FUNCTIONAL ADAPTATIONS OF THE POSTCRANIAL SKELETON OF TWO MIOCENE BORHYAENOIDS (MAMMALIA, METATHERIA), *BORHYAENA* AND *PROTHYLACINUS*, FROM SOUTH AMERICA

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ABSTRACT. Two Santacrucian borhyaenoids, *Borhyaena tuberata* and *Prothylacinus patagonicus*, are analyzed from a functional-adaptive perspective. Seven extant placental and marsupial models are examined in order to interpret the locomotor adaptations of the two fossils. These carnivorous models are characterized by various hunting types and locomotor habits, and the association of their skeletal adaptive features with diet, substrate preference, and locomotor performance permits a functional interpretation of the postcranium of *Borhyaena* and *Prothylacinus*. The analysis shows that the forelimb of *Prothylacinus* is modified to provide strength and flexibility for controlled climbing. This taxon exhibits semiplantigrade fore- and hind feet. Its vertebral column was flexible, and the hindlimb suggests an active predatory mode of hunting. The tail was muscular, heavy, and was probably used as a balancing organ. By comparison, the forelimb of *Borhyaena* indicates a more terrestrial mode of life, with a digitigrade forefoot, and more parasagittal movements. The tail was lighter and less muscular than in *Prothylacinus*. Both fossils are characterized by a powerful neck musculature related to predatory habits.

KEY WORDS: functional analysis, Metatheria, Miocene, South America.

THIS paper presents a functional analysis of the postcranial skeleton of *Borhyaena tuberata* and *Prothylacinus patagonicus* (Santa Cruz Formation, Patagonia) in order to reconstruct the potential locomotor activities of these two fossil mammals. *Borhyaena* and *Prothylacinus* both belong to the borhyaenoid superfamily (Marshall 1978, 1979). The borhyaenoids were highly carnivorous South American marsupials, known from deposits that range in age from early Palaeocene to late Pliocene. The oldest specimen known, and one of the best preserved borhyaenoids, is *Mayulestes ferox* from the early Palaeocene of Tiupampa (Santa Lucía Formation, Bolivia). The detailed analysis of the postcranial skeleton of *Mayulestes* (Muizon 1998; Argot 2001, 2002, 2003) highlighted primitive adaptations within the superfamily and permits a better understanding of the locomotor behaviour of younger taxa.

The postcranial remains of five different borhyaenoid taxa have been obtained from the Santa Cruz beds of Patagonia: *Borhyaena tuberata*, *Cladosictis patagonica*, *Prothylacinus patagonicus*, *Pseudonotictis pusillus*, and *Sipalocyon gracilis* (Marshall 1978, 1979, 1981). More than 40 myr separate *Mayulestes ferox* from these species. Therefore, analysis of the locomotor diversification of contemporaneous taxa, in comparison with their ancestor, is of particular interest. *Borhyaena* and *Prothylacinus* are in the same size range and represent the two largest taxa of the Miocene series. They are therefore described and analyzed together. *Cladosictis*, *Pseudonotictis*, and *Sipalocyon* belong to a smaller size range, and are described and discussed elsewhere (Argot in press).

Dealing with two predators of the same size that coexisted in the same environment raised questions as to their different adaptions and biological roles. The postcranial skeletons of *Borhyaena* and *Prothylacinus* were described by Sinclair (1906), and discussed briefly by Muizon (1998), based on postcranial remains collected during J. B. Hatcher's Patagonian expeditions. Sinclair (1906) emphasized the unusual proportions of the Santacrucian forms (i.e. large head, long neck, and short limbs), and hypothesized that both taxa were terrestrial, *Prothylacinus* because of the reduction of the hallux, *Borhyaena* because of the shape of its ungual phalanges. More recently, Muizon (1998) briefly compared some adaptive features

of these taxa with the same features observed in *Mayulestes ferox*. In his study, Muizon (1998) noted the mobility of the joints of the forelimb of *Prothylacinus*, and particularly the capacity for considerable pronation-supination, a feature not highlighted by Sinclair (1906). For *Borhyaena*, Muizon (1998) remarked that the long bones of the forearm exhibit distinctive features which reduced the mobility of the manus. However, neither Sinclair (1906) nor Muizon (1998) analyzed the axial skeleton or the extremities (the manus of *Borhyaena* and the manus and foot of *Prothylacinus*).

In the present paper, *Borhyaena* and *Prothylacinus* are described in relation to the same complex of postcranial features which were found relevant for *Mayulestes* (Argot 2001, 2002, 2003). An interpretation of these features is then given, based on skeletal and myological features characterizing selected model species. The latter include one carnivorous marsupial and various living placental carnivores, despite structural differences due to historical constraints. This choice may be justified on the basis of the carnivorous dental adaptations of borhyaenoids, and because, except for the recently extinct *Thylacinus cynocephalus*, there are no other living carnivorous marsupials in the size range of the fossils. The extant eutherian models have been chosen within a broad adaptive range, and are representative of the different families of Carnivora. They are: *Arctictis binturong* (binturong), *Canis lupus* (grey wolf), *Gulo gulo* (wolverine), *Hyaena hyaena* (striped hyaena), *Neofelis nebulosa* (clouded leopard), and *Ursus malayanus* (Malayan sun bear). These species represent predators with very different hunting and locomotor strategies.

This paper deals only with conclusions that can be reached from analysis of adaptive modifications related to locomotion. No palaeoenvironmental details will be discussed.

MATERIAL AND METHODS

The description of the postcranial skeleton of the two Santacrucian borhyaenoids deals primarily with the most complete specimens, as a reconstruction of locomotor adaptations requires well-preserved post-cranial elements. Nevertheless, some other more fragmentary specimens are used occasionally in order to complete the analysis. The postcranial skeleton of *Prothylacinus patagonicus* is known only from two specimens, specimen PU 015700 being the most complete and well preserved. A second specimen (MACN A 706–720) provides information on the manus. The postcranial skeleton of *Borhyaena tuberata* is known from more specimens, although most of these are only fragmentary. Specimen PU 015701 forms the basis of a comparative analysis with *Prothylacinus*. The other specimens provide information on the humerus, the calcaneum, and some vertebrae. A seventh specimen was referred to *Borhyaena excavata* by Sinclair (1906), but to *B. tuberata* by Marshall (1978). It is slightly smaller than PU 015701 but is used here as it includes a skull and five well-preserved cervicals. Listed below are the bones that have been used for the description and interpretation of the postcranial skeleton of each taxon.

Prothylacinus patagonicus PU 015700: atlas, axis, third, fourth and fifth cervicals, one pre-diaphragmatic thoracic vertebra (T?7), three associated thoracic vertebrae (T?10–12), three associated lumbar vertebrae (L?4–6), sacrum (two vertebrae), five caudals (Ca?3–4 and Ca?7–9); parts of the left and right scapulae, right humerus, right ulna, right and left radii, right scaphoid; right and left parts of the innominate (without the pubis), right and left femora, right patella, right tibia and fibula, parts of the left pes: all tarsal bones except the calcaneum, Mt I and Mt III.

Prothylacinus patagonicus MACN A 706–720: two cervicals (C?3–4), and three damaged caudals; right and left ulnae, parts of the left manus: magnum, unciform, pisiform, lunate, Mc II, III, and V, three proximal phalanges, four intermediate phalanges, four ungual phalanges.

Borhyaena tuberata PU 015701: all cervicals except the fourth, one prediaphragmatic thoracic vertebra (T?7), two proximal caudals (Ca?3–4); right scapula, right and left ulnae (the left one without the distal extremity), right and left radii, parts of the manus: right scaphoid, lunate, and trapezium, left pisiform and magnum, part of the left unciform, parts of all left metacarpals except Mc I, four proximal phalanges, three intermediate phalanges, four ungual phalanges; left femur.

Borhyaena tuberata MACN A 6203–6265: the diaphragmatic vertebra, three damaged lumbars; distal extremities of the left and right humeri; a fragmentary right innominate (around the acetabulum).

Borhyaena tuberata MACN A 2074–2078: distal half of the left humerus, right radius (incomplete); right calcaneum.

Borhyaena tuberata PU 015473: right Mc V.

Borhyaena excavata PU 015120: atlas, axis, third, fourth and fifth cervicals.

All fossil specimens come from the Santa Cruz Formation in Patagonia (Santacrucian, end of early Miocene), and were collected during various expeditions between 1889 and 1899 (Sinclair 1906; Marshall 1978, 1979).

The skeletal comparisons consider myological and eco-ethological data available for the living carnivores. The myological inferences concerning *Borhyaena* and *Prothylacinus* rely on personal data obtained during dissections of various taxa of living Guyanese didelphids (genera *Caluromys*, *Didelphis*, *Metachirus*, *Micoureus*, *Monodelphis*, and *Philander*), with additional carnivore data taken from Davis (1964), Miller *et al*. (1964), and Barone (1967). I have also made myological observations for two placental Carnivora, the giant panda (*Ailuropoda melanoleuca*), and the small-toothed palm civet (*Arctogalidia trivirgata*). As noted by Davis (1964), the myological differences observed between the models are related on the one hand to variations in the site of attachment of muscles, and on the other to considerable variations in the relative weights of the muscle groups in relation to their function. For example, Canidae and Hyaenidae exhibit advanced adaptations towards cursorial locomotion by comparison with felids and especially ursids, in which adductors, abductors and rotators play an important role. These differences, at the skeletal level, can be particularly informative regarding locomotor adaptations in the fossils. I have limited references to biomechanical studies performed on living forms such as electromyography and gait analysis, because such results have proved of limited use for interpreting the morphology of fossils.

Abbreviations used. MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MNHN, Muséum national d'Histoire naturelle, Paris, France; PU, Peabody Museum of Yale University, New Haven, USA.

DESCRIPTION OF *BORHYAENA* AND *PROTHYLACINUS*

Axial skeleton

Cervical vertebrae (Text-fig. 1). The dorsal arch of the atlas is large and robust in both taxa. It exhibits a constant anteroposterior depth in *Prothylacinus*, with straight anterior and posterior edges. There is no well-defined dorsal sulcus between the dorsal arch and the anterior articular facets. In contrast, in *Borhyaena* the anterior and posterior edges of the dorsal arch are convex (compare Text-fig. 1c and d), although not to the extent observed in *Mayulestes*. The facets that articulate with the occipital condyles are relatively more concave in *Borhyaena* than in *Prothylacinus*, and are separated from the dorsal arch of the atlas by a sulcus. The transverse processes of the atlas are robust and well-developed laterally in both taxa, but are not expanded posteriorly.

The articulation between the skull and the atlas clearly differs between the fossils. The main difference is related to the orientation of the occipital condyles (compare Text-fig. 1a and b). The condyles of *Borhyaena* protrude posteriorly, and are oriented more horizontally than in *Prothylacinus*. Therefore, in a neutral posture, the angle between the atlas and the skull is sharper in *Prothylacinus* than in *Borhyaena*. The occipital crest is prominent posterodorsally in both taxa.

The neural process of the axis is extremely well-developed in both taxa (Text-fig. 1e–f). The anterior tip of this process reaches the posterior edge of the atlantal dorsal arch when articulated. Although partially broken in all specimens observed, this process also clearly extends posteriorly above the third cervical vertebra. As a consequence of this posterior extension, the neural process of the third cervical, well-preserved in *Borhyaena*, is inclined posteriorly and exhibits an anterior border that runs parallel to the posteroventral border of the axial neural process (see Sinclair 1906, pl. 52, figs 1–2). The posterior cervical neural processes are more vertical, and slightly inclined anteriorly on C6 and C7.

Inferior lamellae develop on the ventral edge of the transverse processes of cervicals C3–C6. In *Prothylacinus*, these lamellae form a small extension protruding anteriorly on C3 (Text-fig. 1g) and C4, and a well-extended flange on C5 (C6 is unknown). On the sixth cervical of *Borhyaena*, the lamellae are prominent ventrally (Text-fig. 1h). Their
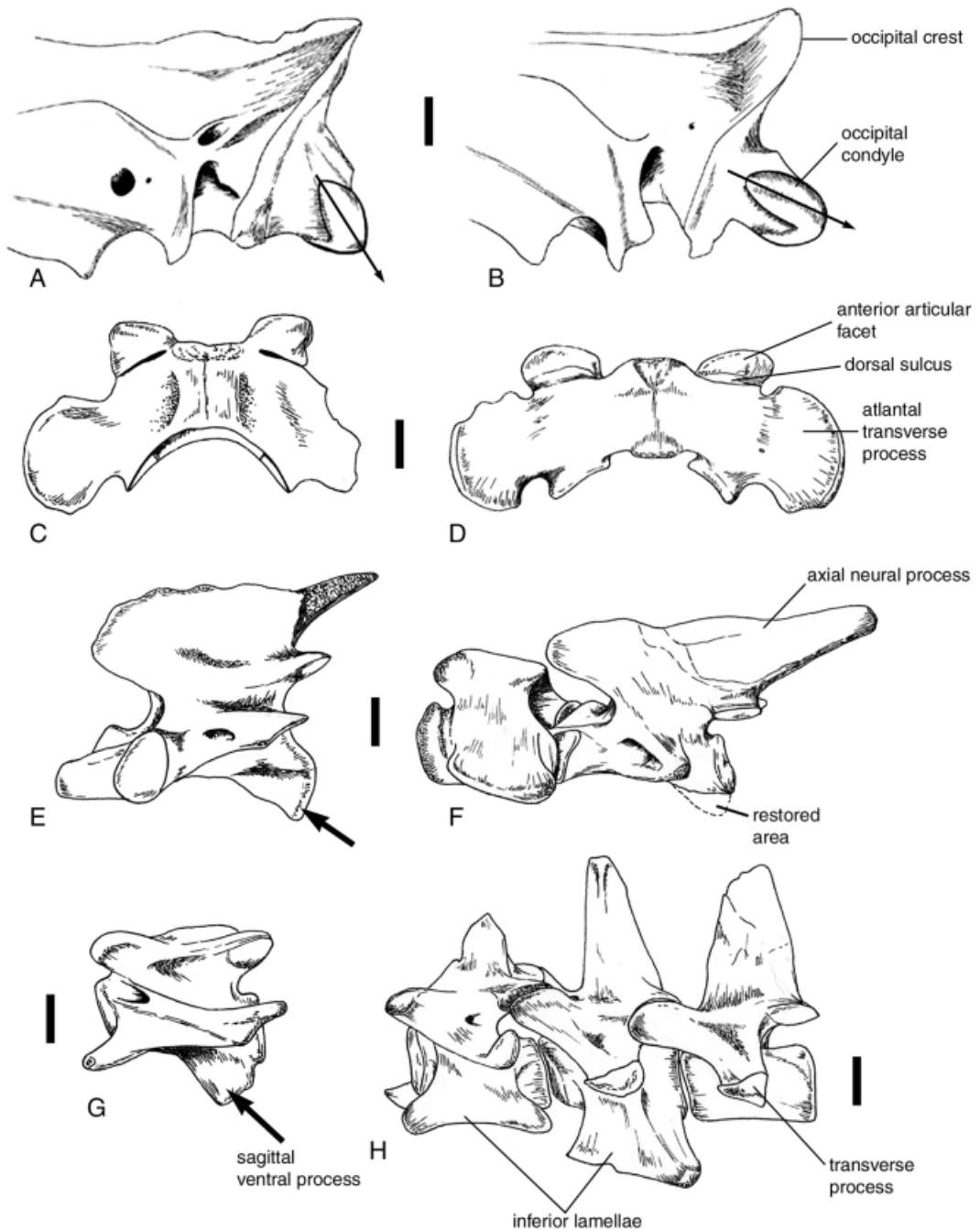
TEXT-FIG. 1. A–B, posterior part of the skull in lateral view, showing the orientation of the occipital condyles (arrow). A, *Prothylacinus patagonicus* PU 015700. B, *Borhyaena tuberata* PU 015120. C–D, atlas in dorsal view. C, *Prothylacinus patagonicus* PU 015700. D, *Borhyaena tuberata* PU 015701. E–F, axis in lateral view. E, *Prothylacinus patagonicus* PU 015700; the arrow underlines the strong ventral process. F, *Borhyaena tuberata* PU 015701; the axis and atlas are articulated, and the sagittal ventral process of the axis is broken. G–H, posterior cervical vertebrae. G, third cervical in lateral view in *Prothylacinus patagonicus* PU 015700, showing the development of the ventral process. H, C5–7 in lateral view in *Borhyaena tuberata* PU 015701. Scale bars represent 10 mm.

development is remarkable compared to those of living didelphids. Another remarkable feature of borhyaenoids is the development of sagittal ventral processes. In *Prothylacinus*, the bodies of the axis, C3, and C4, exhibit a strong triangular process that protrudes ventrally at the posterior extremity of the sagittal crest (Text-fig. 1E–G). The fifth cervical is too damaged for comparison, but the crest seems to be bifid posteriorly. The process of the axis and C3 of *Borhyaena* are also well developed.

Neural processes of the thoracolumbar area, anapophyses, and mammillary processes (Text-fig. 2A–G). In *Borhyaena* and *Prothylacinus* the single preserved pre-diaphragmatic vertebra (supposedly T7, Sinclair 1906) exhibits a long, slender neural process (Text-fig. 2A–B). The posterior inclination of this process does not differ significantly between these taxa (*c*. 50–55 degrees), but the process is longer in *Borhyaena* than in *Prothylacinus* when compared to the length of the vertebral body.

The diaphragmatic vertebra represents the transition between two modes of articulation (tangential vs. radial). In *Prothylacinus*, this vertebra is associated with two posterior thoracic vertebrae, and therefore probably represents T10 or T11 (Text-fig. 2C). It is characterized by a pair of processes that are prominent dorsally and located lateral to the articular facets of the prezygapophyses, as if this vertebra began a trend towards a radial articular mode. Such processes are absent on the diaphragmatic vertebra of *Borhyaena* (specimen MACN 6203–6265). The last thoracics are tightly articulated, a morphology that stabilizes the vertebral column anterior to the lumbar region. Anapophyses contribute to this stabilization. In *Prothylacinus*, the anapophyses are well developed on the last thoracics (the anterior lumbars are unknown), a morphology that allows them to bind the prezygapophyses of the following vertebra (Text-fig. 2C). Compared to the last thoracics, the last lumbars of *Prothylacinus* exhibit very reduced anapophyses (a small pit can be seen on L5 but not on L6: Text-fig. 2F), and this increases the flexibility of the posterior lumbar region. In *Prothylacinus*, as in *Mayulestes*, the anteroposterior lengthening of the vertebrae through the lumbar region is moderate.

In *Prothylacinus*, the neural process of the diaphragmatic vertebra (T?10) is broken, but the remaining part clearly indicates that it was inclined posteriorly, forming an angle of approximately 70 degrees with the vertebral column. The neural process of the following vertebra, although also broken, was approximately perpendicular to the vertebral column, whereas the neural process of the third vertebra in the series was inclined anteriorly. Therefore, the thoracic vertebra following the diaphragmatic one represents the anticlinal vertebra, which is T?11 (Text-fig. 2C). This anterior position clearly differs from the situation observed in *Mayulestes*, in which the anticlinal was probably the third lumbar (Muizon 1998; Argot 2003; Muizon and Argot 2003). The neural processes of the last lumbar vertebrae are robust, as long as the dorsal arch of the vertebra, and are clearly inclined anteriorly (Text-fig. 2F). On L6, the angle of inclination of the process to horizontal is approximately 65 degrees. In *Borhyaena* (MACN 6203–6265), the neural processes of the lumbar vertebrae are poorly preserved. Nevertheless, one neural process is approximately perpendicular to the longitudinal axis of the column, while another is clearly inclined anteriorly (Text-fig. 2D). This suggests that the anticlinal vertebra was a lumbar in *Borhyaena*.

Lumbar transverse processes (Text-fig. 2E–G). These processes are well preserved only in *Prothylacinus*. They protrude anteriorly and show a concave anterior border. The anterior tip protrudes anteroventrally beyond the limit of the vertebral body, a condition very similar to that on the fifth lumbar vertebra of *Mayulestes*. The processes are deflected downward, and this deflection is particularly emphasized by their ventral concavity (Text-fig. 2E), a condition that restricts their lateral development. In *Borhyaena*, the lumbar processes are too poorly preserved to permit useful comparisons. However, while in *Prothylacinus* the base of the lumbar processes is dorsally located (at the junction between the vertebral body and the root of the pedicles), it is located more ventrally in *Borhyaena*, a position that may reduce the ventral concavity.

