LEONARD RADINSKY

Endocasts of Amphicyonid Carnivorans

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ABSTRACT

Endocranial casts of 10 genera of amphicyonids, ranging in age from about 35 my to 10 my, reveal evolutionary trends of increase in relative brain size and expansion and increased folding of the neocortex. Amphicyonids had a distinctive pattern of cerebral convolutions, characterized by the presence of a long ectolateral sulcus, a short sulcus between the caudal ends of the ectolateral and suprasylvian sulci, and a complete, unopercularized ectosylvian sulcus. The ectolateral sulcus is a derived character amphicyonids share with canids, in contrast to a derived feature of basicranial circulation that links amphicyonids to ursids.

INTRODUCTION

The Amphicyonidae are an extinct family of carnivorans that lived during middle Tertiary time, from about 40 to 10 million years ago. Most amphicyonids were medium-sized to very large, and ranged in appearance from wolflike to bearlike. Some workers believed they were most closely related to the Canidae (e.g., Romer, 1966; Bonis, 1969), but the most recent studies have stressed affinities with the Ursidae (e.g., Hunt, 1977; Ginsburg, 1977). During the course of a survey of carnivoran brain evolution, I prepared several new endocasts of amphicyonids that extend our knowledge of the neuroanatomy of this group. The purpose of the present paper is to review what is known about the external neuroanatomy of amphicyonids, to describe evolutionary trends, and to call attention to features that may help to assess the phylogenetic relationships of the family.

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5 —   — 5

10 —   — 10
            amphicyonine

15 —   *Amphicyon   Pliocyon*   — 15

         Amphicyon
20 —   — 20
         Daphoenodon

25 —   *Temnocyon*   *Cynelos   (Ysengrinia)* — 25

30 —   *Daphoenus*   *Brachycyon*   — 30

35 —   *Daphoenus (Daphoenictis)   Pseudocyonopsis*   — 35

40 —   — 40
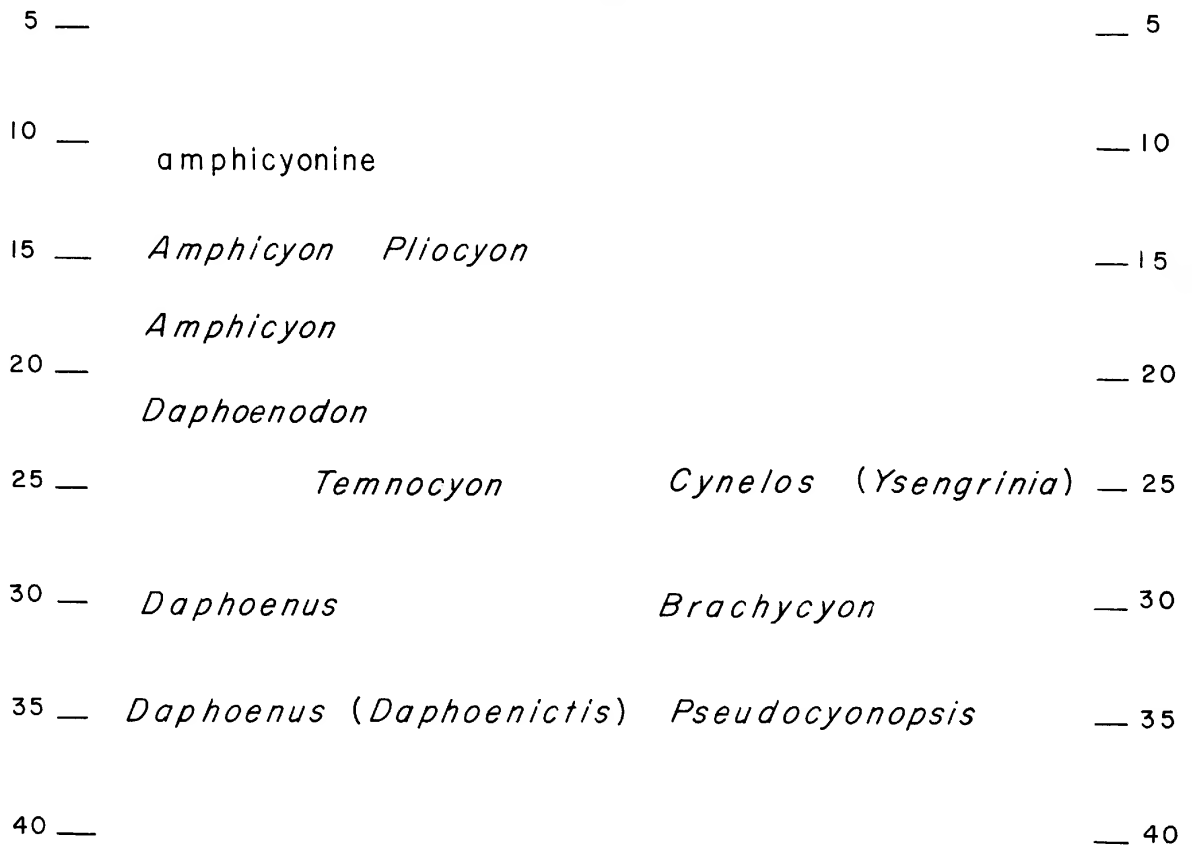
FIG. 1.   Temporal distribution of amphicyonid genera for which endocasts are known. Numbers at sides indicate millions of years ago. North American occurrences are at left; European at right. Parentheses indicate genera for which only a little of the endocast is preserved. See text for more detailed taxonomy and stratigraphic information.

