyuroidea, the Caenolestoidea, and the Phalangeroidea, with the exception of the Potoroidae, the urogenital sinus is of considerable length and this may justly be regarded as the primitive condition. In all members of the Potoroidae the urogenital sinus is extremely short, a condition which is not primitive.

FIG. 13 (opposite page).—Urogenital system in Macropodidae. Dorsal view. (Two small crosses represent position of each os uteri. Two larger crosses represent position of connexion of ureters with neck of bladder.) (This applies to figs 13 and 15.)

FIG. 14.—Urogenital system in Macropodidae. Lateral view.

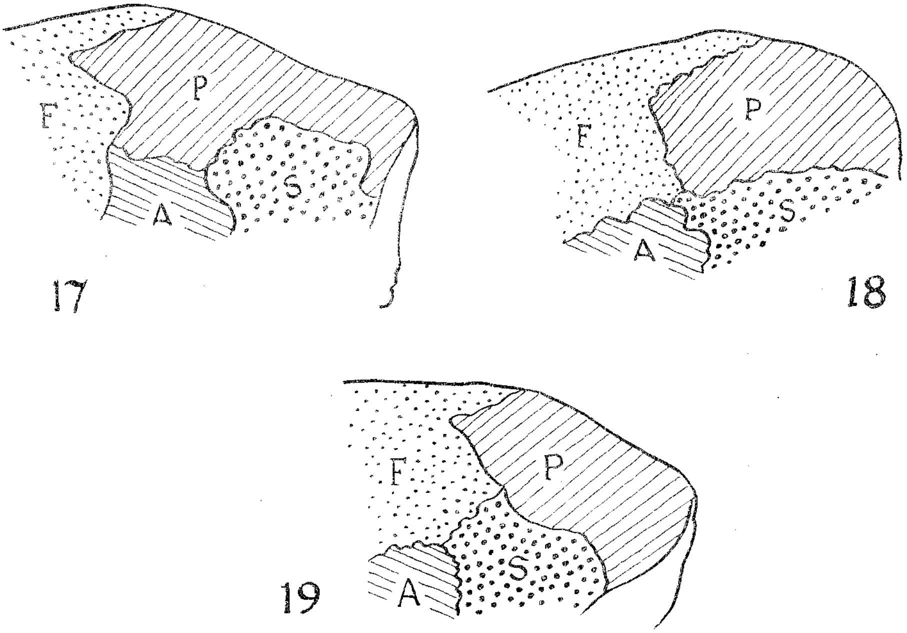
FIG. 15.—Urogenital system of *Potoroüs*. Dorsal view.

FIG. 16.—Urogenital system of *Potoroüs*. Lateral view.

5. The Attachment of the Urinary Bladder (figs 14, 16)

Both the Perameloidea and the Potoroidae differ in a marked manner from all other marsupials in the extreme forward position of the attachment of the urinary bladder. As a consequence, the urethra is inordinately long in relation to the size of the other parts of the female urogenital system. By comparison the urethra of the Macropodidae is short and the attachment of the bladder conforms to the arrangement found in the remaining marsupial groups. The extreme anterior attachment of the bladder in the Potoroidae (fig. 16) marks this family as having departed from the normal and more primitive condition found in the Macropodidae (fig. 14) and the rest of the Phalangeroidea.

To sum up, a survey of these main features of the urogenital system makes it evident that this system in the Potoroidae is highly specialized and can readily be distinguished from that of the Macropodidae. Also it seems clear that in the course of evolution the general set-up of the female urogenital system of the Potoroidae has departed considerably from the generalized marsupial condition which the members of the Macropodidae share with most of the major groups of the Marsupialia.



Arrangement of the temporal bones throughout the Marsupialia.

FIG. 17.—Condition in the super-families Didelphoidea, Dasyuroidea (except *Thylacinus*). Caenolestoidea and Phalangeroidea (except Potoroidae).

FIG. 18.—Condition in *Hypsiprymnodon* (Potoroidae).

