Chapter 8

New Material of *Osbornodon* from the Early Hemingfordian of Nebraska and Florida

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ABSTRACT

New cranial and dental material from the early Hemingfordian of Florida and Nebraska permits recognition that *Tephrocyon scitulus* Hay, 1924, a poorly established taxon from the Texas Gulf Coast, belongs to the genus *Osbornodon* (Hesperocyoninae, Canidae). *O. scitulus* is a transitional species that partially fills a large morphological and stratigraphical gap within the *Osbornodon* clade. Compared to *O. renjiei* and *O. sesnoni*, *O. scitulus* possesses derived characters such as large frontal sinus, high sagittal crest, narrow infraorbital canal, short bulla, and broad premolars. *O. scitulus* differs from *O. wangi* in larger size and relatively wider P3 and shorter P4. On the other hand, *O. scitulus* is distinguishable from *O. iamonensis* and later species in its primitive characters such as rostrum not elongated, paroccipital process not expanded posteriorly, mastoid process not reduced, and p4 not differentially enlarged relative to p3.

INTRODUCTION

Osbornodon belongs to the subfamily Hesperocyoninae (Wang, 1994), a small group of archaic canids with short legs and a curious mixture of hyper- and hypocarnivorous dental morphologies. The *Osbornodon* clade is initially characterized by relatively hypocarnivorous dental features such as a basined talonid on the lower carnassial (m1) and enlargement of M2 and m2. Later species of the genus developed moderately hypercarnivorous characters such as enlarged frontal sinuses and p4 enlarged relative to p3, features paralleling some later bone-crushing borophagine canids (subfamily Borophaginae). These characters establish the *Osbornodon* clade as generally having the most hypocarnivorous dentition of the hesperocyonines. *Osbornodon* also evolved the largest size among hesperocyonines and was the last to become extinct in the early Barstovian.

Six species of *Osbornodon* are currently recognized. Members of the *Osbornodon* clade are easily identified during the late Arikareean and early Hemingfordian, when medium-sized species such as *O. iamonensis* first appear, bearing clearly recognizable characteristics of the clade. In the Whitneyan and early Arikareean, prior to the appearance of these more typical forms, two putatively ancestral species, *O. renjiei* and *O. sesnoni*, possess only some incipient characteristics of the genus (including basined talonid of m1 and enlarged second molars). There is thus a large morphological and temporal gap between the early forms and the later diverging taxa.

Recently, the University of Kansas acquired a collection of fossil mammals of early Hemingfordian age from a private collector in Florida. The excellently preserved specimens from the Miller Locality were retrieved from underwater sites in the Suwanee River of northern Florida. Represented in the Miller Locality are a partial skull and several lower jaws belonging to a transitional species

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of *Osbornodon* that bridges the morphological gap between *O. sesnoni* and *O. iamonensis*. Using the new Miller materials, a small sample of mostly fragmentary jaws in the Frick Collection of the American Museum of Natural History from Dunlap Camel Quarry, Runningwater Formation of northwestern Nebraska, can now be referred to the Florida species. Finally, knowledge derived from the combined new materials of Nebraska and Florida permits recognition that a hitherto neglected species, *Tephrocyon scitulus* Hay, 1924, based on one-and-a-half teeth from the early Hemingfordian of the Texas Gulf Coast, belongs to the same taxon.

INSTITUTIONAL ABBREVIATIONS:

F:AM   Frick Collection, American Museum of Natural History
KUVP   Natural History Museum, University of Kansas
TMM-TAMU   Texas A&M University collection in Texas Memorial Museum of University of Texas.

SYSTEMATIC PALEONTOLOGY

CLASS MAMMALIA LINNAEUS, 1785

ORDER CARNIVORA BOWDICH, 1821

SUBORDER CANIFORMIA KRETZOI, 1943

INFRAORDER CYNOIDEA FLOWER, 1869

FAMILY CANIDAE FISCHER DE WALDHEIM, 1817

SUBFAMILY HESPEROCYONINAE MARTIN, 1989

Osbornodon Wang, 1994

Osbornodon scitulus (Hay, 1924)

Tephrocyon scitulus Hay, 1924: 3, pl. I, figs. 2, 3.
Cynodesmus scitulus (Hay, 1924): Hesse, 1943: 167.
Cynodesmus iamonensis (Sellards, 1916): Wilson, 1960: 986.

HOLOTYPE: TMM-TAMU 2380, right maxillary fragment with P3 alveolus, P4 and partial M1 (fig. 8.1).

TYPE LOCALITY: TAMU locality 20, Garvin Gully, Oakville Formation (early Hemingfordian), 1.5 miles northeast of Navasota, Grimes County, Texas (Hesse, 1943). The Garvin Gully local fauna is correlative with faunas in the Runningwater Formation of
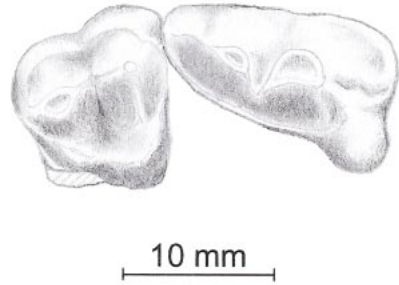

10 mm

Fig. 8.1. Occlusal view of TMM-TAMU 2380, holotype of *Osbornodon scitulus* (Hay, 1924) from Garvin Gully, Grimes County, Texas.

Nebraska and the Thomas Farm Local Fauna of Florida (Tedford et al., 1987).

REFERRED SPECIMENS: Miller Locality (early Hemingfordian), Suwannee River, Dixie? County, Florida: KUVP 114471, left ramal fragment with c1–p1 alveoli and p2–m1; KUVP 114475, left maxillary fragment with P3 alveolus, P4–M1, and M2 alveolus (fig. 8.3B); KUVP 114497, partial skull with right P2–M1 and M2 alveolus and alveoli of left C–M2 (fig. 8.2); KUVP 114506, partial right ramus with c–p1 alveoli and p2–m2 (fig. 8.3C, D); and KUVP 114517, partial right ramus with c–p1 alveoli, p2–m2, and m3 alveolus.

