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11

Evolution of the marsupial brain: Does it reflect the evolution of behavior?

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SUMMARY

Data on the brain morphology of 28 species of marsupials were re-examined to determine whether they contained information as to the evolutionary history of the Marsupalia, and if we could help establish relationships between the evolution of brain and behavior. A phylogenetic tree was reconstructed based on the standardized volumes of 11 brain components; the tree was rooted using similar brain volume data from two edentates and two rodents. Using the triple-permutation test for comparing phylogenies, this tree was shown to be statistically related to the accepted phylogeny of the group, and to be even more closely related to the taxonomic classification of marsupials at the order level. The brain evolutionary tree was then statistically compared to phylogenetic hypotheses concerning the evolution of four categories of behavior: habitat, diet, locomotion, and sociability. Correlations between brain components and the categories of behavior were also studied in order to associate the development of brain parts to the development of behavioral traits. The discussion contains an eco-ethological, a taxonomic and a neurological interpretation of these results.

INTRODUCTION

Marsupials present such a unique set of morphological and anatomical characteristics that their monophyletic origin can hardly be questioned. In particular, the marsupial brain is quite different from that of placental mammals (Johnson *et al.*, 1982a, b); it is characterized by unique qualitative features such as lack of corpus

ANIMALS IN THEIR ENVIRONMENT: A TRIBUTE TO PAUL PIRLOT

callosum, different position of the hippocampal commissure, medial position of the dorsal cochlear nucleus as well as lateral position of the ventral nucleus of the inferior olive, and different branching of the spino-cerebellar fibers (Johnson, 1977). On the other hand, marsupials present important *quantitative* differences in brain size and composition (Moeller, 1970, 1973; Nelson and Stephan, 1982) associated with a wide variety of ecological and behavioral adaptations (Eisenberg and Wilson, 1981; Pirlot, 1981). Monophyly and within-group variability make the Marsupialia especially suitable for studying the evolution of adaptations and behavior from a neurological standpoint.

For several years, Paul Pirlot worked on the morphology of marsupial brains, using serial sectioning, staining and microscopic measurement of brain parts, a technique allowing to obtain fairly accurate reconstructions of the brain component volumes (Pirlot, 1981; the method is described in detail in that primary reference). In this, Pirlot was following the pioneering work of Stephan (1959, 1967) and co-workers (Stephan and Bauchot, 1959; Stephan and Andy, 1962, 1964, 1969; Stephan and Spatz, 1962; Bauchot and Stephan, 1964, 1966, 1968, 1969; Pirlot and Stephan, 1970; Stephan *et al.*, 1970; Stephan and Pirlot, 1970).

In the present paper, the data presented by Pirlot (1981) on the brain morphology of 28 marsupial species are re-examined in order to answer the two following questions:

(1) How much phylogenetic information about the Marsupialia does this data set contain? — Previous studies based on qualitative and quantitative characters (Bauchot, 1979a, b; Switzer *et al.*, 1980; Bauchot, 1982; Kirsch and Johnson, 1983; Kirsch *et al.*, 1983; Johnson *et al.*, 1984; Pettigrew, 1986; Lapointe, 1992) have shown the usefulness of brain data in phylogenetic studies of mammals (see also Campbell, 1975). We want here to assess and quantify the phylogenetic information embedded in brain component volumes, to justify their use in evolutionary studies of marsupials.

(2) What are the relationships between brain evolution on the one hand, and the evolution of ecological and ethological characters in this group? — The idea that the evolution of behavior may reflect itself in the evolution of brain component volumes stems from the theory of cerebral localization of brain functions, which represents a basic paradigm of neuropsychology. That theory, first formulated by Gall (1851) and firmly grounded in empirical evidence by Broca (1861 and following papers) and Brodmann (1909), states that the brain is divided into discrete areas assigned to specific roles and behaviors. If so, brain volumes may contain ecological as well as phylogenetic information concerning marsupials. Mapping ecological, behavioral and neurological characters on the marsupial phylogeny may reflect their relative rates of change, as well as the convergence and parallelism events in the different lineages.

To answer the first question, a phylogenetic tree reconstruction method was used on the brain morphology data, and the resulting tree was statistically compared to the accepted phylogeny of the marsupials; comparisons were also made with the taxonomic classification and with the geographical distribution of marsupials.

For the second question, the brain evolutionary tree was statistically compared to phylogenetic hypotheses concerning the evolution of four categories of behavior relative to habitat, diet, locomotion, and sociability. The correlation between brain

LAPOINTE, LEGENDRE

components and the categories of behavior was also studied in order to associate the development of brain components to the development of behavioral traits.

Table 1 : List of the species of mammals considered in this paper, together with their taxonomic positions

Cohort	Order	Family	Species
Marsupialia	Paucituberculata	Caenolestidae	<i>Lestoros inca</i> <i>Caenolestes obscurus</i>
		Didelphidae	<i>Marmosa murina</i> <i>Marmosa domina</i> <i>Thylamys sp.</i> <i>Metachirus nudicaudatus</i> <i>Philander opossum</i> <i>Didelphis m. aurita</i> <i>Didelphis m. marsupialis</i> <i>Didelphis virginiana</i> <i>Caluromys lanatus</i>
	Diprotodontia	Dasyuridae	<i>Antechinus flavipes</i> <i>Sminthopsis murina</i> <i>Dasyurus viverrinus</i> <i>Sarcophilus harrisii</i> <i>Perameles nasuta</i> <i>Isoodon obesulus</i> <i>Vombatus ursinus</i> <i>Potorous tridactylus</i> <i>Macropus eugenii</i> <i>Setonix brachyurus</i> <i>Thylagale billardierii</i> <i>Macropus rufogriseus</i> <i>Macropus giganteus</i> <i>Trichosurus vulpecula</i> <i>Petaurus breviceps</i> <i>Petauroides volans</i> <i>Pseudochirus peregrinus</i> <i>Dasyurus novemcinctus*</i> <i>Euphractus sexcinctus**</i>
		Phalangeridae	
		Petauridae	
		Vombatidae	
		Macropodidae	
		Dasypodidae	
		Rodentia	
		Muridae	<i>Mus musculus***</i> <i>Mesocricetus auratus***</i>

Marsupialia from Pirlot, 1981; * from Pirlot, 1980; ** from Pirlot and Kamiya, 1980;
*** from Ouedraogo, 1974.

ANIMALS IN THEIR ENVIRONMENT: A TRIBUTE TO PAUL PIRLOT

MATERIALS AND METHODS

The Pirlot (1981) data set contains 28 species (Table 1) representing 8 families and all three living orders of marsupials (Kirsch, 1977). A single brain has been analyzed per species; considering the large amount of effort that has to be devoted to the analysis of each brain, the work tries to maximize the number of species covered, thus increasing diversity at the expense of replication. The rationale for this is found in Stephan *et al.* (1981), who have shown that within-species variability is small compared to that between species. In addition to the 28 species of marsupials, brain morphology data on non-marsupial species found in other papers by Pirlot and co-workers (Ouedraogo, 1974; Pirlot, 1980; Pirlot and Kamiya, 1983) was used as the outgroup. Primitive species from different but related taxa are used as an outgroup in a phylogenetic analysis to determine the position of the root of a tree; they may also suggest the ancestral state of the characters (Wiley, 1981). Following Eisenberg's (1980) concept of what constitutes a primitive mammal, two species of edentates were chosen (the nine-banded armadillo *Dasypus novemcinctus* and the six-banded armadillo *Euphractus sexcinctus*), along with two rodents (the house mouse *Mus musculus* and the golden hamster *Mesocricetus auratus*). The root of the marsupial tree is located at the point on the tree where all marsupials separate from the members of the outgroup; the outgroup data will not be used any further in the analyses.