FIG. 19.—Condition in Potoroidae (except *Hypsiprymnodon*), *Thylacinus* (Dasyuroidea), and the super-family Perameloidea.

THE TEMPORAL BONES (figs 17-20)

As already indicated, certain bones of the temporal region of the skull provide an interesting contribution to our problem. These bones are the frontals, parietals, alisphenoids, and squamosals. In all marsupials, with the exception of the super-family Perameloidea, the family Potoroidae, and the genus *Thylacinus*, the parietal at each side of the skull makes a wide contact with the alisphenoid thus separating the frontal from the squamosal (fig. 17). This is the condition found in the Macropodidae, so that this family follows the normal and presumably archaic marsupial pattern in this respect. On the other hand, the members of the Potoroidae show the reverse condition, that is to say, the frontal and squamosal meet over a relatively wide front with the consequent wide separation of the parietal and alisphenoid (see fig. 19). At first sight it is difficult to explain how such a complete reversal of bone arrangement and relationship could have been brought about, and the evidence of *Hypsiprymnodon* is important in this connexion. In this genus it is found that the relationship of these bones follows the potoroid pattern with this important qualification, that the junction of frontal with squamosal is a very narrow one so that the parietal and alisphenoid almost meet (fig. 18). Thus the condition in *Hypsiprymnodon* represents a transition from one extreme phase to the other and shows how the change has been brought about (see fig. 20, *(a)*-*(e)*).

Fig. 20 shows five stages in the transition from one extreme condition to the other. Fig. 20 *(a)* is the condition in the typical marsupial including the Macropodidae. Fig. 20 *(b)* is merely a variant of *(a)*. Fig. 20 *(c)* is a hypothetical stage in which all four bones meet. Fig. 20 *(d)* is the *Hypsiprymnodon* plan, and finally fig. 20 *(e)* shows the condition in the more highly specialized members of the Potoroidae.

It is clear from the above description that the arrangement of the four bones in the Potoroidae is a departure from the primitive condition found in most marsupials including the Macropodidae. The condition in *Hypsiprymnodon* approaches more closely to the primitive condition than the other genera of the Potoroidae, but is definitely of the potoroid type. We may conclude, therefore, that with regard to the temporal bones, the Potoroidae depart considerably from the normal marsupial condition found in the Macropodidae. A reference to fig. 21 will, perhaps, make this clear. The main phalangerine-macropod stem (A, D, E, and F) carries the bone-relation shown in fig. 17. Stem G, which represents the point of divergence of the Potoroidae from the main stem, would contain species, all now extinct, which probably showed the condition seen in fig. 20 *(b)* (in the most ancient forms), and the condition in fig. 20 *(c)* in still later but now extinct forms, and finally at the point where H and J fork, a condition somewhat similar to the *Hypsiprymnodon* condition (fig. 20 *(d)*).

PHYLOGENETIC CONSIDERATIONS

I have already expressed the view (Pearson, 1947) that both the kangaroos and rat-kangaroos 'may have arisen from the same primitive phalangerine stock, but in the course of subsequent evolution have both become specialized in different ways', that is to say, they are collateral groups derived from a common ancestor. Tate (1948) has interpreted my views to mean 'that the Macropodidae comprise two families derived independently from the phalangeroid stock'. This interpretation which might suggest that the two groups deviated from the main line at two different levels would not accord with my views. I conceive both families (fig. 21, E and G) as having sprung from a common stock (fig. 21, D) which itself had branched from the main phalangerine stem (fig. 21, A) at an earlier stage. This was demonstrated in a previous paper (Pearson, 1947, fig. 2). Any basic characters which the Macropodidae and Potoroidae may have in common could be explained, therefore, on the ground that they were collaterals having a considerable degree of common heritage. Any resemblances which the two families may possess, such as certain features of dentition and foot structure may be due to nothing more than the circumstance that these two collateral families, derived from the same common stock, are living for the most part under somewhat similar conditions. That is to say, these resemblances may be the outward and visible sign of the effects of a common environment upon the gene complexes of two closely related families which have many genes in common.