Caudal vertebrae (Text-fig. 2H–I). In *Borhyaena* and *Prothylacinus*, two anterior caudals are preserved (Ca?3–Ca?4: Sinclair 1906) and are as long as the first sacral vertebra, i.e. they are approximately two-thirds the length of the last lumbars. These vertebrae are more robust in *Prothylacinus* than in *Borhyaena*. The neural processes are reduced to a small posterodorsal prominence on the sagittal crest, while the prezygapophyses protrude dorsally but are not widely divergent. Only the basal part of the transverse processes is preserved, but it suggests that the robust processes were perpendicular to the vertebral axis in one caudal (Ca?3), and inclined posteriorly in the other (Ca?4). In *Borhyaena*, the vertebral body of the preserved caudals is less massive than in *Prothylacinus*, with relatively more slender transverse processes. The prezygapophyses are more divergent than in *Prothylacinus*, and the articular facets are shorter. The foramen vertebrale is narrower and more rounded in *Borhyaena* than in *Prothylacinus*, in which it is much wider than high. As in cervical vertebrae, the vertebral body is oblique in lateral view (with prominent anterodorsal and posteroventral borders), an obliquity which may have slightly increased the flexibility of the tail.
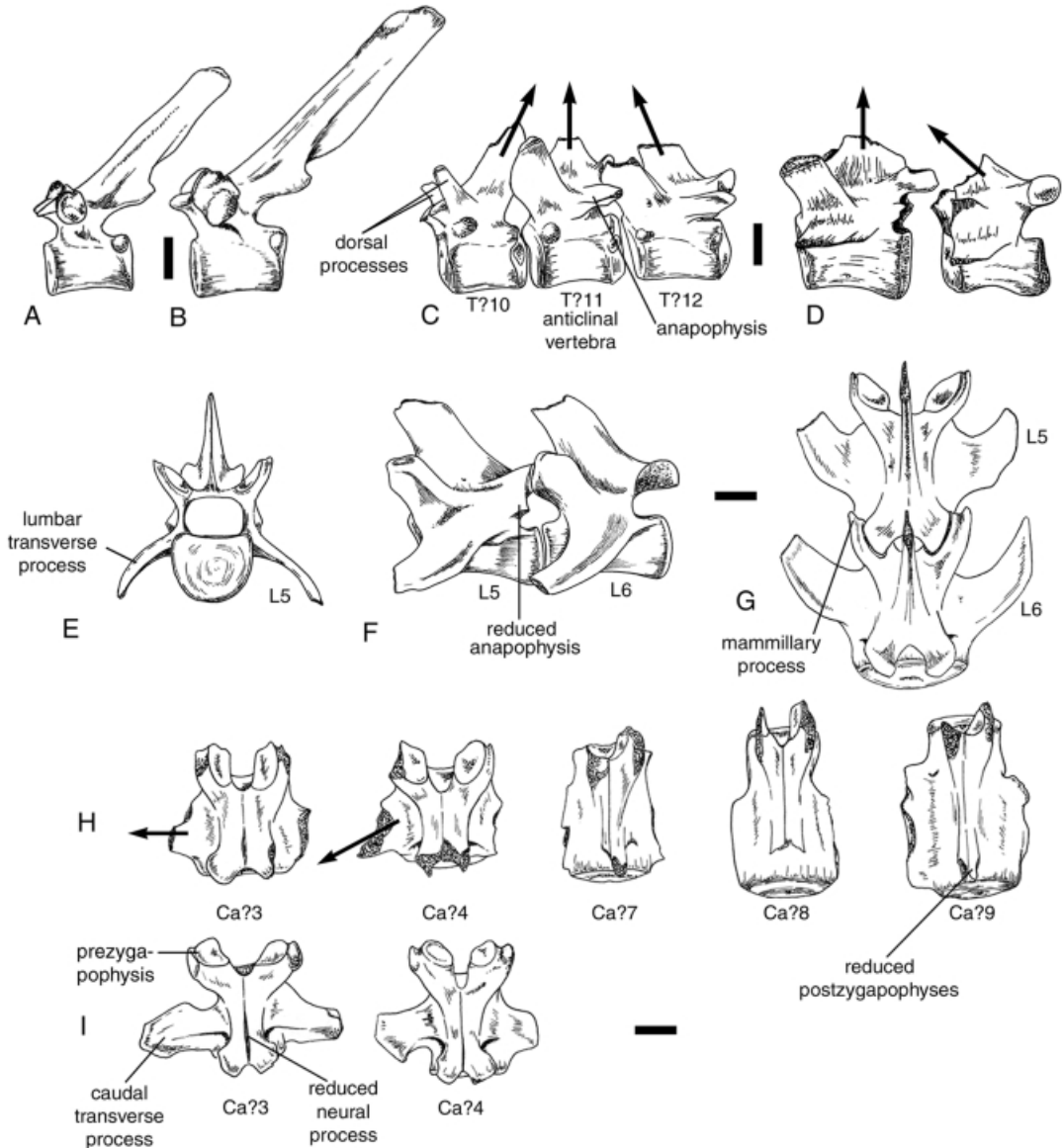
TEXT-FIG. 2. A–B, pre-diaphragmatic (T?7) vertebra in lateral view. A, *Prothylacinus patagonicus* PU 015700. B, *Borhyaena tuberata* PU 015701. C–D, location of the anticlinal vertebra; the arrows show the orientation of the neural processes. C, posterior thoracic vertebrae in lateral view in *Prothylacinus patagonicus* PU 015700; T?10 is the diaphragmatic vertebra and T?11 is the anticlinal vertebra. D, two isolated lumbars of *Borhyaena tuberata* MACN 6203–6265; the left vertebra may be the anticlinal vertebra because of the vertical neural process. E–G, posterior lumbar vertebrae of *Prothylacinus patagonicus* PU 015700, showing the orientation of the neural and transverse processes. E, L5 in anterior view. F, L5–6 in lateral view. G, L5–6 in dorsal view. H–I, caudal vertebrae in dorsal view. H, *Prothylacinus patagonicus* PU 015700. I, *Borhyaena tuberata* PU 015701. Scale bars represent 10 mm.

Three posterior caudal vertebrae are also preserved in *Prothylacinus* (Ca?7–9). They are very robust and much longer than Ca?3 and Ca?4. The zygapophyses are damaged, but the postzygapophyses are clearly reduced compared to those of the anterior caudals. The neural canal is clearly visible on the two shortest vertebrae, but it is very reduced on the longest one (Ca?9). The transverse processes are broken at their base, but formed broad lateral wings extended

along the distal two thirds of the vertebral bodies. The length of the tail of *Borhyaena* and *Prothylacinus* is difficult to estimate, but from the length and robustness of Ca?9 in *Prothylacinus*, the tail of this taxon may have had 25 or 30 vertebrae. Without the last caudals, no estimate of prehensility can be made. From the size of the animal, the tail was certainly unable to support the total body weight. The tail of *Borhyaena* was clearly lighter and more slender.

Pectoral girdle and forelimb

Glenohumeral joint and brachium (Text-fig. 3). The glenoid cavity of the scapula has a pear-shaped outline in both taxa, but it is more robust in *Prothylacinus* (compare Text-fig. 3D and E) due to the massive supraglenoid tuberosity and the width of the neck. The anterior part of the glenoid cavity is more slender and much more ventrally deflected in *Borhyaena* than in *Prothylacinus*. The humeral head of *Prothylacinus* that articulates with the glenoid cavity of the scapula is rounded in proximal view (Text-fig. 3G) and not twisted in relation to the distal extremity. In posterior view (Text-fig. 3F), the articular surface is convex medially but flat laterally, perhaps reflecting the development of the greater tubercle and thus the tendons of the spinati muscles. In lateral view (Text-fig. 3H), the articular surface extends further posteriorly than in *Mayulestes*. No reliably associated humeral head is known for *Borhyaena*.

The scapula of *Prothylacinus* is more robust than that of *Borhyaena*, particularly in the thick axillary and vertebral borders, and the short, thick neck, but the supra- and infraspinous fossae are well developed in both fossils (Text-fig. 3A–C). The anterior border meets the neck of the scapula abruptly and this increases the area of the supraspinous fossa. This contrasts with the condition in *Mayulestes* in which the supraspinous fossa is triangular. The infraspinous fossa is triangular in outline, widening towards the vertebral border. It is relatively broader in *Prothylacinus* than in *Borhyaena*. The massive scapular neck, as well as the height of the scapular spine, further suggests well-developed spinati muscles. On the humerus of *Prothylacinus*, the greater tubercle, where the supraspinatus inserts, is taller than the head. It is also prominent anteriorly (i.e. it forms a sharp angle with the anteroposterior axis of the head: Text-fig. 3G), and this increases the depth of the bicipital groove. On the posterolateral side of the greater tubercle, there is a broad fossa for the insertion of the infraspinatus.

The deltopectoral crest of the humerus is extremely long (extending along the proximal two-thirds of the humeral diaphysis: Text-fig. 3I), and characterized by a prominent distal extremity. Along the distal third of this crest, the distal part of the pectoralis insertion is well defined. The strength of the pectoralis muscles is confirmed in *Prothylacinus* by a fragment of manubrium that exhibits a relatively well-developed sagittal crest, in contrast to that of *Borhyaena*. The lesser tubercle of the humerus of *Prothylacinus* is appressed against the humeral head (Text-fig. 3G), a condition different from that of *Mayulestes*. The insertion of the teres major is emphasized by a well-developed crest on the medial side of the humerus, but the caudal angle of the scapula (from where the teres major originates), although reinforced, is not extended posteriorly (contrary to *Mayulestes*). The latissimus dorsi insertion is located in the bicipital groove, at approximately midshaft, more distally than the teres major insertion (Text-fig. 3I).

Humeroulnar and radioulnar joints (Text-fig. 4). In *Prothylacinus*, the anterior part of the humeral trochlea is separated from the capitulum by a slightly convex area. In *Borhyaena*, the equivalent region of the trochlea is separated from the capitulum by a deeper groove, and is more developed proximally (Text-fig. 4B$_{I–III}$). This condition is reflected on the ulna, in which the coronoid process is more oval in outline, and less prominent medially in *Borhyaena* than in *Prothylacinus* (Text-fig. 4B$_{IV}$). The posterior part of the humeral trochlea is asymmetrical in *Prothylacinus*, because of the distal protrusion of its medial margin (Text-fig. 4A$_{II}$). The olecranon fossa is deep, and is wider than the articular facet located below it. It is more extended medially, consistent with the prominent medial lip of the anconeal process of the ulna (i.e. the upper margin of the trochlear notch). By comparison, the anconeal process of *Borhyaena* is narrower (Text-fig. 4B$_V$). It is also more prominent anteriorly and, consistently, the humeral trochlea is narrower and more concave posteriorly than in *Prothylacinus* (compare Text-fig. 4A$_{III}$ and B$_{III}$).

In *Prothylacinus*, the radial head is oval in outline, but the proximal articular facet is rounded, with thickened medial and lateral borders. Moreover, the enlarged ulnar articular surface is convex. The posterolateral border protrudes proximally, and the capitular eminence is elevated on the anterior margin. On the ulna of *Prothylacinus*, the articular facet of the radial notch forms an angle of approximately 120 degrees with the coronoid process, but this angle is smaller in *Borhyaena* (compare Text-fig. 4A$_V$ and B$_V$). The radial head of *Borhyaena* is more compressed anteroposteriorly, and has more slender margins than that of *Prothylacinus*. It is also relatively smaller: in proximal view, with the radius and ulna in articulation, the area of the radial head is approximately as large as that of the coronoid process in *Prothylacinus*, but is clearly smaller in *Borhyaena*. This suggests a reduced loading of the radial head in *Borhyaena*. The radius of *Prothylacinus* is also characterized by the angle formed between the transverse axes of the proximal and distal epiphyses, an angle of approximately 50 degrees (Text-fig. 4A$_{VI}$). Because of this angle, the ulnar articular facet is oriented posteromedially when the ulna and radius are articulated, whereas in *Borhyaena* (in
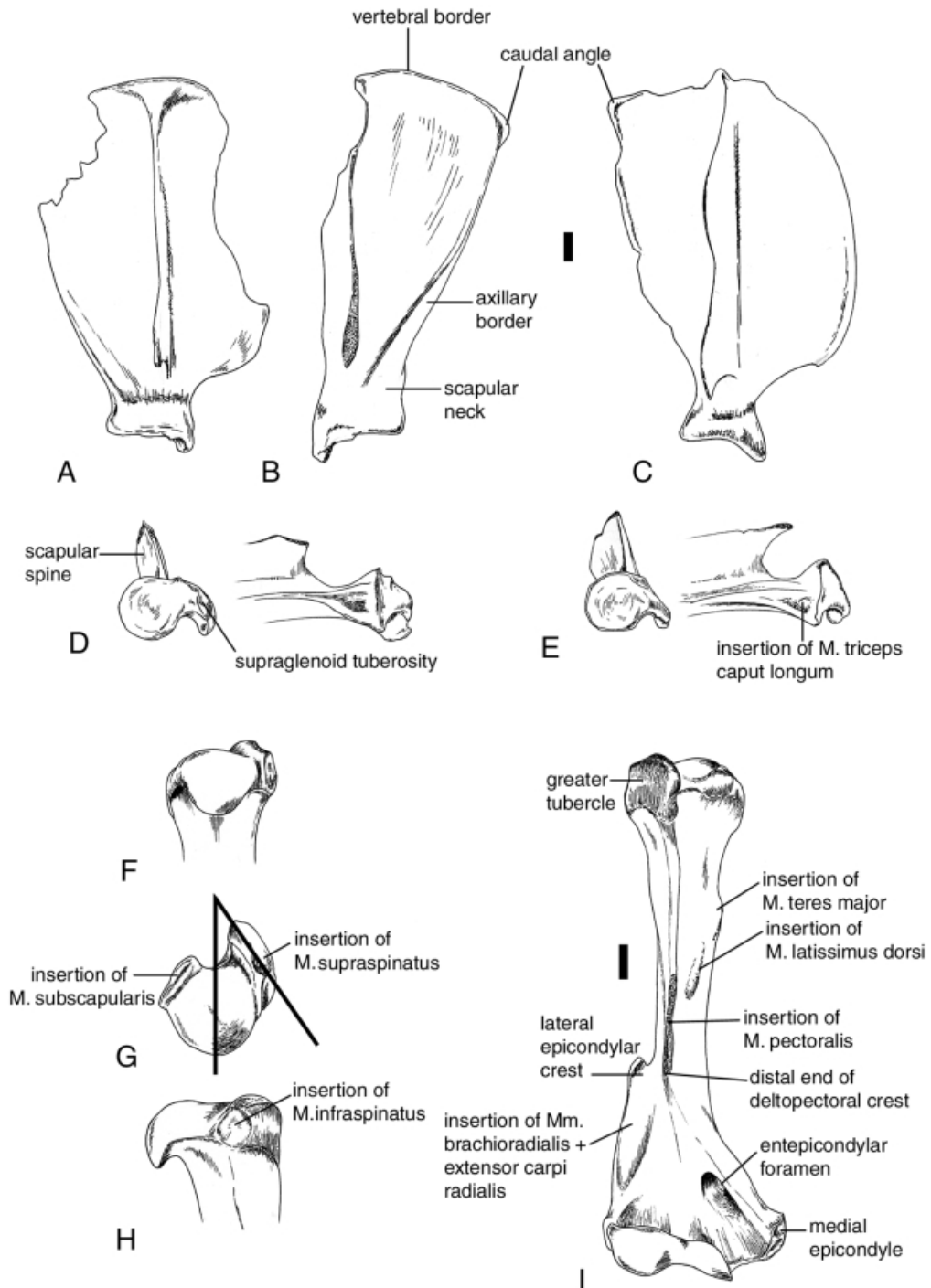
TEXT-FIG. 3. A–C, scapula in lateral view. A–B, *Prothylacinus patagonicus* PU 015700 (A, right scapula and B, left scapula). C, *Borhyaena tuberata* PU 015701. D–E, glenoid cavity of the right scapula; left, distal view; right, posterior view. D, *Prothylacinus patagonicus* PU 015700. E, *Borhyaena tuberata* PU 015701. F–H, right humeral head in *Prothylacinus patagonicus* PU 015700. F, posterior view; G, proximal view; H, lateral view. I, right humerus in anterior view in *Prothylacinus patagonicus* PU 015700. A–C, I, scale bars represent 10 mm. D–H are not to scale.
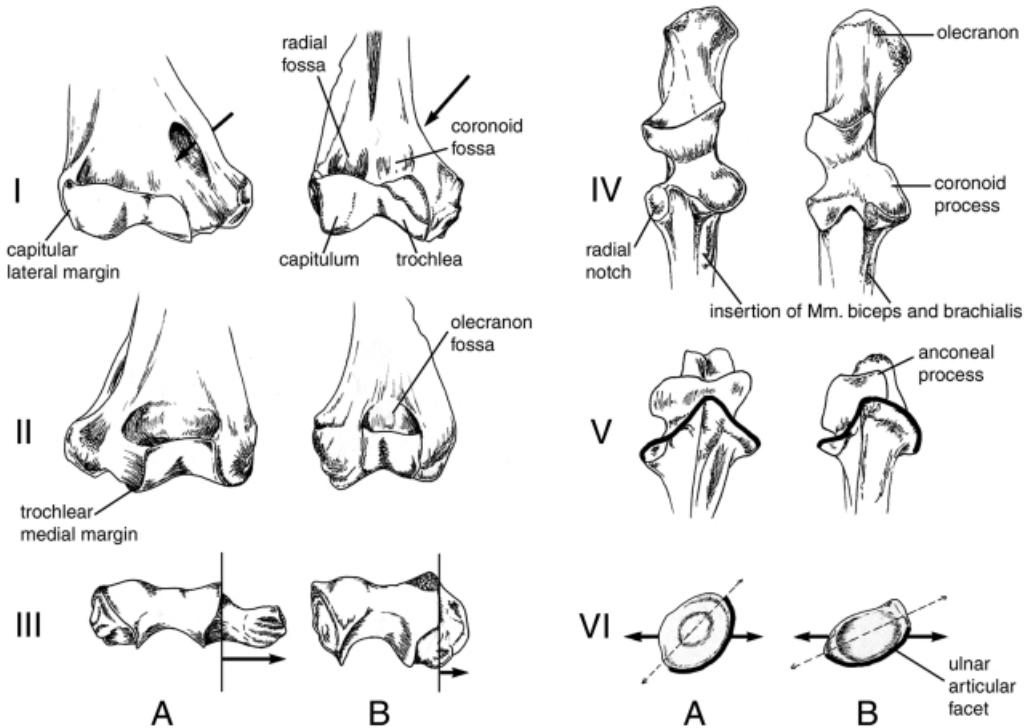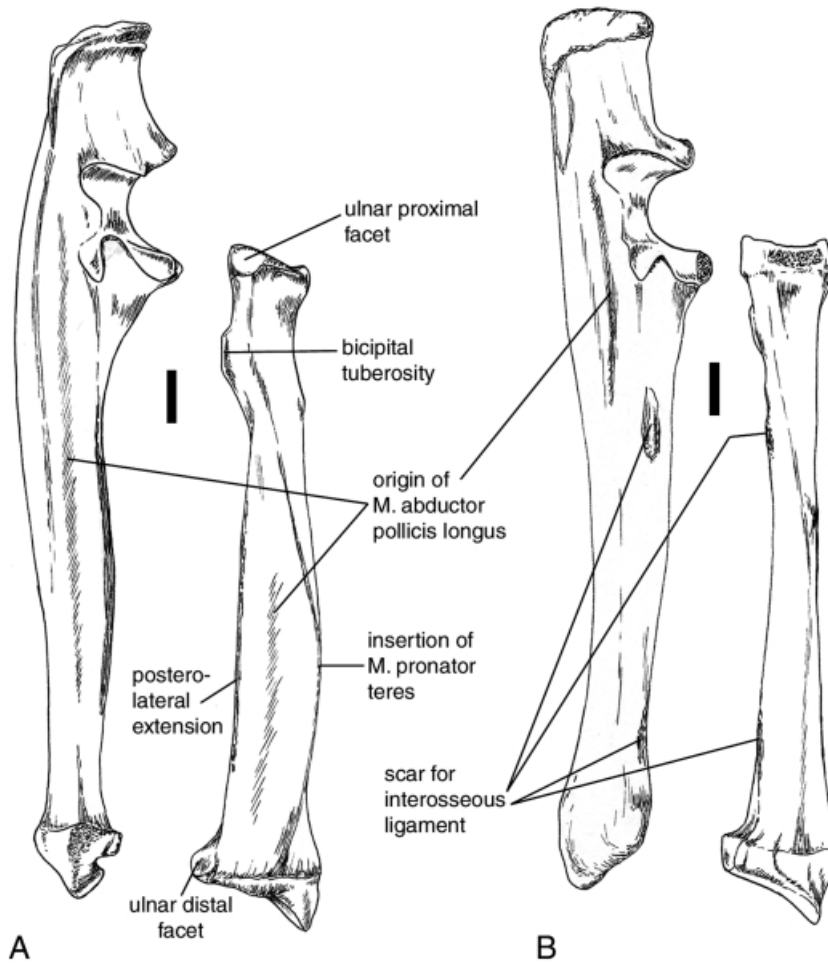
TEXT-FIG. 4. Elbow joint. A, *Prothylacinus patagonicus* PU 015700. B, *Borhyaena tuberata* MACN 2074–2078 (humerus) and PU 015701 (ulna and radius). I–III, distal extremity of the right humerus. I, anterior view; II, posterior view; III, distal view. IV–V, trochlear notch of the right ulna. IV, anterior view; V, anterodistal view. VI, right radial head in proximal view; the dashed line represents the long axis of the proximal epiphysis, the full line the long axis of the distal epiphysis; the bold part of the circumference represents the ulnar articular facet. Not to scale.

which the radius does not exhibit the same twist), the ulnar articular facet is oriented more posteriorly. This means that the radius is located more anteriorly in relation to the ulna in *Borhyaena*, and more laterally in *Prothylacinus*.

