('Bridger B') of the Bridger Formation, within the middle Eocene Bridgerian North American Land Mammal 'Age' (NALMA), placing it at 49 to 46.7 Ma (Prothero 1998). This new specimen expands our knowledge of basal carnivoramorphans in general, and increases the known carnivoramorphan diversity in mid-Bridgerian age rocks of southwestern Wyoming. We thoroughly describe this specimen, offer a diagnosis of the new taxon, and incorporate it into the currently most comprehensive available matrix for analysing basal carnivoramorphan relationships (Wesley-Hunt and Flynn 2005; Spaulding and Flynn 2009).

## METHODS

All descriptions of the new taxon are from direct examination of the type specimen: DMNH 19585. Comparisons to other taxa were made, if possible, by direct examination of type specimens or casts of type specimens housed in the American Museum of Natural History Fossil Mammal collection. In rare instances, such as the European genera *Paroodectes*, *Paramiacis*, and *Messelogale*, if original material was unavailable, comparisons were made with published descriptions, photographs and illustrations.

Body mass was reconstructed as 1.34 kg, using the equation from Legendre and Roth (1988) based upon regressions of m1 area. (Equation used: $\ln \text{mass} = 1.653\ (\ln \text{area of m1 in mm}^2) + 1.897$).

The phylogenetic position of DMNH 19585 was assessed by coding the morphology of the type specimen for incorporation into the matrix of Wesley-Hunt and Flynn (2005). Three additional basal carnivoramorphan taxa, *Quercygale* (e.g. Wesley-Hunt and Werdelin 2005), *Viverravus acutus* of Polly *et al.* (2006) and '*Miacis*' *uintensis*, are incorporated into this analysis, based upon coding in Spaulding and Flynn (2009). The final matrix was comprised of 44 taxa coded for 99 characters. The possible non-independence of characters 43 (M1 size metastyle compared to parastyle) and 44 (M1 size parastyle compared to metastyle) of the original Wesley-Hunt and Flynn (2005) matrix was dealt with: #43 was eliminated as it does not vary within carnivoramorphans and its inclusion or elimination does not affect the results of the analysis. Table 1 presents the character codings of DMNH 19585.

**TABLE 1.** Coding of *Dawnsonicyon isami*, DMNH 19585, for inclusion in cranio-dental matrix of Wesley-Hunt and Flynn (2005).

| | |
|---|---|
| DMNH 19585 | ?011???0?? 00???????? ????0????? ?????????? 1011001102 100121101? ?????0???? ???????000 01000110?? 00?0????? |

The matrix was analysed in PAUP* version 4.0b (Swofford 2000). We selected the heuristic search option with TBR branch swapping and ran the analysis for 1000 replicates. Bootstrap values were also generated with PAUP* version 4.0b, with 1000 separate bootstrap replicates comprised of 10 trials each. Decay index scores were found using TreeRot (Sorenson 1999).

*Abbreviations.* AMNH, American Museum of Natural History, New York; DMNH, Denver Museum of Natural History, Denver; LP4, anterior-posterior length of fourth upper premolar, likewise for Lp3, Lp4, LM1, Lm1, and Lm2; MM1, distance from anterior labial border of paracone to posterior lingual border of protocone; MP4, maximum distance between the anterior border of the protocone and posterior border of metastylar blade; NALMA, North American Land Mammal 'Age'; Tm1, trigonid length of lower first molar; Twm1, talonid width of lower first molar; WP4, maximum width of 4th upper pre-molar, similar definitions for Wp3, Wp4, WM1, Wm1, and Wm2; WPM1, length of parastyle of first upper molar. Dental terminology for premolar cusps follows Flynn and Galiano (1982).

## SYSTEMATIC PALEONTOLOGY

### CARNIVORAMORPHA Wyss and Flynn, 1993

### Genus DAWSONICYON gen. nov.

*Type species. Dawsonicyon isami* sp. nov.

*Derivation of name.* Named after Mary Dawson, in honour of her exceptional contributions to the study of fossil mammals, particularly fossil carnivoramorphans.

*Diagnosis.* An early-diverging carnivoramorphan (presence of carnassial shear restricted to P4/m1 in adults) possessing the following plesiomorphic conditions: an unfused scaphoid and lunate, the presence of m3, the lack of expanded braincase with an anteriorly located fronto-parietal suture and the presence of the third trochanter of the femur.

*Differential diagnosis.* Differs from crown clade Carnivora in lacking synapomorphies of that clade.

Differs from all Viverravidae in: an M1 paracone that is much smaller than the protocone; retaining M3/m3; P4 parastyle cusp is not well developed and defined; and m2 talonid not elongate and lacking an enlarged hypoconulid.

Differs from all other early-diverging (non-Carnivora) carnivoramorphans, in the following unique apomorphies of this new taxon: a p4 lingual basin that is deep and defined, with a clear raised rim on its lingual margin; on the M1 a large stylar shelf that diminishes in size substantially posteriorly, until it is hardly noticeable and small parastyle development; presence of well-developed medially positioned hypocone on M1 and M2 among early carnivoramorphan taxa traditionally placed in the paraphyletic 'Miacidae' (many of which also retain the primitive condition of M3/m3, as in this new taxon):

Differs from all '*Miacis*' (also paraphyletic as traditionally configured) species in its unique combination of the following features: clear diastemata surrounding all premolars except P4; lack of strongly developed parastyle on M1; presence of broad parastylar shelf on M1; absence of strong metastyle on M1 and M2; presence of well-developed, relatively medially positioned hypocone on M1 and M2; well-developed metaconule on M1; strongly developed p4 lingual basin; paraconid and metaconid confluent at their bases on m2; relatively unelongated m2 talonid; and cristid obliqua joins with the protoconid on m3. See 'Discussion' for detailed explication of diagnostic distinctions from individual species currently assigned to '*Miacis*'.

Differs from *Messelogale* (tentative distinctions, as *Messelogale* is predominantly known from deciduous teeth) in: basined lower molars; presence of M3/m3; and diastemata between all premolars.

Differs from *Miocyon* in: the lack of a relatively short and deep mandible; premolars not extremely small when compared to molars; p2 not single rooted; p3 and p4 roughly equal in size; M1 parastyle not large; M2 not elongated anteroposteriorly relative to other taxa; M3 less highly reduced: cusps besides the protocone are identifiable; much smaller than all known specimens of *Miocyon*.

Differs from *Oodectes* in: accessory cusps on lower premolars; relatively lower crowned premolars with respect to molar trigonid heights; m2–m3 much smaller; P4 parastyle smaller; P4 metastyle wing long; lack of large projecting metastyle or parastyle on M1.

Differs from *Quercygale* in: presence of M3/m3; basined p4; basined lower molars; reduced M1 parastyle; and presence of hypocones.

Differs from *Palearctonyx* in: nonquadrate upper molars; premolars not small when compared to the molars; molars not low crowned with bunodont cusps; P4 protocone located farther anteriorly; and P4 metastyle wing long.

Differs from *Paramiacis* in: presence of hypocone; presence of basined p4; higher trigonid of m1; and paracone and metacone aligned with one another mesiodistally.

Differs from *Paroodectes* in: strongly developed p4 lingual basin; low trigonids on m2 and m3; more highly reduced m3; and a larger P4 metastyle.

Differs from *Procynodictis* in: lack of lingual inflection on lower premolars; lower molar talonids basined; M1 parastyle wing much smaller; paracone set back farther posteriorly on the tooth and larger than the metacone; cingulae not reduced, paraconule and metaconule cristae not reduced, and M3/3 not absent.

Differs from *Tapocyon* in: lack of an elongated parastyle on M1; mandible not exceptionally robust and lacks a deep symphyseal region; M1 protocone not conical; M1 not highly compressed anteroposteriorly; p2 roughly equal in size to p3; m1 talonid relatively wider and possesses more than one posterior talonid cusp; and m1 paralophid not anteroposteriorly directed to the same degree (more transverse in *Tapocyon*); much smaller than all known specimens of *Tapocyon*.

Differs from *Uintacyon* in: mandible neither short nor robust and lacks a deep symphyseal region; premolars slightly larger relative to the molars and possess accessory cusps; lower molars have basined talonids; upper molars have well-developed hypocones; parastyle is not well developed; and m3 not flat crowned.

Differs from *Vassacyon* in: mandible neither short nor robust and lacks a deep symphyseal region; premolars slightly larger relative to the molars and possess accessory cusps; lower molars have basined talonids; m2 is reduced; and m3 not flat crowned.

Differs from *Vulpavus* in: non-quadrate shape of upper molars, shearing retained on upper molars; lower molar trigonids not low, and talonid basins not equal to or broader than trigonids.

Differs from *Xinyuictis* in: presence of hypocone on M1; retention of metaconule on M1; wider talonid basins on m1–m2; and a relatively smaller paraconid on m2.

Differs from *Zodiocyon* in: presence of hypocone on M1; M1 with reduction of stylar shelf adjunct to the metacone; larger metaconule on M1; reduction of metastyle on M2; lower molars with basined talonids; and m1 trigonid is less open. (Comparisons based on images and descriptions only).

### *Dawsonicyon isami* sp. nov.
Text-figures 1–7

*Derivation of name*. After Isam L. Spaulding Jr., the senior author's paternal grandfather.

*Holotype*. The holotype and only known specimen is DMNH 19585 (Text-figs 1–7), a partial skull, pair of mandibles, and partial postcranial skeleton, comprised of all seven cervical vertebrae, 8 thoracic vertebrae, 5 lumbar vertebrae, the sacrum, 13 caudal vertebrae, distal fragments of both scapulae, right and left humeri, right and left ulna and radius, right lunate, the pelvic girdle, right and left femur, right and left tibia, distal right fibula, right and left astragalius, right and left calcaneius, right cuboid and ectocuniform, and a number of metacarpal or tarsal bones and phalanges that are of uncertain attribution (Collected by RKS and crew, Sweetwater Co, Wyoming, USA).

*Type horizon.* The type and only specimen is from the Black's Fork Member of the Bridger Formation – roughly in the middle of the Bridgerian NALMA, placing it within the middle Eocene, *c.* 49 to 46.7 Ma (Prothero 1998), in Br-2 (Gunnell *et al.* 2009).