For each animal, the volume (in mm³) of each of 11 brain components had been measured (Pirlot, 1981): bulbus olfactorius (BO), neocortex (NX), rhinencephalon (RH), schizocortex (SZ), septum (SE), striatum (ST), hippocampus (HI), diencephalon (DI), mesencephalon (ME), cerebellum (CE), and medulla oblongata (MO).

Since the size of the animals included in this analysis, and also the volume of their brains, varied greatly, from the 10-cm *Sminthopsis murina* to the 1.5-m tall *Macropus giganteus*, data were transformed to remove these differences prior to the analysis, because they would tend to dominate the results of most statistical procedures and might prevent us from bringing out finer differences. Several methods are available for doing so. Among the most popular is to use *progression indices* (Stephan, 1967) instead of raw measurements; principal component analysis of the log-transformed data, followed by removal of the size factor, which is often concentrated in the first principal component (Blackith and Reymont, 1971); or division of each value either by the body mass of the animal, or by the total volume of the brain (Pirlot, 1981). In the present case, this last, very simple, solution was used (division of brain component volumes by the total brain volume), since it produced well-behaved (i.e., symmetrical) distributions for all transformed brain component variables (Table III of Pirlot, 1981).

Using the transformed data, a Euclidean distance matrix was computed for the animals. The phylogenetic tree reconstruction method of De Soete (1983a) was applied to this matrix to obtain an additive tree (cladogram) minimizing the sum of squared differences between the additive (or *path-length*) distances representing the additive tree and the original Euclidean distances. This method was preferred to other "distance methods" for tree reconstruction, such as those of Fitch and Margoliash (1967) or Cavalli-Sforza and Edwards (1967), for it had been shown to produce better

LAPOINTE, LEGENDRE

results (De Soete, 1983b) because it constructs the topology of the tree and optimizes branch lengths simultaneously (Swofford and Olsen, 1990).

The resulting additive tree was compared in turn (a) to the best available hypothesis about the phylogeny of the group, (b) to the classification of marsupials (Kirsch, 1977), and (c) to a geographic division of the species into American and Australian taxa. The taxonomic, geographic, and phylogenetic relationships are given in Figure 1. The triple-permutation method of Lapointe and Legendre (1992) was used to test the statistical significance of the similarity of these pairs of trees; the method is also summarized in Legendre *et al.* (1994).

The evolutionary tree based on brain morphology data was then compared to the evolution of four categories of behavior relative to habitat, diet, locomotion, and sociability. To make this comparison possible, each behavioral characteristic had to be transformed into a tree. This was done in the following four steps:

(a) Each behavioral characteristic was mapped onto the phylogeny of the group, as shown in Figure 1. Following Eisenberg (1980), the ancestral states were chosen to be: forest dweller, insectivorous, low sociability, and climber-walker.

(b) The order in which the behavior states descend from one another along the tree was noted and transcribed in the form of four behavior state trees, represented in coded form by arrows and parentheses in Table 2b.

(c) Behavioral state trees were transformed into full patristic species trees for the given behavior characteristic, using the method described by Legendre and Lapointe (1995).

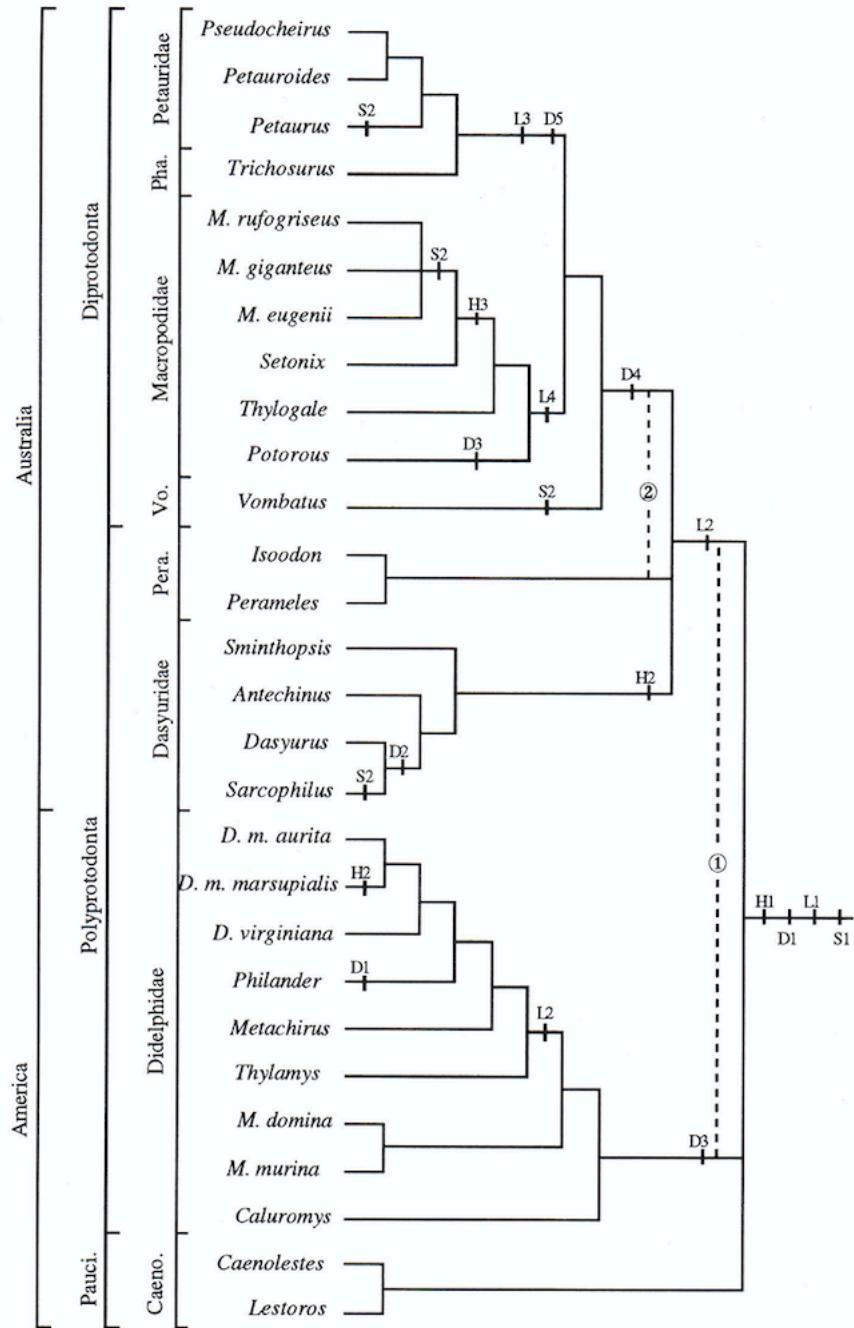
(d) Each of these new rooted trees was compared to the brain evolutionary tree using the triple-permutation test of Lapointe and Legendre (1992).

In order to determine which of the brain components are more likely to be associated with the development of each behavioral state, the various states of the behavioral variables were coded into as many binary (0, 1) variables. Correlations were computed between each of these binary variables and all 11 standardized brain component volumes. Kendall's non-parametric correlations were used since the behavioral state variables are binary-coded, not continuous. To facilitate interpretation of these correlation coefficients, the brain components were each recoded into three states (small, medium, large) and mapped onto the marsupial phylogeny. Correlations were also computed between brain component volumes, taxonomy (orders and families), and geography to interpret brain evolution in marsupial taxa.