The following institutional abbreviations are used:

AM, American Museum of Natural History
CM, Carnegie Museum
F:AM, Frick American Mammals, Department of Vertebrate Paleontology, American Museum of Natural History
FMNH, Field Museum of Natural History

GEN, Museum d'Histoire Naturelle
LY, Université Claude Bernard
MCZ, Museum of Comparative Zoology
MNHN, Museum National d'Histoire Naturelle
PU, Princeton University
SDSM, South Dakota School of Mines

THE EVIDENCE

EARLY AMPHICYONIDS: Amphicyonids appeared about 35 to 40 my in North America and Europe, and the oldest known amphicyonid endocasts are from early to middle Oligocene deposits (about 30 to 35 my) from the European amphicyonines *Pseudocyopsis* and *Brachycyon,* and the North American daphoenines *Daphoenus* and *Daphoenictis. Daphoenus* is the best known of these
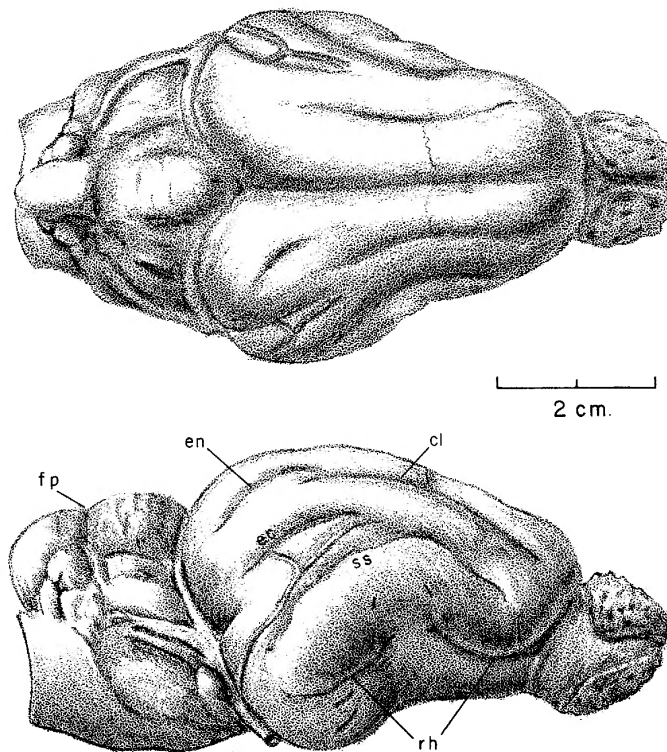
2 cm.

FIG. 2. *Daphoenus hartshornianus*. SDSM 51121, ×1. *Abbreviations*: cl, coronolateral sulcus; ec, ectolateral sulcus; en, entolateral sulcus; fp, *fissura prima*; rh, rhinal fissure; ss, suprasylvian sulcus.

genera, and is represented by several endocasts, one of which was briefly described by Scott and Jepsen (1936). The specimen figured by Edinger (1956, fig. 5) under the name *Daphoenus* (AM 6946) is an endocast of the canid *Mesocyon*.

The brain of *Daphoenus* (fig. 2) had three main neocortical sulci, a relatively straight coronolateral sulcus that paralleled the dorsal midline, a gently arched suprasylvian sulcus that approximately paralleled the rhinal fissure, and an ectolateral sulcus that in three of the six specimens I examined extended rostrally to contact the suprasylvian sulcus. In addition, there was a short, variably developed entolateral or postlateral sulcus that is sometimes confluent with the caudal end of the coronolateral sulcus, a short sulcal notch in the caudal border of the temporal lobe between the ends of the ectolateral and suprasylvian sulci, and finally, in some spec-

imens, variably developed dimples under the suprasylvian sulcus that mark the beginnings of an ectosylvian sulcus. In one of the *Daphoenus* endocasts (PU 12588), the ectosylvian sulcus is expressed as a complete arch, the suprasylvian sulcus is longer and more arched than in the other specimens, and the rostral end of the coronolateral sulcus is bowed out laterally. There is not enough evidence to indicate whether the more advanced condition of neocortical folding in this specimen represents a species-specific difference, or merely one extreme of individual or intraspecific variation. The cerebellum was widely exposed, and the configurations of the vermis, with a sharply marked *fissura prima*, the ansiform lobules and the paraflocculus are discernible on *Daphoenus* endocasts.