*Occurrence and age.* 'Bill's *Smilodectes* BLM locality' (DMNS loc. 885), located in T 16N R 110W, Sweetwater County, Wyoming. Fossils come from a slate green coloured mudstone in the Bridger Formation. The approximately 1-m-thick horizon lies about 4–5 m below Gazin's (1965) Sugar White Layer. The fossil bed is laterally persistent throughout the exposures in this township. The horizon consistently produces specimens of partial skeletons of *Smilodectes gracilis*, titanotheres, carnivoramorphans, rodents and other mammals. Other mammals from the locality include *Smilodectes gracilis*, *Sciuravus nitidus*, *Palaeosyops* sp., *Helaletes* sp., *Hyrachyus* sp., *Omomys carteri, Orohippus* sp., *Hyopsodus* sp., *Thinocyon muselinus*, and *Sinopa* sp.

*Diagnosis.* As for the genus.

### *Description*

*Lower Dentition.* The right mandible preserves c1-p2, a damaged m1, and m2. The left mandible contains i3-m3 (Text-figs 1B, 2C–E).

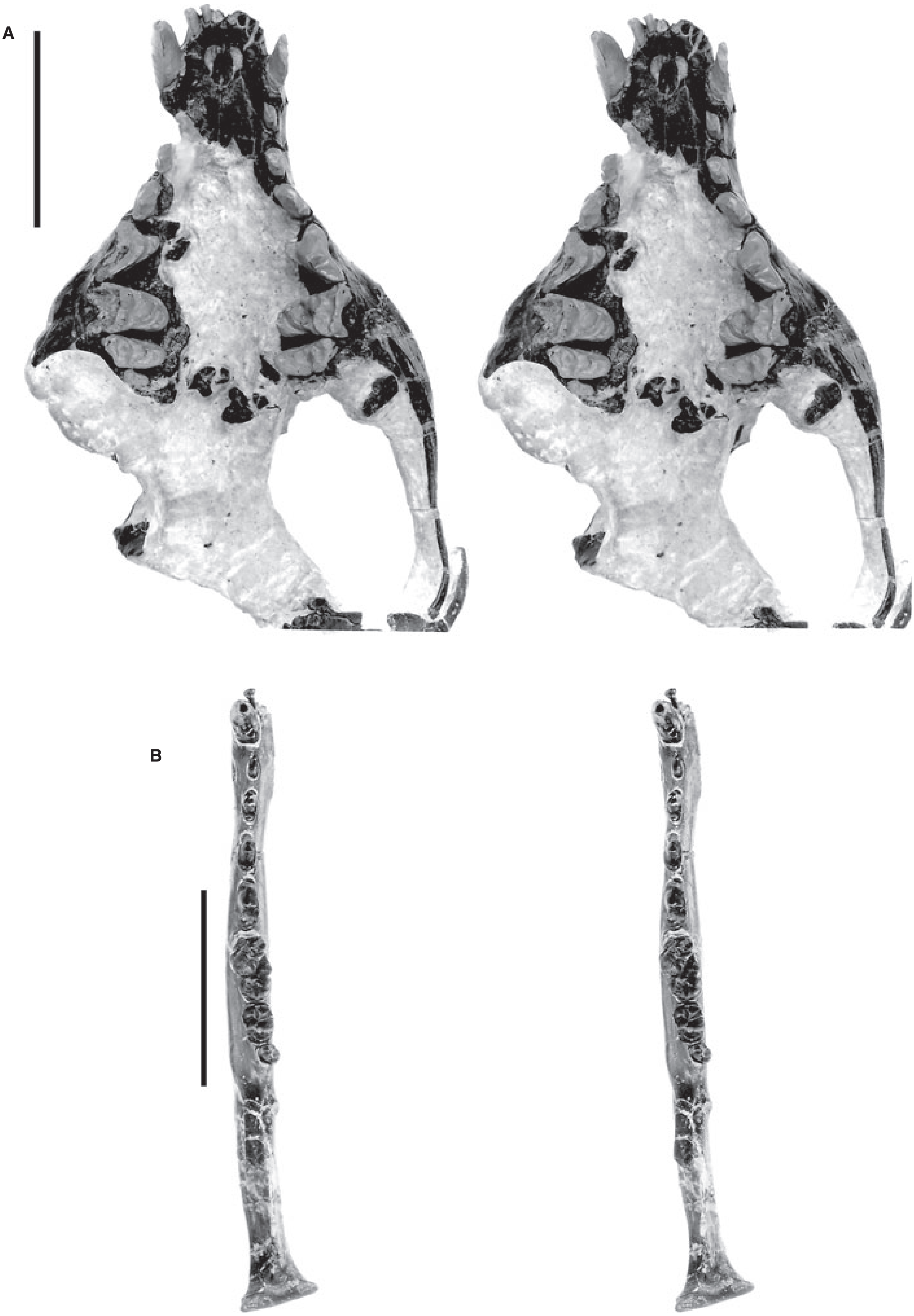
The i3 has one main central cusp flanked by two small cusps. The canines are large and robust at the base and thin dorsally as they curve posteriorly. All four premolars are separated from their adjacent teeth by diastemata. The premolar series increases in size from p1 to p4, with the p4 being much larger than p3 and p1 much smaller than p2. The anteriorly inclined p1 has a main cusp and one very small posterior accessory cusp. No accessory cusps occur on p2, but a small bump is present on the anterior occlusal surface and a small cingular cusp occurs on the posterior margin. The anterior part of the slightly larger p3 is missing; a small cingular cusp is present on its posterior portion. Both p2 and p3 have small 'basin-like' depressions on their posterior lingual surfaces, but these are not clearly developed. An anterior cingular cusp is present on p4. The p4 also has a well-developed posterior accessory cusp that is separated from the main cusp by a clear notch. There is also a well-developed posterior cingular cusp. The p4 further differs from more anterior premolars by having a cingulum on the buccal margin of the tooth and a well-developed lingual 'talonid' basin bordered by the posterior accessory and cingular cusps as well as a lingual rim. This rim originates from the posterior cingular cusp and runs anteromedially to define the back and side walls of the basin. Because of this basin, the outline of the tooth widens noticeably towards the posterior end. All the premolars have narrow ridges running along their occlusal surfaces parallel to the long axes of the teeth. The ridges on the p4 are less well developed when compared with the anterior premolars.

The m1 has a high trigonid with three distinct, well-developed cusps forming an acute angle ('closed' trigonid). The protoconid is the largest cusp, followed by the much smaller paraconid, and the metaconid is the smallest cusp. The paracristid orientation is difficult to determine because of the poor preservation of m1 in both jaws, but it seems to run roughly anteromedially–posterolaterally. The protocristid clearly runs slightly posteromedially. No cingulum is present on the lingual margin of the tooth, and although the buccal margin is heavily damaged, a very weak anterobuccal cingulum can be seen. The talonid is much lower and shorter than the trigonid, while their widths are roughly equal. The sub-vertical cristid obliqua runs from the posterior midpoint of the protocristid to the hypoconid, and has a very well-developed shear facet on its buccal surface. The talonid is simple in its morphology; it has a distinct basin rimmed by the cristid obliqua, hypoconid, hypoconulid, entoconid, and entocristid. The latter two cusps are not highly differentiated from each other and are much smaller than the hypoconid, but they nevertheless are recognizable as distinct cusps.

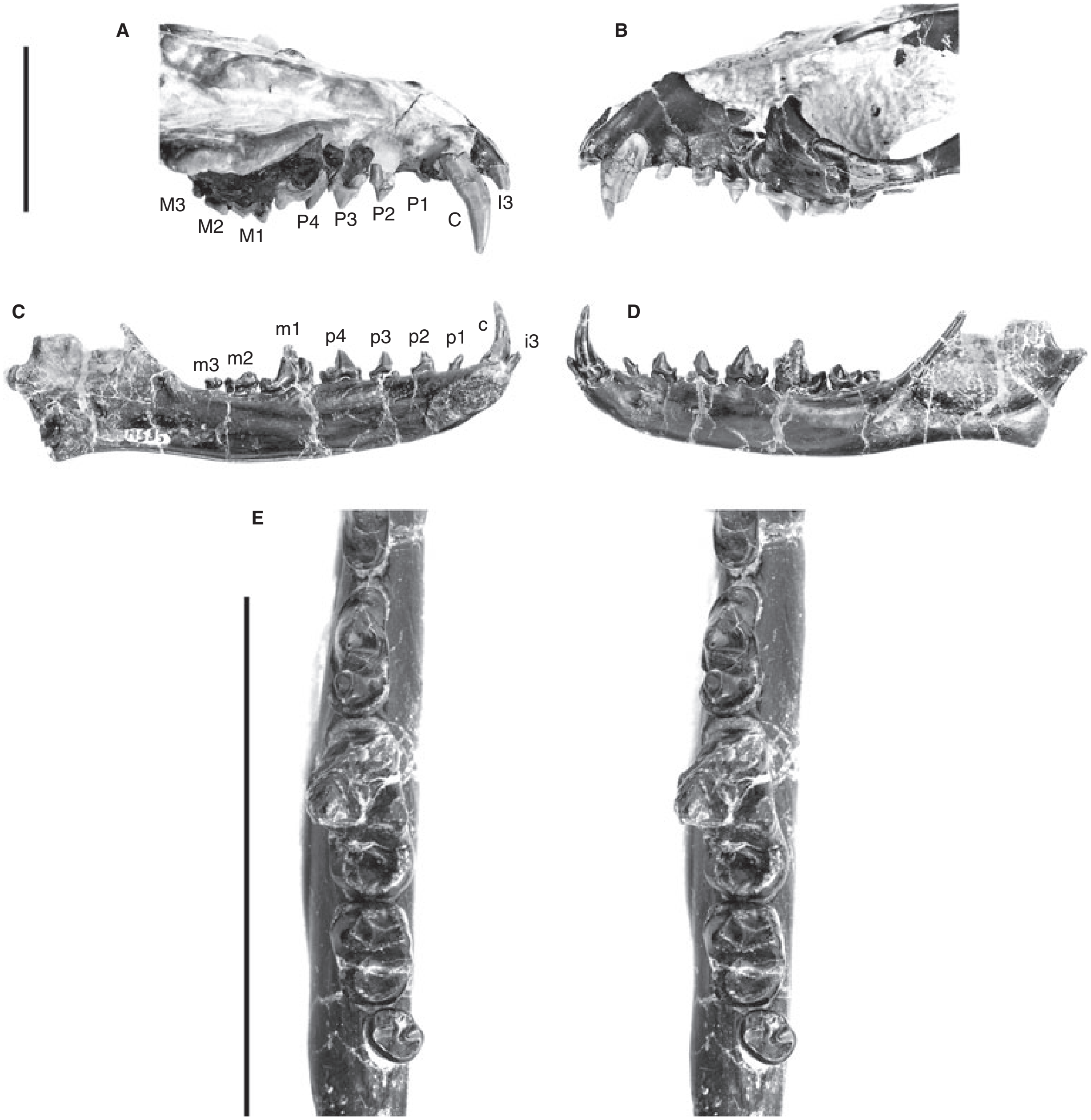
The m2 is roughly half the length of m1, while their widths are similar. The trigonid of m2 is much lower than that of m1, and the protoconid is just barely the largest cusp. The trigonid is somewhat anteroposteriorly compressed, resulting in a 'closed' trigonid basin, where the similarly sized paraconid and metaconid are confluent with one another at their bases. There is a weak cingulum on the buccal border of the tooth, and the hypoconulid and entoconid are not easily differentiated. The talonid basin of m2 is broader and shallower than the corresponding structure on m1. The m3 is roughly half the size of m2 in overall area. This tooth is orientated diagonally relative to the rest of the tooth row because of postmortem deformation and rotation. The occlusal surface features on this tooth are low and rather indistinct; this condition is not because of wear of the tooth surface but rather is the original form of the reduced structure. The readily identifiable features of m3 are the protoconid, cristid obliqua, and a distinct entoconid on the rim of the talonid basin.