RESULTS AND DISCUSSION

The phylogenetic tree based on brain morphology is presented in Figure 2, which brings out the neurological similarities among the 28 species of marsupials; the outgroup shows where to root the tree. Two groups are clearly distinct on this tree. The first cluster includes all polyprotodonts and paucituberculates, whereas the second represents all diprotodonts. The correlation with Kirsch's (1977) classification into Paucituberculata, Polyprotodonta, and Diprotodonta reflects this dichotomy (Table 2a). Had we used Aplin and Archer's (1987) classification (i.e., division into Ameridelphia including Didelphidae and Caenolestidae, and Australidelphia including

ANIMALS IN THEIR ENVIRONMENT: A TRIBUTE TO PAUL PIRLOT



LAPOINTE, LEGENDRE

Table 2 : Results from the triple-permutation tests of significance between the evolutionary tree based on brain morphology (Fig. 2), and **a** aspects of the evolutionary history or **b** phylogenetic hypotheses about the evolution of four categories of behavior. The models are considered fixed, so only the brain morphology tree was permuted (999 permutations)

Brain morphology tree tested against...		Correlation coefficient	Probability of H ₀
a) Comparison of the brain tree to evolutionary history:			
Taxonomy	(Kirsch, 1977)	0.79015	0.001
	(Aplin and Archer, 1987)	0.25602	0.003
Geography			
	R → America → Australia	0.33723	0.001
	R → Australia → America	0.32776	0.002
Phylogeny			
	(Fig. 1 unresolved)	0.73514	0.001
	(node ① resolved)	0.73791	0.001
	(node ② resolved)	0.75573	0.001
b) Comparison of the brain tree to ecological/ethological hypotheses:			
Habitat selection	R → 1 → (2, 3)	0.22314	0.010
Diet	R → 1 → (2, 3, 4 → 5)	0.59912	0.001
Sociability	R → 1 → 2	0.33325	0.003
Locomotion	R → 1 → (2a,2b → (3,4))	0.49660	0.001

Habitat selection: **R** root, **1** forest, **2** ubiquitous, **3** prairie. Diet: **R** root, **1** insectivorous, **2** carnivorous, **3** omnivorous, **4** herbivorous, **5** frugivorous-folivorous. Sociability: **R** root, **1** low, **2** high. Locomotion: **R** root, **1** climber-walker, **2a** walker (American), **2b** walker (Australian), **3** climber, **4** jumper.

← **Figure 1 :** Phylogenetic relationships among the families of marsupials, updated from Kirsch (1977) and Archer (1984). Relationships among species within families are drawn from Baverstock *et al.* (1987, 1989), Flannery (1989), Kirsch *et al.* (1990a, b), Springer and Kirsch (1991), Springer *et al.* (1992), Kirsch *et al.* (1996), and Krajewski *et al.* (1992). Dashed lines represent possible relationships based on neurological data (see text). On this phylogeny are mapped the eco-ethological characters representing habitat selection (**H1** forest, **H2** ubiquitous, **H3** prairie); diet (**D1** insectivorous, **D2** carnivorous, **D3** omnivorous, **D4** herbivorous, **D5** frugivorous-folivorous); sociability (**S1** low, **S2** high); and locomotion (**L1** climber-walker, **L2** walker, **L3** climber, **L4** jumper) of marsupials after Frith and Calaby (1968), Ride (1970), Hershkovitz (1972), Keast (1972), Collins (1973), Tyndale-Biscoe (1973), Hunsaker (1977), Hunsaker and Shupe (1977), Dawson (1983), Strahan (1983), Marshall (1984), Russell (1984), Lee and Cockburn (1985), and Eisenberg (1989). The top of the figure presents the geographic and taxonomic (orders, families) variables used in the statistical analysis.

ANIMALS IN THEIR ENVIRONMENT: A TRIBUTE TO PAUL PIRLOT

Diprotodontia, Dasyuridae and Peramelidae) instead of Kirsch's, the correlation would have dropped from 0.790 to 0.256.

The brain tree (Fig. 2) is also significantly related to the geographic radiation models of marsupials presented in Table 2a. The alternative models are: (R → America → Australia), in which America is considered to be the cradle of marsupials (Clemens, 1968); and (R → Australia → America) (Kirsch, 1979). They both lead to significant and very similar correlations of 0.337 and 0.328 (Table 2a). Thus our results do not discriminate between these alternative hypotheses.

Finally, the tree derived from brain characters is significantly correlated with the phylogeny of marsupials presented in Figure 1. We tried to improve the fit of the brain tree by resolving some of the trichotomies of the phylogeny (dashed relationship levels in Figure 1). At the order level, the best correlation ($r = 0.738$) is obtained when the Didelphidae are a sister-group of the Dasyuridae-Peramelidae-Diprotodontia clade (Table 2a). A significant increase in correlation was also obtained when the Peramelidae-Dasyuridae-Diprotodontia trichotomy was broken and the peramelids were moved into the diprotodont clade ($r = 0.756$). The *Macropus* trichotomy is the only one whose resolution did not lead to an improvement in fit.

1. ECO-ETHOLOGICAL INTERPRETATION

Table 2b presents the results of the tests comparing the brain tree to the four eco-ethological models: habitat selection, diet, sociability, and locomotion. These correlations, along with those in Table 3, can be used together with the mapping of the eco-ethological characters on the Marsupial evolutionary tree (Fig. 1) to determine the associations between behavioral adaptations and brain component development.

A. Habitat selection

According to Eisenberg (1980), primitive marsupials were forest dwellers (i.e., *sylvan* *sensu* Hershkovitz, 1972). Indeed, most didelphids, caenolestids, phalangerids, petaurids, and peramelids still inhabit forested areas of several types (Ride, 1970; Collins, 1973). Dasyurids, however, along with some didelphids (e.g., *D. marsupialis*), can be defined as ubiquitous (i.e., versatile *sensu* Hershkovitz, 1972); they live in pasture lands, forests, scrubs, and cultivated and urban areas (Hunsaker, 1977; Strahan, 1983). On the other hand, most kangaroos (Frith and Calaby, 1968) can definitely be described as prairie-dwellers (i.e., *pastoran* *sensu* Hershkovitz, 1972), except for rat-kangaroos (e.g., *P. tridactylus*) and some forest-dwelling species (e.g., *T. billiardierii*). The radiation of marsupials (Fig. 1) from forest-dwellers to ubiquitous species and prairie-dwellers (see model in Table 2b) is significantly correlated with brain evolution (see also Fig. 3). As illustrated in Table 3, the BO, RH, SZ, DI, and CE are smaller, while the NX and SE are larger in species inhabiting prairies. Only the BO and RH are enlarged in ubiquitous species. No special brain morphology is significantly associated with forest-dwellers (Table 3).