A partly exposed natural endocast of *Daphoenictis*, from the early Oligocene, was
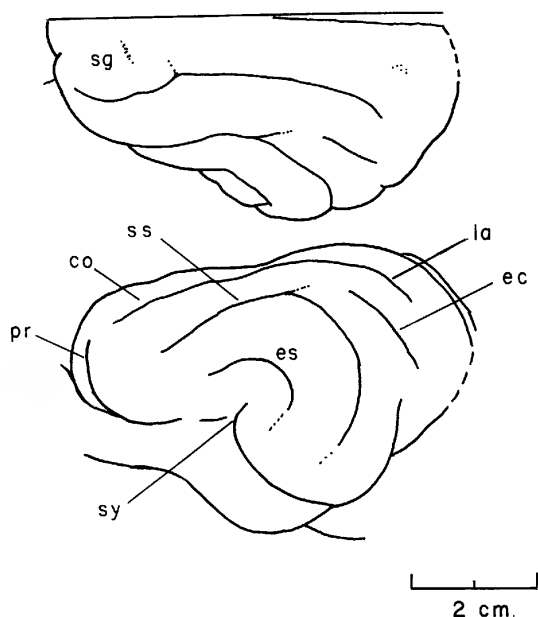
FIG. 3. *Daphoenodon superbus*. CM 1589A, ×¾. *Abbreviations*: co, coronal sulcus; ec, ectolateral sulcus; es, ectosylvian sulcus; la, lateral sulcus; pr, presylvian sulcus; sg, sigmoid gyrus; ss, suprasylvian sulcus; sy, sylvian sulcus.

briefly described by Hunt (1974, p. 1037), who noted that it had an ectolateral sulcus developed as in *Daphoenus,* with its rostral end confluent with the suprasylvian sulcus.

The brain of *Pseudocyonopsis* is known from an endocast from the French Quercy Phosphorites, described by Beaumont (1964) under the name *Amphicyon ambiguus.* (The species *A. ambiguus* was placed in *Pseudocyonopsis* by Ginsburg, 1966.) *Pseudocyonopsis ambiguus* had a neocortical sulcal pattern similar to that of *Daphoenus,* with well-developed coronolateral, ectolateral, and suprasylvian sulci. The ectolateral sulcus contacted the suprasylvian sulcus rostrally. It is not clear whether there was a notch between the caudal ends of the ectolateral and suprasylvian sulci. The brain of *Pseudocyonopsis* was a bit more advanced than that of *Daphoenus* in having a longer entolateral sulcus, a more arched suprasylvian sulcus, a better developed ectosylvian sulcus, and a notch at the junction of anterior

and posterior limbs of the rhinal fissure that suggests incipient development of a sylvian sulcus. In addition, there was a presylvian sulcus delimiting a portion of the frontal lobe, the coronal sulci were bowed out laterally, and there is a small depression in the dorsal midline that suggests incipient development of a cruciate sulcus.

An incomplete endocast of *Brachycyon,* from middle Oligocene (Stampian) deposits near Marseilles, was described by Ginsburg (1966). It suggests a brain similar to that of *Pseudocyonopsis,* with a depression marking the beginnings of a sylvian sulcus, and with a complete ectosylvian sulcus. There was a short sulcal notch between the caudal ends of the suprasylvian and ectolateral sulci (called the postlateral sulcus by Ginsburg), and a well-developed ectolateral sulcus which did not contact the suprasylvian sulcus. Ginsburg's figure indicates a small sulcus medial to the coronal sulcus, which may indicate incipient development of a cruciate sulcus.