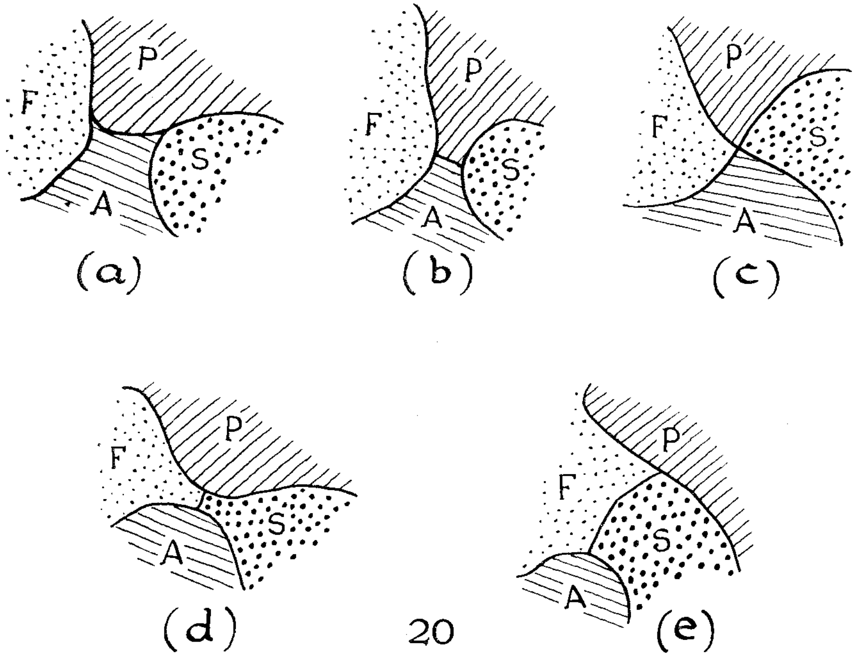


FIG. 20.—Diagrammatic representation of the arrangement of the temporal bones in the Marsupialia.
a—Typical marsupial condition (except Peramaloidea, Potoroidae, and *Thylacinus*).
b—A varient of fig. *a*.
c—A hypothetical stage when all four temporal bones meet.
d—*Hypsiprymnodon*.
e—Condition in Perameloidea, Potoroidae (except *Hypsiprymodon*), and *Thylacinus*.

Tate (1948) saw difficulties in the proposed establishment of a separate family for the rat-kangaroos. He considered that it would involve not only the invocation of convergence to explain similarities in structure of the hind limbs of both families, but also the further admission of a ' very complex ' convergence to account for the similarity between the third and fourth premolars in both families as well as the replacement of the third premolar and milk fourth premolar by the permanent fourth premolar. He regarded these two sets of ' unrelated examples of morphological identity—foot structure and premolar structure' as pointing much more strongly to real relationship than to convergence, a relationship which justified the widely accepted view that both groups should be placed in the same family.

Convergence, which implies a similarity of structure acquired by two or more unrelated forms, need hardly be invoked in support of my case, as I too, in company with Dr. Tate, admit the basic relationship of the two families, as may be seen from fig. 21. Certain similarities in dentition and foot structure in the two families are not due to convergence but rather to inheritance from common ancestors (stem D) and any differences there may be are due to *divergences.* Divergence has produced the differences; heredity has accounted for the resemblances. In particular, there is the major divergence of the basal potoroid stock (stem G) from the phalangerid-macropod line involving important specializations of the female urogenital system and new arrangement of some of the temporal bones. Thus the two families possess homologous features in dentition and foot structure and also important morphological divergences.

ANALYSIS OF FIG. 21

My conception of the phylogenetic relationships of the Macropodidae and the Potoroidae are explained diagrammatically in fig. 21. A close examination of this phylogenetic tree is necessary in order to follow my views on this question. These are set out below.