*Upper Dentition.* Of the upper dentition, the right I2-C1 and P4-M3 are preserved, with damage to the P4 and M1. On the left side, I2-M2 are present (Text-figs 1A, 2A–B).

As in other basal carnivoramorphans, DMNH 19585 had three pairs of upper incisors, indicated by a combination of premaxilla alveoli and preserved teeth. Only the right I2 can be described in detail; it is curved on its buccal surface, with a straight lingual surface, resulting in a triangular shape in occlusal view. The canines are large and have a slight posterior curvature. The first three premolars have diastemata between them and adjacent teeth; those flanking P1 are the largest. The three anterior premolars are relatively small, increasing steadily in size from P1 to P3. All of the first three premolars have ridges on their occlusal surfaces; anteriorly these ridges run anteromedially to posterolaterally, while posteriorly they run parallel to the long axis of the tooth. P1 is single rooted and slightly procumbent, with a very small bump on its posterior border; its tip is broken. P2 was broken into many fragments but has been fully restored. No accessory cusps are present, and there is a very small posterior cingular cusp; this basal cusp is buccal to the axial ridge and forms a very tiny buccal basin. P3 also lacks an anterior accessory cusp and one definitive posterior accessory cusp; however, a slight rise in the posterior edge of the main cusp could be considered an additional rudimentary accessory cusp. A weak cingulum is present around the entire margin of P3; it is most



**TEXT-FIG. 1.** A–B, *Dawsonicyon isami* gen. et. sp. nov. holotype DMNH 19585 stereo-pairs of dentition in occlusal view. Scale bar represents 2 cm.



**TEXT-FIG. 2.** A–E, *Dawsonicyon isami* gen. et. sp. nov. holotype DMNH 19585 dentition in side view. A, right view of cranium. B, left view of cranium. C, buccal view of left mandible. D, buccal view of left mandible. E. stereo-pair of lower dentition in occlusal view: restricted to p4-m3. Scale bar represents 2 cm.

pronounced on the posterobuccal margin, creating a well-developed posterior cingular cusp that is separated from the main cusp by a clear notch, with a very small associated buccal basin.

P4 has a very small protocone, projecting far anterolingually. The posterior edge of the protocone aligns with the middle of the paracone, and anteriorly the protocone barely extends past the front edge of the paracone. The paracone is angled posteriorly and lacks a well-developed parastyle wing or parastylar cusp; only a small cusp arising from the cingulum is present at its anterior margin. The metasylar blade is moderately elongate, buccally directed, possesses an irregular occlusal edge and is clearly separated from the paracone by a well-developed metastylar notch. The whole tooth is ringed by a cingulum, which is slightly better developed on the inner surface of the tooth than elsewhere.

The M1 is a transversely elongated rectangle, a standard shape for basal carnivoramorphans, and it does not vary much in width anteroposteriorly or buccolingually. The protocone appears deflected anteriorly by the well-developed hypocone that is formed via a swelling of the cingulum. The hypocone and protocone are roughly the same size. Pre- and post-protocristae lead to the well-formed paraconule and metaconule, respectively. A notch in the cristae separates the paraconule from the protocone while no such feature exists to clearly separate the metaconule. The paraconule is slightly larger than the metaconule and they are well separated by a basin. The bases of the paracone and metacone also are well separated, with the paracone being much larger than the metacone. A large stylar shelf lies buccally to the paracone and metacone. This shelf broadens anteriorly to eventually reach the breadth of the paracone at its base. The metastyle is only very weakly developed, but there is a distinct metastylar cusp. The parastyle is developed to some degree, has a weakly developed stylar cusp and is slightly anteriorly directed. The entire crown is surrounded by a cingulum, which is very well developed on the lingual margin of the tooth, but becomes faint on the buccal side. Both the anterior and posterior cingulae diminish in size at a position about even with the bases of the metacone and paracone buccally. The outer border of the tooth forms a roughly straight line, but with the parastyle projecting slightly in occlusal view.

M2 is *c.* 2/3 the size of M1 in overall area. The parastyle is much more pronounced than in M1, but only projects far in a buccal direction (it has no anterior deflection). A massive hypocone is created by a swelling of the inner cingulum, and is mostly separated from the much smaller protocone via a basin, but a small connecting ridge runs from the apices of the hypocone and protocone. The paracone and metacone are not well separated; the paracone is higher than the metacone. The metaconule is not a distinct cusp, although the paraconule is. There is a small basin on the stylar shelf portion of the parastylar wing.

M3 is two-rooted and extremely small, being only about a quarter of the overall size of the M2. The tiny size of this tooth has resulted in the loss of most identifiable features relative to likely ancestral conditions; however, a small trigon basin, the pre-paracrista, and a clear division can still be identified between the protocone region and the paracone/metacone region (see Table 2 for dental measurements).

*Mandible.* The coronoid and angular processes are broken on both of the gracile dentary bones, but a strong coronoid crest is preserved. The condyloid process is present on the left ramus, showing that its height is slightly taller than the dorsal tip of the m1. This structure has a smooth convex articular surface that widens medially and trends medioventrally. Each jaw possesses two mental foramina, one beneath p1 and a second below p3. The mandibular foramen is situated in the middle of the ramus, just below the condyloid process, and is well developed. The ramus as a whole is rather shallow; the dentary is just barely taller than the total height of the m1. The lower border overall is gently convex, with a concave portion found under the deep masseteric fossa. The weakly developed symphyseal region extends from the anterior end of the mandible to below the middle of p2.

**TABLE 2.** Standard dental measurements for DMNH 19585.

| | | | |
|---|---|---|---|
| LP4 | 7.03 | Lp3 | 3.87 |
| WP4 | 4.31 | Wp3 | 1.91 |
| MP4 | 7.07 | Lp4 | 5.29 |
| LM1 | 5.02 | Wp4 | 2.52 |
| WM1 | 7.19 | Lm1 | 6.26 |
| MM1 | 8.2 | Wm1 | 3.95 |
| WPM1 | 1.3 | Tm1 | 3.78 |
| | | Twm1 | 3.4 |
| | | Lm2 | 4.14 |
| | | Wm2 | 3.21 |

All measurements are in centimetres.
After Wesley and Flynn 2003.

*Skull.* The skull of DMNH 19585 is fragmentary, but there is not much distortion of the preserved elements, as the skull is held together by the original matrix, providing a rough estimate of overall shape. Each premaxilla contains three incisors and the anterior component of the incisive foramen. Posteriorly, the premaxilla extends to the midpoint of the base of the canines on the roof of the mouth, and on lateral surface of the rostrum it extends to the posterior margin of the canine. The maxilla is partially preserved and contains a round infraorbital foramen above the anterior portion of P4. Not enough of this bone is present ventrally for the position of the palatine foramen to be determined. The dorsal skull profile appears to have been relatively straight in life with the postorbital constriction occurring anterior to the fronto-parietal suture. It is difficult to determine the size of the postorbital processes because of breakage, but they were at least as pronounced as that of *Vulpavus profectus*, if not more so, but likely not as large as in *Oodectes*. The skull itself appears rather slender, except for widely flaring zygomatic arches; the degree of flaring likely has been exaggerated by the deformation of the skull. The squamosal overlaps the jugal at roughly the same location as the fronto-parietal suture.

The glenoid fossa is deep and faces anteriorly. It is bounded posteriorly by a very well-developed postglenoid process. A rather wide Glaserian fissure lies medial to the postglenoid process, serving to mark the boundary between the squamosals and basisphenoid. There is a clear groove running through the Glaserian fissure, which marks the presumed passage of the inferior ramus of the stapedial artery (Wang and Tedford 1994). Behind the postglenoid process is a large postglenoid foramen. This is the only portion of the auditory region that is preserved on the main body of the skull, but isolated left and right petrosals were recovered with the specimen.