Morphology of the ulna and radius (Text-fig. 5). The ulnae and radii of *Borhyaena* and *Prothylacinus* have a distinct morphology. In *Prothylacinus*, the posterior border of the ulnar diaphysis is convex along its proximal half, whereas in *Borhyaena* it is straight proximally and concave distally. In *Borhyaena*, the olecranon is very robust, deep and wide. It protrudes medially (Text-fig. 4B$_{IV}$), which may reflect the development of the medial head of the triceps. The straight ulnar diaphysis, as well as the orientation of the olecranon with respect to the ulnar shaft (angle defined in Walker 1974 and Van Valkenburgh 1987) indicates that the triceps acted in more extended stances in *Borhyaena* than in *Prothylacinus*. In the latter, the olecranon has less caudal curvature, and the anterior tip of the olecranon is more prominent proximally than the posterior one.

The supraglenoid tuberosity of the scapula (origin of biceps brachii) is much more robust in *Prothylacinus* than in *Borhyaena*. Consistently, the bicipital tuberosity of the radius is much larger in *Prothylacinus*, and is more distally located than in *Borhyaena*. On the ulna of *Prothylacinus*, the biceps and brachialis insert in a deep fossa located just distal to the coronoid process. In *Borhyaena* this insertion is more medially located, and it is shallower.

The medial epicondyle (M. flexor digitorum profundus humeral head) is much more prominent in *Prothylacinus* than in *Borhyaena* (Text-figs 3I, 4A$_{I-III}$). In the former, the epicondyle is separated from the trochlea by a deep groove, whereas in *Borhyaena* the epicondyle is appressed against the trochlea. Therefore, the distal humeral extremity of *Borhyaena* is much more symmetrical than that of *Prothylacinus*. Moreover, in *Borhyaena* (MACN 2074–2078 and MACN 6203–6265, with poorly preserved distal humeri), unlike *Prothylacinus*, there is no medial epicondylar crest and no entepicondylar foramen. Medially, the ulna of *Prothylacinus* bears a deeper fossa (M. flexor digitorum profundus ulnar head) than *Borhyaena*, extending from the apex of the olecranon to the middle of the diaphysis.

TEXT-FIG. 5. Right ulnae and radii in lateral view. A, *Prothylacinus patagonicus* PU 015700. B, *Borhyaena tuberata* PU 015701. Scale bars represent 10 mm.

Furthermore, the radial diaphysis of *Prothylacinus* exhibits a very well-developed posterolateral extension which extends towards the ulnar shaft (Text-fig. 5A), similar to the extension developed in the arboreal didelphid *Caluromys*. It houses a deep medial fossa for a robust attachment of the radial head of M. flexor digitorum profundus, in contrast to *Borhyaena*.

The lateral ulnar fossa (M. abductor pollicis longus origin) is deeper and much longer in *Prothylacinus* than in *Borhyaena*, extending almost the entire length of the diaphysis. Moreover, the extension of the radial diaphysis in *Prothylacinus* further increases the space for M. abductor pollicis longus origin. In *Borhyaena* the ulnar lateral fossa is shorter and shallower. The long bones of the forearm were tightly associated in *Borhyaena*, as shown by two scars for the attachment of a strong interosseous ligament: a prominent proximal one lies on the radius distal to the bicipital tuberosity, and a weaker one lies near the distal epiphysis.

The anterior edge of the radial diaphysis in *Prothylacinus* is convex distally and the insertion of the pronator teres extends along the distal three quarters. By comparison, the radius of *Borhyaena*, although of the same length, is more slender and less curved (Text-fig. 5B). Moreover, there is a difference between the taxa in the distal articulation of the ulna and radius. In *Prothylacinus*, the ulnar facet is particularly large, convex and prominent, in contrast to *Borhyaena*. This morphology, in conjunction with a strong interosseous ligament, suggests a more stabilised distal articulation in *Borhyaena*.

Radiocarpal joint and manus (Text-fig. 6). In *Borhyaena* the distal epiphyses of the radius and ulna are more or less equivalent in width, whereas in *Prothylacinus*, the distal radial epiphysis is almost twice as wide as that of the ulna (Text-fig. 6A–B). As the total width of the wrist is equivalent in the two taxa, this demonstrates the robustness of the distal ulna in *Borhyaena*, in contrast to the predominant role of the scaphoradial articulation in *Prothylacinus*. The scaphoradial articulation is very different in the two taxa. In *Borhyaena* the distal radial epiphysis is deeper than in *Prothylacinus*, and the articular facet is more convex anteroposteriorly. In contrast, the articular facet in *Prothylacinus* is slightly concave and more sharply angled in relation to the styloid process. Similarly, the scaphoid of *Prothylacinus* is wider than that of *Borhyaena*, but shorter anteroposteriorly. The scaphoids of both taxa bear a transversely extended proximal groove. In lateral view, the proximal facet of the scaphoid in *Prothylacinus* is deflected strongly anteriorly, a position that may increase the range of dorsiflexion. By comparison, the same facet in *Borhyaena* is horizontal and approximately parallel to the distal articular facets. The palmar process (M. flexor carpi radialis insertion) protrudes more radially in *Prothylacinus*, and more ventrally in *Borhyaena*, reducing the degree of radial deviation of the manus in the latter.

The pollex is unknown in both taxa, but some indication of its orientation is given by the Mc II of *Prothylacinus* and by the trapezium of *Borhyaena*. In *Prothylacinus* the internal side of Mc II is rough and lacks any well-defined articular facet. This implies that Mc I and Mc II were not tightly articulated, allowing relatively free movements of Mc I. Mc II was closely articulated with Mc III, but its distal epiphysis is more asymmetrical than that of Mc III, suggesting that the palmar side of the phalanges of the second digit faced slightly medially during flexion. In *Borhyaena*, the trapezium exhibits a facet for Mc I that is slightly deeper than wide, oriented distally, and is concave anteroposteriorly. It is similar to the distal facet on the magnum for Mc III, and therefore suggests that Mc I and Mc III laid parallel to one another.

In *Prothylacinus*, the left Mc II, III, and V are complete, while in *Borhyaena* all left metacarpals are known except Mc I, but only Mc IV and V are complete (Text-fig. 6C–D). The Mc III in *Prothylacinus* is only 80 per cent of the length of Mc IV in *Borhyaena*, a condition that implies a shorter palm in the former considering that the forearm bones of the two taxa are of similar length. A relative lengthening of metapodials in *Borhyaena* is consistent with a more digitigrade stance, as already suggested by the reduced dorsiflexion range at the scaphoradial joint. In *Prothylacinus* the proximal articular facet of the unciform is strongly helical, and this may increase the convergence of the external digits towards the inner side of the palm. Unfortunately, the unciform of *Borhyaena* is damaged, precluding comparisons. In *Prothylacinus*, Mc V is robust and relatively longer than that of *Borhyaena* compared to the rest of the hand, which implies a more important role in grasping habits. The proximal end of Mc V bears a dorsolateral fossa in both taxa for the insertion of M. extensor carpi ulnaris. The proximal articular facet is particularly asymmetrical in *Borhyaena* (it extends further dorsally than ventrally, and is depressed laterally while the medial ridge is dorsally prominent). In *Prothylacinus*, Mc V exhibits an asymmetrical distal epiphysis and has a twisted diaphysis, i.e. the transverse axis of the proximal facet lies at an angle to the transverse axis of the distal epiphysis. The shape of the distal articular facet (with a prominent internal condyle and an internal groove that is deeper than the external one) suggests a slight convergence of the fifth digit during flexion. One of the proximal phalanges known for *Prothylacinus* has a proximal articular facet that is asymmetrical, consistent with the shape of the distal epiphysis of Mc V. Moreover, the diaphysis of one of the intermediate phalanges is slightly twisted, and these two phalanges together probably increased the convergence of the fifth digit towards the other digits during flexion. By comparison, the distal epiphysis of Mc V is not asymmetrical in *Borhyaena*.

The proximal phalanges are longer in *Prothylacinus* than in *Borhyaena*, in absolute size (see Appendix), and compared to the palm length. In *Prothylacinus*, the longest proximal phalanx known represents 51 per cent of the length of Mc III, whereas in *Borhyaena*, it represents only 38 per cent of the length of Mc IV. The proximal phalanges of *Borhyaena* are also more robust, deeper dorsoventrally at their proximal ends, and have a dorsal border that is not flat but convex (Text-fig. 6E–F). The intermediate phalanges (Text-fig. 6G–H) are particularly short and robust in *Borhyaena*, and are as wide as long. The longest represents 67 per cent of the longest proximal phalanx, versus 91 per cent in *Prothylacinus*. In addition, the intermediate phalanges of *Prothylacinus* exhibit a deep fossa on the palmar side.

Four ungual phalanges of a single manus have been preserved for each taxon. They are anteroposteriorly shorter and more rounded in cross-section in *Borhyaena* than in *Prothylacinus*. Moreover, these phalanges exhibit a transversely convex dorsal border in *Borhyaena*, and the tips are cleft. In *Prothylacinus* they are twice as deep dorsoventrally as in *Borhyaena* (Text-fig. 6I–J), with a sharper and more strongly curved dorsal margin. In *Borhyaena*, the proximal articular facet is wider than high, and is only weakly concave, whereas it is higher than wide in *Prothylacinus*. The flexor tubercle is also much larger in *Prothylacinus*.

Pelvic girdle and hindlimb

The innominate and hip joint (Text-fig. 7). In *Prothylacinus* the ilium is blade-like and quadrangular in outline (Text-fig. 7A). It is aligned with the ischium, unlike that of *Mayulestes*. Moreover, the expansion dorsal to the
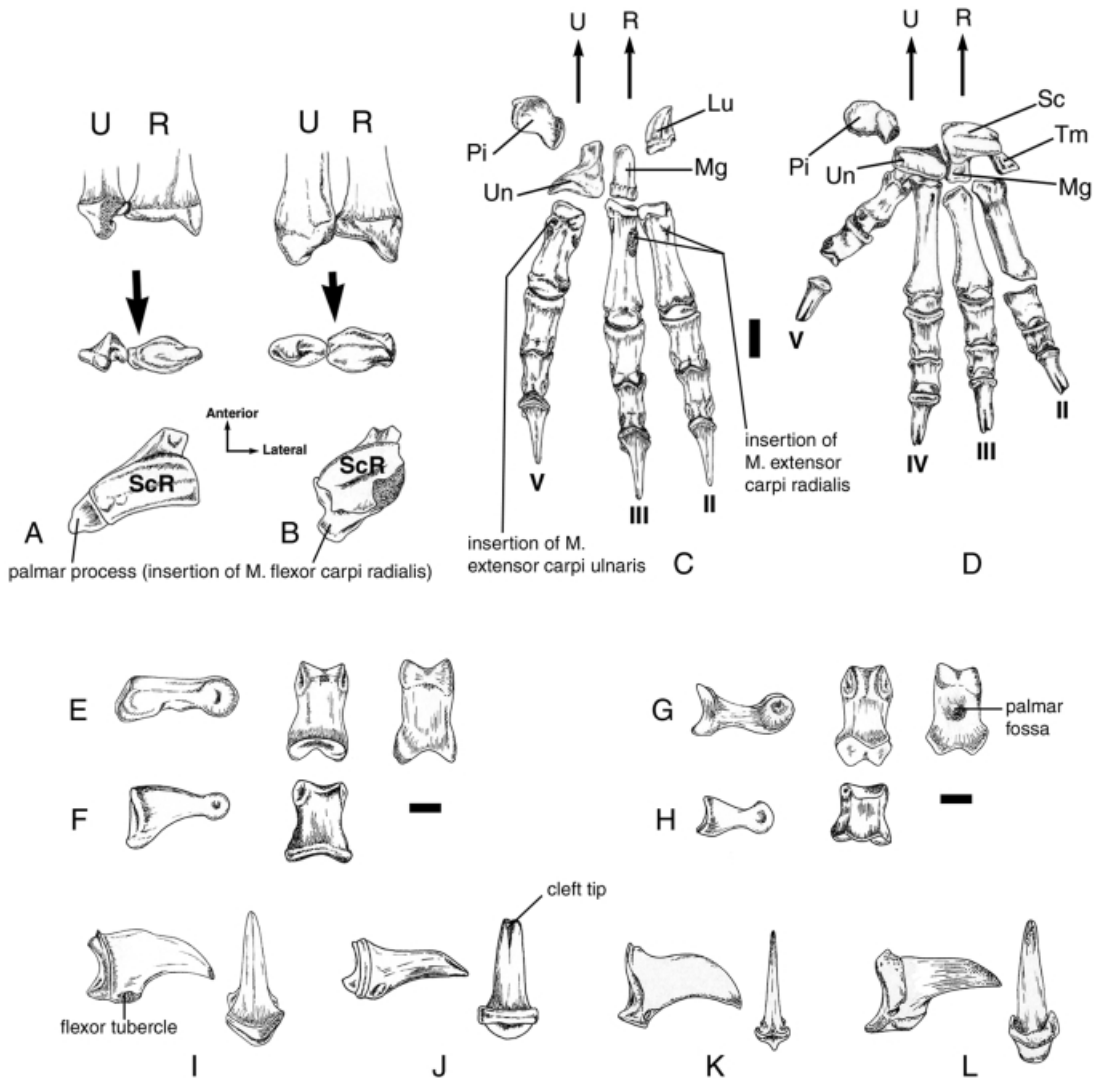
TEXT-FIG. 6. A–B, proximal radiocarpal joint. Top, distal end of the right ulna and radius in anterior view. Middle, the same in distal view. Bottom, right scaphoid in proximal view. C–D, general morphology of the manus in dorsal view; the association of the phalanges is conjectural. Abbreviations: Lu, lunate; Mg, magnum; Pi, pisiform; R, radius; Sc, scaphoid; ScR, scaphoradial joint; Tm, trapezium; U, ulna; Un, unciform. E–F, proximal phalanges; from left to right: lateral, dorsal, and ventral views. G–H, intermediate phalanges; from left to right: lateral, dorsal, and ventral views. G, *Prothylacinus patagonicus* PU 015700; H, *Borhyaena tuberata* PU 015701. I–L, ungual phalanges. Left, lateral view. Right, dorsal view. A, C, E, G, I, *Prothylacinus patagonicus* PU 015700 (ulna, radius, and scaphoid) and MACN 708–720 (manus). B, D, F, H, J, *Borhyaena tuberata* PU 015701. K, *Arctictis binturong* MNHN 1975–78. L, *Canis lupus* MNHN 1984–08. C–D, scale bar represents 10 mm. E–H, scale bars represent 5 mm. The other elements are not to scale.

sacral articulation is more pronounced than in *Mayulestes*. Although little of the ilium of *Borhyaena* is preserved (Text-fig. 7B), the dorsal expansion of the ilium is similar to that of *Prothylacinus*. The large space located dorsal to the sacrum and the outward deflection of the anterior part of the ilium seen in dorsal view (Text-fig. 7C) suggest a well-developed lumbar epaxial musculature. Along the ventral margin of the iliac blade, the iliacus fossa is restricted to a slender strip. The femoral lesser trochanter, where the M. iliacus inserts, is robust, but it is posteriorly located and less
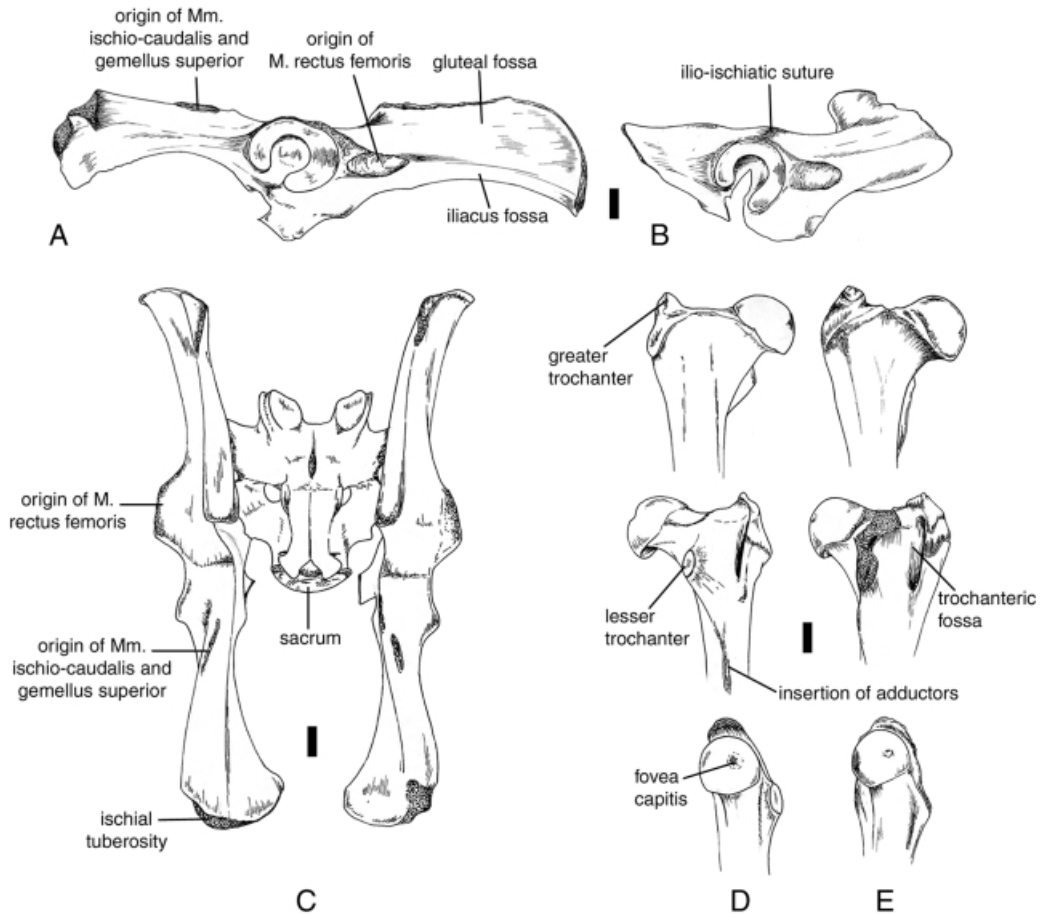
TEXT-FIG. 7. A–B, innominate in lateral view. A, *Prothylacinus patagonicus* PU 015700. B, *Borhyaena tuberata* MACN 6203–6265. C, innominate of *Prothylacinus patagonicus* PU 015700 in dorsal view, articulated with the sacrum. D–E, proximal extremity of the femur. From top to bottom: anterior, posterior, and medial views. D, *Prothylacinus patagonicus* PU 015700. E, *Borhyaena tuberata* PU 015701. Scale bars represent 10 mm.

prominent medially in the Miocene taxa than in *Mayulestes*. M. rectus femoris originated on a prominent, rugose tuberosity anterior to the acetabulum in both taxa. In *Prothylacinus*, the tip of the ischial tuberosity and the posterior ramus of the ischium are poorly preserved, but the preserved part is not deflected strongly outward, as seen in dorsal view. The dorsal ramus of the ischium is very robust, and the ischium represents 46 per cent of the total length of the innominate.

The acetabular articular surface is oriented more laterally in *Prothylacinus* than in *Borhyaena*, while the ventral part of the articular facet extends more posteriorly (Text-fig. 7A–B). In *Borhyaena* the dorsal border is more prominent and the anterior part of the articular surface faces more posteriorly. A slight constriction of the articular surface at the level of the ilio-ischiatic suture can be observed in *Prothylacinus*. In both taxa the acetabulum is very close to the sacral articulation, the neck of the ilium being particularly short and thick. The length of the iliac neck relative to the total length of the innominate is 4·5 per cent in *Prothylacinus*, versus 16·5 per cent in *Mayulestes*.

In *Borhyaena* and *Prothylacinus* the femoral head is circular in medioproximal view (Text-fig. 7D–E, below), and the articular surface does not extend towards the greater trochanter. The fovea capitis (ligamentum teres insertion) is larger in *Prothylacinus*. In medial view, the femoral head is slightly wider anteroposteriorly and the protrusion of the head above the anterior side of the diaphysis is more important than in *Borhyaena*. The greater trochanter is taller than the femoral head in *Mayulestes* and to a lesser extent in *Borhyaena*, but it just reaches the level of the head in

Prothylacinus (Text-fig. 7D–E, top). In both *Borhyaena* and *Prothylacinus*, the lower border of the lesser trochanter extends distally, reaching the area of insertion of the adductors (Text-fig. 7D, middle), a region which is more rugose in *Prothylacinus*.

Knee joint (Text-fig. 8). The distal epiphysis of the femur is quadrangular as seen in distal view in both taxa, and is wider than deep (compare Text-fig. 8A$_I$ and B$_I$). The groove of the femoral trochlea is well defined in *Prothylacinus*, the lateral ridge being slightly longer and more prominent than the medial one, although the difference is weaker than in *Mayulestes*. *Prothylacinus* is the only borhyaenoid for which an ossified patella is known, probably in relation to an increased leverage for M. quadriceps femoris. In *Prothylacinus* the anterior tuberosity of the tibia (where M. quadriceps femoris inserts) is prominent (Text-fig. 8A$_{IV}$), giving a triangular shape to the proximal part of the tibial diaphysis, unlike that of *Mayulestes*. It is located much more distally than the level of the tibial condyles, probably in relation to the presence of the patella. The anterior tibial crest is thick and straight. In *Borhyaena*, the medial lip of the femoral trochlea is damaged on the only femur known, and there is no ossified patella, nor any reliably associated tibial head known for this taxon.