Stem A

Stem A represents the ancestral phalangerine stock from which all members of the super-family Phalangeroidea may be assumed to have arisen. Its members possessed a generalized diprododont dentition suited to an omnivorous diet. In conformity with such a diet they possessed a simple stomach and a small caecum. Such arboreal animals had a syndactylous pes with a functionally apposable hallux. The fourth toe was only slightly longer than the other toes.

In the skull the alisphenoid was in contact with the parietal over a broad front, thus widely separating the frontal from the squamosal. The female urogenital system was built on the same generalized pattern found to-day in the primitive Didelphoidea. That is to say, there was a short cul-de-sac on each side, and the extreme antero-posterior length of the vaginal complex was shorter than the urogenital sinus. In all probability, at this phylogenetic stage the right and left Müllerian ducts were still completely separated throughout life.

Stem A is represented as having divided into two important branches, stem B which give rise to the recent families Phalangeridae and Vombatidae with which we are not concerned in the present discussion, and the other, stem D, from which arose the common ancestors of the Macropodidae and the Potoroidae.

Stem D

Stem D was probably evolved in response to changes in climatic conditions which resulted in the gradual replacement of rain forests by low scrub and sparsely timbered country which later in their turn gave place to grass plains. This gradual change in habitat would be accompanied by certain structural modifications in the hind limbs involving gradual hypertrophy of the hind limbs in general and the enlargement of the fourth toe and the consequent reduction of the fused second and third digits of the foot and the ultimate loss of the hallux. It should be noted, however, that at this stage the hypertrophy of the hind limbs and the lengthening of the fourth digit of the pes could not have proceeded very far and a functional apposable hallux was undoubtedly still present.

This gradual change in foot structure was probably accompanied by a transition from the type of omnivorous diet common to most small arboreal mammals living in the rain forests to the more strictly herbivorous diet usual in the denizens of low scrub and thickets on the edge of the open plains. This, again, changed to the more specialized grazing habits of the inhabitants of the grass plains living under more arid conditions. Such changes in habitat and habit would be reflected in dental adaptations and in the consequent specializations of the alimentary canal which were called forth in response to new conditions.

According to Abbie (1939) the changed diet of the Macropodidae and the Potoroidae results in the greater development of the masseter muscle. Hence the presence of a well-developed masseteric fossa and masseteric canal in these families. The masseteric canal is not present in the phalangerines and hence it must have made its first appearance in stem D.

However, these specializations in dentition and in other respects which ultimately were to produce the Macropodidae and Potoroidae were not fully developed at this stage, but stem D marked a definite departure from the phalangerine condition. This departure which was probably governed to a certain degree by the gradual change in habitat conditions already referred to resulted in the development of characteristics which in the aggregate ultimately produced the immediate ancestors of the Macropodidae and Potoroidae, which differed from the prototypal phalangerine stock in a number of respects, including the following:—

1. The third premolars gradually became restricted to immature individuals and were morphologically very similar to the permanent fourth premolars.
2. The deciduous fourth premolars became molarized in shape so as to be scarcely distinguishable from the true molars. The permanent fourth premolars gradually increased in size.
3. In nearly all cases the permanent fourth premolar replaced the third premolar and the deciduous fourth premolar.
4. The masseteric canal gradually developed in the mandible.
5. The gradual hypertrophy of the hind limbs and other changes in the pes, such as the dominance of the fourth digit, the loss of the hallux, and the reduction of the second and third digits.

With the exception of these five characters, stem D probably differed little from stem A, that is to say, the female urogenital system retained the generalized phalangerine condition, the arrangement of the temporal bones was unaltered, the alimentary canal possessed a simple stomach and small caecum, the hind limbs perhaps showed slightly greater development, and the fourth digit of the pes showed the beginning of the elongation which ultimately became a feature in most of the descendants of this stem.