From Dunlap Camel Quarry, Runningwater Formation (early Hemingfordian), Dawes County, Nebraska: F:AM 61302, right isolated P4 (fig. 8.3A); F:AM 61302A, maxillary fragment with M1–2 (possibly belonging to the same individual as F:AM 61302; fig. 8.3A); F:AM 61304, left partial ramus with c–p2 alveoli, p3–m2, and m3 alveolus; F:AM 61305, left partial ramus with p1 alveolus–m1 and m2–m3 alveoli; F:AM 61306, right partial ramus with c broken–m2 and m3 alveolus; F:AM 61307, left partial ramus with p1 alveolus, p2 broken, and p3–m2; F:AM 61308, left partial ramus with p3 alveolus–m1 and m2–m3 alveoli; F:AM 61309, left partial ramus with p1 and p3–p4 (p2 and m1–m3 alveoli); and F:AM 61310, right partial ramus with p1 alveolus, p2–p3 both broken, and p4–m2.

EMENDED DIAGNOSIS: *Osbornodon scitulus* is readily distinguished from earlier species,
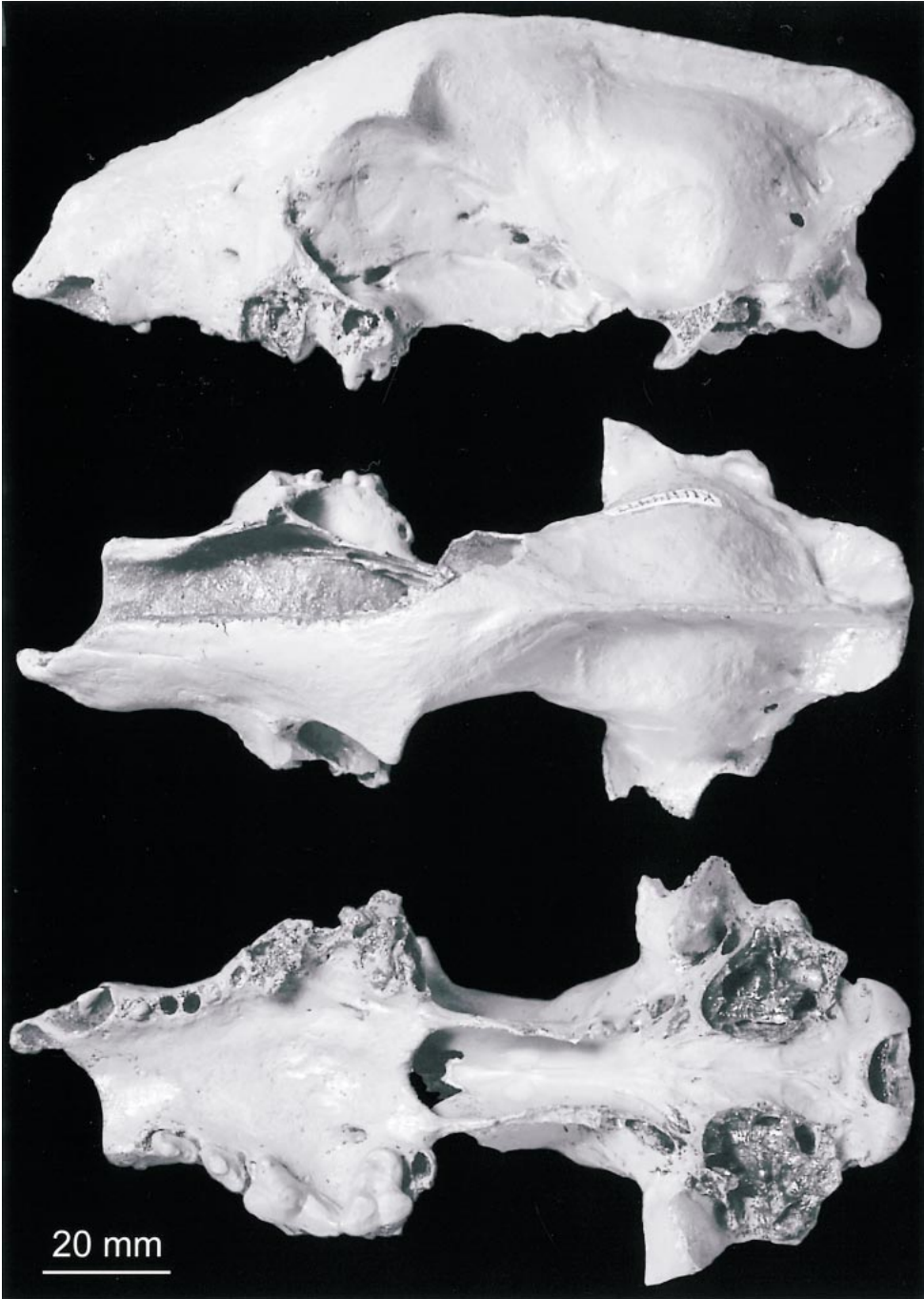
Fig. 8.2.　Lateral, dorsal, and ventral views of skull of *Osbornodon scitulus* (Hay, 1924), KUVP 114497 from Miller Locality, Florida.
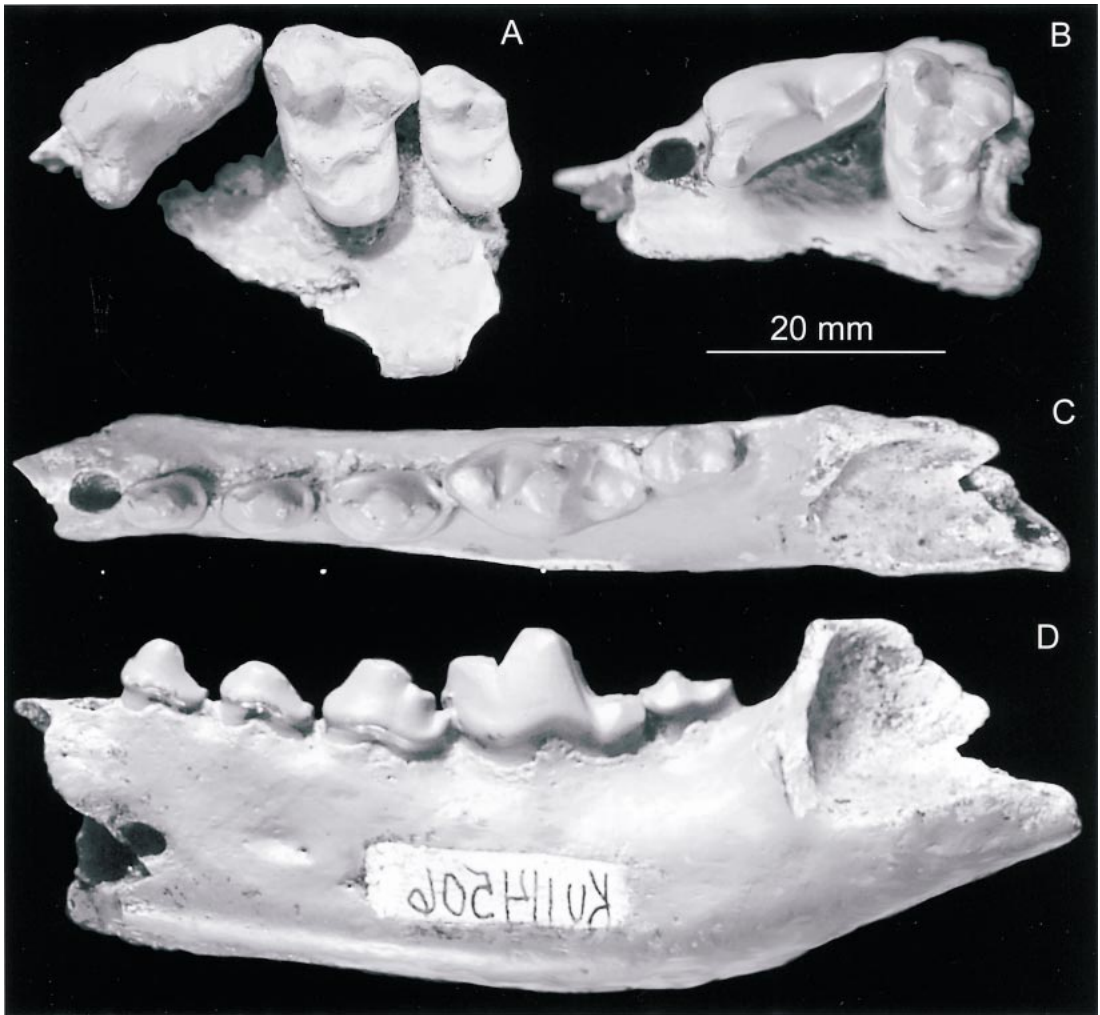
Fig. 8.3. Teeth of *Osbornodon scitulus* (Hay, 1924). **A,** Occlusal view of P4 (F:AM 61302) and M1–2 (F:AM 61302A) from Dunlap Camel Quarry (all reversed from right side). **B,** Occlusal view of P4–M1 (KUVP 114475) from Miller Locality. Occlusal (**C**) and lateral (**D**) views of lower jaw and teeth (KUVP 114506) from Miller Locality (both reversed from right side).