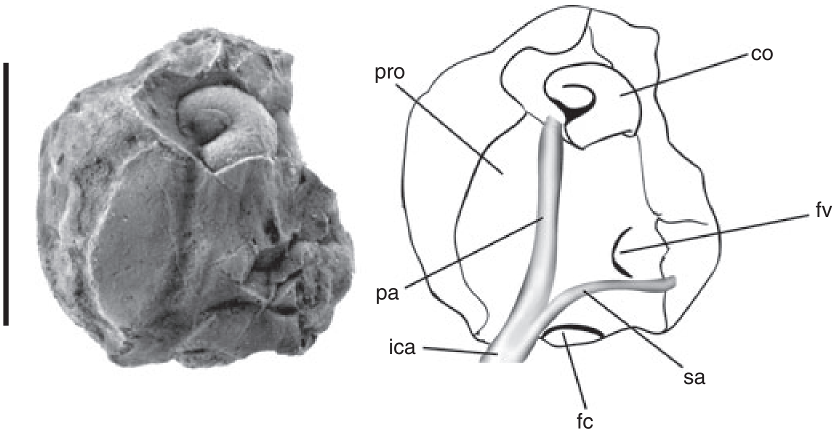
The right petrosal is highly damaged, providing no additional morphological information beyond that observed in the much more complete, but still damaged, left petrosal. The petrosal is rounded in shape, although the degree of roundness relative to other early-diverging carnivoramorphans and the extent of isolation of the petrosal are difficult to determine because of damage around the edges. Nevertheless, it is evident that the petrosal did not contact the basisphenoid anteriorly, as the anterior surface of the petrosal is smooth with no indication of breakage or contact with other elements. It appears likely that the element was in contact with the basioccipital medially; there is a broken expanse of bone, which extends the profile of the petrosal past the coiled cochlea. In carnivoramorphan taxa where the petrosal does not contact the basioccipital, such as *Vulpavus profectus* (Wang and Tedford 1994), the medial surface of the petrosal is smooth and rounded with no trace of a flat, shelf-like process.

A distinct groove runs laterally across the promontorium just anteriorly to the fenestra cochlea. Past the fenestra cochlea this groove meets a second groove, running roughly perpendicular to the first and along the entire preserved length of the promontorium. These features are interpreted (based upon Wang and Tedford 1994) as evidence of the internal carotid artery entering the ear region and travelling across the ventral surface of the promontorium. Once it passed the fenestra cochlea, the artery branched into the promontorial (anteriorly) and stapedial (posteriorly) branches of the internal carotid artery. The position of the grooves indicates that the internal carotid artery was laterally positioned, as seen in many other early carnivoramorphan taxa, such as *Miacis parvivorus* (Wang and Tedford 1994). No crown Carnivora taxon possesses such a pattern, as the internal carotid artery has either shifted to be medially positioned upon the promotorium, or it has become extrabullar (Wesley-Hunt and Flynn 2005). Additional short, shallow, irregular grooves and ridges are seen on the ventral surface of the promontorium, also as seen in *Miacis parvivorus* (Wang and Tedford 1994). Text-figure 3 illustrates the promontorium, with the hypothesized arteries and their courses superimposed upon it.

*Skeleton.* Study of basal carnivoramorphans traditionally focused primarily on craniodental morphology (Text-fig. 4). Specimens that include postcranial material exist in museum collections in larger numbers than one would suppose from examining the literature. Here, we compare DMNH 19585 to the few previously published, thoroughly described taxa: *Procynodictis vulpiceps* (published as *Miacis gracilis*, Clark, 1939 – this original description is supplemented with personal observations of the specimen), *Vulpavus* (Heinrich and Rose 1997), '*Miacis*' *petilus* (Heinrich and Rose 1995), and '*Miacis*' *uintensis* (Spaulding and Flynn, 2009). We also briefly compare DMNH 19585 to two described Viverravidae taxa, *Didymictis* (Heinrich and Rose 1997) and *Viverravus acutus* (Heinrich and Houde 2006). Comparisons are not as detailed between DMNH 19585 and the viverravids, as the ancestral character states for the Viverravidae remain unclear (e.g. the two well-known taxa, *V. acutus* and *Didymictis*, show many differences between them, making basal optimizations for the clade equivocal).

*Scapula.* Both the right and left scapulae are represented by the glenoid region, with the right being more complete. The supraglenoid tubercle extends beyond the glenoid fossa, creating a concave mediolaterally compressed feature. This morphology is shared with the Viverravidae and *Procynodictis*; all other known non-viverravid basal carnivoramorphans possess a less well-developed supraglenoid tubercle, giving a much more open appearance to the glenoid. A distinct coracoid process is present medially, a featured shared with all known basal Carnivoramorpha. Although the bone is broken just beyond the glenoid fossa, there is no evidence of a scapula notch as ascribed to *Vulpavus*. The remaining scapular spine has a well-developed acromion process that extends well past the glenoid fossa, curving anteriorly as it does so. This morphology is similar to that seen in '*M.*' *uintensis* and dissimilar to the short acromion seen in *Procynodictis,* although comparisons to other taxa are limited by the lack of preservation of this region of the material. It is unclear how large the metacromion process was, as the boundary of the spine ventral to the base of the acromion process is rough and broken.

*Humerus.* The left humerus is complete, whereas the right humerus is represented only by fragments (Text-fig. 5C). The greater tuberosity does not extend above the rounded head of the humerus. The greater tuberosity remains in contact with the head for its entire width, except for the clearly defined bicipital groove. In life this groove most likely housed the tendon of the *m. biceps brachii* (Heinrich and Rose 1997). This greater tuberosity morphology agrees with all known non-Viverravidae basal carnivoramorphans, whereas in viverravids the greater tubercle rises above the humeral head and is relatively twisted with respect to the long axis of the shaft. The lesser tuberosity is distinct proximally, but distal to the head it soon diminishes in size, leaving only a faint marking ridge down the shaft. Distally the greater tuberosity gives rise to a distinctly compressed and elevated deltopectoral crest, a feature found to this degree in all other basal carnivoramorphans save *Procynodictis* but not in any known Viverravidae. The full extent of this feature is not certain,



**TEXT-FIG. 3.** *Dawsonicyon isami* gen. et. sp. nov. holotype DMNH 19585 petrosal. Line drawing shows hypothesized pattern of the internal carotid artery. Scale bar represents 5 mm. co, cochlea; fc, fenestra cochleae; fv, fenestra vestibuli; ica, internal carotid artery, pa, promontory artery; pro, promontorium; sa, stapedial artery.

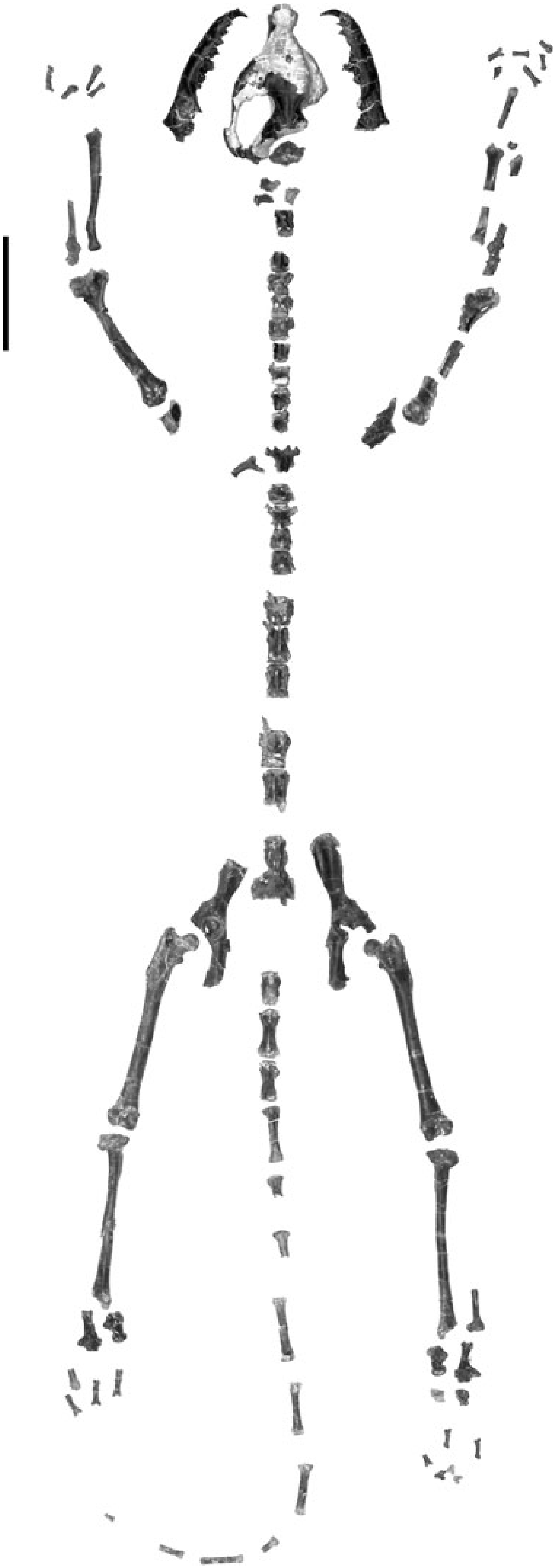
as the crest is broken just after after it rises from the shaft. The small unbroken distal portion, as well as isolated fragments, suggests that this was at least a somewhat prominent feature, developed to a degree comparable to that in *Miacis parvivorus* and *M. petilus*, although probably not as much as in *M. uintensis* and *Vulpavus*. Distally this feature ends approximately at the midshaft.

A supinator crest ridge extended from the distal extreme of the bone to about where the deltopectoral crest diminishes distally. As the crest travels proximally, it curves around the back of the shaft such that at the proximal extreme, it aligns with the midline of the humeral head. As with the deltopectoral crest, the full extent of this feature is unknown, as it is broken off very shortly after its origination. This crest is well-developed in all basal carnivoramorphans with the exception of *Didymictis* and *Procynodictis*.