It is of interest to note that the change from the omnivorous diet of the prototypal phalangerines to the more strictly herbivorous (arboreal) diet of the recent phalangers, on the one hand, and the herbivorous (grazing) diet of the kangaroos, on the other, has been accompanied by certain modifications of the stomach and caecum which have their counterpart in the eutherian mammals. As we have seen, the primitive phalangers which were omnivorous had a simple stomach and a short caecum. In the recent phalangers which are herbivorous the stomach is still simple but the caecum is long, varying in length from 14 per cent to 20 per cent of the total length of the intestine. In the Macropodidae and

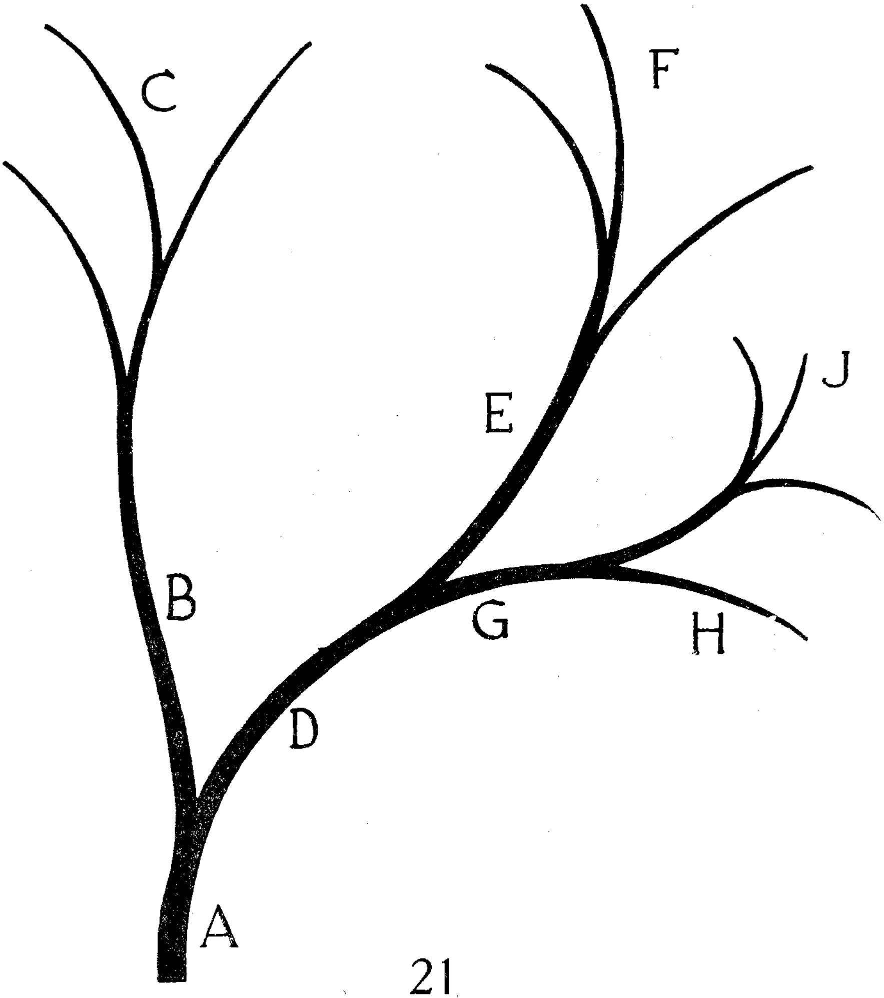


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FIG. 21.—Phylogenetic Tree of the super-family Phalangeroidea, particularly to show the relationship between the Macropodidae and the Potoroidae.

A—Primitive phalangeroid stock.

B—Ancestral stem from which families Phalangeridae and Vombatidae arose.

C—Recent Phalangeridae and Vombatidae.

D—Divergence from the main phalangeroid stem, representing the common ancestors of the kangaroo group (Macropodidae and Potoroidae).

E—Ancestral stem from which recent members of family Macropodidae have arisen.

F—Recent Macropodidae.

G—Divergence from the phalangeroid-macropod line, representing the stem from which recent members of family Potoroidae have arisen.