O. renjiei and *O. sesnoni*, in its possession of several derived cranial and dental characters: larger size, presence of a large frontal sinus and domed forehead, high sagittal crest, vertically narrowed infraorbital canal, shortened bulla, baseline of P3 offset from that of P4, and shortened and widened lower premolars. On the other hand, *O. scitulus* differs from *O. iamonensis*, *O. brachypus*, and *O. fricki* in its relatively primitive morphology: smaller size, rostrum not elongated, infraorbital canal not narrowed to a thin slit,

paroccipital not posteriorly expanded, mastoid process not reduced, and p4 not prominently enlarged relative to p3.

DESCRIPTION AND COMPARISON: Cranial morphology is based entirely on KUVP 114497, a partial skull missing only the upper right half of the snout and forehead (fig. 8.2). Although this skull is incomplete, much of the morphology is preserved at least on one half, except the frontmost part of premaxillary, zygomatic arch, and ventral halves of the bullae. When preserved, the
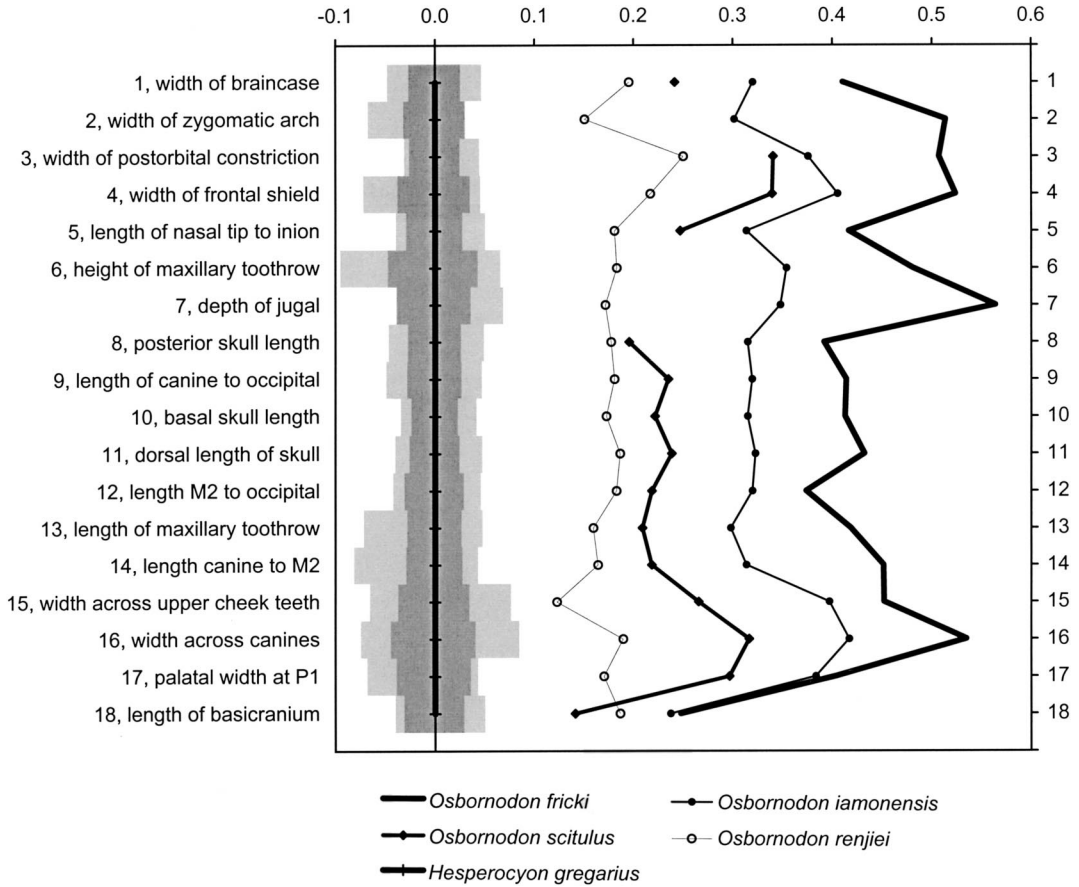
Fig. 8.4. Log-ratio diagram (sensu Simpson, 1941) of cranial measurements for species of *Osbornodon*, using *Hesperocyon gregarius* as standard (straight line at zero axis). See Wang (1994) for definitions of measurements and data on other species of *Osbornodon*. Darkly shaded bars represent one standard deviation above and below the means and lightly shaded bars represent upper and lower ranges for *Hesperocyon gregarius*.

bones are in excellent condition and are completely undistorted. The following descriptions and comparisons mainly use morphological characters that have been proven useful in the phylogeny of *Osbornodon* (Wang, 1994).