LAPOINTE, LEGENDRE

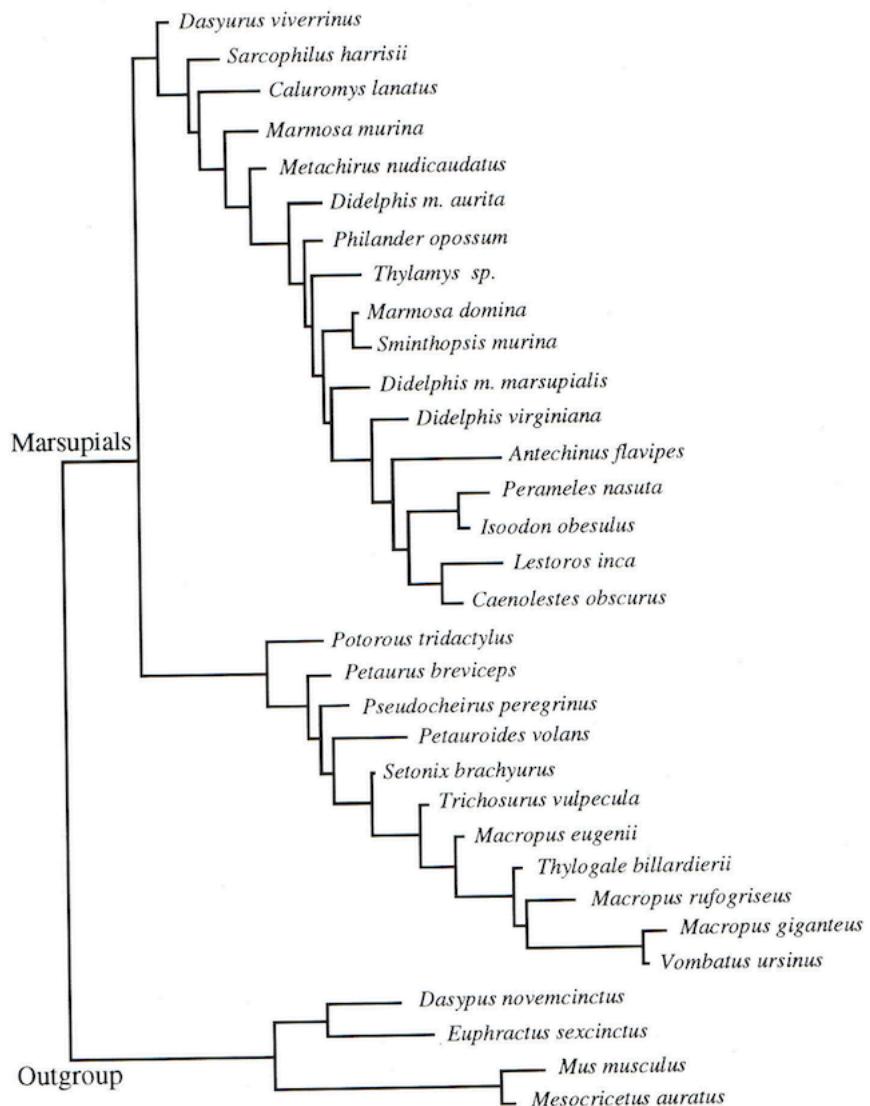


Figure 2 : Phylogenetic tree based on brain characters

Table 3 : Nonparametric correlation coefficients (Kendall's tau) between the binary-coded behavioral state variables (rows) and the 11 standardized brain component variables (columns)

Brain component variables	1 BO	2 NX	3 RH	4 SZ	5 SE	6 ST	7 HI	8 DI	9 ME	10 CE	11 MO
Habitat selection											
1- Forest	0.11	-0.17	0.09	0.11	-0.18	-0.01	0.24	0.08	0.07	0.15	0.15
2- Ubiquitous	0.26*	-0.20	0.25*	0.17	-0.05	0.18	-0.14	0.20	-0.15	0.14	-0.02
3- Prairie	-0.44‡	0.44‡	-0.40†	-0.34*	0.29*	-0.18	-0.17	-0.33*	0.07	-0.36†	-0.18
Diet											
1- Insectivorous	0.51‡	-0.56‡	0.50‡	0.34*	-0.50‡	0.12	0.36†	0.23	-0.20	0.30*	-0.07
2- Carnivorous	0.08	0.06	0.01	-0.09	-0.01	0.06	-0.29*	0.01	0.26*	-0.04	0.13
3- Omnivorous	0.19	-0.19	0.24	0.27*	-0.11	-0.33	0.24	0.32*	-0.25	0.15	-0.02
4- Herbivorous	-0.48‡	0.58‡	-0.52‡	-0.48‡	0.31*	-0.06	-0.27*	-0.50‡	0.03	-0.51‡	-0.18
5- Frugifolivor.	-0.39†	0.23	-0.34*	-0.16	0.40†	0.34*	-0.24	-0.13	0.35†	0.05	0.23
Sociability											
1- Low	0.38†	-0.49‡	0.41‡	0.41‡	-0.37*	0.14	0.46‡	0.45‡	-0.13	0.39†	0.07
2- High	-0.38†	0.49‡	-0.41‡	-0.41†	0.37*	-0.14	-0.46‡	-0.45‡	0.13	-0.39†	-0.07
Locomotion											
1- Climber-walker	0.25	-0.28*	0.27*	0.19	-0.36†	-0.08	0.20	0.39†	-0.21	0.25	-0.18
2- Walker (all)	0.42†	-0.37†	0.39†	0.30*	-0.21	-0.09	0.05	0.16	-0.04	0.17	0.18
3- Climber	-0.39†	0.23	-0.34*	-0.16	0.40†	0.34*	-0.24	-0.13	0.35†	0.05	0.23
4- Jumper	-0.43‡	0.53‡	-0.45‡	-0.42†	0.27*	-0.10	-0.05	-0.48‡	-0.05	-0.50‡	-0.23
2a- Walker (Am.)	0.28*	-0.21	0.32*	0.20	-0.09	-0.35†	0.07	0.14	-0.03	0.08	-0.10
2b- Walker (Aus.)	0.23	-0.24	0.16	0.16	-0.16	0.21	-0.01	0.06	-0.01	0.12	0.29*

Abbreviations for the brain components as in the text. * 0.01< p≤0.05; † 0.001< p≤0.01; ‡ p≤0.001.