H—Sub-family Hypsiprymnodontinae.

J—Sub-family Potorinae.

Potoroidae, with the exception of *Hypsiprymnodon*, the stomach is complicated and the caecum is short varying in length from 1·8 per cent to 4·2 per cent of the total length of the intestine.

Stem D branched in two directions, stem E representing the continuation of the main phalanger-macropod line from which recent Macropodidae (F) have been derived; and G which was the basal stem from which recent Potoroidae have sprung. The phalangerine-macropod line passed through A, D, E, and F, and in this series a gradual change took place from an arboreal animal with an omnivorous diet to ground-living forms with cursorial and in the most extreme development, a saltatorial type of locomotion. These changes were accompanied by changes in morphology of the hind limbs which culminated in the highly specialized hind limbs and feet of the kangaroos. At the same time, these more specialized forms acquired the true grazing habit which was reflected in the special type of dentition of the true kangaroos.

Stem E

Stem E represents the ancestral Macropodidae, and on the whole it followed the ancestral phalangerine plan (stem A) with certain modifications, which we have already seen in stem D. In fact, the main features of stem E were already present in stem D and differed only from the latter in degree of specialization. For example, the pes became more elongated with special emphasis on the fourth digit. The hallux probably became greatly reduced and finally disapeared. The temporal bones remained as in stems A and D. The simple stomach gradually assumed complications and the caecum became still more reduced in size. The female urogenital system retained the general phalangerine plan and the dentition became more suited to the grazing habit. The fourth premolars were relatively insignificant and during the growth of the skull were gradually pushed forward to make way for the developing molars. Accompanying this gradual change in habitat along the Phalangerid-Macropod line certain morphological changes took place. In the main, however, the phalangerine characteristics persisted, modified, of course, by superficial influences which gradually affected foot structure, dentition, and the alimentary canal. However, the more deep-seated characters, such as those associated with the female urogenital system and the disposition of the temporal bones, did not change materially from the typical phalangerine arrangements.

Stem G

Stem G may be regarded as the ancestral line from which the recent Potoridae (sub-families Potoroinae and Hypsiprymnodontinae) have been derived. Raven and Gregory (1946) have dealt with the question of the 'adaptive branching of kangaroos', as they termed it, in an interesting manner. There is no question that the influences of habitat have wrought certain clear-cut changes in such characteristics as foot-structure and dentition, but it may be questioned whether the results produced by a study of the effects of environment are in themselves sufficient to justify the conclusions to which systematists have come. If by 'adaptive branching' Raven and Gregory mean nothing more than the response of structure to habit and habitat, then I am willing to fall into line. If, however, the diagram which serves to illustrate their thesis represents a phylogenetic tree of the true kangaroos and rat-kangaroos, it would appear that due consideration has not been given to structures which are least affected by environmental changes. Hence my conception of the phylogeny of these groups given in fig. 21 differs fundamentally from theirs. Stem G is vital in this connexion, as it is at this point that the Potoroidae departed from the phalangerine-macropod line to develop certain morphological characteristics which clearly separate them from the ancestral phalangerine stock and also from the Macropodidae.

If, for example, the rat-kangaroos, including *Hypsiprymnodon*, differed from the true kangaroos only in such external features as dentition and foot-structure, it would be justifiable to regard all forms which were derived from this stem as being sufficiently homogeneous to justify their being placed in a single family. However, it has been shown in the present paper that the Hypsiprymndontinae and the Potoroinae are united by two fundamental characteristics, the specializations of the female urogenital system in which they differ from all other marsupials including the Macropodidae, and the arrangement of the temporal bones in which they differ from the Macropodidae and all other marsupials with the exception of the Perameloidea. These two fundamental departures from the normal marsupial plan must have taken place *after* stem G had been established since it has been shown that all recent derivatives from stem G, the Hypsiprymnodontinae and the Potorinae alone possess this unique combination of attributes and in this respect differ from all other members of the Phalangeroidea. Moreover, these two departures can hardly be regarded as adaptations 'in relation to habitat'.