In *Borhyaena*, the medial femoral condyle is slightly wider than the lateral one, and is asymmetrical as the external border is more developed proximodistally than the internal one (Text-fig. 8B$_{II}$). This condition is unknown in other borhyaenoids. In *Prothylacinus*, the femoral condyles have a similar width and length (Text-fig. 8A$_{II}$), but the medial condyle is slightly more prominent distally than the lateral one. The condyles are as long as the trochlea seen in lateral view (Text-fig. 8A$_{III}$), and they are not flattened posteriorly. The intercondyloid space is deep and broad. On the tibia, the facets that articulate with the femoral condyles are more or less rounded seen in proximal view. The medial facet is crescent-shaped, and is more concave near the intercondyloid eminence. The lateral facet is flat and the external margin is angular, due to the width of the fibular facet that faces posteriorly (Text-fig. 8A$_{IV}$).

Morphology of the tibia and fibula (Text-fig. 8C). No complete tibiae or fibulae of *Borhyaena* are known. The tibia of *Prothylacinus* is straight in anterior and lateral views, in contrast to *Mayulestes*. The lateral side of the tibia is concave proximally (M. tibialis anterior origin). Along the distal part of the anterior crest, a scar marks the insertion of a strong interosseous ligament. The insertion of the gracilis and semitendinosus caput ventrale is well defined along the medial side of the anterior crest, and extends until the middle of the shaft. Proximally, the insertion of the medial collateral ligament is not well defined compared to arboreal didelphids. Posteriorly, a slender, sharp proximal crest represents the origin of M. peroneotibialis.

The fibular shaft of *Prothylacinus* is triangular in cross-section due to the development of the medial crest that extends towards the tibia. The fibular head of *Prothylacinus* is narrow, while the proximal tibial articular facet is broad, representing more than half the medial side of the head. It does not suggest an articulation with the femur. The corresponding facet on the tibia is oriented posteriorly. Another posteriorly oriented proximal articular facet on the fibula suggests a well-developed parafibula. Distally, the groove for the peroneal tendons is wide and shallow. The distal tibial facet protrudes medially and faces mediodistally. On the tibia, the corresponding facet is elongated anteroposteriorly and faces laterally.

Tarsal joints (Text-fig. 9). All the tarsal bones except the calcaneum are known for *Prothylacinus*, whereas the calcaneum alone is known for *Borhyaena*. For comparison, the calcaneum of *Mayulestes* is known (Muizon 1998; Argot 2002), as are all the tarsal bones of *Sipalocyon* (Szalay 1994, pp. 204–210). Compared with *Sipalocyon*, the lateral astragalotibial facet of the astragalus of *Prothylacinus* (Text-fig. 9A) is more convex transversely, but it also exhibits a posterior astragalotibial facet (the posterior continuation of the lateral astragalotibial facet, *sensu* Szalay 1994, p. 207). The corresponding lateral facet on the tibia is oval in outline, concave, and almost perpendicular to the diaphysis in lateral view. The tibial malleolus is very prominent as in the other borhyaenoids, and exhibits an internal facet that is convex and sharply angled from the lateral facet. The anteroposterior axis of the tibial malleolus is perpendicular to the transverse axis of the distal epiphysis, in contrast to *Mayulestes*. On the astragalus, the medial astragalotibial facet represents a long groove for the guidance of the tibial malleolus. The astragalofibular facet is small, as in *Sipalocyon*. The upper margin of the astragalar head is more oblique in anterior view in *Prothylacinus* than in *Sipalocyon*, and the astragalonavicular facet of *Prothylacinus* does not exhibit a distal astragalar tuber (a lateral prominence on the upper margin of the facet) in contrast to *Sipalocyon* (Szalay 1994, figs 7.17–7.19).

There is no astragalus known for *Borhyaena*, but a left astragalus has been referred to a Deseadan borhyaenoid, *Pharsophorus lacerans* (MACN 52–367) (Marshall 1978). This taxon is similar in size to *Borhyaena* (based on mandibular remains, Marshall 1978), and this astragalus is the only part of the postcranium referred to that taxon. A study of the teeth has suggested the existence of an ancestor-descendant relationship between *Pharsophorus* (Deseadan) and *Borhyaena* (Colhuehuapian and Santacrucian) (Marshall 1978), and therefore it is of interest to compare this astragalus with that of *Prothylacinus*. In *Pharsophorus* (Text-fig. 9B), the lateral astragalotibial facet is
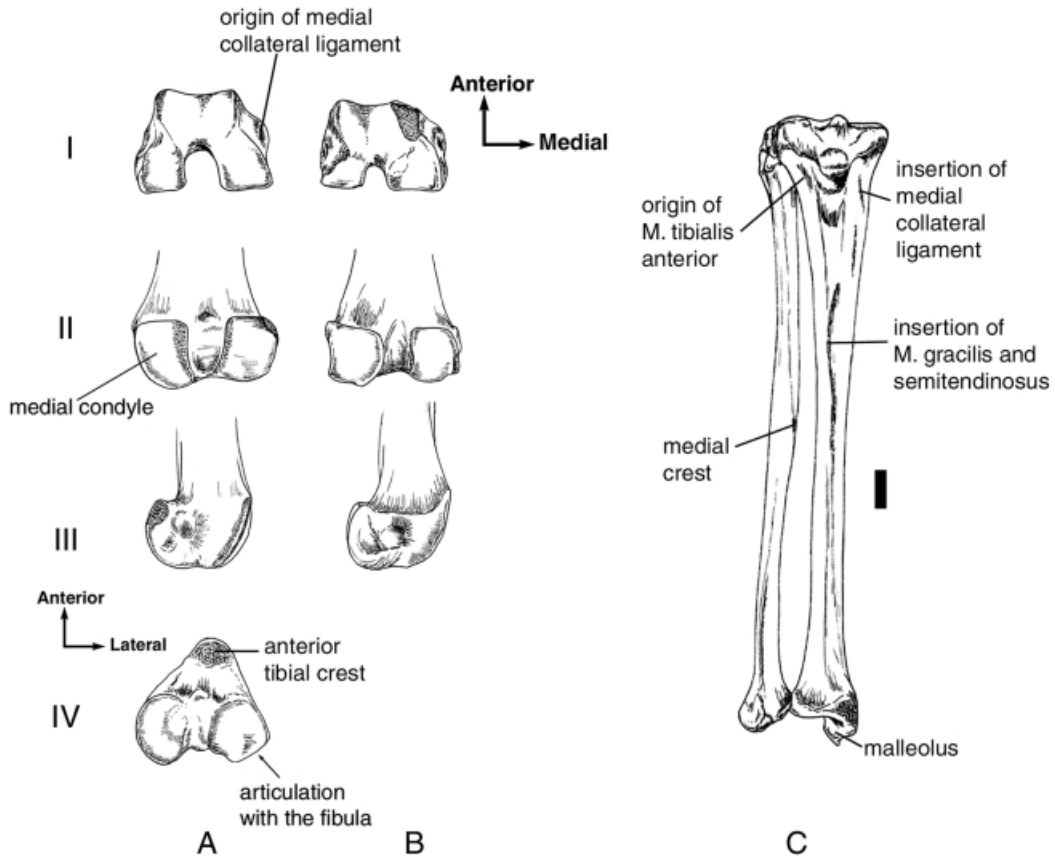
TEXT-FIG. 8. A–B, knee joint. I–III, distal epiphysis of the right femur. I, distal view; II, posterior view; III, lateral view. IV, proximal epiphysis of the right tibia in proximal view (unknown in *Borhyaena*). A, *Prothylacinus patagonicus* PU 015700. B, *Borhyaena tuberata* PU 015701. C, right tibia and fibula in anterior view in *Prothylacinus patagonicus* PU 015700. Scale bar represents 10 mm.

less convex transversely than in *Prothylacinus*. Ventrally, the calcaneoastragalar facet does not exhibit the same orientation, as its longitudinal axis is almost perpendicular to the longitudinal axis of the astragalus (angle of approximately 80 degrees between the two axes). In contrast, this angle is of approximately 50 degrees in *Prothylacinus*. *Sipalocyon* is intermediate, but more similar to *Prothylacinus*. The astragalar head is relatively wider transversely in *Pharsophorus*, and less oblique in anterior view than in *Prothylacinus*.

The calcaneum of *Prothylacinus* is unknown, but a right calcaneum of *Borhyaena* is available (Text-fig. 9C). On this calcaneum, the calcaneoastragalar facet is well-developed, anteroposteriorly convex, and wider than long. As the articular surface is not preserved, the area of the calcaneofibular facet (if exists) cannot be evaluated. The transverse axis of this facet is perpendicular to the longitudinal axis of the calcaneum and to the long axis of the sustentacular facet, a condition that is consistent with the morphology and orientation of the corresponding facets on the astragalus of *Pharsophorus*. Seen in anterior view, the two facets of the calcaneum are oriented dorsally, in contrast to *Mayulestes*, in which the calcaneoastragalar facet is oriented medially. The facet of the sustentaculum tali is longer than wide, concave proximodistally, and reaches the smoothly concave calcaneocuboid facet distally. The two facets of the astragalocalcaneal joint are separated by a groove that is relatively deeper than in *Sipalocyon*. The calcaneum of *Borhyaena* lacks a peroneal process, in contrast to that of *Mayulestes* or *Sipalocyon*. The apex of the tuber calcanei is not preserved.

The pes (Text-fig. 9D). The pes is unknown in *Borhyaena* but all tarsal bones (except the calcaneum) and two metatarsals of the left pes are known for *Prothylacinus*. The cuboid bears a small posterior groove for the tendon of the
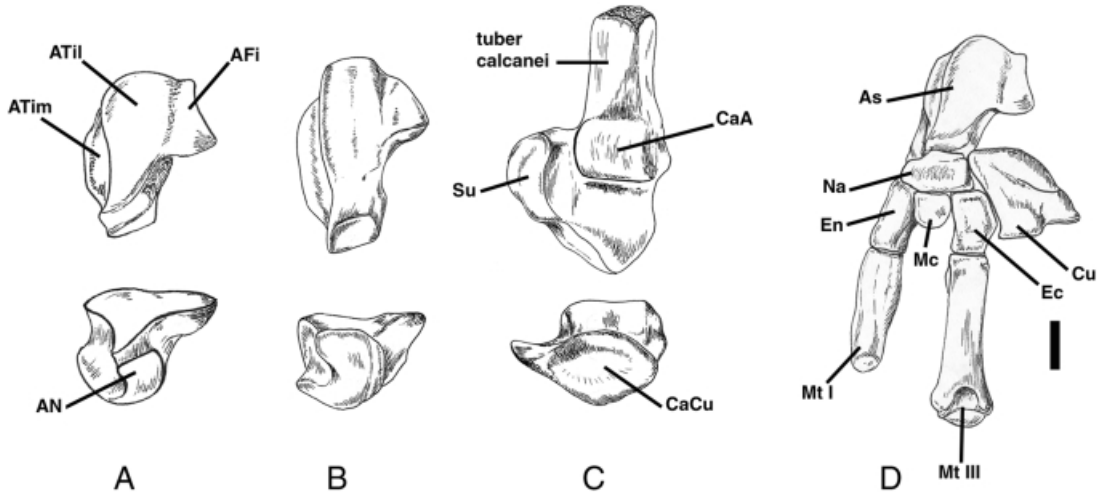
TEXT-FIG. 9. Ankle joint bones and pes. A, left astragalus of *Prothylacinus patagonicus* PU 015700 in dorsal (top) and anterior (bottom) views. B, left astragalus of *Pharsophorus lacerans* MACN 52–367 in dorsal (top) and anterior (bottom) views. C, right calcaneum (reversed) of *Borhyaena tuberata* MACN 2074–2078 in dorsal (top) and anterior (bottom) views. D, left hind foot in dorsal view in *Prothylacinus patagonicus* PU 015700. Abbreviations: AFi, astragalofibular facet; AN, astragalonavicular facet; As, astragalus; ATil, astragalotibial lateral facet; ATim, astragalotibial medial facet; CaA, calcaneoastragalar facet; CaCu, calcaneocuboid facet; Cu, cuboid; Ec, ectocunei-form; En, entocuneiform; Mc, mesocuneiform; Mt I, first metatarsal; Mt III, third metatarsal; Na, navicular; Su, sustentacular facet. A–C are not to scale. D, scale bar represents 10 mm.

peroneus longus. Above the peroneal groove, a prominent globular posterior tuberosity reflects the strength of the calcaneocuboid ligament, and possibly contact with the ground. The proximodistally elongated entocuneiform is very compressed transversely. Proximally, it has two facets, one for the navicular and the other for the mesocuneiform. Distally, it articulates with Mt I by a small, narrow facet. The first metatarsal lacks the characteristic shape of a metatarsal and is clearly vestigial. It is transversely compressed and rugose, and bears two proximal articular facets. That for the entocuneiform faces proximally, is triangular in outline, and is both narrow and elongated dorsoventrally. The facet for Mt II is oriented laterally, and is large and flat. Mt I did not articulate distally with a phalanx, but it is relatively long (65 per cent of Mt III). The third metatarsal is robust, with a large, globular head that is compressed dorsoventrally, and a transversely compressed proximal end. The proximal articular surface is slightly convex dorsoventrally, wider dorsally than ventrally, and slightly deflected dorsomedially. This metatarsal is short (21 per cent of the tibial length), and barely longer than Mc III.

MUSCULOSKELETAL ADAPTATIONS OF EXTANT MODELS USED IN THE INTERPRETATION OF FOSSIL SPECIES

The seven extant models chosen are: *Arctictis binturong* (Viverridae), *Canis lupus* (Canidae), *Gulo gulo* (Mustelidae), *Hyaena hyaena* (Hyaenidae), *Neofelis nebulosa* (Felidae), *Thylacinus cynocephalus* (Thylacinidae), *Ursus malayanus* (Ursidae). (For the sake of brevity, and because a single species per genus is studied, specific names will be omitted in the text.) A single species within each family has been chosen in order to avoid the possibility that morphological resemblances due to phylogenetic contraints might be considered adaptive for some common roles. Moreover, these Recent species were selected as being of similar size range, in order to limit problems related to skeletal allometry. A classification of these models according to their obligate locomotor and hunting strategies is undertaken on Table 1, and Table 2 compiles numerical data. The categories reported in Table 1 are, of course, not entirely distinct as behaviours occur along a continuum. However, the goal of such a classification is to avoid unnecessary complexity, and to characterize primary behavioural tendencies that might influence the morphology of

TABLE 1. Locomotor and hunting behaviour categories of living models. The categories are adapted from Taylor (1974, 1989) and Van Valkenburgh (1985). The data compiled are from Ogilvie (1958), Krott (1960), Ondrias (1961), Kruuk (1976), Rieger (1979), Nowak and Paradiso (1983), MacDonald (1984), Van Valkenburgh (1985, 1987), Taylor (1989), Lawrence (1997), and Heinrich and Biknevicius (1998).

Behavioural category	Definition	Models
Locomotor type		
Arboreal	Rarely on the ground, usually forages and shelters in trees; usually exhibits particular specializations for climbing	*Arctictis binturong* *Ursus malayanus*
Scansorial	Adept climber which also forages on the ground during a considerable proportion of its time	*Neofelis nebulosa* *Gulo gulo*
Terrestrial	Never climbs, and exhibits incipient to highly specialized running adaptations	*Canis lupus* *Hyaena hyaena* *Thylacinus cynocephalus*
Hunting type		
Ambush	Short distance rush frequently preceded by a stalk	*Neofelis nebulosa*
Pounce/Pursuit	A moving search which usually ends in either a pounce or a chase; small prey chased and grabbed, large prey usually scavenged; omnivorous diet	*Hyaena hyaena* *Gulo gulo*
Pursuit	A typically long distance chase; no grappling with prey	*Canis lupus* *Thylacinus cynocephalus*
Occasional	Rarely hunts at all; mainly eats vegetable matter	*Arctictis binturong* *Ursus malayanus*

TABLE 2. Measurements of living models. The data are compiled from the same references used for Table 1. The great amount of variation observed for the weight of *Canis lupus* and *Hyaena hyaena* follows Bergmann's rule, i.e. the size is related to the latitude of the habitat (Rieger 1979; Lawrence 1997).

Species	Head and Body length (m)	Tail length (m)	Shoulder height	Weight (kg)
Arctictis binturong	0·61–0·96	0·56–0·89	no data	9–16
Gulo gulo	0·65–1·05	0·17–0·26	c. 0·45 m	7–32
Neofelis nebulosa	0·60–1·10	0·55–0·91	c. 0·7–0·8 m	16–23
Thylacinus cynocephalus	0·80–1·30	0·50–0·65	c. 0·6 m	15–35
Hyaena hyaena	1·00–1·20	0·25–0·47	0·60–0·94 m	25–55
Canis lupus	1·00–1·60	0·35–0·56	c. 0·7 m	20–80
Ursus malayanus	1·00–1·40	0·03–0·07	c. 0·7 m	27–65

the postcranial elements. Hence, these models may be used to identify the potential locomotor capabilities of the fossils.

One of the main problems of model-based analyses is that the natural history of some of the models is poorly known. For example, the time that the rare and nocturnal clouded leopard (*Neofelis nebulosa*) spends in trees is not well established, although it is considered to be a skilful climber. It is reported to be able to run down trees head first, clamber upside down on the undersides of branches, and swing by one foot before dropping directly onto deer or wild boar that are its main terrestrial prey (MacDonald 1984). It seems to hunt monkeys, birds and squirrels in trees, but also deer, boars, goats, and porcupines on the ground or from an elevated post, and it is therefore classified as scansorial. Together with jaguars, which are also forest dwellers and good climbers, clouded leopards have the shortest forelimbs and lumbar region (relative to vertebral column length) among the big cats (Kiltie 1992).

The binturong (*Arctictis binturong*) is a highly arboreal and slow-moving form that eats mainly vegetable material. However, it is reported to be able to move at speed and 'strike like a snake' (Ogilvie 1958, p. 1). *Arctictis* is characterized by a heavily built tail that is very muscular at its base, and strongly prehensile in the last third. The Malayan sun bear (*Ursus malayanus*) is said to be an adept climber because of its low weight and large foreclaws (Nowak and Paradiso 1983; MacDonald 1984), but the time it spends in trees is poorly established.

Wolverines (*Gulo gulo*) are reportedly well adapted for carrion feeding, as their skull structure, dentition, and strong jaws allow them to feed on frozen meat and to crush large bones (Hornocker and Hash 1981). As a consequence of this scavenging lifestyle, *Gulo* does not appear to be a serious competitor to efficient sympatric hunters such as coyotes, wolves, and pumas, but it may compete directly with black and grizzly bears for available carrion. It is reported to climb trees, either to escape enemies (wolves or bears), or to hide the remains of prey or carrion if the nature of the substrate precludes burial (Krott 1960). When hunting, wolverines do not move with stealth, nor stalk their prey like felids, or chase swiftly like wolves. Rather, they pursue relatively slowly, but with enormous endurance, a mode of hunting that is particularly efficient on snow-covered areas (Krott 1960).

For the extinct Tasmanian tiger (*Thylacinus cynocephalus*), little is known of the ecology, behaviour, preferred habitat, or preferred method of hunting. Information is reduced to statements of farmers and hunters, or to observations made on captive animals. The consensus is that *Thylacinus* was solitary, hunting mostly by scent, wearing down the quarry by chasing it for hours, and securing it with a final rush when the quarry showed signs of exhaustion (Smith 1982). It has therefore been classified as a 'pursuit predator' like the wolf, although Smith (1982) noted that this method of trotting relentlessly after its prey was perhaps suggested by its external morphological resemblance to the wolf. Unlike *Canis lupus*, it was certainly not capable of fast pursuits over longer distances, wolves depending upon both speed and stamina in overhauling prey (Taylor 1989; Szalay 1994).

Axial skeleton

Atlas and axis: movements of the head (Text-fig. 10). The skulls of *Canis*, *Gulo*, and *Hyaena* are characterized by a well-developed sagittal crest that is prominent posteriorly (Text-fig. 10B–C), reflecting the development of the jaw musculature (especially M. temporalis). The occipital crest is prominent in *Neofelis* and *Thylacinus* (Text-fig. 10A), suggesting a powerful neck musculature for active predation, while both crests are particularly reduced in *Arctictis* and *Ursus* that eat mainly vegetable matter. The powerful head-neck-shoulder musculature of hyaenas enables them to carry heavy carcass material (Rieger 1979). Striped hyaenas are known to be particularly adapted for crushing bones. The carnassial teeth exert pressure estimated at over 15·4 kg/sq cm (Kruuk 1976; Rieger 1979), a pressure that has to be relayed by the jaw and neck musculature, with consequences for the cervical skeleton. In active predatory taxa like *Canis*, *Neofelis*, and especially *Hyaena*, the cervical vertebrae are long and extremely robust compared to the thoracolumbar vertebrae, a condition clearly related to their feeding habits. The prominence of the occipital crest of *Borhyaena* and *Prothylacinus* is therefore compatible with a powerful neck musculature and with active predatory habits, but the orientation of the occipital condyles suggests distinct habits between them.