LATER AMPHICYONIDS: A new wave of amphicyonids appeared in the early Miocene of North America (Arikareean, about 20 to 25 my), replacing the Oligocene daphoenines, and endocasts are now available for two genera, *Daphoenodon* and *Temnocyon.* The brain of *Daphoenodon superbus* (fig. 3) is known from two endocasts, AM 27568 and CM 1589A. It appears to have been at a similar stage as that of *Pseudocyonopsis* and *Brachycyon,* with incipient sylvian and well-developed ectosylvian sulci, a relatively long and arched suprasylvian sulcus (compared to *Daphoenus*), a presylvian sulcus, and beginnings of expansion of the sigmoid gyri (= cortex between the coronal sulci). A transversely oriented depression within the sigmoid gyrus may represent incipient development of a cruciate sulcus. The ectolateral sulcus did not contact the suprasylvian sulcus, there was a sulcal notch between the caudal ends of the ectolateral and suprasylvian sulci, and the entolateral sulcus was not well developed. Details of cerebellar morphology are blurred on the endocasts of *Daphoenodon* and the other post-Oligocene amphicyonids, presumably owing to their
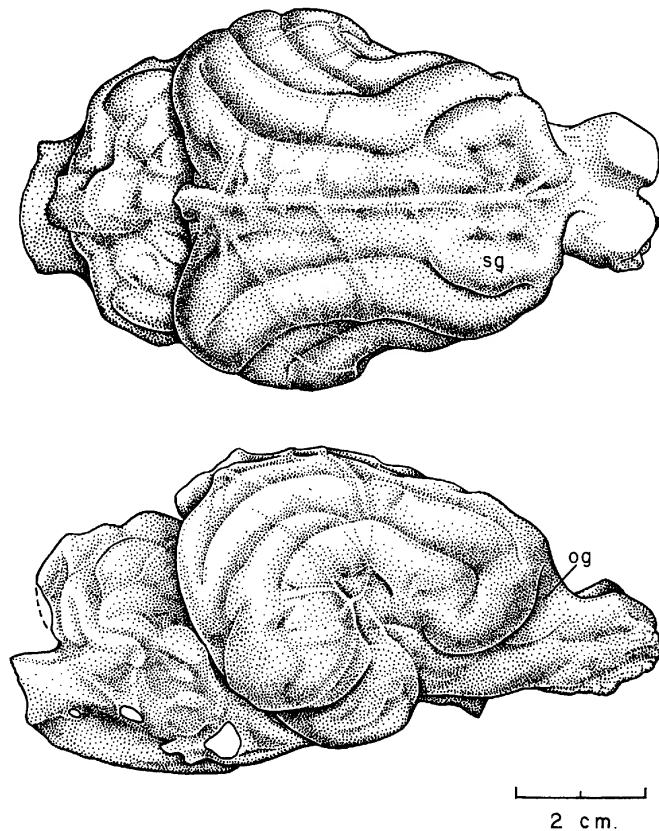
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FIG. 4.   *Cynelos rugosidens,* from the Gervais skull (MNHN), ×¾. *Abbreviations*: og, orbital gyrus; sg, sigmoid gyrus.

relatively large size. The endocast from AM 27568 is larger than that of CM 1589A, and shows more neocortex between the suprasylvian sulcus and rhinal fissure.

The one endocast known for *Temnocyon* (F:AM 54134) suggests a brain similar to that of *Daphoenodon.* The frontal region is shattered in F:AM 54134, but one portion preserves the imprint of a short sulcus that extended rostrolaterally from the dorsal midline in the middle of the sigmoid gyrus, and probably represents the cruciate sulcus.

Endocasts of European amphicyonids that were approximate contemporaries of *Daphoenodon* and *Temnocyon* are known for species of *Cynelos* and *Ysengrinia,* from the French St. Gerand-le-Puy Aquitanian deposits (about 25 my). An excellent *Cynelos* endocast was first described by Gervais (1872),

under the name *Cephalogale rugosidens,* then figured by Edinger (1929, fig. 127) as *Amphicyon* (*Cephalogale*) *rugosidens,* by Piveteau (1961, p. 814) as *Amphicyon ambiguus,* and by Beaumont (1962) as "*Amphicyon*" cf. *rugosidens.* A second *Cynelos* endocast, from a skull referred to as the Julien skull by Hunt (1977), is also now available.