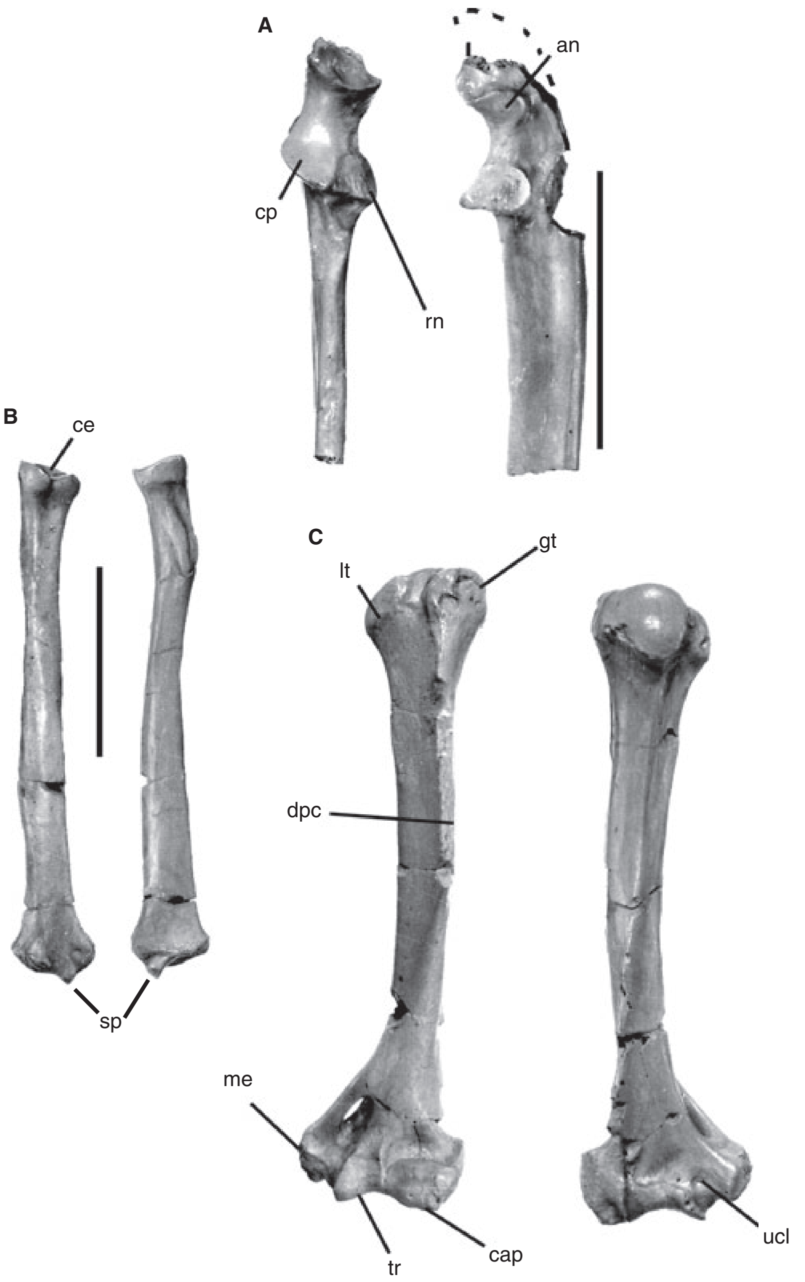
A pronounced entepicondylar foramen is present on the humerus; its medial boundary runs at roughly a 45-degree angle to the main shaft. Distally this boundary joins with the medial epicondyle. The medial epicondyle has a well-defined neck and it curves posteriorly relative to those latter two features, as seen in '*M.*' *petilus*. The trochlea has a shallow angle to it, and consequently does not extend far distally to the cylindrical capitulum, resembling *Vulpavus* but in contrast to all other described basal carnivoramorphans. A distinct ridge of bone on the anterior surface separates the trochlea and capitulum. The capitulum is not rounded as in *Vulpavus* and the viverravids, but is relatively more cylindrical in overall shape, as in '*M.*' *petilus*, *Procynodictis*, and '*M.*' *uintensis*.

Proximal to the articulation facets, a distinct and deep radial fossa is present. There is a distinct shallow pit for the ulnar collateral ligament on the posterior surface, between the posterior trochlea and the medial epicondyle. Lateral to the posterior trochlea surface is an L-shaped boundary to the capitular articulation surface. Proximal to the articular surfaces, the olecranon fossa is shallow and circular as in '*Miacis*' *petilus* and *Vulpavus*, and unlike the deep and rectangular fossa of '*Miacis*' *uintensis* and *Procynodictis*. The fossa is solid, with no trace of a perforation, dissimilar to the state found in *Didymictis* (Heinrich and Rose 1997) and some living Carnivora, such as canids.

*Ulna.* Both ulnae are present, although somewhat fragmentary (Text-fig. 5A). The right ulna preserves almost intact proximal and distal regions. On the proximal surface in all known basal carnivoramorphans, no groove is seen for the *m. triceps brachii* tendon as occurs in many Carnivora, although there is a distinct ridge of bone running mediolaterally across the surface, set back from its anterior edge. The olecranon process is robust, but not square in shape; it is noticeably taller than it is wide. This process is roughly 70% the length of the semilunar notch. This shape is shared with *Vulpavus* and '*M.*' *petilus*, to the exclusion of *Didymictis*, *Procynodictis*, and '*M.*' *uintensis*, which all possess



**TEXT-FIG. 4.** *Dawsonicyon isami* gen. et. sp. nov. holotype DMNH 19585 full specimen. All identifiable material is laid out in roughly natural positions relative to neighbouring elements. Note that the association of metapodials and phalanxes with fore or hindlimb is uncertain. Scale bar represents 5 cm.



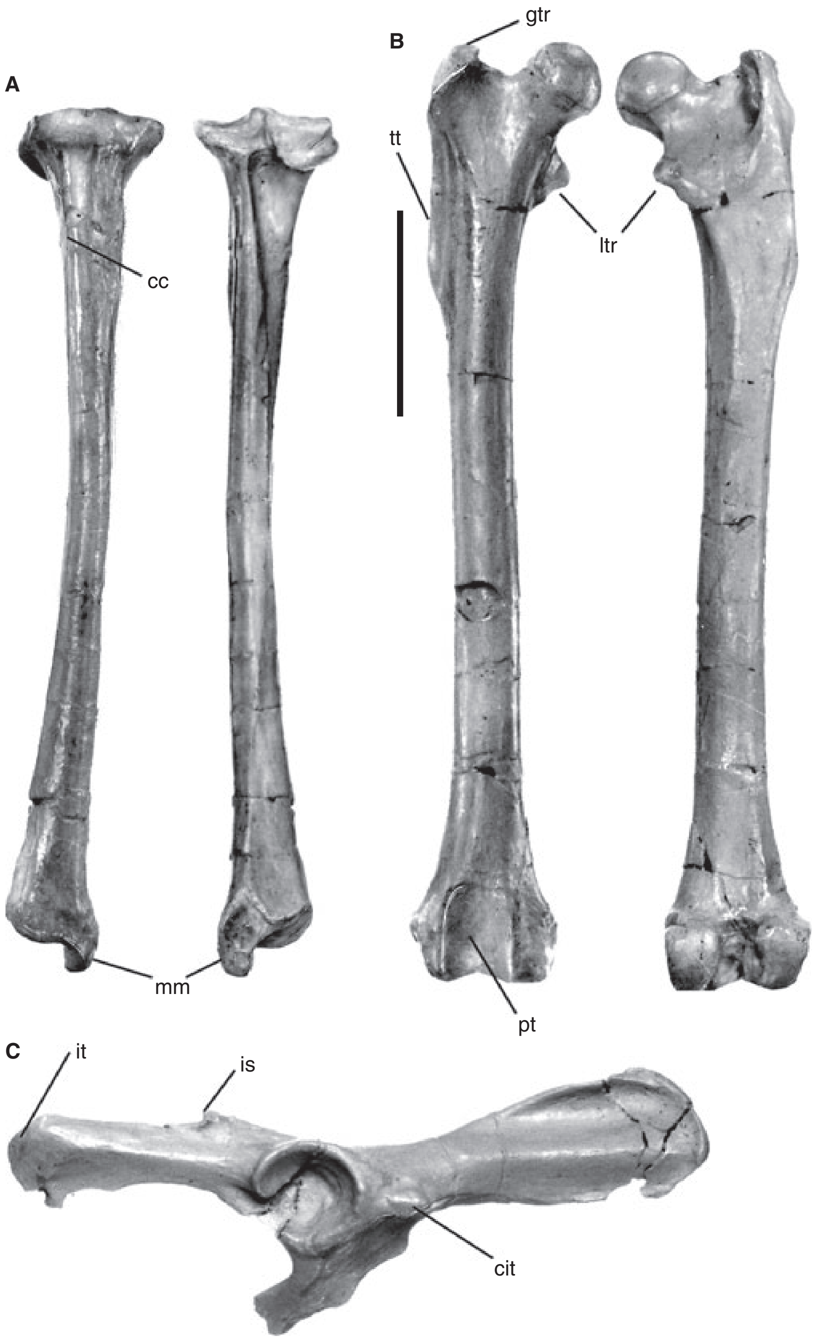
**TEXT-FIG. 5.** A–C, *Dawsonicyon isami* gen. et. sp. nov. holotype DMNH 19585 forelimb elements. A, anterior and lateral views of proximal left ulna. B, anterior and posterior views of left radius. C, anterior and posterior views of left humerus. All scale bars represent 2 cm. Figure B and C share the same scale bar. an, anconeal process; cap, capitulum, ce, capitular eminence, cp; coronoid process, dpc; delto-pectoral crest; gt, greater tuberosity; lt, lesser tuberosity; me, medial epicondyle; rn, radial notch; sp, styloid process; tr, trochlea; ucl, site of ulnar collateral ligament.

more laterally compressed processes. The anconeal process borders the semilunar notch proximally, and is not very well developed, a feature with a taxonomic distribution similar to the shape of the olecranon process, but with the addition of a similar morphology also seen in *V. acutus*. The medial edge of the anconeal process bends to reach father proximally than the lateral edge, creating a double-lobed appearance. The somewhat square-shaped radial notch is flat and faces anterolaterally, unlike the more anterior position in the Viverravidae. The coronoid process extends outwards a considerable distance, creating the distal boundary of the semilunar notch. Distal to the coronoid process, the probable insertion point of the *m. brachialis* occurs on the anterior surface of the shaft, as in *Vulpavus* and *Didymictis* but unlike the lateral position in '*M.*' *petilus*, *Procynodictis*, and '*M.*' *uintensis*. The distal end of the ulna has a distinct articular surface for the radius and a well-developed styloid process.