In *Canis* and especially in *Hyaena*, the occipital condyles are prominent posteriorly (Text-fig. 10C), and are more horizontal as seen in lateral view than in arboscansorial taxa. The anterior facets of the atlas are particularly concave in *Hyaena*, wrapping the occipital condyles tightly. By comparison, the arboscansorial *Arctictis* and *Neofelis* have less prominent occipital condyles, with a long axis that is almost vertical in lateral view (Text-fig. 10A). These differences in the orientation of the occipital condyles, and therefore in the neutral position of the skull, are probably related both to the hunting methodology and locomotor substrate. Striped hyaenas, in particular, are characterized by a low horizontal head posture when walking (Kruuk 1976). This posture seems to be partly related to their searching behaviour, aimed at obtaining small food items from dense vegetation, catching insects and small vertebrates, finding fruits, and scavenging (Kruuk 1976). In terrestrial East African viverrids, the head is also carried low (Taylor 1970), apparently in relation to a similar search behaviour. This head posture is not usual in arboscansorial taxa, which may need more head mobility, aided by the reduced stability of the atlantocranial articulation. The orientation of the occipital condyles of *Borhyaena* recalls that of hyaenas, as do the laterally prominent zygomatic arches.

The neural process of the axis is more prominent anteriorly in active predators than in *Arctictis* or *Ursus*. In *Canis* and *Hyaena*, it reaches the level of the anterior tip of the dens (Text-fig. 10I) and then covers a large part of the dorsal arch of the atlas, which is particularly long compared to the other taxa. However, the axial neural process does not
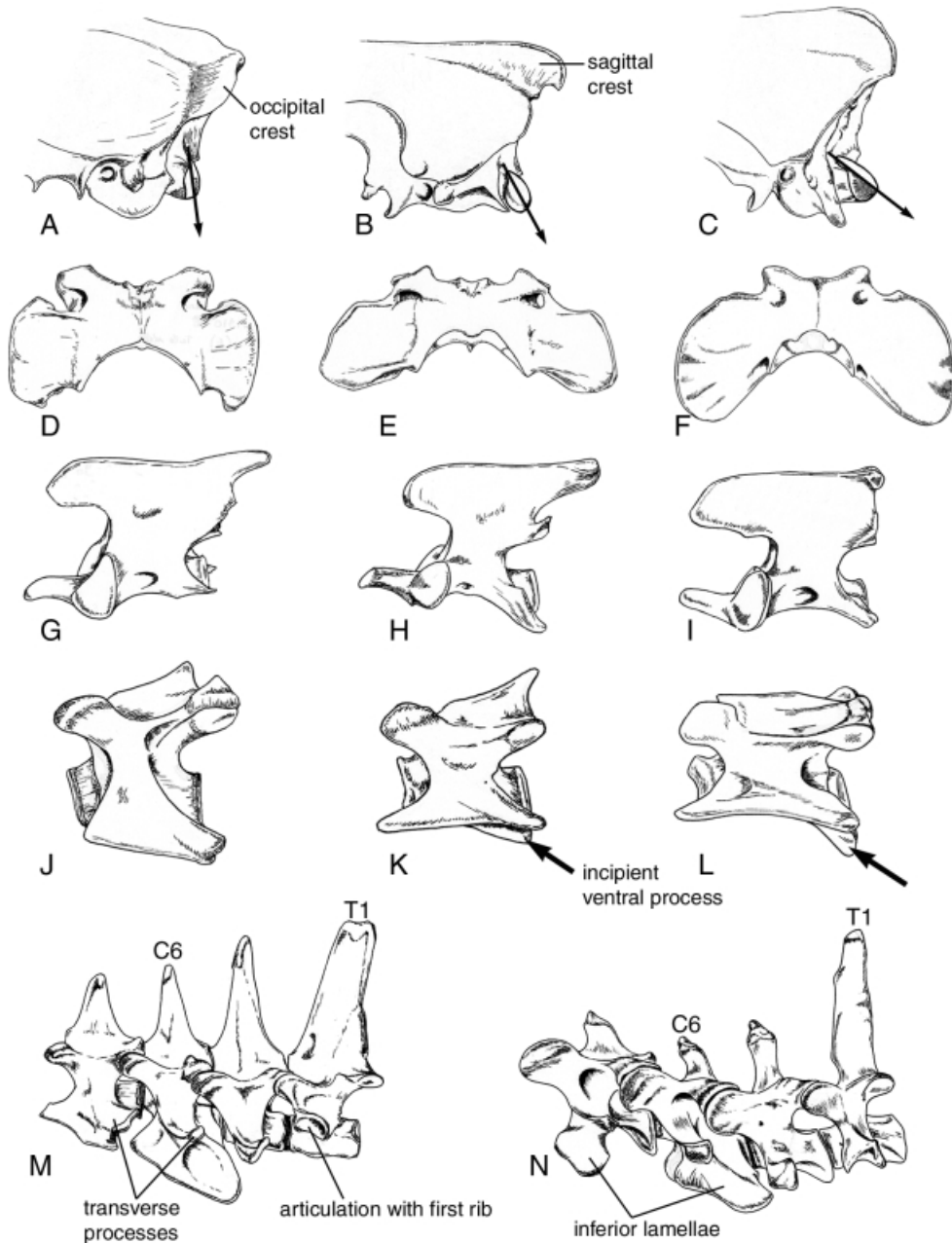
TEXT-FIG. 10. A–C, posterior part of the skull in lateral view showing the orientation of the occipital condyles (arrows). D–F, atlas in dorsal view. G–I, axis in lateral view. A, D, G, *Neofelis nebulosa* MNHN 1992–3 (skull) and MNHN 1961–101 (atlas and axis). B, E, H, *Gulo gulo* MNHN 1935–3. C, F, I, *Hyaena hyaena* MNHN 1910–90. J–L, third cervical in lateral view. J, *Gulo gulo* MNHN 1935–3. K, *Thylacinus cynocephalus* MNHN 1891–61. L, *Canis lupus* MNHN 1984–08; the arrow shows the presence of a ventral sagittal process in *Thylacinus* and *Canis*. M–N, posterior part of the cervical area in lateral view, from C5 to T1. M, *Gulo gulo* MNHN 1935–3. N, *Hyaena hyaena* MNHN 1910–90. Not to scale.

protrude posteriorly in either of these taxa to the extent observed in borhyaenoids (Text-fig. 10G–I). In *Hyaena* the posterior border of the axial neural process is vertical, as seen in lateral view (Text-fig. 10I), while in *Canis* this border is inclined anteriorly and its posterior tip fails to reach the level of the postzygapophyses. In both taxa, this posterior tip is thick and bifid. On the atlas of *Hyaena*, the transverse processes form broad flanges, extended well posteriorly (Text-fig. 10F). Together, therefore, the axial neural process and atlantal transverse processes indicate that M. obliquus capitis caudalis is quadrangular in dorsal outline, with fibres oriented ventrolaterally. In contrast, in *Gulo*, *Neofelis*, and *Thylacinus*, the posteriorly extended axial neural process and the laterally extended atlantal transverse processes increase the fan shape of the muscle (with fibres oriented anteroventrally). In *Neofelis*, but also in *Hyaena*, the anterior atlantal facets of the axis are extended dorsoventrally, a condition which may improve the rotational capability of the atlantoaxial articulation and relate to the habit of killing small living prey (up to the size of a bat-eared fox for striped hyaenas; Kruuk 1976) by grabbing and shaking. Two other muscles, more superficial than the obliquus capitis caudalis, originate from the neural process of the axis: M. rectus capitis dorsalis major, which originates from the anterior region, and M. spinalis capitis, which originates from the posterior tip. They are both fan-shaped in dorsal view as they insert largely on the occipital crest and, as such, may also play a role in the rotation of the head, especially when the moment arm is increased by the posterior extension of the axial neural process. Therefore, the posteriorly extended axial neural process of borhyaenoids, as well as the laterally expanded atlantal transverse processes, suggest a good rotational capability of the head.

Processes of the posterior cervical vertebrae (Text-fig. 10). In *Canis* and *Hyaena* the cervical neural processes are reduced but, by comparison, the neural processes of the first thoracics are extremely high and robust (Text-fig. 10N). In arboscansorial taxa such as *Arctictis* or *Neofelis*, the cervical neural processes are more developed, but the neural process of C7 is very similar to that of T1 in height, robustness, and inclination, indicating that the neck musculature originating from the apex of the first thoracics (especially M. splenius) had a relatively reduced pull. This may reflect the diet of each animal: *Arctictis* being mainly frugivorous, it may use its fore feet to carry food to its mouth (although detailed data are lacking concerning this particular behaviour) whereas hyaenids and canids grab and kill prey with their jaws. The well-preserved cervical neural processes of *Borhyaena*, which are tall, robust, and anteriorly inclined on C6 and C7, suggest powerful neck extensors (Mm. spinalis and multifidus cervicis, biventer, splenius), and this development might be related to the weight of the head. The nuchal ligament is strong in canids (Miller *et al*. 1964) but unknown in didelphids, and its presence cannot be inferred in borhyaenoids.

The cervical transverse processes seem to be relatively shorter and more prominent dorsally in *Borhyaena* than in *Prothylacinus*. Based on living taxa, various muscles attach on these processes, especially the longissimus cervicis, the levator scapulae dorsalis, and the scalenus. The longissimus cervicis extends the neck and turns it to one side in a unilateral action. It is the most dorsal muscle of the series and therefore the dorsal protrusion of the transverse processes in *Borhyaena* might reflect the pull exerted by this muscle, in combination with the weight of the head.

In *Hyaena*, the inferior lamellae form well-developed flanges (short anteroposteriorly but prominent ventrally) from C4. They are better developed on C3–C5 than in *Canis*. They are also well-developed from C4 in *Borhyaena*, contrary to *Prothylacinus* (see Sinclair 1906, pl. 52, figs 2–3). The ventral projection of these lamellae may increase the mechanical advantage of the cervical flexors (especially M. longus capitis), as their attachment is then shifted farther from the centre of the vertebral body. The development of M. longus capitis is confirmed by the presence of two well-defined symmetrical fossae on the basicranium of *Borhyaena* and *Prothylacinus*, anterior to the foramen magnum.

The sagittal ventral processes noticed in borhyaenoids are not developed to the same extent and strength in extant taxa. However, the axis, C3, and C4 of *Canis* and *Thylacinus* do exhibit a sharp crest of this kind (Text-fig. 10K–L). A sagittal crest is also developed in *Arctictis*, and especially in a viverrid with more predaceous habits, the oyan (*Poiana richardsoni*). Based on the dissection of the small-toothed palm civet (*Arctogalidia trivirgata*), this strong crest is related to well-differentiated bundles of the M. longus colli. The size of the borhyaenoid crests therefore suggests a particularly powerful flexor.

Position of the diaphragmatic and anticlinal vertebrae, and neural processes of the thoracolumbar area (Text-fig. 11A–H). The position of the diaphragmatic vertebra is important because subsequent vertebrae function more like lumbar vertebrae than thoracics (Pridmore 1992; Shapiro 1993): the radial articular mode restricts lateral bending and long-axis rotation. The position of the diaphragmatic vertebra is variable among the taxa examined (Table 3). Because of the different number of thoracolumbar vertebrae, the number of post-diaphragmatic lumbar-like vertebrae is also variable, from seven in *Ursus* to ten in *Thylacinus* (Table 3). A relatively short lumbar area moves the centre of gravity closer to the hindlimbs and prevents torques on the vertebral axis produced by the propulsive thrust of the hindlimbs (Shapiro 1995). In *Arctictis*, *Gulo*, and *Ursus*, like *Prothylacinus*, the transverse processes of the diaphragmatic vertebra protrude anterodorsally, suggesting a functional trend towards a radial articular mode and development of the mammillary processes.

TABLE 3. Distribution of thoracolumbar vertebrae and position of the diaphragmatic and anticlinal vertebrae in extant taxa. Abbreviations: L, lumbar vertebra; T, thoracic vertebra.

Specimens	Number of thoracics	Number of lumbars	Total (T + L)	Number of post-diaphragmatic vertebrae	Position of diaphragmatic vertebra	Position of anticlinal vertebra
Arctictis binturong MNHN 1975–78	14	6	20	9	T11	T11
Neofelis nebulosa MNHN 1961–101	14	7	21	9	T12	T12
Ursus malayanus MNHN 1913–505	15	4	19	7	T12	absent
Gulo gulo MNHN 1935–3	15	5	20	8	T12	T12
Hyaena hyaena MNHN 1910–90	15	5	20	8	T12	T13
Thylacinus cynocephalus MNHN 1891–61	13	6	19	10	T9	T10
Canis lupus MNHN 1984–08	13	7	20	10	T10	T11

The diaphragmatic vertebrae of *Arctictis*, *Gulo*, and *Neofelis* (Text-fig. 11A) are characterized by an extremely reduced neural process. This reflects the strong posterior inclination of processes on previous vertebrae (these processes showing a slow and regular decrease in height and an increase in their posterior inclination towards the anticlinal vertebra), in contrast to the anterior inclination of those on the following vertebrae. Therefore, in these taxa the diaphragmatic vertebra is also the anticlinal one, and the contrast between anterior and posterior parts of the thoracolumbar area is particularly marked. This is unexpected for *Arctictis*, which is usually characterized by cautious and quite slow movements (Nowak and Paradiso 1983). However, this animal is also reported to be skilful and able to move at speed (Ogilvie 1958), although details are lacking. It is worth noting that it also shows well-developed anapophyses and compact vertebrae (with very short, broad neural processes) in the middle part of the thoracolumbar region, two features that help to stabilize the vertebral column. By comparison, anapophyses are relatively reduced in the lumbar region of *Neofelis* but stabilization is provided by an anteroposterior elongation of the neural process on L4–6, which reduces the space available for the interspinous ligaments or muscles.

In contrast, the axial skeleton of *Ursus* lacks an anticlinal vertebra. The pre-diaphragmatic neural processes are tall, with a broad apex and a concave anterior border (Text-fig. 11F). The basal part is inclined posteriorly while the apical part is vertical, a condition very similar to that in *Canis*. Slijper (1946, p. 98) considered the basal posterior inclination to be a response to the force exerted by the deep rotatores, whereas the vertical apical part suggests that the traction exerted by Mm. semi-spinalis and multifidus dorsi is probably reduced, as compared to felids where the neural processes are more strongly inclined posteriorly. The post-diaphragmatic neural processes are vertical, a condition probably partly related to the short post-diaphragmatic area (Slijper 1946, pp. 101–102), and that reflects the reduced pull exerted by M. longissimus dorsi. Since ursids are not obligate cursors, they show no strong flexion and extension of the vertebral column and, therefore, no strong anticliny (Slijper 1946). The stabilization of the middle thoracolumbar area of this taxon is also provided by the anapophyses, that are almost as high as the prezygapophyses of the following vertebra.

In the terrestrial taxa the diaphragmatic and anticlinal vertebrae are not the same (Table 3). In these taxa the anticlinal neural process is not reduced (see *Hyaena*: Text-fig. 11B), since the inclination of the neural processes between the pre- and the post-diaphragmatic regions is less important. The anapophyses are particularly reduced in *Thylacinus* (Text-fig. 11H), by comparison with the two terrestrial eutherians, a condition that recalls the reduction observed in the posterior lumbar region of *Prothylacinus*. However, the orientation of the borhyaenoid neural processes is more similar to that of arboscansorial taxa.

The length and posterior inclination of the anterior thoracic neural processes reflect in particular the role of the multifidus and semi-spinalis dorsi, muscles that insert on the apex of the neural processes, and exert posteriorly directed pull (Slijper 1946). This is not true for the most anterior processes where the neck musculature attaches. In *Hyaena* the first five neural processes are hypertrophied, indicating the powerful nuchal musculature required by the
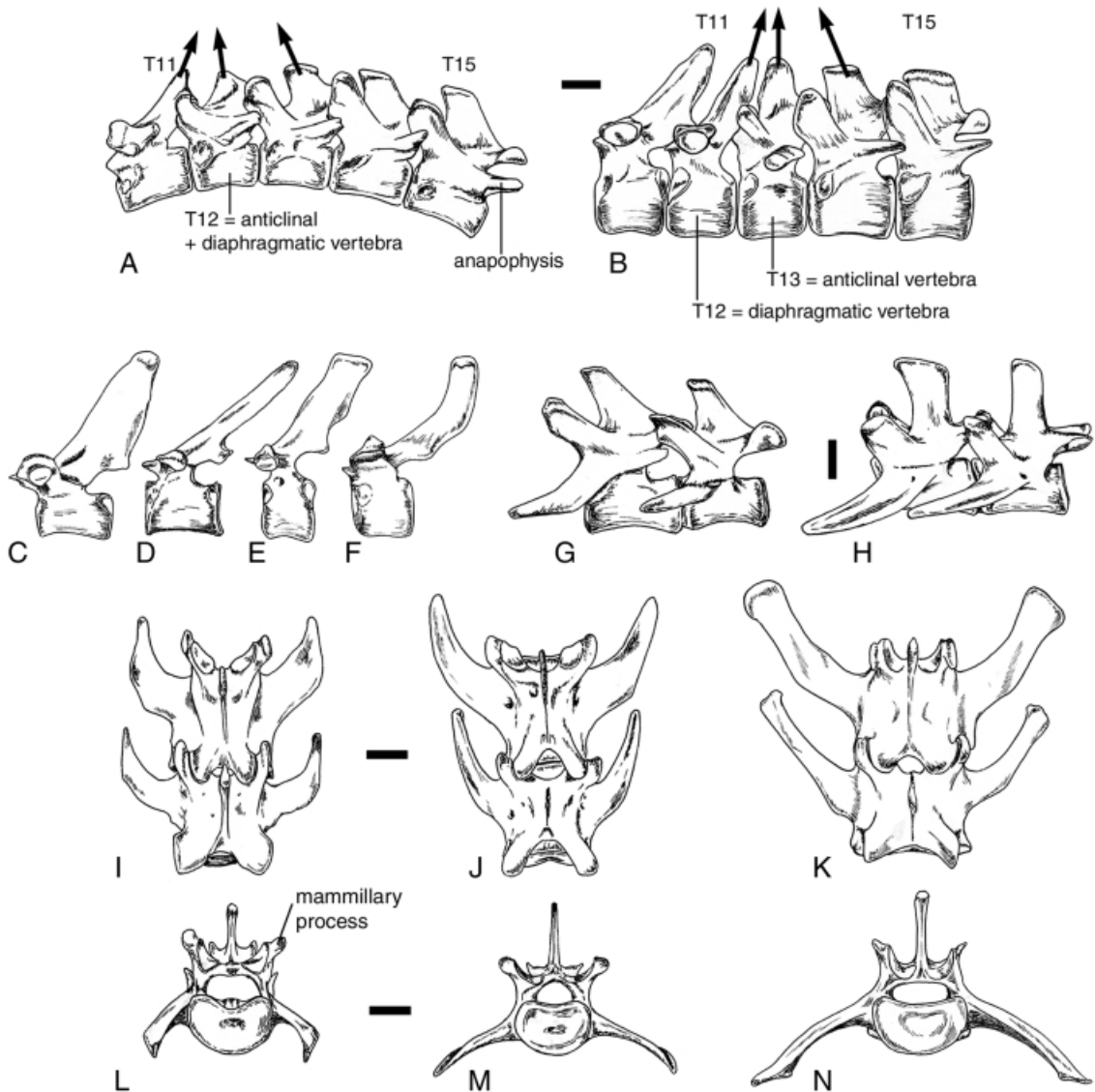
TEXT-FIG. 11. A–B, posterior thoracic vertebrae (T11–15) in lateral view. A, *Gulo gulo* MNHN 1935–3. B, *Hyaena hyaena* MNHN 1910–90. C–F, pre-diaphragmatic (T7) vertebra in lateral view. C, *Gulo gulo* MNHN 1935–3. D, *Thylacinus cynocephalus* MNHN 1891–61. E, *Hyaena hyaena* MNHN 1910–90. F, *Ursus malayanus* MNHN 1913–505. G–H, posterior lumbar vertebrae in lateral view. G, L4–5 in *Gulo gulo* MNHN 1935–3. H, L5–6 in *Thylacinus cynocephalus* MNHN 1891–61. I–K, two last lumbar vertebrae in dorsal view. I, L4–5 in *Gulo gulo* MNHN 1935–3. J, L5–6 in *Thylacinus cynocephalus* MNHN 1891–61. K, L6–7 in *Canis lupus* MNHN 1984–08. L–N, penultimate lumbar vertebra in anterior view. L, L4 in *Gulo gulo* MNHN 1935–3. M, L5 in *Thylacinus cynocephalus* MNHN 1891–61. N, L6 in *Canis lupus* MNHN 1984–08. Scale bars represent 10 mm. C–F are not to scale.

weight of the head and feeding habits. At the diaphragmatic level, the bundles of the multifidus dorsi become thinner and shorter, whereas the semi-spinalis dorsi blends with the longissimus dorsi and ilio-costalis to form a common epaxial muscular mass, the erector spinae. The force exerted by this mass is involved in the anterior inclination of the neural processes in post-diaphragmatic vertebrae. In living didelphids the three muscles are not completed fused. The most powerful part (longissimus dorsi lumborum), attaches laterally to mammillary processes and not to neural

processes, and the anticlinal vertebra is L3 in *Metachirus*, the most agile terrestrial didephid (Argot 2003). By comparison, the anterior position (T?11) of the anticlinal vertebra of *Prothylacinus* suggests the development of more powerful back extensors, that were probably united in a common mass and generated tensile forces directly from the apex of the neural processes. In the pelvis, the deflection of the anteroventral part of the ilium, and its dorsal extension above the sacrum are consistent with a well-developed epaxial musculature in the lower back (i.e. ilio-costalis + longissimus dorsi lumborum, extended between the ilium and the last ribs). As in *Mayulestes*, the anteroposterior lengthening of the vertebrae through the lumbar region is moderate in *Prothylacinus*, a condition related in *Mayulestes* to increased mobility by comparison with living didelphids (Argot 2003). This, together with the anterior position of the anticlinal vertebra, suggests a flexible axial skeleton, in contrast to *Borhyaena* in which the anticlinal was probably a lumbar vertebra.