The brain of *Cynelos* (fig. 4) was slightly more advanced than that of *Daphoenodon* in having a more expanded sigmoid gyrus (cortex medial to coronal sulcus), with variably developed dimples suggesting incipient subdivisions, and a more expanded orbital gyrus (rostral to the presylvian sulcus). The sylvian sulcus is represented by a short notch, and the ectosylvian and suprasylvian sulci were about as tightly arched as in the more ad-
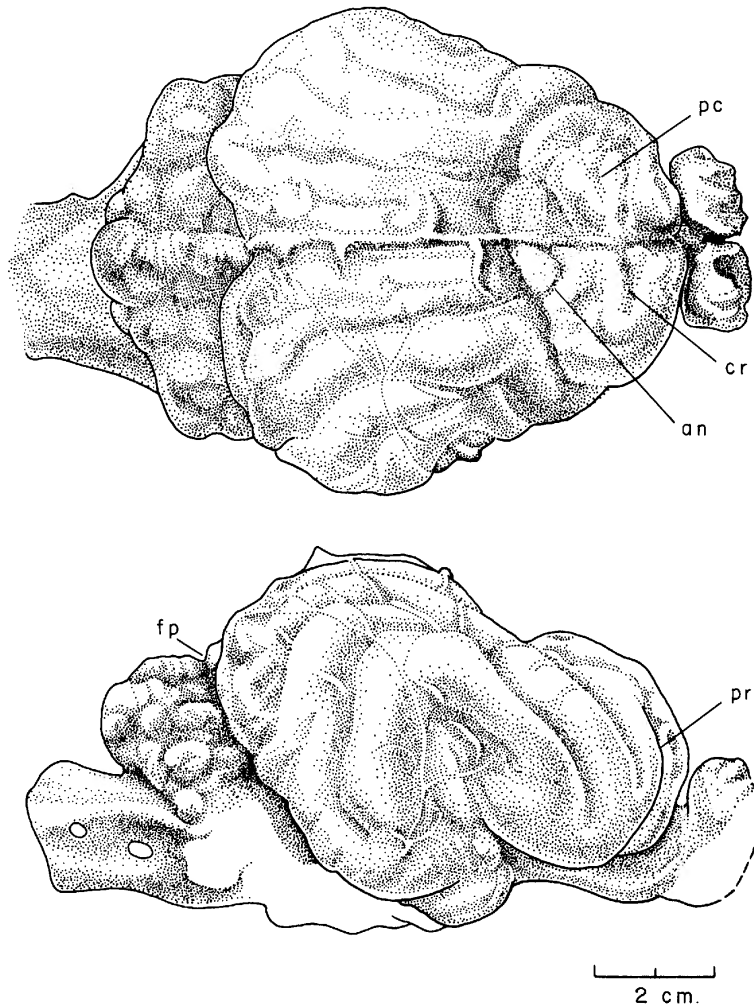
FIG. 5. *Pliocyon* cf. *P. medius*. F:AM 54334, ×¾. *Abbreviations*: an, ansate sulcus; cr, cruciate sulcus; fp, *fissura prima*; pc, postcruciate dimple; pr, presylvian sulcus.

vanced of the two *Daphoenodon* endocasts (AM 27568). The ectolateral sulcus contacted the suprasylvian sulcus in one but not the other of the two *Cynelos* endocasts, and the entolateral sulcus was moderately well developed in one but absent in the other.

The endocast of *Ysengrinia* preserves only a portion of the frontal lobe and olfactory bulb, and appears similar to corresponding portions of the *Cynelos* endocasts. The sigmoid gyrus was equally expanded, and subdivided by secondary dimples.

The next record of amphicyonid brains is a partial endocast of *Amphicyon*, from the

Thomas Farm middle Miocene (about 18 my). It shows relatively longer and more tightly arched ectosylvian and suprasylvian sulci, and a more sunken-in insular region (within the arch of the ectosylvian sulcus), than in the older amphicyonid endocasts, suggesting a higher and more rostrocaudally compressed brain. The lateral gyrus was relatively narrow and there is no trace of an entolateral sulcus. The frontal region is not preserved on this endocast, but a short section of the coronal sulcus is present, and its curvature suggests that the sigmoid gyri were expanded at least as much as in *Cynelos*.

Still more recent amphicyonid endocasts are known from the Barstovian late Miocene (around 12 to 16 my), from *Pliocyon* cf. *P. medius* and *Amphicyon frendens*. The *Pliocyon* endocast (F:AM 54334) is an excellent specimen, with slight damage only in the frontal region (see fig. 5). It indicates that the brain of *Pliocyon* was advanced over that of *Cynelos* and the older amphicyonids in having a more expanded frontal lobe. Expansion of the sigmoid gyri is reflected in the bowed-out coronal sulci, the appearance of an ansate sulcus, a laterally extending cruciate sulcus, and a dimple representing the postcruciate sulcus. A long presylvian sulcus delimited an expanded orbital gyrus. The ectosylvian and suprasylvian sulci were relatively long and tightly arched, as in the older Thomas Farm *Amphicyon* endocast described above, and there was a short sylvian sulcus. The lateral gyrus was relatively broad, and was subdivided by an entolateral sulcus. The occipital lobe overlapped the cerebellum more than in the older amphicyonids, extending to about the level of the *fissura prima* of the vermis.

The endocast of *Amphicyon frendens* (F:AM 54415) is dorsoventrally crushed and also shattered in the frontal region. From what is preserved, it appears that the sigmoid gyri were not expanded around a transversely oriented cruciate sulcus as in *Pliocyon*, but rather were dimpled, as in *Cynelos*. The lateral gyrus is relatively narrow, with no trace of an entolateral sulcus, and the occipital lobe did not cover as much of the cerebellum as in *Pliocyon*.