Skull (figs. 8.2, 8.4). KUVP 114497 is a medium-sized hesperocyonine. The rostrum is short, in contrast to the elongated state in more derived *Osbornodon*. The nasal process of the premaxillary is not in contact with the frontal, but is separated by the nasal-maxillary suture of about 10 mm long. This is characteristic of the hesperocyonines, in contrast to most borophagines in which premaxillary and frontal meet. The cross section of

the infraorbital foramen is oval shaped, measuring 4.7 × 2.4 mm in its long (vertical) and short (horizontal) axes, a condition intermediate between *O. sesnoni* and *O. iamonensis*. In lateral view, the skull is prominently domed at its forehead, due to the enlargement of frontal sinuses. This approaches the condition in *O. iamonensis*, but is in sharp contrast to the flat forehead in *O. sesnoni*. The breakage at the right forehead allows unobscured observation of the sinus development. The frontal sinus expands posteriorly to the frontal-parietal suture or slightly beyond, causing a posteriorly shifted postorbital constriction. At its maximum depth, the sinus is more than 16 mm deep just be-

low the highest point of the forehead. The postorbital process of the frontal is incomplete. Judging from the remaining parts, the frontal sinus probably penetrated into the process. The sinus is partially partitioned by a median septum at the posterior end. The sagittal crest is high and is formed by a thin blade at least 7 mm on top of the braincase. The nuchal crest is fan shaped in posterior view and slightly overhangs the occipital condyles.

Except the missing tympanic bones, the basicranium is well preserved. The bulla is short with its anterior margin beginning at the posterior border of the glenoid fossa, a derived character shared by all late *Osbornodon*. The mastoid process is not depressed, as it is in *O. iamonensis* and later diverging taxa. Although both paroccipital processes are broken near the bases, the remaining parts suggest that the processes are not posteriorly expanded as in *O. iamonensis* and further elaborated in *O. fricki*.

The lower jaw is robust, especially in its breadth, in contrast to the more slender ramus in the canine canids. The horizontal ramus is nearly of identical depth along much of the cheek teeth region. There are two mental foramina, the anterior one between the two roots of the p2 and the posterior one generally between the p3 and p4. The ascending ramus is mostly not preserved. The masseteric fossa is deep and slightly pocketed at its lower border, a character that is further developed in *Osbornodon brachypus*.

Cranial Measurements (defined in Wang, 1994): Width of braincase: 49.5 mm; width of postorbital constriction: 26.1; width of frontal shield: 37.4; length of nasal tip to inion: 145.8; length of posterior skull: 99.6; length of canine to occipital: 140.3; basal skull length: 146.2; dorsal length of skull: 154.0; length of M2 to occipital: 76.0; length of maxillary toothrow: 50.0; length of canine to M2: 60.0; width across upper cheek teeth: 51.0; width across canines: 30.0; palatal width at P1: 19.0; length of basicranium: 35.5.

Teeth (figs. 8.1, 8.3, 8.5): No upper incisor is known. The partial I3 alveolus on KUVP 114497 indicates a rather large I3. Consistent with its relatively short rostrum,