LAPOINTE, LEGENDRE

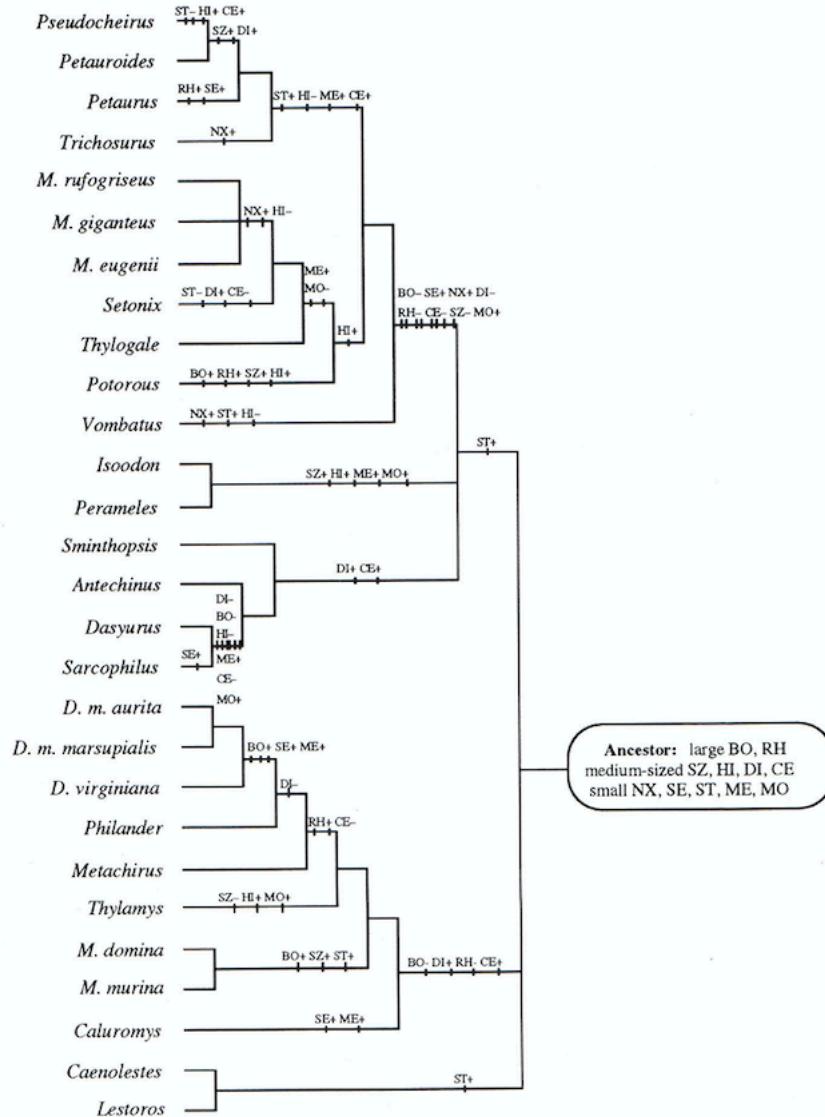


Figure 3 : Mapping of the 11 standardized brain components, each divided into three size states, onto the phylogenetic tree of the marsupials. Character state changes represent an increase (+) or a decrease (-) in the volume of a particular brain component on a given branch, with respect to the hypothetical ancestor described in the Figure.

ANIMALS IN THEIR ENVIRONMENT: A TRIBUTE TO PAUL PIRLOT

B. Diet

As primitive mammals, early marsupials were probably insectivores (Eisenberg, 1980). The paucituberculates and most of the polyprotodonts are still insectivores (Hershkovitz, 1972; Collins, 1973). From this ancestral state, some dasyurids (Guiler, 1970) became carnivores (e.g., *S. harrisii*), most didelphids became omnivores (Hunsaker, 1977), and the macropodids and vombatids became herbivores, grazers or browsers (Raven and Gregory, 1946). From the herbivorous state, the petaurids and phalangerids became frugivores and/or folivores (Ride, 1970) as they became climbers (Fig. 1). The trophic radiation of marsupials is highly correlated with brain differentiation (Table 2b). Insectivorous species are characterized by large BO and RH, two related structures of the olfactory system. They also have large SZ, HI, and CE, but reduced NX and SE (Table 3). The omnivorous state shows a reduction of the ST and enlarged SZ and DI, whereas carnivorous dasyurids differ from primitive insectivores only in their reduced HI and enlarged ME (Table 3). The herbivorous species (including folivores and frugivores) are very distinct from the non-herbivorous marsupials. Grazing kangaroos have significantly larger NX and SE, a condition reflecting their higher evolutionary level, accompanied by reduced BO, RH, SZ, HI, DI, and CE (Table 3). Frugivorous possums (*Phalangeridae* and *Petauridae*) have further enlarged ST and ME, compared to the herbivorous macropods.

C. Sociability

Primitive marsupials are solitary asocial animals; higher sociability appeared independently in several families (Fig. 1) including some dasyurids (Eisenberg *et al.*, 1975; Croft, 1982), the large kangaroos (Croft, 1989), and some possums (Biggins, 1984). The social level of a species can be defined in terms of social organization, dominance hierarchy, communication skills, territoriality, or parental care (Hunsaker and Shupe, 1977; Russell, 1984). Whereas some species are typically solitary animals, others live in herds (e.g., *Macropus*), communicate extensively (e.g., *Sarcophilus*), or show complex hierarchical structures (e.g., *Petaurus*). Brain component characteristics are therefore not clearly associated with sociability, as can be seen in Figure 3. The NX and SE are probably the most important brain parts associated with social level (Pirlot, 1981), their enlargement being correlated with higher sociability (Table 3). Most other brain components are negatively correlated with high sociability.

D. Locomotion

Ancestors of the marsupials were probably climber-walkers (Eisenberg, 1980). Primitive paucituberculates and most didelphids are semi-arboreal (climber-walkers) or terrestrial animals (Hershkovitz, 1972; Hunsaker, 1977) with some very good climbers (Eisenberg and Wilson, 1981), whereas the Australian polyprotodonts evolved into terrestrial marsupials (Collins, 1973). On the other hand, diprotodont radiation led to jumping kangaroos, walking semi-fossorial wombats, and climbing or even gliding possums (Ride, 1970). As the primitive state (Fig. 3), climbing-

LAPOINTE, LEGENDRE

walking is characterized by larger RH and DI, and reduced NX and SE, compared to other species (Table 3). The derived walkers, exhibiting enlarged BO, RH, SZ and a reduced NX, can be separated into two groups according to taxonomic or geographic differences (Fig. 1); American walkers are characterized by large BO and RH and a small ST, while the Australians have an enlarged MO. Climbing species are characterized by reduced BO and RH, and enlarged SE, ST, and ME. Interestingly, the CE is not larger in climbing species; it is greatly reduced in kangaroos, along with a reduction of the BO, RH, SZ and DI (Table 3). Jumpers also exhibit large NX and SE, the latter feature shared with climbers.

2. TAXONOMIC INTERPRETATION

Table 4 presents the correlation coefficients computed for each of the 11 brain components and the binary-coded families of marsupials. These values can be used to show neurological similarities among marsupial lineages in conjunction with evolutionary trends of brain components mapped on the marsupial phylogeny (Fig. 3).

A. Caelonestidae

Two species represent the South-American Paucituberculata in this study (Table 1). The caenolestids are primitive animals that share all the eco-ethological states of the hypothetical ancestor of the marsupials; that is, they are forest-dwellers, primarily insectivores, climbing-walking animals, with no social organization (Hershkovitz, 1972; Collins, 1973). The brain of caenolestids is similar to that of peramelids and didelphids (Fig. 2) to which they are related either eco-ethologically or geographically. In Figure 2, the caenolestids are found in the same large group as all polyprotodonts, probably indicating some phylogenetic relationship as well as neurological similarities. The brains of *L. inca* and *C. obscurus* are characterized by relatively large BO and RH compared to other marsupials. However, the NX, SE, and MO are reduced, an indication of their low sociability and relatively primitive brain (Table 4).

B. Didelphidae

This is the best represented group in our study (Table 1), including 9 species from two distinct subfamilies: genera *Marmosa*, *Thylamys*, *Philander*, *Metachirus*, and *Didelphis* represent the Didelphinae, whereas *Caluromys* is from the subfamily Caluromyinae (Marshall, 1984). This taxonomic distinction suggests that there may be eco-ethological separation of the two subfamilies. The woolly possum (*C. lanatus*) is an omnivorous species typically adapted to living in trees or on the ground (Hunsaker, 1977). On the other hand, most didelphines (Handley, 1976) are terrestrial (except the genus *Marmosa*), some species exhibiting an insectivorous preference in diet (e.g., *P. opossum*). The brain of *Caluromys lanatus* is but remotely related to that of the didelphines (Fig. 2, 3), but as a family, the Didelphidae are characterized by a brain similar in composition to that of the caenolestids; that is, they have reduced NX and ST but very large RH, SZ, and DI

Table 4 : Nonparametric correlation coefficients (Kendall's tau) between the binary-coded taxonomic and geographic states (rows) and the 11 standardized brain component variables (columns)