The youngest amphicyonid endocast available is from an undescribed braincase (amphicyonine, sp. indet., AM 2792), probably from Clarendonian deposits (10–12 my). It is damaged in the occipital region and lacks the cerebellum. In preserved portions it resembles the *Pliocyon* endocast, and shows nicely the sigmoid gyri expanded around a rostralaterally oriented cruciate sulcus.

DISCUSSION

EVOLUTIONARY TRENDS: The main evolutionary trends seen in the fossil record of amphicyonid brains are expansion and increased folding of the neocortex, and increase in relative brain size. Expansion and increased folding of the neocortex are nicely illustrated by a morphological series of endocasts of *Daphoenus-Cynelos-Pliocyon* (fig. 6). Note the appearance and expansion of the orbital gyrus; the expansion of the sigmoid gyrus, reflected in the bowing out of the coronal sulcus and the eventual development of a cruciate sulcus; the lengthening and increasingly tight folding of the suprasylvian and ectolateral sulci, and the appearance of ectosylvian and sylvian sulci as the temporal lobe (and frontal lobe) expanded; and the increasing overlap of cerebellum by cerebrum. Similar trends in neocortical expansion patterns can be seen in other families of carnivorans (see, e.g., Radinsky, 1973, 1975a), and the cruciate sulcus evolved independently at least five times (Radinsky, 1971).

The expansion and increased folding of neocortex appears to indicate an increase in relative amount of neocortex (compared to rest of brain). However, that might not be the case. The apparent increase in relative amount of neocortex may be accounted for, at least in part, by allometry—in particular, the scaling relationships of surface area to volume. Brains of later amphicyonids were larger than those of early amphicyonids, in part owing to the larger body size of the later species, and in part to the trend towards increasing relative brain size (see table 1). As noted by Le Gros Clark (1947, and references cited therein), the neocortex is organized as a thin sheet, and can increase only by areal expansion, while the underlying subcortical matter expands as a volume. With increasing brain size there is relatively less surface area (since surface area is proportional to a radius squared while volume is proportional to a radius cubed), and for the neocortex sheet to keep pace, in volume, with the increasing volume of subcortical tissue, it must expand disproportionately areally. This is reflected in increased folding and apparent relative expansion of the neocortex over the rest of the brain with increasing brain size. Whether there was an actual in-

TABLE 1
Relative Brain Size in Amphicyonids

	Endocast Volume (cm^3)	Skull Length (SL, cm)	Body Length (cm)	Estimated Body Weight (gm)[a]	Encephalization Quotient (EQ)[b]
Daphoenus hartshorni-anus[c]	56 (AM 9757; SDSM 51121)	16.5	5.6 SL[d] = 92.4	18,594	0.64
Daphoenus vetus[c]	65[r] (PU 12588)	18.5	5.6 SL[d] = 103.6	25,411	0.61
Pseudocyonopsis ambiguus	68[r] (GEN)	17.5[r]	5.6 SL[e] = 98	21,834	0.70
Cynelos rugosidens[c]	115 (LY)	24	5.0 SL[f] = 120	37,954	0.82
Daphoenodon superbus	133[r] (CM 1589)	22.8	5.2 SL[g] = 118.6	36,723	0.97
Pliocyon cf. *P. medius*	240 (F:AM 54334)	29.3[r]	4.5–5.0 SL[h] = 131.9–146.5	49,080–65,438	1.19–1.44

[a] From the relationship between body length (L) and body weight (P) in 54 species of modern carnivores: P = 0.080 L$^{2.73}$ (Radinsky, 1978, p. 820).

[b] The Encephalization Quotient (EQ) of a species is its brain size (E, gm or cm^3) divided by the brain size expected in the average living mammal of that species' body weight (P, gm). In the average living animal, E = 0.12 P$^{0.67}$. Thus $EQ_i = E_i/0.12\ P_i^{0.67}$. In a large suite of modern carnivores, EQ ranges from 0.53 to 1.60 (Radinsky, 1978, p. 823).

[c] EQ estimates for these species differ slightly from those given in Radinsky, 1978, because additional data on skeletal dimensions allow improved estimates of body weights.

[d] Proportions from Scott and Jepsen, 1936, p. 74.

[e] Body proportions modeled after *Daphoenus*.

[f] Proportions from Ginsburg, 1977, p. 42.

[g] Proportions from Romer, 1966, p. 237.

[h] Modeled after *Cynelos* (Ginsburg, 1977) and *Amphicyon major* (Bergounioux and Crouzel, 1973).

[r] = restored.

crease in relative volume of neocortex compared to the rest of the brain in amphicyonid brain evolution cannot be determined from the available data.

The parallel evolution of the same general pattern of neocortical convolutions with increasing brain size in various carnivoran lines—in particular, the pattern of arcuate folds arranged concentrically around the sylvian sulcus—may reflect constraints on folding patterns imposed by inheritance of a common pattern of thalamocortical connections from the Eocene common ancestor of modern carnivorans.