the upper premolars are closely spaced with slight imbrication between P2 and P3. The P2 is two-rooted with a small anterior accessory cusp located on the anterolingual corner. There are an indistinct posterior accessory and a cingular cusp. The left P3 on KUVP 114497 (broken off) has two roots, whereas the right P3 has three, with the third root located on the lingual side of the tooth. This extra root supports a small bulge in the middle of the tooth and is responsible for a significantly wider P3 than most other species of *Osbornodon* (fig. 8.5). In lateral view, there is a slight offset between the horizontal baselines of the P3 and P4, more so in the holotype. The degree of this offset in KUVP 114497, however, is no more than that in *O. sesnoni*, in contrast to more prominent offsets in *O. iamonensis* and later species. P4–M3 are present in all three localities of *O. scitulus* (Garvin Gully, Miller, and Dunlap Camel). The P4 has a moderately developed lingual cingulum in all specimens, and the labial cingulum generally is indistinct. The protocone is closely appressed to the base of the paracone and leads to a ridge on the latter cusp. There is an incipient development of a parastyle formed at the junction of an anterior cingulum and a well-developed anterior ridge on the paracone, although this parastyle is not a fully formed cusp as is often seen in the borophagine canids. The M1 is transversely wider than it is long and is constricted on the posterior border, in contrast to the more quadrate outlines in the M1s of borophagines. The parastyle is reduced. The paracone is higher than the metacone. The metaconule is small and located at the base of the metacone, in contrast to generally larger and more lingually positioned metaconules in borophagines. The lingual cingulum (hypocone) is restricted to the posterolingual corner of the tooth rather than more anteriorly extended as in the borophagines. On F:AM 61302A, the cingulum also shows a tendency of becoming a cusp with slight enlargement along the middle section of the cingulum and a low peak on top of this enlargement. M2 is preserved only in F:AM 61302A. It is relatively large, as is typical of species of *Osbornodon*, in contrast to the
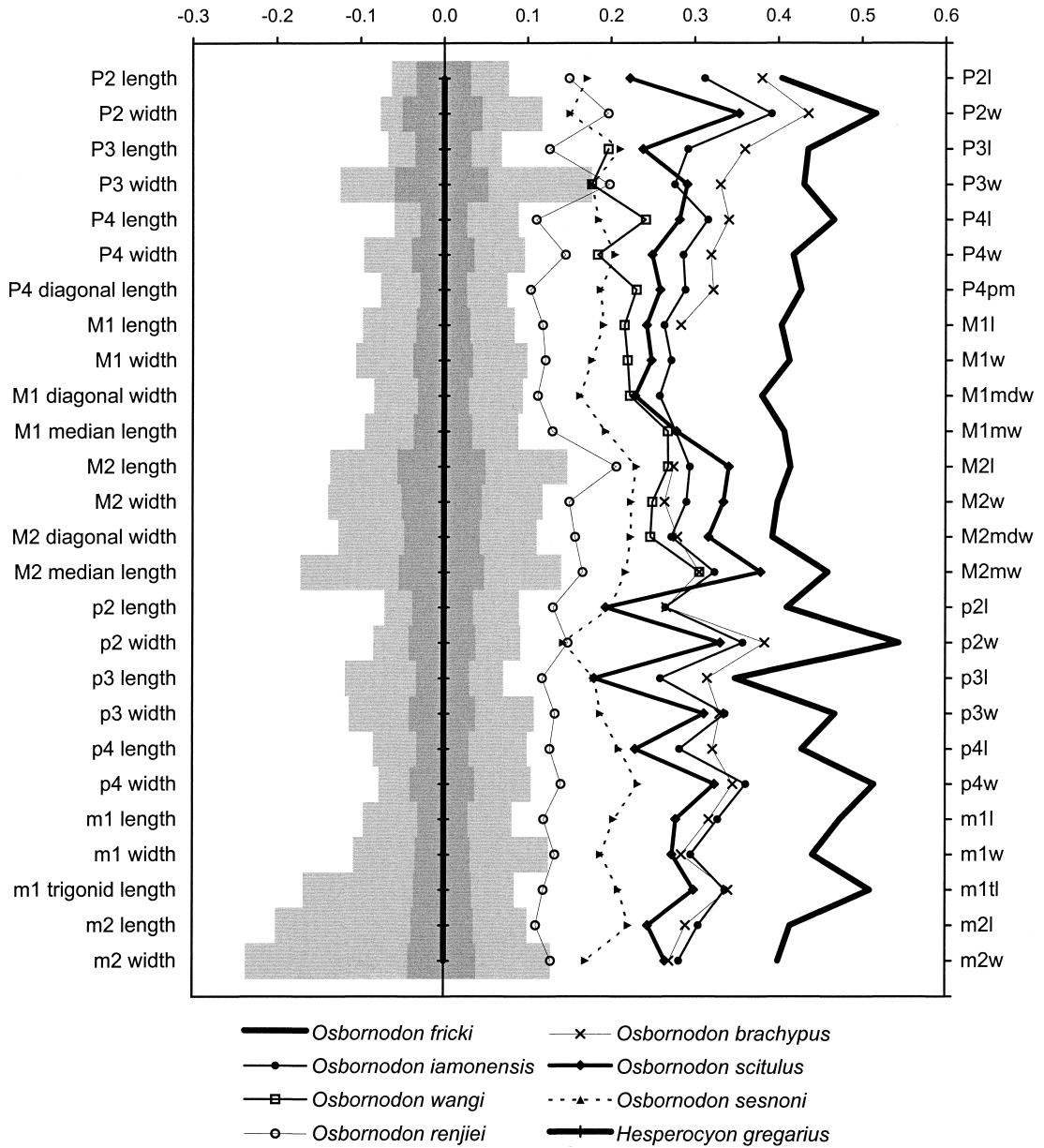
Fig. 8.5. Log-ratio diagram (sensu Simpson, 1941) of dental measurements for species of *Osbornodon*, using *Hesperocyon gregarius* as standard (straight line at zero axis). See tables 8.1 and 8.2 for dental measurements of *O. scitulus* and Wang (1994) for definitions of measurements and data on other species of *Osbornodon*. Darkly shaded bars represent one standard deviation above and below the means and lightly shaded bars represent upper and lower ranges for *Hesperocyon gregarius*.

opposite trend in most other hesperocyonines. The apparently large size of M2 relative to M1 in *O. scitulus* as plotted in figure 8.5 may reflect that F:AM 61302A, the only M2 in *O. scitulus*, is a large individual. The M2 has an oval occlusal outline and a broad and low posterolingual cingulum. The parastyle is relatively well developed, but the metastyle is reduced. The metaconule is also extremely reduced, and

represented by a tiny swelling at the posterior end of the postprotocrista.

No lower incisors are preserved. Alveoli for the lower canines indicate an oval cross section for the roots. The p1 has one root (alveolus only). The p2 is double rooted and has a single main cusp. The anterior and posterior cingular cusps are represented by faint swellings at the base of the main cusp. The p3 has a small, but distinct, posterior accessory cusp (present in KUVP 114517 and 114471 but absent in KUVP 114506), and the cingular cusps remain indistinct as in the p2. The p4 has further enlargement of the posterior accessory cusp just behind the main cusp. The posterior cingular cusp also begins to take the shape of a small cusp, although the anterior accessory cusp is still largely indistinct. On KUVP 114517, there is a tiny ''metaconid'' at the posterolingual base of the main cusp on the p4. The p4 on KUVP 114471, on the other hand, apparently had suffered from periodontal disease, and its anterior root and the surrounding dentary are severely eroded. The lower carnassial (m1) has the mesocarnivorous construction typical of the genus. The cutting blade is not markedly elongated as is in the Caninae. Cingula on labial and lingual sides are either indistinct or lacking. The basined talonid has the entoconid and hypoconid nearly equal-size, with the entoconid slightly taller than hypoconid in unworn specimens. The crestlike entoconid and hypoconid are mostly anteroposteriorly oriented, with the hypoconid directed slightly more lingually than the entoconid, and enclosing a longitudinal basin, which opens posteriorly. The entoconid and hypoconid show no sign of transverse cristids that are commonly seen in derived borophagines and canines. The m2 is relatively short and has little or no cingulum except at the anterolabial corner. There is a short platform at the location of the paraconid on KUVP 114506, which is not present in KUVP 114517. Wear on the m2s makes it difficult to judge the relative heights of the protoconid versus metaconid and the hypoconid versus entoconid. The m3 is absent in KUVP 114506 but present in KUVP 114517 (represented by double-rooted alveoli).