*Radius.* Both right and left proximal and distal radii were recovered (Text-fig. 5B). The radial head is relatively circular in outline (measuring 0.58 by 0.68 cm), a round radial head is shared by all non-Viverravidae basal carnivoramorphans (with the roundest heads found in *Vulpavus*), while the viverravids have a more oval morphology. A distinct capitular eminence is present, as in all known basal carnivoramorphans except *Vulpavus*, medial to an indentation in the anterolateral surface of the rim. Distal to the head is a distinct bicipital tuberosity. The distal radius is somewhat compressed anteroposteriorly, unlike the condition in known viverravids. There is a well-developed styloid process and a low-lying extensor tubercle. A deep and well-rounded articulation with the distal ulna is present.

*Manus.* The only bone recovered that undoubtedly can be attributed to the manus is the left lunate. This bone clearly is a separate element with no signs of fusion with the scaphoid, in contrast to the condition in most basal carnivoramorphans other than some specimens of *Vulpavus* (Matthew 1909) and *Vassacyon* (Matthew 1915). Relative to the available comparative taxa, this bone most closely resembles that of *Vulpavus* (Heinrich and Rose 1997). It is a narrow bone, much longer anterioposteriorly than it is wide. On its distal concave surface, there are clearly separated facets for articulation with the unciform and the magnum. Its medial margin also is concave.

*Innominate.* The majority of both innominate bones are preserved, lacking only the fragments of the pubis, with the right one more complete (Text-fig. 6C). Prior studies noted limited variation in the pelvic bones of basal carnivoramorphans, and the present specimen does not alter those findings. The iliac



**TEXT-FIG. 6.** A–C, *Dawsonicyon isami* gen. et. sp. nov. holotype DMNH 19585 proximal hindlimb elements. A, anterior and posterior view of right tibia. B, anterior and posterior view of left femur. C, lateral view of right innominate. Scale bar represents 2 cm and applies to all elements. cc, cnemial crest; cit, caudal iliac tubercle; gtr, greater trochanter; is, ischial spine; it, ischial tuberosity; ltr, lesser trochanter; pt, patellar trochlea; tt, third trochanter.

blade is ventrally wide for half of its length, and then its ventral margin tapers to a narrow edge, as in all known basal carnivormorphans. The lateral side of the iliac blade has a gently sloping ridge running approximately along its midline; the blade is concave anteriorly and posteriorly to this ridge. Immediately anterior to the acetabulum is a well-defined cranial inferior tubercle. The acetabulum is fully enclosed, save for an opening in its posteroventral quadrant. Posteriorly, close to the acetabulum, is a well-defined ischial spine; this placement agrees with that in other non-Viverravidae basal carnivoramorphans, whereas viverravids have a more posteriorly placed spine. The ischial tuberosity is not well developed, and the ischium does not widen at the tuberosity.

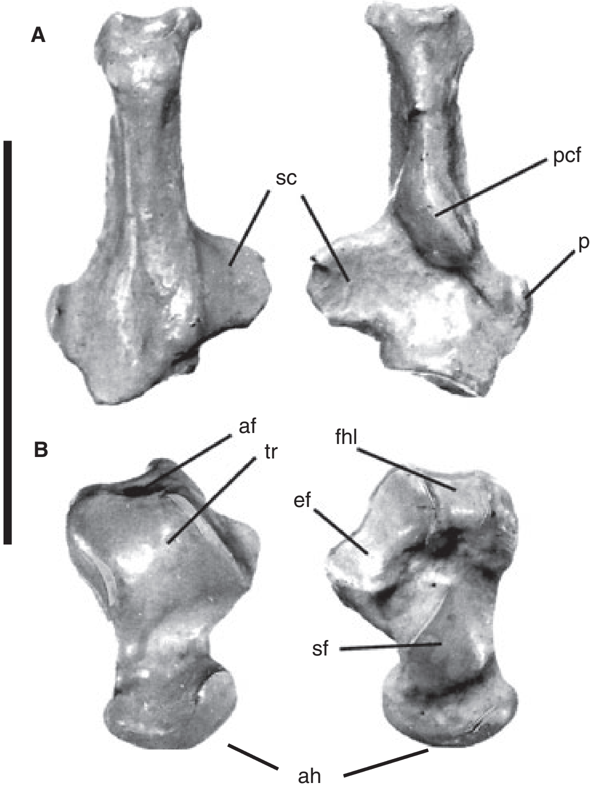
*Femur.* Both femora are complete (Text-fig. 6B). The round femoral head extends very slightly beyond the greater trochanter and its articular surface runs down the short femoral neck, as in other basal non-Viverravidae carnivoramorphans. The fovea capitis is large and directed medially. Again, as in other non-viverravids, the ridge of bone connecting the head with the greater trochanter is uniform for the entirety of its length. A trochanteric fossa is present and occupies roughly the entire posterior area of the greater trochanter. The intertrochanteric crest becomes flush with the shaft before it reaches the well-formed, medially projecting lesser trochanter. The medial projection resembles most non-Viverravidae carnivoramorphans, whereas the Viverravidae, *Procynodictis*, and *M. uintensis* all have a more posteriorly projecting trochanter. On the lateral margin of the shaft, the third trochanter is present but not prominent. It reaches its maximum development just distal to the lesser trochanter, resembling other basal non-viverravid carnivoramorphans. The posterior surface of the straight shaft is smooth, lacking ridges associated with muscle attachments.

The distal end of the femur has a broad and flat patellar trochlea that is not bound by high ridges on either side, unlike the condition in the Viverravidae, *Procynodictis*, and *M. uintensis*. Both lateral and medial condyles are roughly the same size and have pitting on their outside edges.

*Tibia.* Both tibiae (Text-fig. 6A) are complete. The lateral condyle is convex and slightly higher than the concave medial condyle. The boundary between the two condyles is marked by a rise on the proximal surface; the exact boundary is indistinct, however, as the rise is not marked by a medial ridge. A sharp ridge extends down the posterior shaft, emanating from the posterior border of the medial condyle. This serves to create a large popliteal notch. On the medial edge of the shaft, near the proximal head, is a small raised tubercle as occurs in other basal carnivoramorphan taxa; its development most closely resembles the slightly larger tubercle of *Vulpavus* rather than that of viverravids. No distinct cnemial crest is noted. The distal tibia has a large medial malleolus, a distinct posterior tubercle as seen in most other basal Carnivormorpha, and a smooth tibia-astragalus articular surface unlike the slightly ridged surface seen in viverravids and *Procynodictis*.

*Fibula.* A distal right fibula is present. The bone is mediolaterally compressed. There is a shallow, medially orientated peroneal groove and a clear anteromedially facing tibia-fibula articulation surface.

*Astragalus.* The right and left astragali are both present (Text-fig. 7B). There is a broad smooth dorsal surface for articulation with the distal tibia, with only the barest trace of a groove upon this surface, resembling the condition in most other basal non-Viverravidae carnivoramorphans, with the exception of *Procynodictis*. The articulation surface has a straight anterior edge, whereas the medial edge of the posterior surface extends farther back than the lateral edge. A dorsally directed astragalar foramen lies anterior to a deep posterior groove. This groove, presumably for the *flexor fibularis* tendon, extends to the ventral surface of the bone. Ventrally the concave ectal and convex sustentacular facets are distinct; the posterior edge of the sustentacular facet barely overlaps with the anterior edge of the ectal facet. The sustentacular facet is also distinct from the flattened astragalar head. This flattened morphology is shared with all other non-viverrvid basal carnivoramorphans, with the exception of *M. uintensis* which has a non-compressed head (as also occurs in the Viverravidae). The astragalar head is orientated so that its



**TEXT-FIG. 7.** A–B, *Dawsonicyon isami* gen. et. sp. nov. holotype DMNH 19585 proximal ankle elements. A, right calcaneus in ventral and dorsal views. B, right astragalus in dorsal and ventral view. Scale bar represents 2 cm. af, astragalar foramen; ah, astragalar head; ef, ectal facet; fhl, facet for tendons; pcf, posterior calcaneal facet; pt, peroneal tubercle; sc, sustentaculum; sf, sustentacular facet; tr, astragalar trochlea.

long axis is roughly perpendicular to the long axis of the body of the astragalus. Its articular facet is smooth and convex, extending farther posteriorly on its lateral than on its medial margin. No cotylar fossa is present on the astragalus, unlike the condition in viverravids.

*Calcaneum.* Both right and left calcanei are present (Text-fig. 7A), as with many of the other skeletal elementals, the specimen more closely resembles other known non-Viverravidae carnivoramorphans than the viverravids. The majority of the calcaneal length is formed by the long, mediolaterally compressed heel. The posterior calcaneal facet, which articulates with the ectal facet, is convex and faces medially. No facet for articulation with the fibula is seen, in contrast to the condition in viverravids. The sustentaculum is prominent and gently concave. On the lateral margin of the anterior region of the bone, there is a well-formed peroneal tubercle, which is larger than that in *M. uintensis*. The cuboid articular facet is circular, slightly concave, and faces slightly medially, unlike its dorsomedial orientation in *Vulpavus*.

*Cuboid.* The right cuboid was recovered and its morphology agrees very closely with that of *Vulpavus*. It is wider proximally than distally, with a wide convex facet on its proximal surface for articulation with the calcaneum. A flat ectocuneiform facet and a clearly separate navicular facet occur on the medial surface. On the lateral margin, there is a prominent tubercle, which runs at approximately 20 degrees to the long axis of the bone. The distal surface of the cuboid bears the articular facets for both metatarsals IV and V. The articular surface for mt IV covers most of the distal surface and is much larger than the surface for mt V, which is on the distolateral surface.

*Entocuneiform.* The right entocuneiform was recovered. It has a markedly concave distal surface for articulation with metatarsal I, traces of a projection on its proximal medial surface, a distinct and slightly concave navicular articulation surface, and a convex surface for articulation with the mesocuneiform. Distal to the articulation with the mesocuneiform, there is a projection which appears to have a convex articulation surface upon it, which most likely articulated with a posterior projection of metatarsal II.