Lumbar transverse processes (Text-fig. 11G–N). *Ursus* has a particularly short lumbar region (four vertebrae). The lumbar transverse processes are horizontally placed and lie perpendicular to the vertebral axis seen in dorsal view. The lumbar processes of *Hyaena* (five vertebrae), although relatively more slender and more prominent laterally, are also horizontally placed. This orientation does not provide for a great mechanical advantage of the quadratus lumborum, as the attachments of this muscle are not located far from the centre of rotation of each vertebra. This condition, combined with the shortness of the lumbar region and vertical lumbar neural processes, suggests reduced mobility of the lumbar spine in these taxa, with reduced sagittal flexion. The morphology of the transverse processes recalls that of ungulates which, as obligate cursors, are also characterized by a limited mobility of the spine in the sagittal plane (Slijper 1946). In contrast, the lumbar transverse processes of *Prothylacinus* are ventrally prominent, a condition that provides ample dorsal space for increased development of the epaxial musculature, and moves the ventral tendons of the quadratus lumborum away from the vertebral axis (Shapiro 1995). In *Canis* (Text-fig. 11K, N) the lumbar transverse processes protrude more anteroventrally than in *Hyaena*, and the seven lumbar vertebrae probably give greater mobility to the lower back. In *Gulo* (five lumbar vertebrae; Text-fig. 11G, I, L) and *Thylacinus* (six lumbar vertebrae, Text-fig. 11H, J, M), the lumbar transverse processes are less prominent anteroventrally than in *Canis*, and are more crescent-shaped in dorsal view (i.e. less divergent laterally). They are much less concave ventrally in *Thylacinus* than in *Prothylacinus*, a condition that could be partly due to the position of their roots, which are located more ventrally on the vertebral body in *Thylacinus*. Similarly, the base of the lumbar transverse processes is located more ventrally in *Borhyaena* than in *Prothylacinus*. However, *Thylacinus* has a ventral sagittal crest along the bodies of the three first lumbars (unknown in *Prothylacinus*) that may reflect a large quadratus lumborum.

Caudal vertebrae (Text-fig. 12). *Arctictis* and *Neofelis* have the longest and most robust tails among the taxa examined, and their tail clearly plays an important role in locomotion. Of the two, *Arctictis* has shorter, more robust caudals with wider, longer transverse processes that are retained further along the caudal series to Ca8 (compare Text-fig. 12A and B). The transverse processes are particularly well developed on Ca1–4. On Ca4–7, the transverse processes bear a dorsal prominence reflecting the strong attachment of the Mm. abductor caudae dorsalis and/or ischio-caudalis. A similar dorsal prominence can be observed in *Neofelis*, but only on more anterior vertebrae (Ca2–4). The wide, robust transverse processes of the most anterior caudals of *Borhyaena* and *Prothylacinus* suggest that they had a tail that was muscular at its base, these processes permitting a strong attachment for Mm. abductor caudae dorsalis, ischio-caudalis, and the deep intertransversarii. As in living didelphids, some muscles moving the hindlimb (Mm. semitendinosus caput dorsale, caudo-femoralis, femoro-coccygeus) probably also originated from these processes. At the level of Ca?7–9 in *Prothylacinus*, the transverse processes formed broad lateral wings extended along the distal two-thirds of the vertebral bodies. This reflects the well-developed basal musculature of the tail, and also the expansion of the fleshy part of Mm. sacro-caudalis (flexor) and longissimus caudae (extensor). Moreover, the lateral crest of the anapophyses of the posterior thoracic vertebrae reflect a robust anterior attachment of the longissimus caudae, which suggests that *Prothylacinus* also had a long tail by comparison with living didelphids. Similarly, *Thylacinus* (Text-fig. 12C) had a muscular tail, much more rigid at its base than in placental Carnivora, and this is reflected by the morphology of the vertebrae which have robust transverse processes that project laterally on Ca1–6. The haemapophyses, strongly keeled in *Arctictis* and reflecting strong attachment of M. sacro-caudalis, are unknown in *Prothylacinus*.

The caudal vertebrae of *Arctictis* retain zygapophyses to the level of Ca12, but they are reduced by Ca6 in *Neofelis* in which the foramen vertebrale disappears on Ca8. Therefore the transition between the anterior and posterior parts of the tail occurs more anteriorly in *Neofelis*. Only the first four caudals of *Thylacinus* have functional zygapophyses, and the prezygapophyses are divergent, with reduced articular facets, resembling *Borhyaena* more than *Prothylacinus*. The prezygapophyses are not reduced on Ca?9 in *Prothylacinus*. Moreover, the neural canal is still visible on Ca?9 in *Prothylacinus*, suggesting an important innervation of the tail. This is consistent with the size of the foramen vertebrale, which is much wider than high in *Prothylacinus*, whereas it is narrower and more rounded in *Borhyaena*, suggesting smaller segmental nerves in the latter.
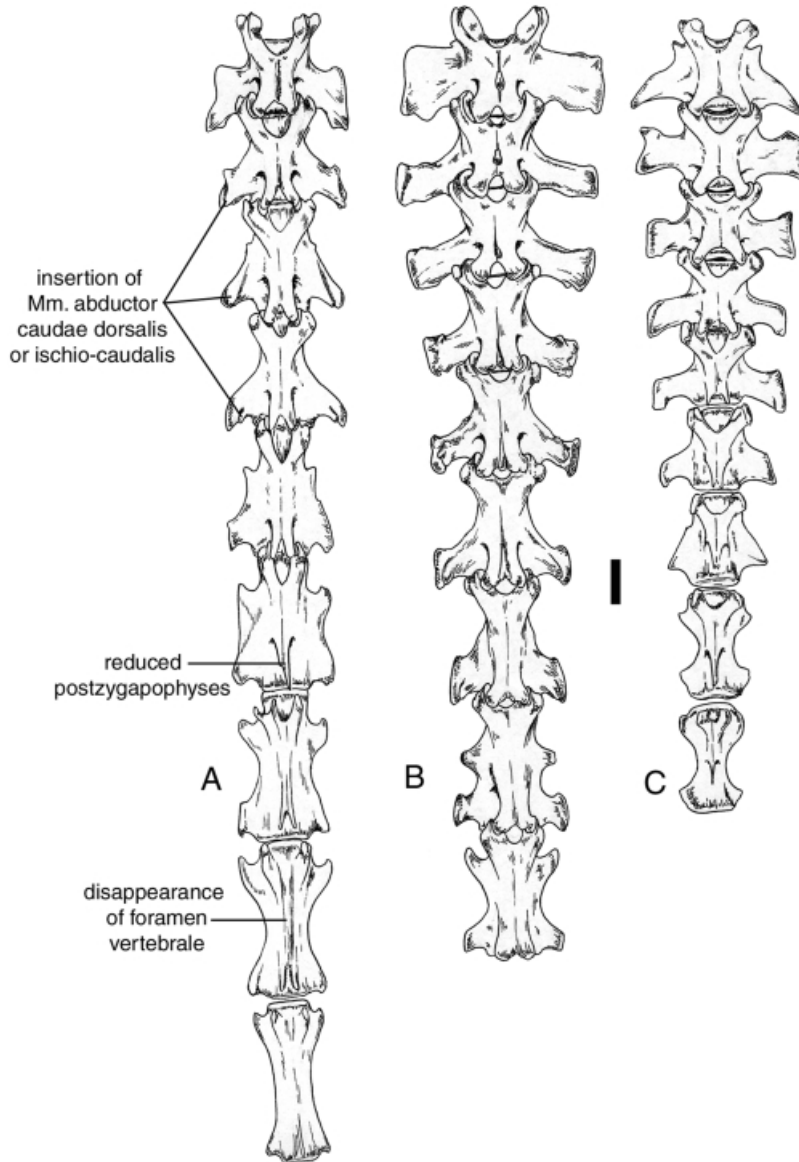
TEXT-FIG. 12. Anterior (Ca1–9) caudal vertebrae in dorsal view. A, *Neofelis nebulosa* MNHN 1961–101. B, *Arctictis binturong* MNHN 1975–78. C, *Thylacinus cynocephalus* MNHN 1891–61. Scale bar represents 10 mm.

The posterior caudals of *Neofelis* are relatively longer and more slender than in *Arctictis*, with reduced processes and zygapophyses. The various differences reflect the different role played by the tail, which is prehensile in *Arctictis* and used as a fifth limb (Ogilvie 1958; MacDonald 1984), in contrast to *Neofelis* in which it serves to provide equilibrium. The absence of posterior caudal vertebrae in *Prothylacinus* does not permit interpretation of its exact role in locomotion, but the morphology of the preserved caudals suggests that the tail had at least a role in equilibrium.

Pectoral girdle and forelimb

Glenohumeral joint and brachium (Text-fig. 13). The glenoid cavity is particularly shallow in *Arctictis* (Text-fig. 13A, E) and *Ursus*, consistent with the high mobility of the shoulder joint required by their lifestyle. The
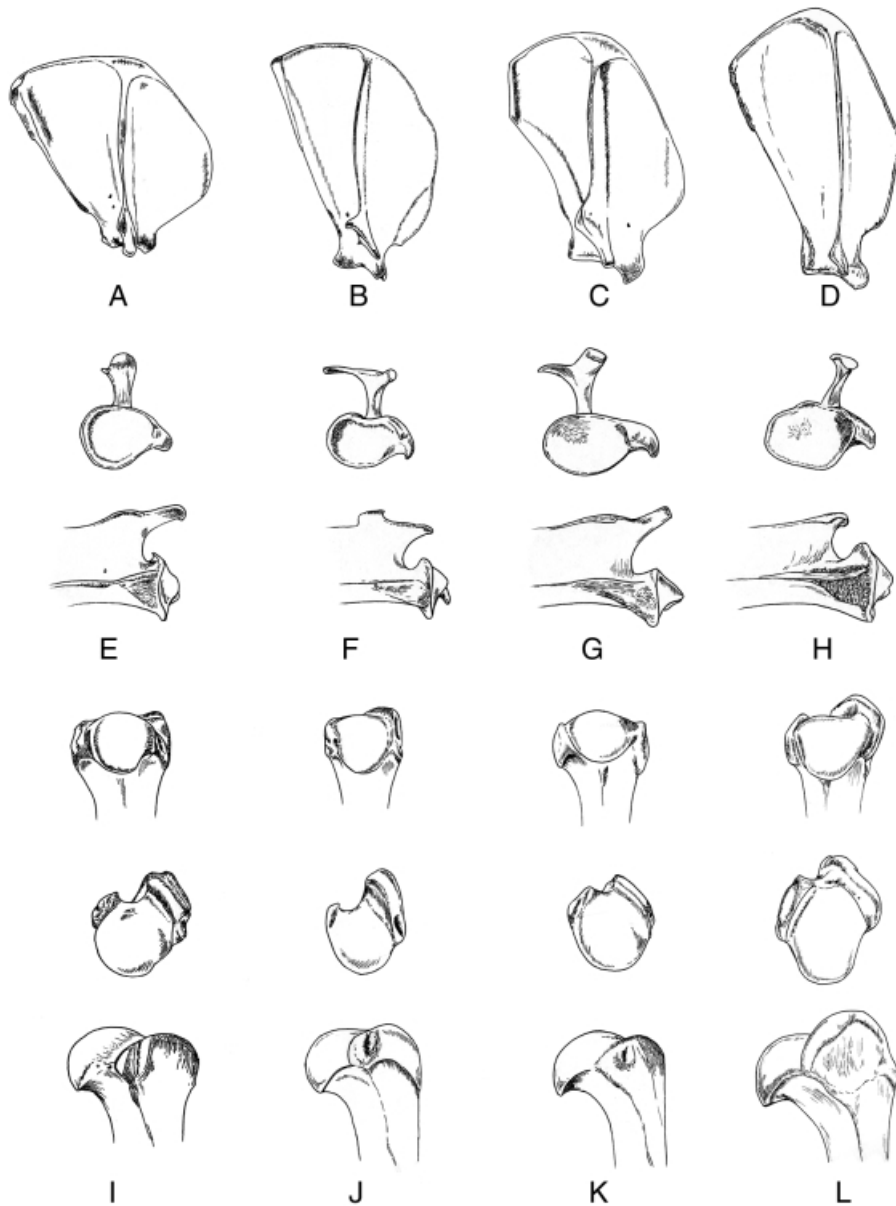
TEXT-FIG. 13. Scapulae and shoulder joint. A–D, right scapula in lateral view. E–H, glenoid cavity of the right scapula. From top to bottom: distal and posterior views. I–L, right humeral head. From top to bottom: posterior, proximal, and lateral views. A, E, I, *Arctictis binturong* MNHN 1975–78. B, F, J, *Neofelis nebulosa* MNHN 1961–101. C, G, K, *Gulo gulo* MNHN 1935–3. D, H, L, *Hyaena hyaena* MNHN 1910–90. Not to scale.

relatively slow locomotion of these taxa reduces the risk of dislocation of the joint despite its low stability. Generally, the morphology of the humeral head is a better indicator of the potential range of movements at the shoulder joint than the glenoid cavity (Text-fig. 13I–L). In *Arctictis* (Text-fig. 13I) and *Ursus* the head is rounded in all directions, and does not protrude posteriorly. Moreover, *Gulo* (Text-fig. 13K) and *Ursus* are characterized by a humerus with extremely low tubercles appressed against the head. The greater tubercle in particular is smaller than the head and does not protrude anteriorly, a feature that greatly restricts the depth of the bicipital groove. In *Arctictis* and *Neofelis* (Text-fig. 13I–J), the

greater tubercle is both more elevated and more prominent anteriorly, providing for a deeper bicipital groove. By comparison, in terrestrial taxa the humeral head protrudes posteriorly, and the head is transversely flattened in posterior view, with a reduced arc of curvature (see *Hyaena*: Text-fig. 13L). In *Hyaena*, the greater tubercle is also particularly prominent proximally, a morphology that might increase the stability of the shoulder joint in the transverse plane. Thus the morphology of the shoulder joint reflects the highly mobile humerus of the arboreal *Arctictis* and *Ursus*, whereas the proximally flattened humeral head of cursorial forms reflects the lateral stability of this joint. The proximal humeral end of *Prothylacinus* is intermediate between these two groups. The rounded humeral head and the shape of the lesser tubercle (low and appressed against the head) reflect a significant range of movement, but the flattened lateral part of the articular facet and a greater tubercle that is much more prominent than in *Arctictis*, *Gulo*, and *Ursus*, indicate powerful Mm. spinati, used as stabilizers of the joint.

   Despite the less prominent greater tubercle of the extant arboscansorial taxa, a common feature shared by *Prothylacinus* and *Arctictis*, *Gulo*, and *Ursus* is the thick, robust scapular neck, related to the size of the supra- and infraspinous fossae, and therefore to the development of the Mm. spinati that stabilize the shoulder joint (Jenkins and Weijs 1979). In climbers, the shoulder must be able to withstand tensile forces in addition to the usual compressive forces acting during quadrupedal locomotion (Oxnard 1968). Oxnard (1968), in his detailed multivariate analysis of the scapula, noted that in Carnivora most of the separation between the most arboreal taxa and others (the study including *Arctictis*, *Canis*, *Gulo*, *Hyaena*, and *Ursus*) is based on the degree to which these taxa are capable of bearing tensile forces in the shoulder region. In the present study the extant taxa clearly show that resistance to tensile forces is partly based on the robustness of the scapular neck, and partly on the development of the infraspinous fossa, which is fan-shaped and broader in arboscansorial taxa.

   In *Prothylacinus*, the robust vertebral border reflects the loads exerted by the M. serratus anterior, a muscle that supports part of the weight of the trunk and plays an important role during climbing (McEvoy 1982). As detailed by Davis (1949), load transmission from trunk to limb is effected chiefly by the medial extrinsic muscles of the shoulder (Mm. serratus anterior, rhomboideus, trapezius, and pectoralis). They were probably well developed in *Prothylacinus*, given not only the thickness of the vertebral border of the scapula, but also the length of the humeral deltopectoral crest. It is worth noting that the general shape of the scapula of *Neofelis* (Text-fig. 13B) is more similar to that of the terrestrial taxa, but unlike *Canis*, *Hyaena*, or *Thylacinus*, the scapular spine is perpendicular to the vertebral border rather than oriented at a sharp angle, thereby increasing the angle between the Mm. trapezius and serratus anterior, and thus the rotational range of the scapula (Oxnard 1968).

   In the arboscansorial taxa with manipulative behavior (and generally in felids and ursids), the deltopectoral crest is long and well developed, increasing the length of insertion of the pectoralis. By comparison, in terrestrial taxa the insertion of the pectoralis is much weaker, but the insertion of the deltoideus pars spinalis is particularly prominent in *Canis* and *Hyaena*. This muscle probably contributes to retraction of the forelimb (McEvoy 1982), like the triceps caput longum, both muscles being well developed in cursorial forms. Moreover, the insertions of the teres major and latissimus dorsi are weaker and more proximally positioned in terrestrial taxa than in arboscansorial ones. The adductors like pectoralis are used both in climbing up and down, head first, when the forefeet usually grip the support at a position just forward of the scapula so that the pectoralis can exert the maximum lateral pressure and thus maximum frictional forces (Taylor 1970). The pectoralis also rotates the humerus internally (McEvoy 1982), and this rotatory component serves to force the distal parts of the forelimb into the medially lying branch when the elbow is flexed. This action may be particularly important when the deltopectoral crest is very long as it is in *Prothylacinus*. In the borhyaenoid, the distal insertions of the teres major and latissimus dorsi also reflect powerful retraction and adduction of the humerus at the glenohumeral joint, consistent with climbing ability.

Humeroulnar and radioulnar joints (Text-fig. 14). The extant taxa reflect the two different patterns observed in *Borhyaena* and *Prothylacinus*, in relation to the primary obligate mode of locomotion. In *Gulo* (Text-fig. 14A) and especially *Arctictis*, the distal humeral end is wide, the trochlear medial lip is not prominent, and the olecranon fossa is imperforate. *Arctictis* has the less stabilized elbow joint, with a distal humeral end that is wider than deep, and a shallow olecranon fossa and trochlear groove. The flatter, less-stabilised humeroulnar articulation of arboscansorial taxa, as observed in *Prothylacinus* compared to *Borhyaena*, would allow the ulna to rock on the humerus during supination (Taylor 1974). The arboscansorial *Ursus* represents a special case (Text-fig. 14B), since the trochlea is very concave posteriorly between a prominent lateral lip and the medial epicondyle, a morphology that probably stabilizes the humeroulnar joint, like the very asymmetrical anconeal process of the ulna. The elbow joint of *Neofelis* is intermediate between the patterns shown by the arboscansorial and the terrestrial placental taxa. In the latter, the humeral trochlea is particularly narrow and concave, lying between a posteriorly prominent lateral lip and the medial epicondyle (Text-fig. 14D). The olecranon fossa is perforated in *Canis* and *Hyaena*, probably increasing the range of extension. The anconeal process on the ulna is asymmetrical, narrow, prominent anteriorly, and with reduced lips (Text-fig. 14H). In *Thylacinus* the humeral trochlea is relatively shallower and wider than in *Canis* and *Hyaena*, and the

lateral lip and the medial epicondyle are less prominent (compare Text-fig. 14c and d). The olecranon fossa is deep, but not perforated. The anconeal process on the ulna is wider, with relatively well-developed lips (Text-fig. 14g). Although *Thylacinus* exhibits various features suggesting a trend toward cursoriality in the dasyuromorph context, its elbow joint appears to be much less specialized than in placental cursors in which the symmetrical humeroulnar articulation greatly restricts movements to a parasagittal plane. The elbow joint of *Borhyaena*, also less specialized than that of placental cursors, appears to favour parasagittal movements compared to that of *Prothylacinus*.

In *Canis* and *Hyaena* the capitulum is separated from the trochlea by a deep, narrow groove that emphasizes the pulley-shape of the distal articular area (Text-fig. 14d). The capitulum is long and narrow, and the radial head of the radius is wider than deep (Text-fig. 14k), a morphology that precludes it from supination since the radial head cannot rotate on the capitulum. The flat lateral part of the radial head articulates with the well-developed lateral lip of the capitulum, increasing the stability of the humeroradial joint. In neither fossil is the lateral border of the capitulum prominent anteriorly or proximally, nor is there a well-marked groove between the lateral margin and the capitular facet. In *Gulo* and *Neofelis* the capitulum is wider than that of highly cursorial placental taxa, and the distal humeral end is less trochlear-shaped. Moreover, the stabilising lateral lip of the capitulum is extremely reduced in *Neofelis*. The humeroradial joint of *Thylacinus* is much more similar to that of *Neofelis* than to *Canis* and *Hyaena*, and appears less stabilised in the metatherian than the eutherian cursors. In *Gulo* and *Neofelis* the radial head is oval, but its proximal articular facet is broader than that in cursorial forms. The capitulum of *Arctictis* is wide and flat, and is separated from the trochlea by a very shallow groove. The radial head is more rounded than in *Neofelis* or *Thylacinus*, and the ulnar articular facet is longer and broader.