Brain component variables	1 BO	2 NX	3 RH	4 SZ	5 SE	6 ST	7 HI	8 DI	9 ME	10 CE	11 MO
Taxonomy											
1- Caenolestidae	0.36†	-0.27*	0.37*	0.07	-0.37*	0.13	0.06	0.00	-0.07	0.06	-0.37†
2- Didelphidae	0.25	-0.26*	0.30*	0.30*	-0.19	-0.43†	0.20	0.45‡	-0.17	0.26	-0.04
3- Dasyuridae	0.16	-0.18	0.16	0.06	-0.09	0.15	-0.15	0.25*	-0.06	0.23	0.05
4- Peramelidae	0.27*	-0.34*	0.20	0.31*	-0.21	0.01	0.36†	-0.04	0.13	0.09	0.31*
5- Vombatidae	-0.13	0.25	-0.21	-0.19	0.11	0.19	-0.25*	-0.27*	-0.09	-0.27*	0.15
6- Macropodidae	-0.43‡	0.53‡	-0.45‡	-0.42†	0.27	-0.10	-0.05	-0.48‡	-0.05	-0.50‡	-0.23
7- Phalangeridae	-0.15	0.17	-0.13	-0.21	0.13	0.27*	-0.21	-0.19	0.09	-0.05	0.05
8- Petauridae	-0.35†	0.16	-0.30	-0.05	0.37†	0.22	-0.15	-0.03	0.34*	0.09	0.23*
Geography ¹											
1- America	0.43†	-0.39†	0.48‡	0.33*	-0.37†	-0.34*	0.22	0.43†	-0.20	0.28*	-0.23
2- Australia	-0.43†	0.39†	-0.48‡	-0.33*	0.37†	0.34*	-0.22	-0.43†	0.20	-0.28*	0.23

¹ This variable also corresponds to the taxonomic classification of Aplin and Archer (1987) separating Ameridelphidae from Australidelphidae. Abbreviations for the brain components as in the text. * 0.01< p≤0.05; † 0.001< p≤0.01; ‡ p≤0.001.

LAPOINTE, LEGENDRE

(Table 4). Because this family is so diversified, however, important differences in brain organization may be found among its members (see Eisenberg and Wilson, 1981; Pirlot, 1981). *Caluromys* has a smaller RH than most other didelphids except *Marmosa*. On the other hand, it possesses enlarged SE, ME, and CE (Fig. 3); the latter condition, which is shared with *Marmosa*, is associated with the arboreal niche of both genera (Eisenberg and Wilson, 1981). All *Didelphis* species are characterized by a larger SE than the Didelphinae subfamily average, whereas the other genera (*Philander*, *Metachirus*, *Thylamys*) are in many respects similar to the hypothetical ancestor (Fig. 3). Like the caenolestids, the didelphid brain resembles that of the peramelids and dasyurids (Fig. 2); this either represents the symplesiomorphic condition or is a case of adaptive convergence of the brain in Australian and American marsupials.

C. Dasyuridae

This family of Australian polyprotodonts is represented by four species in our study (Table 1), including the Tasmanian devil (*S. harrisii*), the only true carnivorous marsupial (Guiler, 1970). Other dasyurids are occasional carnivores (e.g., *Dasyurus*) but insects constitute the largest part of their diet (Blackhall, 1980; Fox, 1982). They are all more or less ubiquitous in habitat selection, and though more comfortable on the ground, some species can climb trees (e.g., *A. flavipes*). *Sarcophilus* and *Dasyurus* are more social than *Antechinus* and *Sminthopsis* (Eisenberg *et al.*, 1975; Croft, 1982). Considering the brain, the former two genera are but distantly related to the other polyprotodonts (Fig. 2, 3), whereas the latter two are more similar neurologically to the didelphids, peramelids, and caenolestids. This fact is reflected in the brain composition of the two subgroups of dasyurids (Fig. 3). Most species have a primitive didelphid-like brain with a large DI (Table 4), whereas the carnivorous Tasmanian devil (*S. harrisii*), along with *Dasyurus*, is characterized by larger ME, MO, and SE, and reduced BO, HI, DI, and CE (Fig. 3). Differences in diet, sociability level, or body size are associated with this large variation within the same family.

D. Peramelidae

The second family of Australian polyprotodonts is here represented by two species only (Table 1). Bandicoots are terrestrial marsupials inhabiting forested areas and having a preferentially insectivorous diet (Heinsohn, 1966; Stodart, 1977). Peramelids are neurologically similar to the caenolestids (Fig. 2). These two families are less variable in brain composition than most other marsupial families (Pirlot, 1981); the brain of the peramelids is very primitive indeed compared to that of the diprotodonts (Fig. 3). The only relevant differences between any other polyprotodont brain and a bandicoot brain lie in the HI, BO and MO, which are larger in *I. obesulus* and *P. nasuta* (Table 4), the latter feature shared with petaurids rather than with didelphids, dasyurids, and caenolestids to which they are related phylogenetically and ecologically (Fig. 1). Bandicoots also exhibit larger SZ and ME than the other diprotodonts (Fig. 3).

ANIMALS IN THEIR ENVIRONMENT: A TRIBUTE TO PAUL PIRLOT

E. Vombatidae

Only one species of wombat is included in this study (Table 1). *Vombatus ursinus* is an Australian marsupial of the Diprotodontia order; it is a semi-fossiliferous forest-dweller with an herbivorous diet (McIlroy, 1976). Compared to the polyprotodont species, the wombat may be considered a social animal (Pirlot, 1981), but less so than kangaroos and possums (Russell, 1984). Our only vombatid is neurologically more similar to the macropods than to any other marsupial (Fig. 2). Its brain shows significant reduction of the HI, DI, and CE (Table 4). It also shares with some kangaroos a large NX and a reduced HI, and with possums, an enlarged ST (Fig. 3). These brain affinities suggest that vombatids are more closely related to macropodids than to phalangerids.

F. Macropodidae

The study includes five kangaroos representing the Macropodinae subfamily (Kirsch, 1977) and one rat-kangaroo (*P. tridactylus*) of the Potoroinae subfamily (Table 1). All species are characterized by their jumping mode of locomotion and their adaptation to the herbivorous niche (Sansom, 1989), except for *P. tridactylus*, which is omnivorous (Guiler, 1971). Most of the larger kangaroos (e.g., members of genus *Macropus*) are prairie-dwellers, using prairies at least to feed at night or dawn (Frith and Calaby, 1968); the potoroo (*Potorous*) is a typical forest-dweller, however (Heinsohn, 1968; Seebeck *et al.*, 1989). Macropods are highly social animals, presenting the most complex social organization of all marsupials (Croft, 1989). They have a unique brain organization. With the exception of the potoroo, all macropods exhibit very similar brains, which resemble more that of the wombats or phalangerids than the brain of rat-kangaroos (Fig. 2). At least four components (BO, RH, SZ, and HI) are obviously larger in potoroines than in macropodines (Fig. 3). Furthermore, the potoroo's NX is less developed (Pirlot, 1981). Besides these differences, kangaroos are very similar to one another, except for the larger NX and reduced HI characterizing the social *Macropus* genus. The only macropodine differing from the group is the quokka (*S. brachyurus*), which exhibits a unique brain composition (Kirsch and Johnson, 1983), with reduced ST and CE, and an enlarged DI (Fig. 3), a combination not found in any other kangaroo (Macropodines or Potoroines). The quokka is clearly an "anomalous wallaby" (Strahan, 1983) from a neurological standpoint.