*Distal carpal or tarsal elements.* Three distal metatarsals or metacarpals are preserved; one is much larger than the other two. It is possible that this size discrepancy indicates that the smaller two are from the manus and the larger from the pes; however, in *Vulpavus profectus* (Matthew, 1909) the distal ends of the metatarsals and metacarpals are roughly equal in size. It is also possible that all three of these bones are from the same manus or pes region, but one that has undergone reduction of one of the digits, as occurs in *Hesperocyon*. The elements are somewhat dorsoventrally compressed and have a rounded dorsal and distal surface for articulation with the proximal phalanges, with a ridge on the ventral surface most likely demarcating the point of attachment of sesamoid bones.

Five proximal phalanges were recovered. They have a concave proximal surface for articulation with the metatarsals or metacarpals, the shaft bows dorsally, and the distal surfaces have a deeply grooved trochlea. Six medial phalanges are present. Five of them have a marked asymmetry to the shaft, with the axial ridge on the medial side. This morphology has been associated with retractile claws (Wesley and Flynn 2003). The sixth phalanx lacks this asymmetry, possibly marking it as belonging to a reduced digit, based on comparisons to modern *Felis silvestris*. Of the asymmetrical phalanges, two of them have similarly asymmetrically ‘shifted’ distal articulation surfaces, while the other three have a standard symmetrical form. This could possibly represent different levels of retractile claw capabilities between the pes and the manus, although this cannot be determined conclusively with the present material. One mediolaterally compressed distal phalanx ‘claw’ was recovered; it is roughly 0.4 cm long, with a gentle curvature.

*Axial Skeleton.* A number of vertebrae were recovered, in various conditions of preservation; 25 of these are in good enough condition to be identified as to their position in the vertebral column. While all seven cervical vertebrae are present, the posterior five have been badly damaged and are identifiable as cervical primarily by the transverse foramen groove on the vertebral bodies. The atlas and axis are represented only by fragments. Five assuredly thoracic vertebrae were recovered; all are similar in size and have some remnant of the conspicuous spinous process. The three best-preserved thoracic vertebrae have spinous processes that extend more posteriorly than dorsally, at about a 30-degree angle. They extend roughly 0.4 cm past the caudal end of the vertebral body, and rise 0.75 cm high, based on the most complete vertebrae. Each vertebral foramen is slightly larger than the centrum of the vertebra. Four other badly damaged vertebrae are assumed to be thoracic based upon size, bringing the total to nine. The bodies of all the vertebrae, except the caudal, are not circular but instead are dorsoventrally compressed.

The five lumbar vertebrae are roughly twice as long as the thoracic vertebrae, but only about 50% wider. All of the transverse processes are somewhat broken, but none appear to have been very large; at a minimum, it can be confidently determined that they were not broad. The mammillary processes are compressed transversely and rise almost to the same height as the anteriorly directed spinous process. The spinous process projects 0.5 cm in front of the vertebral body and rises 0.62 cm high, at about a 20 degree angle to the body. Each vertebral foramen is slightly smaller than the body of the vertebra.

The sacrum incorporates three fused vertebrae. The surface for articulation of the sacrum with the pelvic girdle is about as tall dorsoventrally as the body plus the vertebral foramen. Twelve caudal vertebrae are present, four of them being unsimplified anterior caudals. The elongation of these caudals indicates the animal had a long tail, as the extreme simplification and elongation of the caudal vertebrae only occurs in carnivoramorphans with long tails.

While many rib fragments are preserved, most are fragments with no noteworthy morphology. The exception to this is one rib that is preserved caudally until just past the angle, which has a clearly defined and well-separated head and tubercle (see Table 3 for measurements of selected postcranial elements).

**TABLE 3.** Measurements of the postcranial of DMNH 19585.

| | Humerus | Ulna | Radius | Femur | Tibia |
|---|---|---|---|---|---|
| Greatest length | 6.54 | * | 5.34 | 9.05 | 8.33 |
| Width–proximal | 2.03 | 0.53 | 0.68 | 1.68 | 1.38 |
| Width–midshaft | 0.57 | 0.27 | 0.49 | 0.79 | 0.50 |
| Width–distal | 1.80 | * | 0.86 | 1.42 | 0.94 |

| | Calcaneus | Astragalus |
|---|---|---|
| Width | 1.10 | 0.90 |
| Length | 1.88 | 1.44 |

All measurements are in centimetres. *, measurement could not be taken due to absence of distal ulna.

## FUNCTIONAL INTERPRETATION

DMNH 19585's forelimb can be readily reconstructed as that of a primarily scansorial or arboreal animal. It shares many features with other basal carnivoramorphans, such as *Vulpavus* (Heinrich and Rose 1997), and living carnivorans that indicate a high range of motion at the elbow joint, and in turn an arboreal lifestyle. These features include a small capitular eminence, a trochlea that does not extend more distally than the capitulum, an anconeal process that is flush with the ulna shaft, and a shallow and round olecranon fossa. These conditions indicate an elbow joint more specialized for fluidity and range of motions in the flexed condition, rather than one specialized for stability in the extended condition, as occurs in more terrestrial taxa (Heinrich and Rose 1997).

The hindlimb of DMNH 19585 likewise implies scansoriality or arboreality. Features such as a robust and more posteriorly positioned ischial spine and a rounded femoral head with an expanded articulation surface are two traits found in extant taxa that regularly abduct and laterally rotate the leg (Jenkins and Camazine 1977). The wide and smooth patellar trochlea and a well-developed peroneal tubercle likewise imply a wide range of motion in the knee and ankle joints, respectively (Heinrich and Rose 1997).

## DISCUSSION

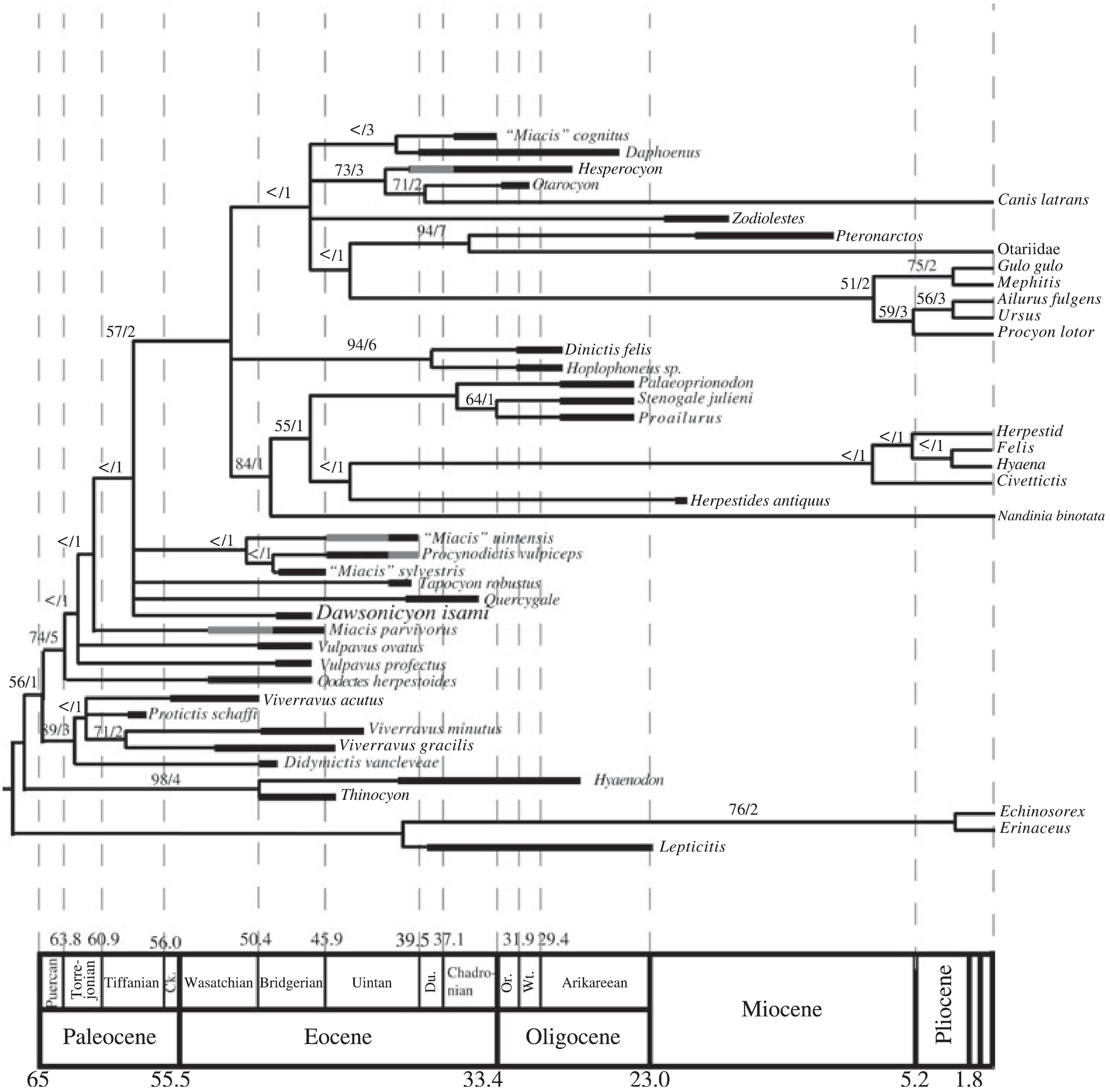
In determining the proper taxonomic assignment for DMNH 19585, special attention must be paid to '*Miacis*'. Species have traditionally been placed in this genus because of the absence of features that link them to any other known genus of basal carnivoramorphan, rather than the presence of any synapomorphic features unique to this almost certainly paraphyletic genus. Matthew's (1909, p. 362) assessment of *Miacis* was: 'Carnassial and tubercule dentition well differentiated, carnassials and premolars moderate to large, tubercular dentition small, lower molars with basined heels, M1 in early forms with small hypocone, slender or moderately deep jaws with the symphyseal region comparatively shallow and loosely sutured and typically a full eutherian dentition, with M3 vestigial or absent in some species.' This is still the best available diagnosis of '*Miacis*', although it contains an unspecified mixture of phylogenetically uninformative plesiomorphic features and apomorphic attributes potentially diagnostic of monophyletic clades. DMNH 19585 agrees with this diagnosis, but it does not fully match that of any previously recognized species of '*Miacis*'. Because of the troublesome nature of this genus, and given the position of the new taxon in the most parsimonious phylogeny as separate from all other taxa previously assigned to the genus, rather than adding an additional species to the wastebasket confusion of '*Miacis*', we consider DMNH 19585 to represent the type species of a novel taxon.