The potential range of movement of the radius depends not only on the general shape of the radial head but also on the size and convexity of the ulnar articular facet (MacLeod and Rose 1993), which is flatter and narrower in cursors. It is also related to the angle between the radial notch and the coronoid process (as seen in didelphids, Argot 2001; and viverrids, Taylor 1974), that is much flatter in *Gulo* and especially *Arctictis* than in the other taxa (Text-fig. 14e–h, bottom). Finally, the supination range is related to the orientation of the radial head relative to the distal end (Text-fig. 14i–k), which is distinct on the extant taxa examined as it is in *Borhyaena* and *Prothylacinus*. In *Arctictis* the transverse axes of the proximal and distal ends of the radius form an angle of approximately 30 degrees, and the ulnar facet is thus oriented posterolaterally in articulation. In *Neofelis* and *Ursus*, the transverse axes of both extremities form an angle of approximately 70 degrees, while in *Gulo* it is intermediate. The condition in *Neofelis* and *Ursus* suggests that the gliding of the radial head on the radial notch is more restricted in *Arctictis* in order to attain a semiprone position of the manus. In cursorial taxa, the transverse axis of the radial head is parallel to that of the distal epiphysis. The difference in orientation of the radial head between *Hyaena* and *Neofelis* implies that in a fully prone position its anterior margin faces the dorsal side of the manus in *Hyaena*, but the internal side in *Neofelis*. The result would be a more abducted humerus and flexed position of the elbow in *Neofelis*, and a more erect and parasagittal position in *Hyaena*. *Neofelis* may supinate its forefeet to some degree when catching prey or grasping supports.

In both *Neofelis* and *Ursus* the radial head is broader than the coronoid process, which is narrow and deflected medially due to the protrusion of the medial lip of the trochlea. This may increase the role of the radius in the transfer of loading from the arm onto the forearm. In *Arctictis* and *Gulo*, as in *Prothylacinus*, the radial head and coronoid process are more equivalent in size, and consequently they provide for a more equivalent loading support.

Morphology of the ulna and radius (Text-fig. 15). The ulnae of the living taxa show three distinct shapes in lateral view (Text-fig. 15a–d). The posterior border is concave in *Canis*, *Hyaena*, and *Thylacinus* (although to a lesser extent in the latter taxon), straight in *Neofelis* and *Ursus*, and extremely convex in *Arctictis*. *Gulo* lies intermediate between the first two groups, with a posterior border that is straight proximally but concave distally. In *Arctictis* the convex posterior border and the anteriorly angled olecranon resemble the condition in arboreal didelphids.

As detailed in the study of the forelimb of *Mayulestes* (Argot 2001, fig. 14), the proximal ulnar convexity, located opposite to the insertion of biceps and brachialis, reflects the combined pull produced by these flexors and extensor (triceps brachii caput longum) of the forearm at the elbow once the manus has secured a grip. When climbing vertically, flexors are used to pull the body up against gravity, bringing the centre of gravity near the support, while the triceps caput longum helps to flex the humerus on the scapula, giving the forelimb a Z shape. The flexors are particularly well developed in climbers, whereas the three heads of the triceps show greater development in cursorial forms. However, as a retractor of the humerus on the scapula, the pull exerted by the long head of the triceps brachii plays an important role in the morphology of the ulna in climbers. The insertion of the biceps and brachialis in *Arctictis* is located more distally to the centre of articulation of the elbow joint than in *Neofelis* and *Ursus*, increasing the mechanical advantage of the muscles. Moreover, the bicipital tuberosity of the radius is long and robust and is also positioned relatively distal to the head. Compared with *Arctictis*, the straight ulna in *Neofelis* and *Ursus* might reflect the lack of grasping ability, since the forces exerted by the triceps and the biceps-brachialis on the ulna are probably strongest when they act against a resistance, i.e. when the manus plays an active grasping role. In *Ursus*, the
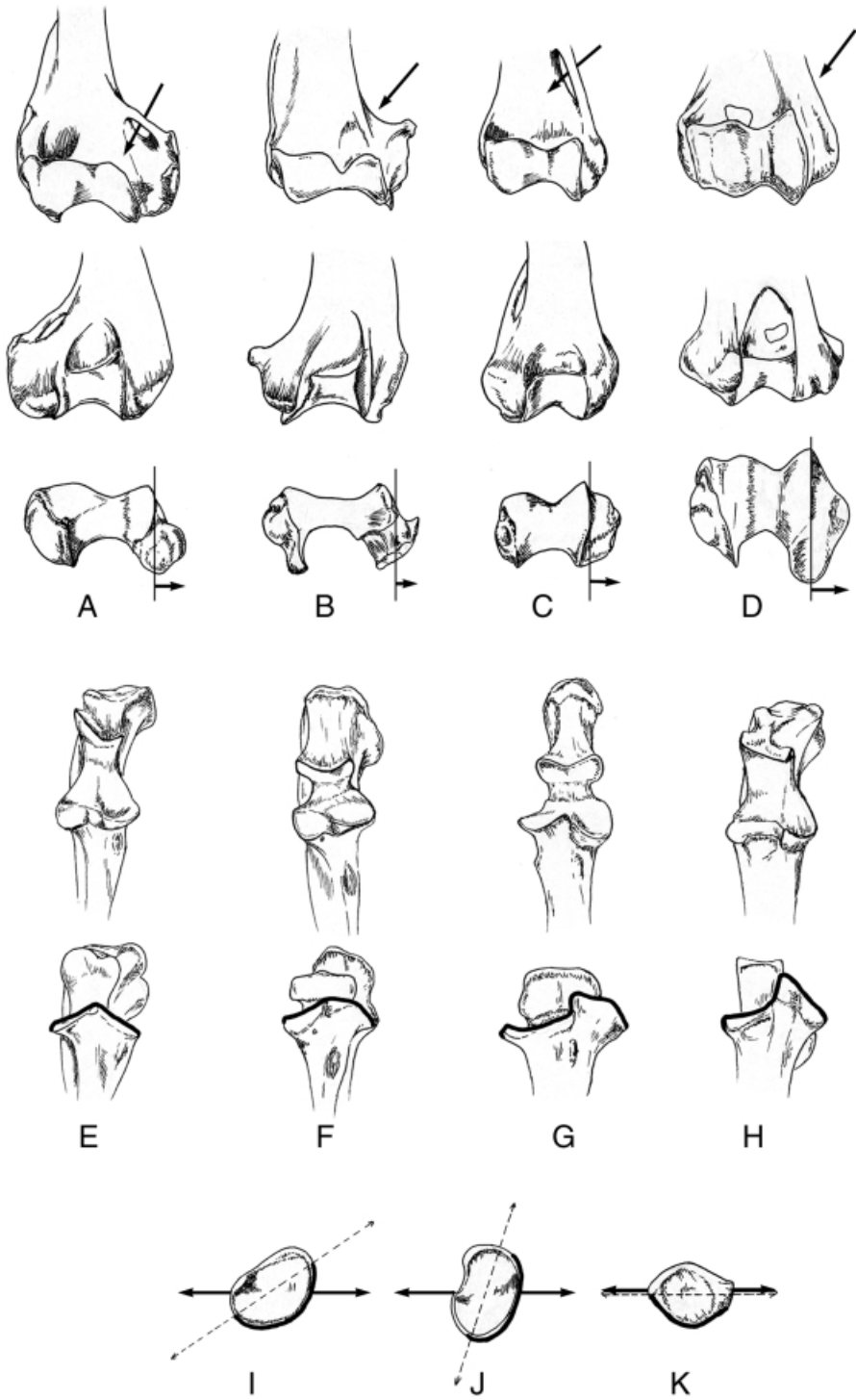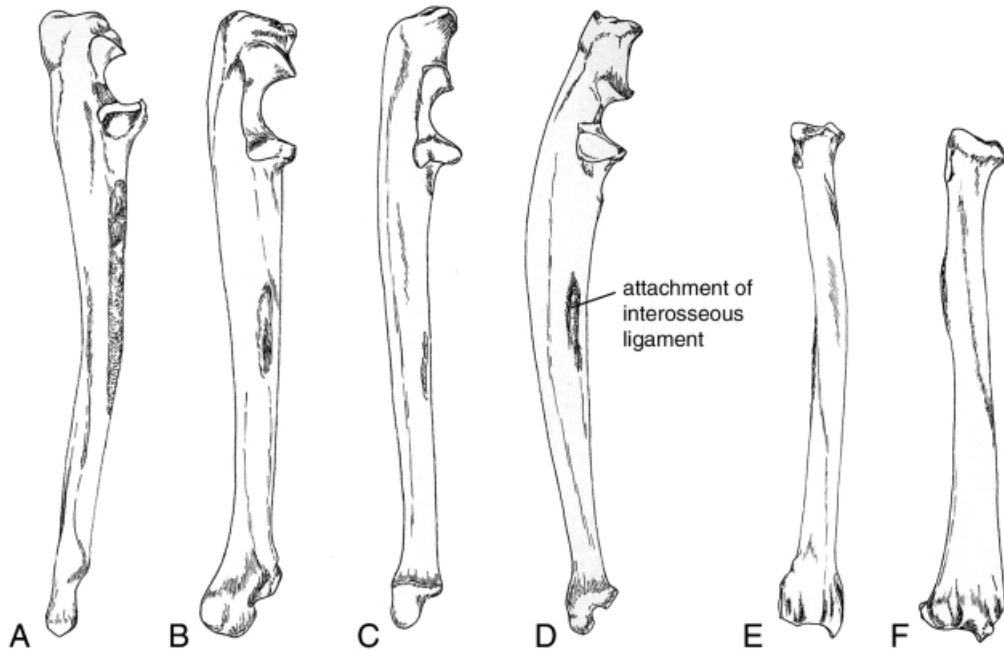
TEXT-FIG. 15. Right ulnae and radii in lateral view. A, E, *Hyaena hyaena* MNHN 1910–90. B, *Gulo gulo* MNHN 1935–3. C, *Neofelis nebulosa* MNHN 1961–101. D, F, *Arctictis binturong* MNHN 1975–78. Not to scale.

palmigrade posture is not related to opposability and grasping ability of the pollex, and the enormous claws preclude obligate grasping, a combination that would explain the straight ulna. The digitigrade *Neofelis* has less grasping ability and belongs with jumping and leaping arboreal species (*sensu* Taylor 1989). In *Gulo* (plantigrade), the straight ulna, weak bicipital tuberosity, and reduced bicipital groove on the humerus reflect more terrestrial habits than those of *Arctictis*. Considering the shape of the ulnar diaphysis of both fossils, as well as the development and location of the bicipital tuberosity, it is clear that flexors played an important role in *Prothylacinus*. *Arctictis* clearly groups with arboreal species, having grasping ability (Taylor 1989) and moving in a controlled fashion, as *Prothylacinus* probably did. In *Canis* and *Hyaena*, the posterior border of the ulna is concave, and the olecranon is short, with a massive apex. Its caudal inclination and the sharp angle between the proximal edge and the long axis of the diaphysis reflect the role of the triceps working from a more extended position than in less cursorial forms (Walker 1974). The insertion of M. brachialis is located proximally, along the medial border of the trochlear notch. On the radius, the bicipital tuberosity is reduced to a small lateral pit. In *Borhyaena* and *Thylacinus*, these features are less specialized than in the obligate placental cursors.

The lateral epicondylar crest, where the Mm. brachioradialis and extensors carpi radialis originate, is particularly reduced in terrestrial taxa. It is stronger in *Arctictis* and *Gulo* but never reaches the development observed in *Prothylacinus*, consistent with the development of the third forearm flexor, M. brachioradialis. The medial epicondyle where the flexors of the manus originate projects medially in the arboscansorial taxa, but it is appressed against the trochlea and protrudes posteriorly in the terrestrial forms, especially in *Canis* and *Hyaena*. This observation is

TEXT-FIG. 14. Elbow joint. A–D, distal extremity of the right humerus. From top to bottom: anterior, posterior, and distal views. A, *Gulo gulo* MNHN 1935–3. B, *Ursus malayanus* MNHN 1913–505. C, *Thylacinus cynocephalus* MNHN 1891–61. D, *Hyaena hyaena* MNHN 1910–90. E–H, trochlear notch of the right ulna. Top, anterior view. Bottom, anterodistal view. E, *Gulo gulo* MNHN 1935–3. F, *Arctictis binturong* MNHN 1975–78. G, *Thylacinus cynocephalus* MNHN 1891–61. H, *Hyaena hyaena* MNHN 1910–90. I–K, proximal epiphysis of the right radius in proximal view. I, *Arctictis binturong* MNHN 1975–78. J, *Neofelis nebulosa* MNHN 1961–101. K, *Hyaena hyaena* MNHN 1910–90; the dashed line represents the long axis of the proximal epiphysis, the full line the long axis of the distal epiphysis; the bold part of the circumference represents the ulnar articular facet. Not to scale.

consistent with Jenkins' (1973) biomechanical study of the humeroulnar articulation in mammals. As the flexor muscles arise from the medial epicondyle, they exert a medial torque in proportion to their distance from the radioulnar axis. This torque may be decreased by either reducing the musculature and shortening the medial epicondyle, or by reorienting the epicondyle so that the flexors pass behind rather than medial to the trochlea, as in *Canis* and *Hyaena*. The prominent medial epicondyle of *Prothylacinus* is therefore consistent with a powerful flexor musculature, in contrast to *Borhyaena*. In this latter taxon, the shorter, shallower medial and lateral fossae on the ulna suggest a reduced abductor pollicis longus and flexor digitorum longus, and thus reduced grasping role of the digits. In contrast, the medial fossa on the ulna (where the ulnar head of the flexor digitorum profundus originates) is particularly long and deep in *Arctictis* as in *Prothylacinus*, an observation that supports the hypothesized development of this muscle in the extinct form, and therefore also its grasping ability.

In the terrestrial taxa, the radius is elliptical in cross-section, i.e. wider than deep along all the diaphysis. It is closely appressed to the ulna, and therefore its anterior convexity (Text-fig. 14E) is related to the posterior concavity of the ulna. In the dog (*Canis familiaris*), M. pronator teres inserts on the proximal third of the radius which is free of muscular insertion beyond that point (Miller *et al.* 1964). This morphology increases the stability of the union between the two bones, and greatly reduces the rotational capabilities of the radius. In cursors, the radius, much more robust than the ulna, becomes the major load-bearing bone of the forearm (Taylor 1989). This difference in size between the radius and ulna is much less marked in *Thylacinus* and especially in *Borhyaena* but the radius is also appressed against the ulna in these taxa. The interosseous space is broader, the radial shaft is more convex (especially in *Arctictis* and *Ursus*), and the insertion of the pronator and supinator muscles is better marked in arboscansorial taxa. The more slender and less curved radius of *Borhyaena*, as well as the weaker insertion of the pronator teres compared to *Prothylacinus* (in which it extends along the distal three quarters of the shaft), probably reduces the capacity for pronation-supination, consistent with the shape of the radial head. The distal facet for the ulna is flat, narrow, and elongated in *Canis* and *Hyaena*, while in arboscansorial taxa this facet is longer than high, slightly concave, and protrudes laterally. It provides for rotational ability of the distal extremity of the radius. Similarly, the distal radioulnar articulation of *Borhyaena*, in conjunction with the presence of a strong interosseous ligament located just above, reflects a more stabilised articulation than in *Prothylacinus*, and thus a restricted rotational range for the radius.

Form and function of the carpus and manus (Text-figs 16–17). The distal ends of the radius and ulna of *Gulo* are more robust than those of *Arctictis*, although the bones are of the same length and both taxa are palmigrade (Text-fig. 16A–B), which may be related to the enlarged extremities of *Gulo*. In *Neofelis*, the distal extremity of the ulna is much more slender than in *Gulo* whereas the radius is equally robust. The carpus as a whole is relatively narrower in *Neofelis*, a condition that may be related to the digitigrade posture. In cursors, the distal extremity of the radius is massive compared to the slender ulna, a feature not shown in *Borhyaena*.

The adaptive differences of the radioscaphoid articulation are clearer on the scapholunar than on the radius. During the support phase, the carpus is rigid and provides for weight transfer in an extended or slightly hyperextended position. During the recovery phase, the proximal carpal joint provides for active flexion of the wrist (Yalden 1970). In *Arctictis* and *Gulo* the orientation of the proximal articular facet of the scapholunar allows an increased range of dorsiflexion when compared with fully digitigrade forms. The range of dorsiflexion at the proximal carpal joint is given as approximately 40 degrees in *Canis* and *Felis*, 45 degrees in *Crocruta*, 50 degrees in *Viverra*, 55 degrees in *Ursus* (Yalden 1970). In fully digitigrade groups like Canidae and Felidae, the limited dorsiflexion only provides for an hyperextended position of the wrist during weight transfer. The carpus of Hyaenidae is very similar in form and mobility to the carpus of Canidae (Yalden 1970). In *Hyaena* (Text-fig. 16C), the distal articular facet of the radius is wide, concave, and has a prominent styloid process and anterior border. The palmar process of the scapholunar that protrudes proximally probably stabilizes the proximal carpal joint. The relatively small range of hyperextension in *Ursus*, but also in the badger (*Meles meles*) and the tayra (*Eira barbara*) does not allow the carpus to touch the ground and, consequently, Yalden (1970) considered these taxa as digitigrade rather than palmigrade. Although the range of dorsiflexion cannot be ascertained in fossils, the morphology of the scaphoradial joint is consistent with a palmigrade position for *Prothylacinus*, and a semi- or fully digitigrade position for *Borhyaena*. Moreover, in *Prothylacinus*, Mc II and especially Mc III bear a rough dorsal area, reflecting the insertion of the extensors carpi radialis. An increase in size of these muscles was already indicated by the development of the humeral lateral epicondylar crest, and is consistent with an increased range of dorsiflexion related to a palmigrade posture.

The metacarpals of *Arctictis* and *Ursus*, two arboreal, palmigrade forms, are short relative to the total forelimb length. In contrast, they attain a maximal length in the terrestrial, cursorial *Canis* and *Hyaena*. The ratios obtained for the three other taxa indicate a more complex functional pattern (e.g. the metacarpals of the digitigrade *Neofelis* are relatively shorter than in *Gulo* whereas the brachial index is similar). It appears that the short metacarpals of *Neofelis* are related to arboreal habits, whereas those of *Gulo*, which are almost as long as in cursors but much more widely spread (compare Text-fig. 17B and D), are related to travelling in soft snow, which requires relatively broad, enlarged
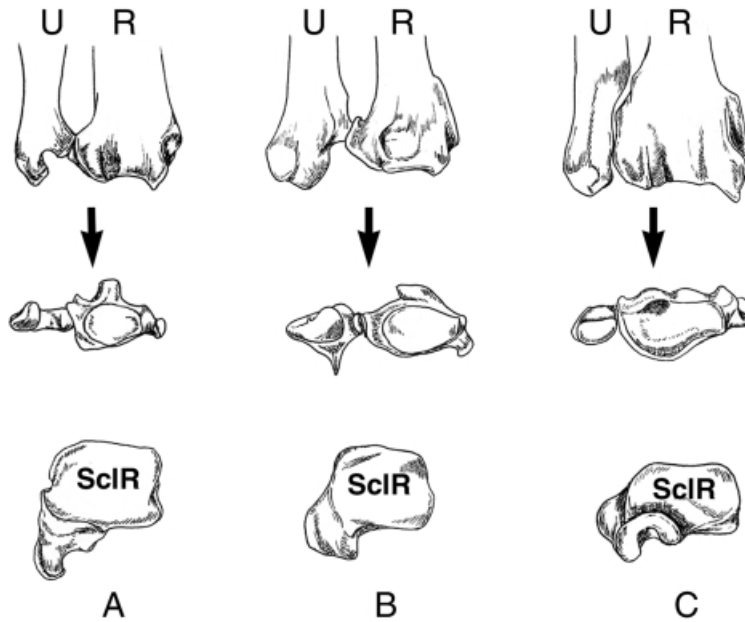
TEXT-FIG. 16. Radiocarpal joint. Top, distal end of the right ulna and radius in anterior view. Middle, the same in distal view. Bottom, right scapholunar in proximal view. Abbreviations: R, radius; SclR, scapholunar-radius joint; U, ulna. A, *Arctictis binturong* MNHN 1975–78. B, *Gulo gulo* MNHN 1935–3. C, *Hyaena hyaena* MNHN 1910–90. Not to scale.

extremities (Krott 1960; MacDonald 1984). The distal ends of the metacarpals are wider and more globular in the four arboscansorial models, whereas in *Canis* and *Hyaena* they are characterized by a sharp sagittal crest and two extremely well-developed sesamoids, reflecting their efficiency as pulleys in cursorial forms. The metacarpals of *Thylacinus* are particularly short relative to the length of its forelimb compared to *Canis* and *Hyaena* (Table 4). This may be due in part to a more limited specialization towards cursoriality, and in part to phylogenetic constraints. Keast (1982, table 1, fig. 5) noted that the ratio of the third metacarpal to the total forelimb length is similar in *Thylacinus* and in smaller dasyurids like *Antechinus* and *Dasyurus* (between 0·10 and 0·12). In contrast, this ratio is uniformly higher in the placentals examined (higher than 0·15), *Canis lupus* having a significantly higher ratio than *Martes* or *Mustela* (p. 678). The lengthening of the metacarpals observed in *Borhyaena* compared to *Prothylacinus*, although much less important than in placental cursors, is consistent with a more digitigrade posture in *Borhyaena*. In *Prothylacinus*, the length of Mc V and the convergence of digit V towards the other digits increased the grasping ability of the manus on curved supports. In *Borhyaena*, the short Mc V and the fact that it was divergent from Mc IV rather than parallel suggest in contrast a relatively reduced role for the external digit during walking.