COMPARISONS: Despite possession of a bicuspid talonid, specimens described in this paper apparently do not belong to the subfamily Caninae. *Osbornodon scitulus* lacks all of the synapomorphies shared by the Caninae: slender rostrum and ramus, presence of diastemata between premolars, narrow premolars, elongated carnassials, and so forth (see Tedford et al., 1995). Differences between *Osbornodon* and certain contemporaneous borophagines are more subtle but still noticeable. Generally borophagines have more quadrate upper molars with a reduced parastyle, well-developed metaconules, and a broad internal cingulum that tends to surround the protocone. Borophagines also tend to have better-developed accessory and cingular cusps on the premolars. Hemingfordian borophagines, however, have not developed the highly domed forehead due to a large frontal sinus that is found in *Osbornodon* (eventually late Miocene borophagines exceeded all other canids in the development of frontal sinuses).

One particular borophagine, *Desmocyon matthewi*, deserves further comparisons. This relatively primitive borophagine is approximately the same size as *Osbornodon scitulus* and is also found in the Miller Locality in Florida and in the Runningwater Formation (but not in the Dunlap Camel Quarry) in Nebraska. In addition to the general distinctions between borophagines and hesperocyonines as outlined above, these two species can be differentiated further on the following characters. *D. matthewi* has an elongated premaxillary that is in contact with the nasal process of the frontal, a unique synapomorphy uniting all borophagines above *Desmocyon*. *Osbornodon*, on the other hand, retains the primitive condition of this character (i.e., no contact of the two bones). Other cranial features of *Osbornodon* useful in its diagnosis against *Desmocyon* include the following: a vertically narrowed infraorbital canal, better developed sagittal crest, more posteriorly extended nuchal crest, and a less posteriorly expanded paroccipital process (compare Wang et al., 1999: fig. 45). Dentally, *Osbornodon* has, relative to *Desmocyon*, a less salient P4 protocone, and lacks transverse cristids between the talonid cusps of the m1.

Potentially even more confusing is *Des-*

mocyon thomsoni, a slightly smaller boro-phagine ancestral to *D. matthewi*. Although *D. thomsoni* is generally chronologically earlier (late Arikareean through early Hemingfordian) than *D. matthewi*, they both occur in the Runningwater Formation but tend to be found in separate horizons (see Wang et al., 1999: 100). Furthermore, *D. thomsoni* lacks two derived characters present in *D. matthewi*: premaxillary meeting frontal and transverse cristid on m1 talonid. Besides these two characters, the above distinctions between *D. matthewi* and *Osbornodon scitulus* can still be applied to the differentiation of *D. thomsoni* and *O. scitulus*, although fragmentary materials are likely to be difficult to distinguish.

DISCUSSION: Since its first description by Hay (1924), no additional material of *Osbornodon scitulus* has been recovered from the type locality in Garvin Gully. Nor has this species received much attention in later studies. The meager one-and-a-half-tooth holotype (TMM-TAMU 2380) has certainly contributed to its obscurity since its initial publication. Hesse (1943) briefly mentioned this species and referred it to *Cynodesmus*, following the then prevalent taxonomic convention (see Wang, 1994, for further discussions about the genus). Wilson (1960) further assigned the Texas specimen to *Cynodesmus iamonensis* (Sellards, 1916), which was originally named on the basis of a maxillary fragment from a well in Griscom Plantation, Florida, now regarded as stratigraphically equivalent to the Hemingfordian Thomas Farm quarry (Bryant et al., 1992). Although *Osbornodon iamonensis* is much larger and morphologically more derived than *O. scitulus* (see below), Wilson's assignment came closest to place the Garvin Gully canid into proper phylogenetic perspective. In his original descriptions, Hay (1924: 3) expressed uncertainties with regard to the identity of this species: "Inasmuch as it appears not to agree with any of the known species it is described as *Tephrocyon scitulus*." He went on to note the size differences between *T. scitulus* and the type species of *Tephrocyon*, *T. rurestris*. The latter, along with other species that Hay had compared, is now known to be a mesocarnivorous borophagine (Wang et al., 1999).

Despite its poor preservation, the M1 of the holotype has an anteroposteriorly short "waist" area with a distinct constricted posterior border behind the metaconule. This posterior constriction, coupled with the poorly developed metaconule, tends to distinguish it from similar-sized Borophaginae and Caninae, and points to the more archaic Hesperocyoninae. Several subtle features of TMM-TAMU 2380 further indicate an affinity to *Osbornodon*. First, the lower alveolar border of the P3 is set off from that of the P4 (see Hay, 1924: pl. 1, fig. 2), a character that involves the reduction of the P3 and p3 relative to the P4 and p4 seen in later *Osbornodon* (and also independently developed in later *Epicyon-Borophagus* clade). Second, the P4 on TMM-TAMU 2380 shows the beginning of a strong anterior cingulum leading down to a distinct anterior ridge on the parastyle. Such a development is commonly followed by a parastyle (pseudoparastyle) in more derived species, as is the case in *O. fricki*. Other features on TMM-TAMU 2380 that corroborate well with an assignment of *Osbornodon* are a large P4 protocone closely appressed to the base of the paracone and a reduced M1 parastyle.

If the above reasoning placing TMM-TAMU 2380 in *Osbornodon* is correct (future findings of additional materials from the type locality will afford a more critical test), it further stands to reason that the new *Osbornodon* materials from Miller Locality and Dunlap Camel Quarry are conspecific with TMM-TAMU 2380. Although both Miller and Dunlap Camel samples contain individuals that are somewhat larger than TMM-TAMU 2380 (e.g., KUVP 114497 and F:AM 61302), they seem to represent the upper extremes within the species, as other smaller individuals (e.g., KUVP 114475) are the same size as or smaller than TMM-TAMU 2380 (see tables 8.1, 8.2). The combined statistics for all three samples yield a coefficient of variation of 4.95 and 4.25 for the upper and lower carnassial teeth, respectively. Such figures are well below the variation of comparable statistics for *O. iamonensis* (7.54 and 5.32), which also includes material from both Nebraska and Florida and has an adequate sample size. Given the new state of knowledge as afforded by materials from Miller

TABLE 8.1
Measurements of Upper Teeth of *Osbornodon scitulus*
See Wang (1994) for definitions of measurements and data for other species of *Osbornodon*

	TMM-TAMU 2380	KUVP 114497	KUVP 114475	F:AM 61302	F:AM 61302a
P2 length	—	8.1	—	—	—
P2 width	—	4.3	—	—	—
P3 length	—	9.9	—	—	—
P3 width	—	5.2	—	—	—
P4 length	16.7	17.7	15.4	16.9	—
P4 width	9.4	9.7	8.9	10.1	—
P4 maximum length	18.1	19.0	17.1	18.4	—
M1 length	11.3	11.7	10.3	—	12.2
M1 width	—	13.0	12.9	—	15.1
M1 maximum diagonal width	—	15.9	14.9	—	16.7
M1 waist length	8.8	8.4	7.4	—	9.4
M2 length	—	—	—	—	7.8
M2 width	—	—	—	—	10.7
M2 maximum diagonal width	—	—	—	—	12.2
M2 waist length	—	—	—	—	7.1

Locality and Dunlap Camel Quarry, *O. scitulus* clearly occupies a transitional position between *O. wangi* and *O. iamonensis* (see phylogeny below).