Stem G probably had the following characteristics, many of which differed but little from those of stem D:—The hind legs were relatively short and the predominance of the fourth digit of the pes was not pronounced. The pes had a well-developed hallux which may still have been functionally apposable. Digital pads were present, the teeth were characterized by the dominance of the posterior premolars and the relatively small size of the molars. The third premolar was probably unlike the fourth premolar. The stomach was simple and the caecum was small. The present specializations of the urogenital system had already begun to take shape and the arrangement of the four temporal bones was such that all four probably met (see fig. 20 *(c)*).

Stems H and J

Stems H and J represent recent Hypsiprymnodontinae and Potorinae respectively. They both agree in having the specialized type of urogenital system, and the disposition of the four temporal bones in which the frontals and squamosals meet. An analysis of foot structure and dentition does not help much in determining the precise relationships of the various genera within the group.

Raven and Gregory talk about the heritage which *Potoroüs* derived from *Hypsiprymnodon* and that '*Bettongia* inherits from *Hypsiprymnodon* . . . most features of its dentition'. I think a much clearer picture would be obtained if we came to the logical conclusion that all recent rat-kangaroos, including *Hypsiprymnodon*, represent the more recent branches of a complicated tree. My view is that the relatively primitive *Hypsiprymnodon* and the more specialized remaining genera of the family have all been derived from a common stock (stem G), and the fact that *Hypsiprymnodon* is more primitive than the other genera of the Potoroidae does not mean that the more specialized genera have 'inherited' certain characteristics from *Hypsiprymnodon*, but from the common stock (stem G) from which all these genera have sprung.

SUMMARY

The object of the present paper is to examine the relationship of the Macropodidae and the Potoroidae. Previous investigators have depended almost entirely upon dentition and foot structure and have, in my opinion, failed to provide an acceptable solution. Bensley (1903) was vague in his conclusions on this question,

but he regarded the Potoroidae as being more primitive than the Macropodidae and thought it possible that the Macropodidae arose from the *Potorous-Caloprymnus* stock, or that both groups arose from a primitive *Dromicia*-like phalanger. In my opinion the first alternative is improbable and the second is more likely to be nearer the truth. Raven and Gregory (1946) agreed with earlier writers who considered *Hypsiprymnodon* to be the only remaining representative of the ancestral stock from which both the rat-kangaroos and true kangaroos have been derived. The evidence given in the present paper claims that this view is quite untenable. It has been shown that the Macropodidae follow the primitive phalangerine plan as regards the female urogenital system and the arrangement of the four temporal bones. On the other hand, *Hypsiprymnodon* and the other genera of the Potoroidae have departed considerably from this plan and it is inconceivable that the rat-kangaroos, which are specialized in these two important respects, could have given rise to the kangaroos. I regard these two groups of structures as being insulated from the effects of habitat, and are thus more static, whereas foot-structure and dentition are unreliable and contradictory witnesses, since they are plastic and responsive to the influences of a changing environment. Gregory (1910) stressed the value of brain, skull, and urogenital system as phylogenetic criteria and issued a timely warning against attaching too much importance to the evidence of the teeth and foot structure.

The resemblances in foot structure and dentition which link the Macropodidae and Potoroidae need not be ascribed to convergence, since the burden of the present claim is that the two families are collateral offshoots from a common ancestral stock. Such resemblances are due to homology and not homoplasy. It is equally true that any changes which took place in the arrangement of the female urogenital organs and in the disposition of the temporal bones along stem G, resulting in considerable specialization, may be regarded as outstanding examples of divergence.