G. Phalangeridae

The common brushtail possum (*T. vulpecula*) is the only phalanger in Pirlot's (1981) data set (Table 1). It is a typical climber but sometimes forages on the ground (Collins, 1973); it inhabits forested areas and feeds on leaves, fruits, and some insects (Ride, 1970; Keast, 1972). It shares its ecological niche with the petaurids (Tyndale-Biscoe, 1973), its sister-group (Fig. 1). Despite the phylogenetic and ecological relationships among Australian possums, the brain of *T. vulpecula* is more similar to that of a kangaroo than a petaurid (Fig. 2). In Table 4, it is only characterized by a larger ST. However, both groups of possums (phalangerids and

LAPOINTE, LEGENDRE

petaurids) possess enlarged ME and ST but a reduced HI compared to the macropods, as well as a larger CE, clearly reflecting their climbing ability (Fig. 3).

H. Petauridae

Ringtail possums are sometimes divided into two distinct families (Aplin and Archer, 1987): the Petauridae family *sensu stricto* includes *Petaurus*, whereas the Pseudocheiridae family encompasses *Pseudochirus* and *Petauroides* (Table 1). Like brushtail possums, ringtail possums are forest-dwellers, arboreal climbers (some species are gliders), and preferentially folivorous or frugivorous (Ride, 1970; Marshall, 1984). They are more socially organized than phalangerids, however (Biggins, 1984). In terms of brain composition, petaurids form quite a homogeneous group (Fig. 2), neurologically related to the kangaroos and phalangerids. The difference between the two groups of ringtail possums (the Petauridae and Pseudocheiridae of Aplin and Archer) is not obvious. *Petaurus breviceps* has somewhat larger RH and SE than *Pseudochirus peregrinus* and *Petauroides volans* (Fig. 3), but this is probably associated with social organization (Henry and Suckling, 1984) rather than phylogenetic relatedness (Fig. 1). The entire family shares with other diprotodonts a reduced BO (Table 4), associated with their shift in diet, and an enlarged SE compared to polyprotodonts. Within diprotodonts, they are also characterized as having an enlarged ME; this is a convergent situation also found in some polyprotodonts sharing similar climbing ability with petaurids.

3. NEUROLOGICAL INTERPRETATION

All correlations presented in Tables 3 and 4 can be interpreted not only in eco-ethological and taxonomic terms but from a neuro-anatomical standpoint as well. One simply needs to read the tables from columns to rows to analyze brain component evolution in relation to phylogenetic, geographical, and eco-ethological characters. Not only can this provide information on brain differentiation, it may also illustrate the neurological radiation of marsupials. [Letters capitalized in brain component names form the abbreviations used throughout this paper]

A. Bulbus Olfactorius

Olfactory structures are obviously related to a species' diet. Insectivorous species exhibit a large BO whereas herbivorous, folivorous and frugivorous marsupials have a reduced BO (Table 3). A large olfactory bulb is generally considered to be the primitive condition in mammals (Stephan, 1967). In marsupials, this condition is found in walkers and climber-walkers (Table 3), which are also assumed to be primitive states in marsupials (Fig. 1). The evolutionary trend in BO is toward reduction (Fig. 3): this structure is fairly large in polyprotodonts and paucituberculates (omnivorous and insectivorous) and becomes smaller in diprotodonts (herbivorous). Caenolestids and peramelids have the largest BO, whereas kangaroos and possums exhibit the smallest BO found in marsupials (Table 4).

ANIMALS IN THEIR ENVIRONMENT: A TRIBUTE TO PAUL PIRLOT

B. Neocortex

The neocortex is the integration center of the brain. As such, neocorticalization provides information on the evolutionary level of a given species (Hofman, 1982). This brain component is generally associated with sociability (Table 3); this may explain its large size in macropods (Table 4). On the other hand, the NX is extremely reduced in peramelids, didelphids, and caenolestids, which are solitary animals (Marshall, 1984). All polyprotodonts have a smaller NX than diprotodonts. In diprotodonts, the trend is toward a larger NX in possums, wombats, and kangaroos (Fig. 3). However, petaurids and phalangerids exhibit a smaller NX than other diprotodonts (Table 3); this is probably a secondary reduction of the NX relative to an increase in the CE required to occupy the arboreal niche (Fig. 3).

C. Rhinencephalon

This brain component encompasses both the rhinencephalon and the piriform lobe in the Pirlot (1981) data; it is therefore functionally related to the BO. The correlation values of the BO and RH with all factors they were compared to are almost identical (Tables 3 and 4). The RH is a primitive brain component that underwent radiation in parallel with the BO in the phylogeny of marsupials (Fig. 3). It is a very large structure in caenolestids and most didelphids (Table 4). However, the RH is smaller in *Caluromys* and *Marmosa* than in other polyprotodonts. It is further reduced in all diprotodonts, particularly the kangaroos and petaurids (Table 4), except for *Potorous* and *Petaurus* (Fig. 3). Differences in diet show that carnivores have a smaller RH than insectivores, whereas frugivores have a larger RH than herbivorous marsupials (Table 3).

D. Schizocortex

As part of the limbic system, with the HI and SE, the SZ controls the interactions of an animal with its environment, as well as memory and learning. The SZ is large in walking insectivorous species, but small in jumping herbivores (Table 3). The trend in SZ evolution has been toward enlargement in the polyprotodonts and reduction in the diprotodonts (Table 4). Petaurids differ from most diprotodonts in that they have a SZ similar to that of the polyprotodonts (Fig. 3). The SZ is larger in solitary animals whereas it reaches its lowest level in kangaroos (Table 3).

E. Septum

This is also a relay component of the limbic system. However, the SE is more closely associated with visceral and behavioral mechanisms (Stephan and Andy, 1962). It shows a pattern of correlations opposite those of the HI and SZ, implying different functions (Tables 3 and 4). Families with a large SZ generally show a reduction of the SE (Fig. 3). Caenolestids have a significantly small SE, whereas no trend was observed for the HI and SZ (Table 4). The reverse is found for petaurids that exhibit a large SE, just like macropods. Among the polyprotodonts, *Didelphis* species, as well as *Caluromys* and *Sarcophilus*, have a larger SE than the average

LAPOINTE, LEGENDRE

marsupial (Fig. 3). This illustrates a situation where slight behavioral differences can mask phylogenetic information within a given family or order.

F. STriatum

This is a relay center for motor connections between the NX and other brain components. However, it does not exactly parallel the evolution of the NX (Fig. 3). While both components are reduced in didelphids and enlarged in most diprotodonts, the ST is somewhat larger in peramelids and dasyurids than in didelphids (Fig. 3). It is also negatively correlated with the NX in kangaroos. The largest ST is found in our phalangerid, *Trichosurus*. It is larger in frugivorous possum climbers and reduced in omnivorous didelphid walkers (Table 3).

G. Hippocampus

The last of the limbic system components is highly correlated with the SZ, to which it is connected. It is an important component for aggressivity control and is, for this reason, reduced in the carnivorous dasyurids compared to the insectivorous peramelids (Tables 3 and 4; Fig. 3). The relative volume of the HI is on the average larger in polyprotodonts than in diprotodonts, but it does not show much variation within these groups. With the exception of bandicoots, where there is a significant increase in HI (Table 4), the evolutionary trend is toward reduction in marsupials (Fig. 3).

I. DIencephalon

This is another integration and relay center that receives and sends connections to all other brain parts, such as the NX. The DI is larger in primitive didelphids (Table 4) but smaller in other polyprotodonts. Further reduction is associated with the passage from insectivores to herbivores (Table 3) and therefore from polyprotodonts to diprotodonts (Table 4). Kangaroos have a reduced DI, just like wombats. Despite their functional association, the DI is negatively correlated with the NX ($r = -0.756$); instead it seems to have paralleled the evolutionary trend of the RH ($r = 0.520$; Fig. 3).