Disproportionate expansion of a particular area of the neocortex may reflect specializa-tion of function (see, e.g., Welker and Campos, 1963). In amphicyonid brain evolution, such relative enlargement of a cortical area is evident primarily in the region of the cruciate sulcus. The cortex around the cruciate sulcus (sigmoid gyrus) contains fore and hind limb representation in primary somatic sensory (tactile) and motor areas, and the multiple independent development of the cruciate sulcus in carnivoran brain evolution may reflect expansion of motor cortex for improved locomotor control (see discussion in Radinsky, 1971). Early stages of expansion of the sigmoid gyrus in amphicyonids were marked by dimpling of the gyrus (see figs. 3 and 4), while in canids and felids the
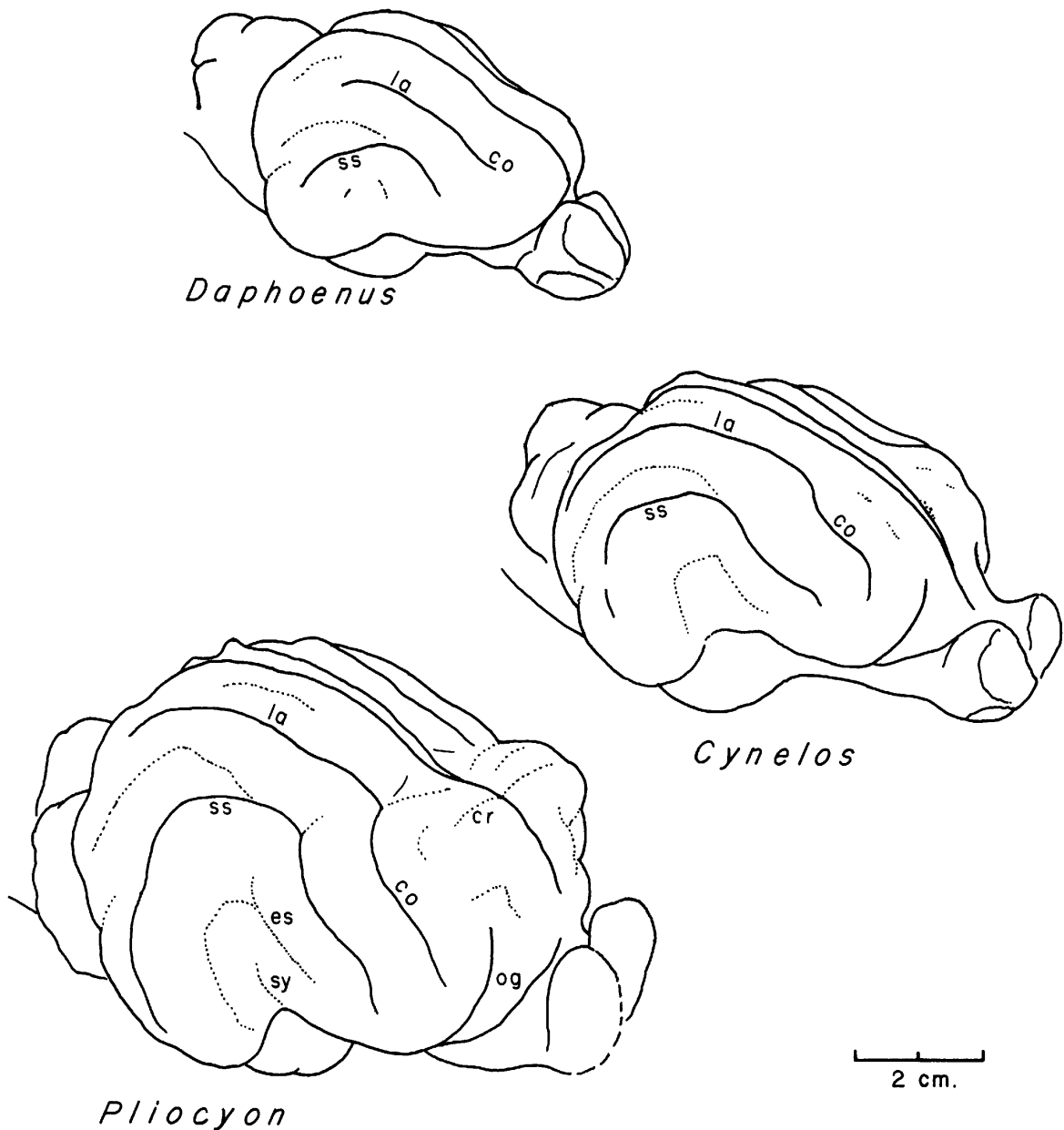
FIG. 6. Endocasts of *Daphoenus*, *Cynelos*, and *Pliocyon* to illustrate the evolutionary trend of expansion of neocortex through time. *Abbreviations*: co, coronal sulcus; cr, cruciate sulcus; es, ecto-sylvian sulcus; la, lateral sulcus; og, orbital gyrus; ss, suprasylvian sulcus; sy, sylvian sulcus. All to scale, approximately ×0.8.

only infolding was the cruciate sulcus itself (see figures in Radinsky, 1973, 1975a). The reason for that difference is not apparent. It may reflect the larger size of the amphicyonid brain (compared to canid and felid brains) when sigmoid gyrus expansion began.