The present series of investigations has been in progress for several years. The ulterior object is to clear up some of the phylogenetic problems of the Marsupialia. In the present paper it is insisted that the evidence shows that the specialized female urogenital system of the Potoroidae has departed from the archaic marsupial plan and differs from the Macropodidae in this respect. It is considered incompatible with the evidence that the Macropodidae should be regarded as an offshoot from a primitive *Hypsiprymnodon*-like rat-kangaroo. Rather is it considered that the two families are collateral branches of a common stock derived from primitive phalangers. The Potoroidae are a specialized offshoot from the phalangerine-macropod line and it is claimed that the evidence of the female urogenital system and the arrangement of the temporal bones lend support to this conclusion and justify the establishment of the family Potoroidae.

REFERENCES TO FIGURES

A—alisphenoid
a.l.v.—anterior extremity of lateral vagina
a.v.c.—anterior vaginal canal
a.v.e.—anterior vaginal expansion
bl.—bladder
cl.—clitoris
d.s.—dorsal remnant of septum
F—frontal
l.ut.—left uterus
l.v.—lateral vagina
m.v.c—median vaginal cul-de-sac
os u.—os uteri
P—parietal
p.l.v.—posterior extremity of lateral vagina
p.v.s.—posterior vaginal sinus
r.s.—receptaculum seminis
S—squamosal
u.b.—opening of ureter into the bladder
u.g.s.—urogenital sinus
u.o.—opening of urethra into urogenital sinus
ur.—ureter
ureth.—urethra
ut.n.—uterine neck
v.s.—ventral remnant of septum

REFERENCES

ABBIE, A. A., 1939.—A masticatory Adaptation peculiar to some Diprotodont Marsupials. *Proc. Zool. Soc. Lond. 109* (ser. B), 261-279.

BENSLEY, B. A., 1903.—On the evolution of Australian Marsupials with remarks on the relationships of the marsupials in general. *Trans. Linn. Soc. Lond.* (2), *9*, part 3, 83-217.

BRASS, A., 1880.—Beiträge zur Kenntniss des welblichen Urogenital-systems der Marsupialen. *Inaug. Dis.* Leipzig.

FINLAYSON, H. H., 1932.—Caloprymnus campestris. Its recurrence and characters. *Trans. & Proc. R.S. South Austr. 56*, 148-167.

GREGORY, W. K., 1910.—The Orders of Mammals. *Bull. Amer. Mus. N.H. 27*. 1-524.

HILL, J. P., 1899.—On the female Urogenital Organs of Perameles, with an account of the phenomena of Parturition. *Proc. Linn. Soc. N.S.W. 24*, 42-82.

————, and FRASER, E. A., 1925.—Some observations on the Female Urogenital Organs of the Didelphyidae. *Proc. Zool. Soc. Lond.*, 1925, 189-219.

LISTER, J. J., and FLETCHER, J. J., 1881.—On the condition of the median portion of the Vaginal Apparatus in the Macropodidae. *Proc. Zool. Soc. Lond.*, 1881, 976-996.

PEARSON, J., 1945.—The Female Urogenital System of the Marsupialia with special reference to the Vaginal Complex. *Pap. Roy. Soc. Tas.*, 1944 (1945), 71-98.

————, 1946.—The Affinities of the Rat-kangaroos (Marsupialia) as revealed by a comparative study of the Female Urogenital System. *Pap. Soc. Tas.*, 1945 (1946), 13-25.

————, 1947.—Some problems of Marsupial Phylogeny. Presidential Address, Section D—Zoology. *Rept. 25th meeting of the Australian and New Zealand Assoc. for the Advancement of Science*, Adelaide, 1946, 71-102.

————, 1950.—A further note on the urogenital system of Hypsiprymnodon moschatus (Marsupialia). *Pap. Roy. Soc. Tas.*, 1949 (1950), p. 203.

RAVEN, H. C., and GREGORY, W. K., 1946.—Adaptive branching of the Kangaroo family in relation to habitat. *Amer. Mus. Nov.*, no. 1309, 1-33, 1948.

TATE, G. H. H., 1948.—Studies on the Anatomy and Phylogeny of the Macropodidae (Marsupialia). *Bull. Mus. Amer. Mus. N.H. 91*, 239-351, 1948.