J. MEsencephalon

Along with the MO, the ME controls the basic functions of life, but it is also correlated with the DI ($r = 0.724$). Because of their important role, these components are not highly variable among species. In fact, the only marsupial family showing any significant correlation with the ME is the Petauridae (Table 4), which has a larger ME than other families. The corollary is that frugivorous-folivorous and climbing marsupials also exhibit a positive correlation with ME volume, whereas climber-walkers and insectivores have a reduced ME (Table 3).

ANIMALS IN THEIR ENVIRONMENT: A TRIBUTE TO PAUL PIRLOT

H. CErebellum

This very important brain component controls spatial orientation and recognition, balance, and movement coordination. The CE is therefore larger in climbing species (Table 3), which need balance and precise coordination to live in trees. Jumpers, however, have an extremely reduced CE; jumping does not seem to require a great deal of balance. Spatial recognition is also less difficult in a prairie than in a forest (Table 3). Like kangaroos, wombats exhibit a reduced CE; this may represent a convergent condition in these two families (Table 4). Besides these exceptions, the evolutionary trend of the CE is more or less constant across marsupial families (Fig. 3).

I. Medulla Oblongata

This small component contains the brain centers that control basic life functions. Peramelids and petaurids have a larger MO, and caenolestids a smaller MO than most other marsupials (Table 4). The remaining families have an intermediate MO. In general, polyprotodonts and diprotodonts do not significantly differ in terms of MO evolution (Table 4). No evolutionary trend is obvious (Fig. 3). However, polyprotodont walkers have a reduced MO compared to diprotodont walkers (Table 3).

CONCLUSION

The following philosophical question often occurs to those who are studying the joint evolution of brain and behavior: which came first? (1) As a first approximation, this co-evolution may be seen as an iterative reinforcement process between a genetically-based pre-adaptation and some behavior; (2) this may lead to the gradual invasion of a new niche; (3) life in the new environment places selection pressure on the quantitative development of certain brain components, which (4) helps reinforce the said behavior, either directly, or by making other aspects of survival and differential reproduction in the new type of environment easier. This is the basis for a model where both brain and behavior (or habitat utilization) may develop simultaneously.

Our results have brought out strong associations between the development of brain components and the emergence of behavioral traits. Thus, they support Gall's, Broca's, and Brodmann's paradigm of cerebral localization of brain functions and extend it to the marsupials. These results are summarized in Figure 4, which shows, for each marsupial family, the increase or reduction in brain parts as well as the eco-ethological changes, compared to the hypothetical ancestor.

The paradigm of cerebral localization of brain functions also receives support from the correlations observed in the present study between brain component development, on the one hand, and behavioral evolution models, on the other. They clearly illustrate that some brain components evolve in association with specific behaviors, while others are not related to any particular characteristic of a species' eco-ethology. For example, the olfactory bulb and rhinencephalon are related to dietary preferences; the neocortex is affected by social level and habitat selection; whereas the cerebellum and locomotion have evolved together. However, the medulla

LAPOINTE, LEGENDRE

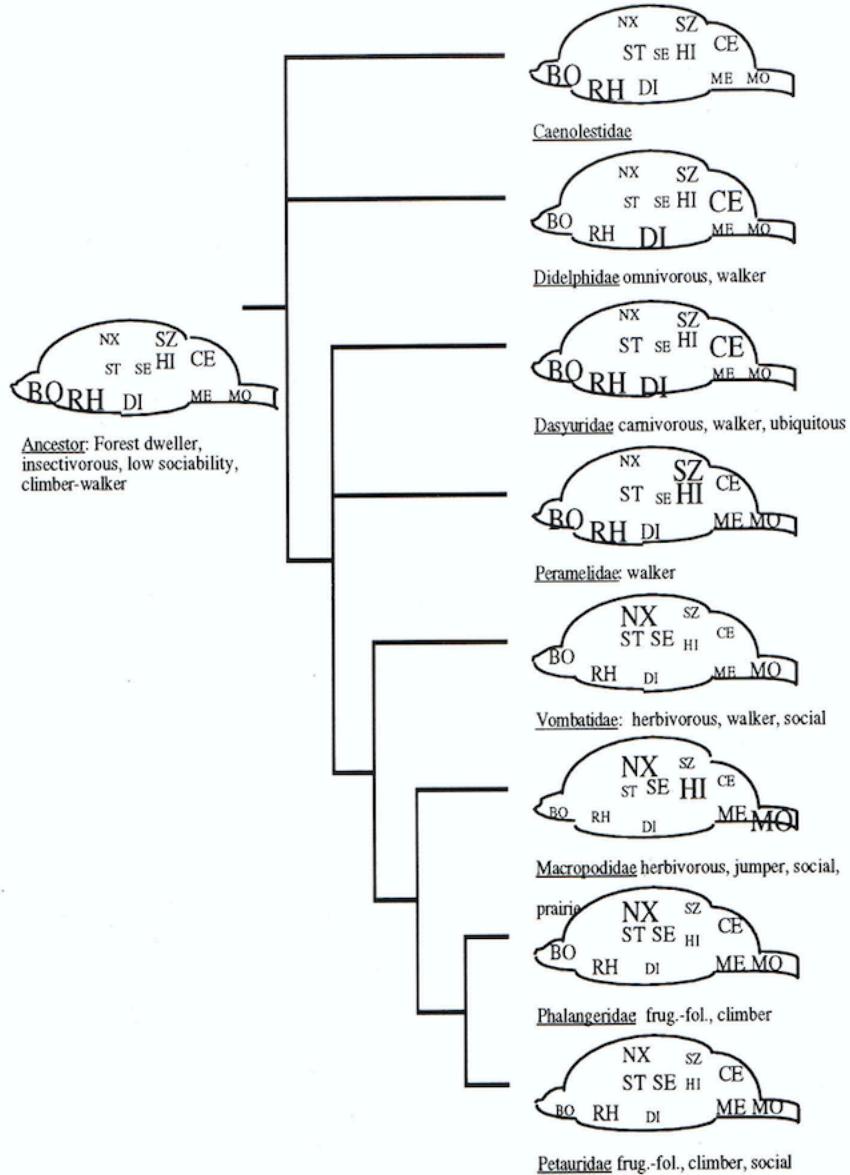


Figure 4 : Evolution of brain and behavior among families of marsupials. Brain components are represented on a schematic view of a sagittal section of a marsupial brain. Each standardized component is divided into three size classes and represented by small, medium or large prints. Behavioral characteristics that differ from the hypothetical ancestor are mentioned besides the family names.

ANIMALS IN THEIR ENVIRONMENT: A TRIBUTE TO PAUL PIRLOT

oblongata and mesencephalon size variations show little correlation with behavior in marsupial families. It is important to keep in mind that while eco-ethological characters can provide information on brain evolution, they may also be correlated with taxonomy, and that ecological pressures as well as phylogenetic inertia have to be taken into account to understand the evolution of the marsupial brain.

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¹ The number following the year of the reference refers to the list of publications of Paul Pirlot at the end of this volume.

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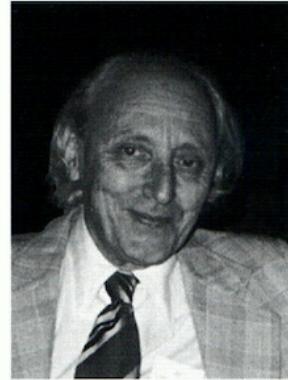
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