The trend toward increase in relative brain size is apparent in even the small sample of amphicyonid endocasts now available to us

(table 1). The earliest amphicyonids had Encephalization Quotients (EQs) of around 0.60 to 0.70, apparently advanced over that of their Eocene miacid ancestors (0.44–0.52 for late Eocene *Procynodictis*; Radinsky, 1978). Five to 10 million years later, *Cynelos* and *Daphoenodon* had EQs of 0.82 and 0.97, respectively, which is within the EQ range of living carnivorans (Radinsky, 1978). Finally, one of the latest amphicyonids, *Pliocyon*, apparently had an EQ between 1.19 and 1.44, which is high even for modern carnivorans. Increase in relative brain size is a common evolutionary trend in mammals, and its significance remains a fascinating, open question.

PHYLOGENETIC SIGNIFICANCE: It has long been recognized that differences in cortical folding patterns distinguish various families of modern carnivorans (Mivart, 1855, and references cited therein). Canids, felids, viverrids, and the arctoid group have distinctive patterns (Radinsky, 1973, 1975a and 1975b). The brains of amphicyonids also had a distinctive pattern of cerebral convolutions, characterized by the presence of a long ectolateral sulcus that usually extended to contact the suprasylvian sulcus, a short sulcus between the caudal ends of the ectolateral and suprasylvian sulci, and, in all but the earliest species, an ectosylvian sulcus that was an unbroken arch and remained exposed (unopercularized) on the lateral surface of the brain.

An ectosylvian sulcus expressed as a complete arch evolved independently in many groups of carnivorans in addition to amphicyonids (paleofelids, canids, ursids, otariids), and in the ursids and otariids it became opercularized, buried by expansion of surrounding gyri (=a derived condition). The short sulcus between ectolateral and suprasylvian sulci occurred only in amphicyonids and, as a variable feature, in a few genera of early canids (e.g., *Mesocyon*). The ectolateral sulcus is rare among carnivorans. Besides amphicyonids, it occurs only in canids and a few species of modern mustelids (*Eira barbara, Galictis vittatus,* and *Martes flavigula*: Theide, 1966, and personal observations). In the early canids the ectolateral sul-

cus was short, and it was only around 15 my, that it appeared as extensive in canids as in amphicyonids (see figures in Radinsky, 1973). Since the ectolateral sulcus is present in only a few mustelids, it obviously evolved independently in those forms. However, the presence of an ectolateral sulcus in the earliest canids and amphicyonids is a shared derived character that may reflect inheritance from a common ancestor.

In modern canids the ectolateral sulcus appears to form the rostral border of a secondary visual field (Radinsky, 1973, fig. 11). The appearance of the ectolateral sulcus in early canids and amphicyonids may therefore reflect early expansion of visual cortex in those families. Such expansion could have occurred independently, or may have been inherited from a common ancestor shared after divergence from the other carnivorans.

Two recent experts on amphicyonids have concluded that amphicyonids are closer phylogenetically to ursids than to any other carnivorans. Hunt (1977) stressed their common possession of an enlarged inferior petrosal venous sinus that contains (or contained) a loop of the internal carotid, a specialization for cooling blood to the brain, and a unique shared derived character in ursids and amphicyonids. Ginsburg (1977) noted that feature plus other aspects of cranial circulation and limb morphology shared by ursids and amphicyonids. To me the most impressive similarity between amphicyonids and ursids is the cranial circulation modification (carotid loop in inferior petrosal sinus). If that shared derived character was inherited from a common ancestor of amphicyonids and ursids, then the ectolateral sulcus evolved independently in canids and amphicyonids (as it has done in a few recent mustelids). On the other hand, if the shared derived character of the ectolateral sulcus in canids and amphicyonids was inherited from a common ancestor, then the cranial circulatory modifications evolved independently in ursids and amphicyonids. In the absence of information on how easy it is (morphogenetically) to modify either the cortical pattern or the cranial circulation, I see no compelling argument for choosing one or the other of those

alternatives. Of course, another possibility
is that both derived features evolved inde-
pendently in amphicyonids.

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