As noted earlier, this decision is supported by the results of the phylogenetic analysis, in which 5 most parsimonious trees of 457 steps each were found. The strict consensus of these five trees is shown in Text-figure 8. *Dawsonicyon isami* does not group with the type species of *Miacis*, *M. parvivorus*. Instead, it is found in a polytomy with *Tapocyon*, *Quercygale*, a small three-member clade of other basal carnivoramorphans, and the crown Carnivora plus the two nimravids included in this analysis. Overall, the tree topology here is almost identical to that of the tree generated in Spaulding and Flynn (2009). The only change seen upon addition of DMNH 19585 in this analysis is that *Oodectes* separated from the polytomy formed by *Vulpavus ovatus*, *Vulpavus profectus*, and all subsequent basal carnivoramorphans.

Although the diagnosis provided features differentiating this new taxon from all other early carnivoramorphans, the retention of many generally primitive (for Carnivoramorpha) features make this taxon superficially resemble many of the species commonly placed in the wastebasket taxon '*Miacis*'. In the following paragraphs, we detail additional features that distinguish *Dawsonicyon isami* from each of the previously named and currently recognized species of *Miacis* ('*Miacis*' *gracilis* is not included elsewhere, as it is now assigned to *Procynodictis vulpiceps*). Quotes indicate the species has been found not to cluster with the type of the genus in recently proposed phylogenies, a lack of quotations indicates the species's relationship with the type has not been tested.

Differs from *Miacis australis* in: P4 protocone relatively reduced; paracone larger than metacone on M1; protoconid-paraconid shearing plate directed less anteroposteriorly; p4 with developed talonid basin; and smaller size.

Differs from *Miacis*? *boqinghensis* in: less well-developed parastyle on M1; presence of hypocone; and smaller pro-



**TEXT-FIG. 8.** Strict consensus of the five most parsimonious trees, each 457 steps long, that were recovered in the phylogenetic analysis. Values associated with nodes represent bootstrap scores followed by Bremer decay support indices. Time ranges indicated by thicker lines. Grey lines indicate uncertainty as to occurrence. Time range information comes from Baskin (1998), Berta (1994), Flynn (1998), Gunnell (1998), Hunt (1991), Hunt (1998*a*, *b*), Martin (1998) and Munthe (1998). Ck, Clarkforkian; Du, Duchesnean; Or, Orellan; Wt, Whitneyan.

tocone on P4. (Comparison based on images and description only).

Differs from '*Miacis*' *cognitus* in: the broad stylar shelf on M1; paracone is larger than metacone on M1–M2; and transpromontorial internal carotid artery.

Differs from *Miacis deutschi* in: lacking a well-developed parastyle and metastyle; presence of molar hypocones; clearly separated paracone and metacone on M1; and clear presence of a metaconule on M1. (Comparison based on images and description only).

Differs from *Miacis exiguus* in: presence of molar hypocones; broad parastylar shelf on M1 and M2; lack of ectoflexus on M1; lack of strong parastyle on M1; stronger development of paraconule and metaconule on M1; development of p4 basin; paraconid and metaconid of m2 confluent at their bases.

Differs from *Miacis hargeri* in: lack of development of parastyle on M1; diastemata separating premolars; strong, medially angled molar hypocones; m2 trigonid compressed; cristid oblique on m3; p4 basin; development of anterior cusps on lower premolars; P4 protocone more reduced; M1 paracone and metacone not conjoined.

Differs from *Miacis hookwayi* (known only from m1 and m2) in: weaker cingulum on m1 and m2; m2 with less elongated talonid basin; m2 trigonid with compressed metaconid and paraconid; back of m1 talonid not 'open' as in *M. hookwayi*.

Differs from *Miacis invictus* (known only from M1) in: less strongly developed parastyle; and presence of hypocone on M1.

Differs from *Miacis latouri* (known only from M1 and M2): in presence of hypocone on M1 and M2; less well-developed parastyle on M1 and M2; lack of ectoflexus on M1; and stronger lingual cingulum on M2.

Differs from *Miacis latidens* in: presence of hypocone on M1 and M2; less-developed parastyle on M1; m3 smaller; morphology of stylar shelf narrows more buccally to metacone.

Differs from *Miacis lushiensis* in: diastemata around lower premolars; less developed anterior accessory cusp on p4; and development of p4 basin.

Differs from *Miacis medius* in: diastemata around upper and lower premolars; development of hypocone on M1 and M2; less developed parastyle on M1; stylar shelf is larger; more reduced M2–M3; P4 relatively smaller, with protocone more posteriorly placed and reduced; upper and lower premolars more mediolaterally compressed; m2 trigonid compressed; development of p4 basin; and smaller anterior accessory cusps on lower premolars.

Differs from *Miacis parvivorus* in: less well-developed M1 parastyle; larger M1 metaconule; more medially directed hypocone on M1; development of p4 basin; shorter m1 talonid anteroposteriorly; and more compressed m2 trigonid.

Differs from '*Miacis*' *petilus* in: development of p4 basin; lack of an elongated m2 talonid; relatively mesiodistally compressed m2 trigonid; cristid obliqua connects to protoconid; smaller posterior accessory cusps on lower molars; and relatively more reduced m3, both in size and elaboration of surface features.

Differs from *Miacis rosei* in: less well-developed M1 parastyle; smaller metastylar shelf on M1; larger M1 metaconule; presence of hypocone on M1; and a more reduced m3 which lacks well-developed trigonid cusps and separation of talonid from the body of the tooth.

Differs from '*Miacis*' *sylvestris* in: lack of well-developed M1 parastyle; development of hypocone on M1 and M2; mesiodistally compressed m2 trigonid; more widely separated metacone and paracone on M1; and larger stylar shelf.

Differs from *Miacis thailandicus* in: M1 not reduced compared to P4; M1 hypocone present; M1 with less well-developed parastyle; presence of M3; and presence of a well-developed basin on p4.

Differs from '*Miacis*' *uintensis* in: relative size of P4 compared to M1; less well-developed parastyle; smaller size; slender jaws; and developed basin on p4.

Differs from *Miacis washakius* in: large M1 parastyle; broad stylar shelf on M1; presence of hypocone on M1 and M2; m2 trigonid compressed mesiodistally; m1 and m2 talonid basins relatively unelongated; development of basin on p4; and no anterior accessory cusps on lower premolars.

Differs from *Miacis winkleri* in: developed p4 basin; lack of strongly developed anterior accessory cusps on premolars; m2 trigonid relatively lower compared to m1; lack elongated m2 talonid basin; and m2 trigonid relatively more compressed. (Comparison based on images and description only).

When character transformations are mapped onto the most parsimonious tree, *Dawsonicyon isami* has a mix of primitive and derived characters. This is not surprising, considering its midpoint position along the paraphyletic stem array of non-viverravid basal carnivoramorphans leading to crown Carnivora. For this discussion, primitive character states are considered to be those predominantly shared by early-diverging taxa such as *Miacis parvivorus*, *Vulpavus profectus*, *Vulpavus ovatus*, and *Oodectes*, whereas derived character states among non-Viverravidae basal carnivoramorphans are those found predominantly in taxa within the clade including later-diverging taxa such as '*Miacis*' *uintensis*, '*Miacis*' *sylvestris*, *Procynodictis vulpiceps*, *Tapocyon*, and *Quercygale*. Primitive traits of *D. isami* include a parastyle with no anterior expansion and M1 with a posterior lingual cingular shelf that is more pronounced than its anterior cingulum. Derived traits of *D. isami* include an M1 parastyle that projects farther buccally than the metastyle, a reduced P4 protocone, and an elongated P4 metastylar blade. Among basal non-viverravid carnivoramorphans, *D. isami* has the unique feature of a hypocone formed by the swelling of the entire cingulum ridge.

## CONCLUSIONS

Based upon comparison to all existing genera of non-Viverravidae basal carnivoramorphans, comparisons to all *Miacis* species, and the results of the phylogenetic analysis, we have erected the new taxon *Dawsonicyon isami*. The recognition of this new faunal element of the Black's Fork Member of the Bridger Formation adds to the known diversity of carnivoramorphans from this unit. A wide variety of carnivoramorphans in the 'Bridger B' informal subunit of the Bridger Formation has been recognized since Matthew's (1909) early, but exceptionally comprehensive and insightful, monograph. Taxa currently known from the Black's Fork Member are *Viverravus*, *Miocyon*, *Oodectes*, *Uintacyon*, *Palearctonyx*, *Vulpavus*, and various species of *Miacis* (*Miacis parvivorus*, *Miacis hargeri*, and '*Miacis*' *sylvestris*) (Flynn 1998). Living carnivorans are one of the most diverse of modern mammalian orders, and it is apparent that this high diversity is not solely a recent development, but also was typical during the early diversification of Carnivoramorpha.

The palaeoenvironment of *D. isami* and its contemporaries was one of a cooling, drying climate; however, the conditions still were much warmer and wetter than in modern southwestern Wyoming (Rose 2006; Roehler 1993). The large lakes that previously characterized the region were rapidly drying out (Roehler 1993), creating changing palaeoecological conditions and new potential adaptive zones for flora and fauna. Only through in-depth anatomical and distributional studies of the carnivoramorphans and other inhabitants of this time slice can we hope to understand how resources were partitioned to allow for such a large number of sympatric, contemporaneous carnivore species from a single clade.

*Dawsonicyon isami* has a unique combination of characters, heretofore unseen in any other basal carnivoramorphan. This highlights the tremendous amount of morphological diversity present even in the early stages of diversification of the clade. Substantial future work will be required to determine the relationships among all of these species, as well as the relative order of character acquisitions across the array of non-viverravid basal carnivoramorphans. This paper also has highlighted the wastebasket taxonomic status of *Miacis*. Again, more detailed systematic work needs to be undertaken to create a coherent, well circumscribed, and monophyletic concept of the genus *Miacis*, including only the type species and its closest relatives (as a clade distinct from all other early carnivoramorphans).

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