PHYLOGENY

Phylogenetic analysis of *Osbornodon scitulus* is presented within the broader framework of hesperocyonine relationships of Wang (1994). The present analysis is restricted to the *Osbornodon* clade and does not attempt to address the uncertainties among different major clades of the Hesperocyoninae. Table 8.3 is a subset of the Hesperocyoninae matrix (Wang, 1994) with minor modifications of character states and polarities (character numbers do not correspond to the original matrix) and with new data from a recently described new species, *O. wangi* (Hayes, 2000). From this matrix, a single shortest tree (fig. 8.6) can be obtained with a length of 25 steps using PAUP 3.1.1 (Swofford, 1993).

Within the genus *Osbornodon*, the transitional nature of *O. scitulus* can be readily recognized. *O. scitulus* is inserted into a formerly long list of synapomorphies shared by *O. iamonensis*, *O. brachypus*, and *O. fricki* (see Wang, 1994: fig. 64). Thus *O. scitulus* possesses, on the one hand, initial developments of derived characters such as high sag-

ittal crest, frontal sinus, widened premolars, and so forth that are shared with *O. iamonensis* and later taxa, and on the other hand, is still primitive in aspects such as unelongated rostrum, unreduced mastoid process, and paroccipital process not posteriorly expanded. The recently established species *O. wangi* consisted of associated upper cheek teeth of a single individual (Hayes, 2000). Dental morphology and proportion of this medial Arikareean species from Florida indicate a taxon well within the *Osbornodon* clade. It would not be surprising if *O. wangi* has acquired some of the derived cranial characters (e.g., 2, 3, 5, 11, 15), even though my cladogram shows primitive states for lack of evidence. In other words, it is likely that morphological distance between *O. wangi* and *O. scitulus* is actually shorter than indicated by the cladogram.

The combination of primitive and derived characters in *O. scitulus* permits more accurate identification of character evolution in the *Osbornodon* clade. Such a transitional position of *O. scitulus* within *Osbornodon* can also be demonstrated in the overall cranial and dental proportions as shown in log-ratio diagrams. Among the four species with cranial measurements, the log-ratio curve for *O. scitulus* (fig. 8.4) is intermediate in many measurements. In particular, *O. sci-*

TABLE 8.2
Measurements of Lower Teeth of *Osbornodon scitulus*
See Wang (1994) for definitions of measurements and data for other species of *Osbornodon*

	KUVP 114471	KUVP 114506	KUVP 114517	F:AM 61304	F:AM 61305	F:AM 61306	F:AM 61307	F:AM 61308	F:AM 61309	F:AM 61310
c1 length	—	—	—	—	—	9.3	—	—	—	—
c1 width	—	—	—	—	—	6.7	—	—	—	—
p1 length	—	—	—	—	—	4.8	—	—	5.0	—
p1 width	—	—	—	—	—	3.6	—	—	3.4	—
p2 length	7.0	7.4	7.1	—	7.8	7.5	—	—	—	—
p2 width	3.4	4.3	3.9	—	4.8	4.4	—	—	—	—
p3 length	7.0	8.2	7.4	—	8.8	9.3	8.7	8.5	8.9	—
p3 width	3.6	4.7	4.3	—	5.4	5.3	5.3	4.7	5.0	—
p4 length	—	10.7	9.5	10.1	10.8	10.6	10.5	10.3	11.2	10.9
p4 width	4.2	6.1	5.7	6.5	6.1	6.0	5.8	5.8	6.0	5.8
m1 length	16.7	16.6	17.1	17.8	18.8	18.1	17.9	18.7	—	18.1
m1 width	6.9	8.2	7.7	8.2	8.5	8.3	7.9	7.7	—	8.1
m1 trig. leng.	10.7	11.9	12.9	12.8	12.9	13.0	12.9	12.5	—	12.6
m2 length	—	8.1	8.1	9.0	—	8.6	9.2	—	—	8.9
m2 width	—	5.7	5.4	6.6	—	6.1	6.1	—	—	6.3
m2 trig. leng.	—	4.2	4.2	5.4	—	5.3	5.3	—	—	5.1

TABLE 8.3
Character Matrix for *Osbornodon* Modified from Wang (1994: table 3)

The chararacter numbers (in parentheses) and their states are designated as follows: (1) rostrum length: 0 = short, 1 = long; (2) frontal sinus: 0 = absent, 1 = present, 2 = further enlarged; (3) infraorbital foramen: 0 = round, 1 = narrowed, 2 = slit; (4) suprameatal fossa; 0 = present, 1 = absent; (5) bulla size: 0 = not shortened, 1 = shortened; (6) paroccipital process orientation: 0 = posteriorly directed, 1 = ventrally directed, 2 = fusion with bulla; (7) paroccipital process elongation: 0 = short, 1 = elongated; (8) paroccipital process posteriorly expanded: 0 = no, 1 = expanded, 2 = further expansion; (9) mastoid process: 0 = not reduced, 1 = reduced; (10) zygomatic arch: 0 = not broadened, 1 = broadened; (11) sagittal crest: 0 = low, 1 = high and thin-bladed; (12) angular process: 0 = not expanded, 1 = vertical expansion; (13) masseteric fossa pocket: 0 = absent, 1 = present; (14) laterally shifted ascending ramus: 0 = no, 1 = yes; (15) lower premolar width: 0 = not widened, 1 = widened, 2 = narrowed; (16) p4 enlargement relative to p3: 0 = no, 1 = yes, 2 = further enlargement; (17) p4 length: 0 = short, 1 = elongated; (18) P4 parastyle: 0 = absent, 1 = present; (19) enlargement of M2 relative to M1: 0 = no, 1 = yes; (20) talonid of m1: 0 = trenchant, 1 = basined. Wang (1994) gives a more detailed explanation of character states.

| Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Hesperocyon gregarius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesperocyon coloradensis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mesocyon-Enhydrocyon clade	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osbornodon renjiei	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Osbornodon sesnoni	0	0	0	?	?	?	?	?	?	?	0	?	0	0	2	0	0	0	1	1
Osbornodon wangi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0	1	1
Osbornodon scitulus	0	1	1	1	1	2	?	0	0	?	1	0	0	0	1	0	1	1	1	1
Osbornodon iamonensis	1	1	2	1	1	2	1	1	1	0	1	1	0	0	1	1	1	1	1	1
Osbornodon brachypus	1	1	2	1	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1
Osbornodon fricki	1	2	2	1	1	2	1	2	1	1	1	1	0	0	1	2	1	2	1	1
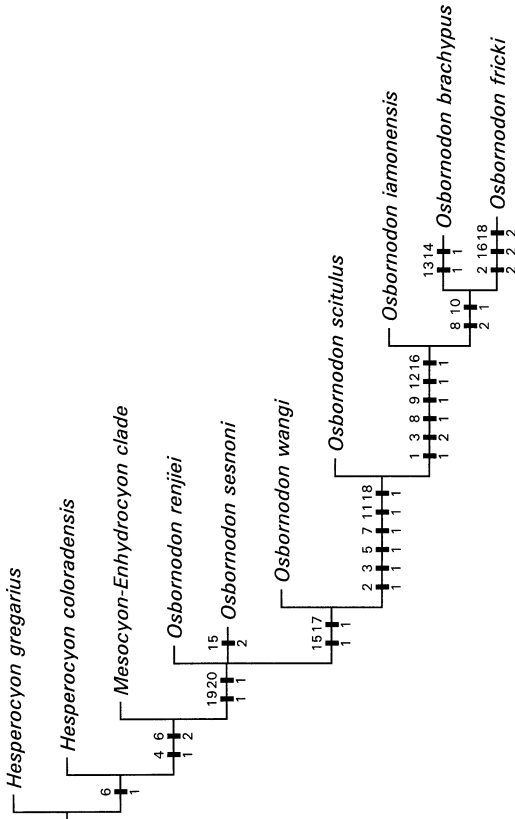
Fig. 8.6. Phylogenetic relationships of *Osbornodon* species using two species of *Hesperocyon* as outgroups, modified from Wang (1994). Character distributions are mapped by ClaDos (version 1.2 of Kevin Nixon). Phylogenetic framework for higher level groups within the family Canidae follows Tedford et al. (1995) and Wang and Tedford (1996). Character numbers above the solid bars and character states below are defined in the character matrix of table 8.3. Differing from a previous cladogram (Wang, 1994: fig. 64), basal *Osbornodon* (*O. renjiei* and *O. sesnoni*) are a trichotomy instead of being fully resolved. This is due to differences in the optimization of character 7 and recoding of character 15. I now consider the narrowed premolars as an autapomorphy for *O. sesnoni*, rather than shared by all advanced *Osbornodon*. The latter share wide but short premolars. Of the six derived characters shared by *O. scitulus* and later diverging species (2, 3, 5, 11, 15, 18), five are missing in *O. wangi* for lack of cranial material (table 8.3). Their placement below *O. scitulus* thus reflects current lack of knowledge; future discovery of more complete material of *O. wangi* will shed light on the actual occurrence of these characters.

tulus has a pattern similar to that of *O. iamonensis*: broadened frontal shield and postorbital constriction, broadened palate (across canines, P1s, and P4s), and shortened basicranium. The dental curve for *O. scitulus* (fig. 8.5) is strikingly similar to those of *O. iamonensis* and *O. fricki*, especially in widened and shortened premolars, and is in contrast to the primitive conditions in *O. renjiei* and *O. sesnoni*, which are more similar to the patterns in *Hesperocyon*. The pattern for *O. wangi* is consistent with those of later species of *Osbornodon*. One measurement that sets *O. scitulus* and *O. wangi* apart is that the former has a relatively narrow P3 compared to that of the latter. In this, *O. wangi* is more like that of *O. iamonensis* and other later species, as was noted by Hayes (2000: 33).

With the establishment of the phylogenetic relationships above, the following evolutionary trends within the *Osbornodon* clade can be observed, along with the general tendency of increasing body size through time. *Osbornodon* is characterized in its initial development by a basined talonid on m1 and slightly enlarged second molars, characters seen in *O. renjiei* but in contrast to the primitive conditions of more trenchant talonid and smaller second molars in *Hesperocyon*. Although also present in the Caninae and Borophaginae, these features are independently derived in *Osbornodon*, because it does not possess other derived characters of the canine and borophagine clades, such as a more distinct metaconule and transverse cristid on talonid cusps. From this initial divergence, *O. sesnoni* developed more slender premolars, an autapomorphic character that was incorrectly assigned as a synapomorphy of more advanced *Osbornodon* by Wang (1994). Beginning in *O. scitulus*, several trends became established: a prominent dome of the forehead due to progressive enlargement of the frontal sinuses, heightening of the sagittal crest, vertical narrowing of the infraorbital canal, shortening of the basicranial area including the bulla, and widening and shortening of the premolars. Besides further elaboration of some of above characters seen in *O. scitulus*, *O. iamonensis* is characterized by initial elongation of the

rostrum, expansion of the paroccipital process posteriorly to form a prominent posterior ridge of the process, and differential enlargement of the p4 relative to p3. *O. brachypus* diverges slightly from the above trends with its low ascending ramus, which is laterally displaced. Otherwise, it is transitional between *O. iamonensis* and the terminal species of the genus, *O. fricki*, which pushes to the extreme many of the trends established in previous species and becomes the largest and terminal taxon among hesperocyonines.

Although the new material of *Osbornodon scitulus* brings us a few morphological steps closer to the more basal species of the *Osbornodon* clade, much remains to be learned about *O. wangi* and how it is related to the earlier species, *O. sesnoni* and *O. renjiei*. In fact, secure knowledge of the identity of the latter two species depends on better knowledge of the intermediate taxa, which are likely to be found in the poorly known medial through late Arikareean of the Gulf Coast, where an early diversification of this archaic canid seems to take place.

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