The pollex is well developed in the palmigrade *Arctictis*, *Gulo*, and *Ursus* (Text-fig. 17A–B), where Mc I has the same robustness as the other metacarpals, and represents more than 75 per cent of the length of Mc II. The pollex is more reduced in *Neofelis* (Text-fig. 17C), where Mc I is less than half the length of Mc II. Nevertheless, the claw of the pollex is large, reflecting its role in climbing and/or grasping objects. In contrast, Mc I is extremely slender in *Canis* (Text-fig. 17D). The pollex of *Thylacinus* is relatively less reduced: Mc I is slightly more than half the length of Mc II, and it is of similar width to the other metacarpals. *Hyaena* does not have a pollex. The absence of a tight articulation between Mc I and Mc II in *Prothylacinus* and the large area of origin for the abductor pollicis longus on the radius and ulna are consistent with a well-developed and relatively free pollex. Its pseudo-opposability cannot be determined but existed in two contemporaneous borhyaenoids, *Cladosictis* and *Sipalocyon* (Argot in press), and would be consistent with the non-parasagittal movements of digits II and V, increasing the grasping ability of the manus. Based on the trapezium, the digit I of *Borhyaena* was not as reduced as in canids or hyaenids, but the similarity in shape and orientation between the articular facets with Mc I and Mc III suggests that the pollex of *Borhyaena* was not opposable. This is consistent with the reduced area of origin for the abductor pollicis longus on the forearm, and with a digitigrade posture.

TABLE 4. Proportions of the limbs. Abbreviations: H, humerus length; R, radius length; McIII, third metacarpal length; PP: proximal phalanx length (phalanx of digit III if associated, maximum phalanx length if not); F, femur length; T, tibia length; MtIII, third metatarsal length; –, measurement not available. In *Prothylacinus patagonicus*, the measurements of the manus are estimated from specimen MACN 708–720, but all the other measurements are from specimen PU 015700. (The ulna is common to both specimens and is of similar length.)

Specimens	Brachial index (R/H)	Crural index (T/F)	Tibio-radial index (R/T)	Intermembral index (H + R + McIII/F + T + MtIII)
Prothylacinus patagonicus PU 015700	0·84	0·87	0·75	0·785
Borhyaena tuberata PU 015701	–	–	–	–
Arctictis binturong MNHN 1975–78	0·79	0·91	0·845	0·91
Gulo gulo MNHN 1935–3	0·82	1·00	0·80	0·89
Neofelis nebulosa MNHN 1961–101	0·82	0·95	0·77	0·82
Ursus malayanus MNHN 1913–505	0·845	0·755	1·06	1·00
Thylacinus cynocephalus MNHN 1891–61	1·01	1·00	0·85	0·815
Canis lupus MNHN 1984–08	1·00	1·05	0·88	0·90
Hyaena hyaena MNHN 1910–90	1·09	0·905	1·16	1·055

Specimens	McIII/ (H + R + McIII)	MtIII/ (F + T + MtIII)	McIII/ MtIII	PP/McIII	MtIII/F
Prothylacinus patagonicus PU 015700	0·11	0·09	0·94	0·515	0·19
Borhyaena tuberata PU 015701	–	–	–	0·38 (digit IV)	–
Arctictis binturong MNHN 1975–78	0·105	0·105	0·915	0·655	0·225
Gulo gulo MNHN 1935–3	0·17	0·17	0·885	0·555	0·405
Neofelis nebulosa MNHN 1961–101	0·14	0·15	0·765	0·665	0·34
Ursus malayanus MNHN 1913–505	0·10	0·095	1·04	0·625	0·19
Thylacinus cynocephalus MNHN 1891–61	0·115	0·14	0·67	0·47*	0·33
Canis lupus MNHN 1984–08	0·17	0·17	0·90	0·395	0·43
Hyaena hyaena MNHN 1910–90	0·175	0·175	1·06	0·335	0·405

* measured on a disarticulated specimen, i.e. the association is doubtful

In digitigrade forms, the proximal phalanges are circular in cross-section and the articular facet for the metacarpal is oriented proximodorsally, increasing the range of dorsiflexion at the joint. In arboscansorial taxa these phalanges are more compressed dorsoventrally, and have a small palmar groove (especially in *Ursus*), in relation to the strong
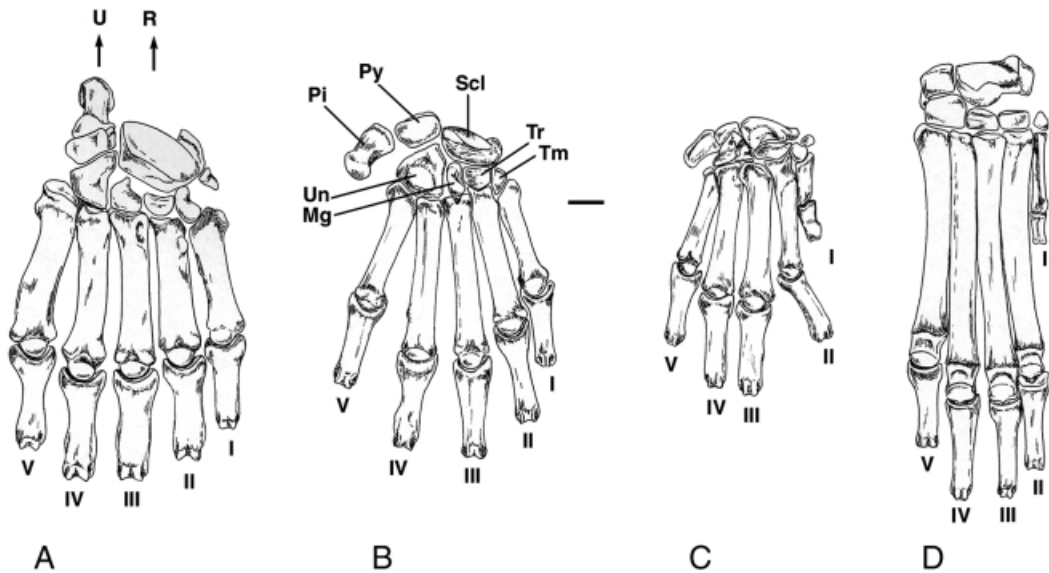
TEXT-FIG. 17. General morphology of the left manus in dorsal view. A, *Ursus malayanus* MNHN 1913–505. B, *Gulo gulo* MNHN 1935–3. C, *Neofelis nebulosa* MNHN 1961–101. D, *Canis lupus* MNHN 1946–1. Compare the development of the pollex and the width of the manus in the various taxa. Abbreviations: Mg, magnum; Pi, pisiform; Py, pyramidal (= cuneiform); R, radius; Scl, scapholunar; Tm, trapezium; Tr, trapezoid; U, ulna; Un, unciform. Scale bar represents 10 mm.

tendons of the flexor digitorum profundus. Relative to metacarpal length, the proximal phalanges are much longer in *Arctictis* and *Ursus*, but also in *Neofelis*, which is consistent with the grasping ability of these forms, long digits providing a better opposition between the palm and the distal segments of the digits (Cartmill 1974; Lemelin 1999). *Neofelis* represents a compromise between the necessity of having long digits for grasping, and the problems this presents for the usual digitigrade posture. In fact, when the palm is off the support, the digits are hyperextended at the metacarpophalangeal and digital joints. The resulting torque at these joints and the bending moments sustained by the phalanges are proportional to the length of the digits, so that long digits are incompatible with a digitigrade posture (Lemelin 1999). In fully terrestrial/cursorial taxa like *Canis* and *Hyaena*, the proximal phalanges are particularly short. The long proximal phalanges of *Prothylacinus* are therefore consistent with a grasping ability for this taxon. Moreover, its intermediate phalanges exhibit a deep fossa on the palmar side, a condition that probably increased the range of flexion of the claws, also consistent with grasping ability. In *Borhyaena*, the short proximal phalanges and their proximal robustness suggest an increased loading at the metacarpophalangeal joint, consistent with the digitigrade posture.

The intermediate and ungual phalanges of *Neofelis* have a specialized shape related to the retractile claws. In *Canis* (Text-fig. 6L), *Hyaena*, and *Thylacinus* the ungual phalanges are wide but not deep, more or less circular in cross-section, and have a blunt dorsal margin. In *Arctictis* they are much deeper and thinner, more concave in lateral view, and with a sharp dorsal margin (Text-fig. 6K). Similarly, the unguals of *Gulo* are deeper and sharper than those of terrestrial forms, permitting the animal to climb out of reach of enemies like grizzlies (*Ursus arctos*) (Van Valkenburgh 1985). The articular facet of the ungual phalanges of *Prothylacinus* is higher than wide, and this probably reflects the increased range of flexion-extension of the claws, as suggested by the fossa on the palmar side of the intermediate phalanges. Their morphology is similar to that of arboscansorial taxa. In *Borhyaena*, the cleft dorsal tip of the ungual phalanges indicates a reduced grasping function, unlike *Prothylacinus* in which the dorsal margin of the claws is sharp.

Pelvic girdle and hindlimb

Form and function of the innominate and hip joint (Text-fig. 18). The basic architecture of the innominate is largely determined by its role in transmitting thrust between the legs and vertebral column, and by its locomotor function in

providing attachment surfaces and lever arms for hip and thigh muscles (Elftman 1929; Davis 1964). Nevertheless, it is also modelled by the urogenital and digestive tracts (e.g. the ventral arch is not only involved in the general stability of the structure, but also in the support of the young, especially in marsupials), and therefore its shape is difficult to understand from an exclusively functional point of view.

The ilia of *Arctictis* and *Neofelis* (Text-fig. 18A, E) are parallel, oval in outline, and have a concave gluteal fossa delimited by thick margins. In *Canis* and *Gulo* (Text-fig. 18B, F), the iliac blades are deeper anteriorly than near the iliac neck, and the anteroventral tip deflected outward, especially in *Gulo*, which has a shorter lumbar region. *Hyaena* (Text-fig. 18C, G) and *Ursus* show the greatest development and outward deflection of the anterior tip of the iliac blades. In these taxa, the gluteal fossa is oriented more dorsally than laterally. The broad iliac crests, expanded in the frontal plane, might be partly related to the width of the trunk and development of the epaxial musculature, since *Hyaena* and *Ursus* have the shortest lumbar region among the taxa studied (Table 3), and thus have the shortest space between the ribs and the iliac crests. Similarly, the outward deflection of the anterior iliac crest allows a great development of the epaxial musculature in *Gulo*, a taxon that is said to be lumbosacrally overbuilt (Krott 1960). A similar outward deflection of the iliac blades also occurs in the marsupial wombat *Vombatus* (Elftman 1929), a powerful digger. The iliac crest of *Canis lupus* (in anterior view) forms an angle of 70–80 degrees with the horizontal plane, versus 45 degrees in *Gulo*, 20 degrees in *Ailuropoda*, and 12 degrees in *Vombatus* (Davis 1964). Davis suggested that a frontal position of the iliac wings increases the efficiency of the glutei and iliacus during an erect and/or burrowing posture in order to stabilize the pelvis and vertebral column. However, this does not explain the similar morphology found in *Hyaena*, except that carrying heavy prey requires a strong build of the lower back. In fact, the effects of the peculiar process of cephalization (massive skull and powerful jaw and neck musculature) cannot be discounted, as noted by Davis (1964): the lower back would be then designed to withstand strong forces acting from the skull in a posterior direction.

Among the taxa examined, *Hyaena* and *Ursus* have the lowest femoral greater trochanter (Text-fig. 18J). However, the particular shape of the ilium it bears does not affect the relative development of the glutei muscles as compared with other Carnivora such as felids and canids (Davis 1964). Moreover, the greater trochanter reaches the level of the femoral head in *Gulo* (Text-fig. 18I), an observation that precludes any inferences on the development of the glutei based only on the iliac shape, which seems to be more dependent upon epaxial musculature.

The ilium of *Thylacinus* (Text-fig. 18D, H) is structurally quite similar to that of *Prothylacinus*. It has broad, quadrangular gluteal fossae, slightly expanded dorsally above the sacral articulation, and with an outward deflection of the anteroventral extremity, suggesting a well-developed epaxial musculature in both taxa. However, there are differences between the innominate of *Prothylacinus* and *Thylacinus*, among them the development of the tuberosity where the rectus femoris originates, and the length of the iliac neck. The iliac neck is particularly short in *Prothylacinus*, the sacral articulation being located just in front of the acetabulum, increasing the stability of the pelvic girdle. Davis (1964, p. 109, fig. 60D) stated that the upward thrust of the legs through the acetabulum is transmitted in such a way that potentially destructive shearing forces are developed along the neck of the ilium. A short iliac neck, as observed in borhyaenoids, may therefore reduce this rotational torque on the sacroiliac articulation, and restrict the displacement of the ilia relative to the sacrum. The greater trochanter is slightly taller than the femoral head in *Thylacinus*, as in *Borhyaena* but not *Hyaena*. In *Prothylacinus*, it barely reaches the apex of the femoral head. *Canis* also exhibits a low greater trochanter but the posterior tip (where the M. gluteus medius inserts) is more prominent than in *Hyaena*. Therefore, it may be hypothesized that the development of the gluteus medius is related to endurance. In *Hyaena*, searching behaviour appears to be adapted towards catching small prey and scavenging (Kruuk 1976), and does not require the same level of endurance as the long chases performed by wolves. The morphology of the proximal femoral extremity in *Borhyaena* and *Thylacinus* suggests an increased endurance, consistent with the fact that *Thylacinus* was not known to be a fast predator, but was reported to trot long distances behind its prey (Smith 1982).

In the extant taxa examined, the lesser trochanter is reduced to a small posterior protrusion (Text-fig. 18I–K, middle), although it is relatively more prominent posteromedially in arboscansorial taxa such as *Gulo* or *Neofelis*. In *Thylacinus*, this trochanter is blade-shaped as in living dasyuromorphs, suggesting phylogenetic rather than functional constraints. The lesser trochanter is located close to the femoral head in *Thylacinus* (Text-fig. 18K), suggesting fast flexion provided by the ilio-psoas. The lesser trochanter of *Prothylacinus* is less prominent medially than in living arboreal didelphids, but is more so than in extant arboscansorial carnivores. Its morphology reflects the role of the ilio-psoas as a flexor more than a rotator of the thigh. Its distal flange, reduced compared to that of *Mayulestes*, reaches the origin of adductors, and is much more rugose than in *Borhyaena*, which is also consistent with climbing ability. The insertion of the adductors is located on the proximal half of the femur, and this may reduce their mechanical advantage compared to that of the forelimb adductors (the pectoralis group), the insertion of which is related to the humeral deltopectoral crest length. The proximal femoral insertion thus provides for adduction but especially fast extension of the thigh.

In *Gulo*, *Hyaena*, and especially *Canis* the ischiatic spines are deflected outward (unlike *Arctictis*, *Neofelis*, and
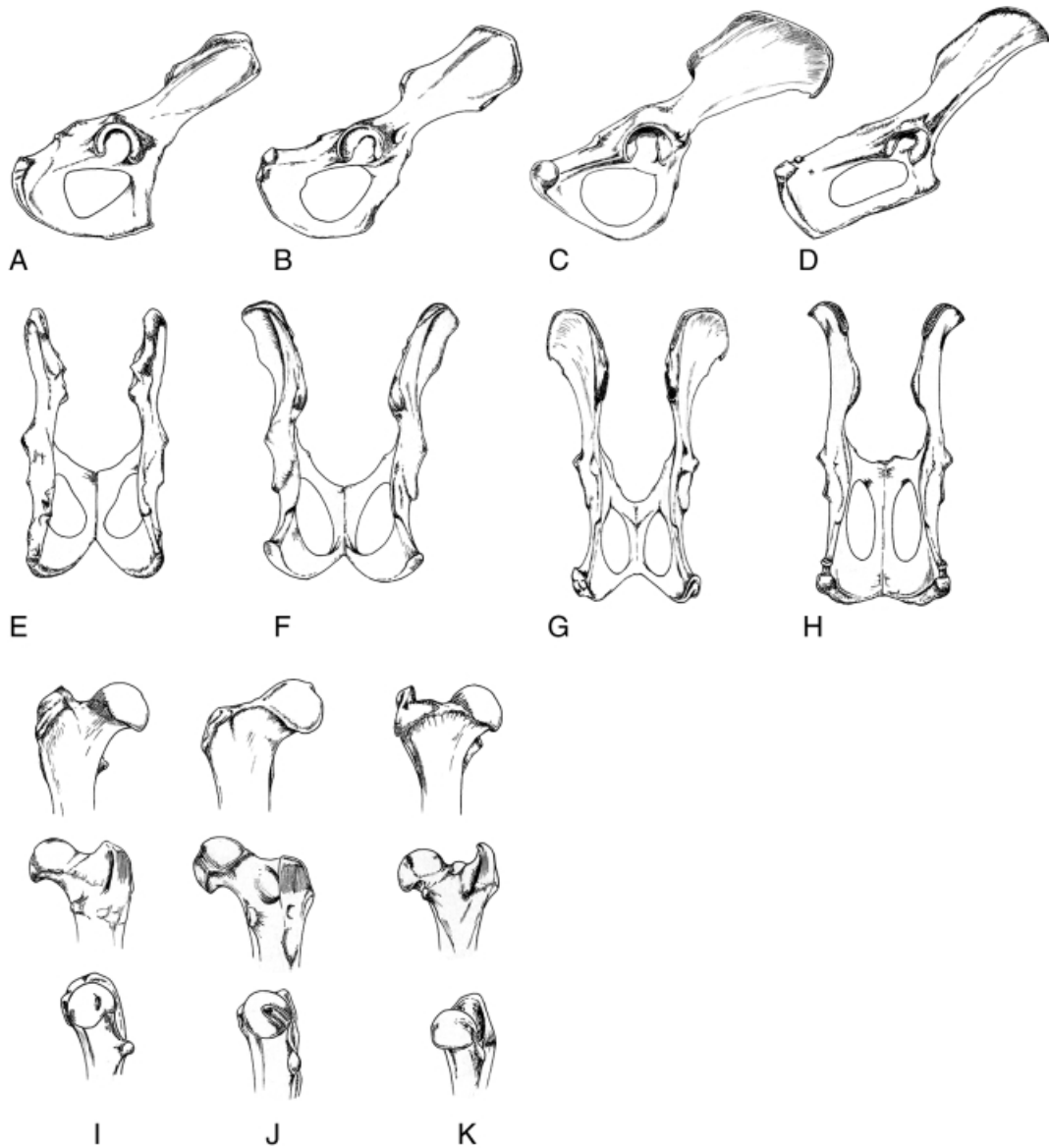
TEXT-FIG. 18. A–D, innominate in lateral view. E–H, innominate in dorsal view. I–K, proximal extremity of the right femur. From top to bottom: anterior, posterior, and medial views. A, E, *Arctictis binturong* MNHN 1975–78. B, F, I, *Gulo gulo* MNHN 1935–3. C, G, J, *Hyaena hyaena* MNHN 1930–220 (innominate) and MNHN 1910–90 (femur). D, H, K, *Thylacinus cynocephalus* MNHN 1891–61. Not to scale.

Thylacinus), and in *Canis* they also protrude anteriorly. The ischium is relatively short (<40 per cent of the total pelvic length) in *Canis*, *Hyaena*, and *Ursus*, and longer in *Arctictis*, *Gulo*, and *Neofelis* (40–45 per cent of the total pelvic length). *Thylacinus* has the longest ischium (>45 per cent of the total pelvic length), and this is comparable with *Prothylacinus*. The biceps femoris, semitendinosus, and ligamentum sacrotuberosum attach to the ischial tuberosity. The short ischium and proximal insertion of these muscles on the tibia of cursors, provide fast extension of the thigh. In *Ursus* the very robust ischiatic spines and the acute angle formed between the innominate and the vertebral column suggest occasional bipedal or sitting postures. Jenkins and Camazine (1977) observed that in Carnivora the outer

surface of the ischium is approximately perpendicular to the middle of the range of abduction (i.e. it is oriented more laterally in arboscansorial forms and more ventrally in terrestrial forms). This is confirmed by the taxa examined here and also supported by quantitative data provided by Davis (1964, p. 111). The descending ramus of the ischium of *Canis lupus* forms an angle of 21 degrees with the horizontal plane, whereas this angle attains 52 degrees in *Gulo*, and 56 degrees in *Ailuropoda*. A long ischium increases the mechanical advantage of the hamstring muscles, and could be partly related to the presence of a long muscular tail (Elftman, 1929). It is worth noting that on the dorsal margin of the ischium of *Prothylacinus*, just posterior to the acetabulum, a rugose tuberosity suggests strong pull exerted by the ischio-caudalis, an adductor of the tail particularly well developed in living arboreal didelphids with a prehensile tail that is muscular and rigid at its base.

There is a greater difference between the form of the acetabulum in *Thylacinus* and that of the placental taxa, than between the placentals themselves. In *Thylacinus* the acetabulum is oval, with an enlarged anterior articular surface due to the prominence of the anterolateral border. The articular surface is also constricted dorsally at the level of the ilio-ischiadic suture. This morphology is very similar to that of living dasyurids, highlighting probable historical constraints exerted at family level. Among the placental models, the acetabulum is deeper in cursorial forms, with an enlarged articular facet and a prominent dorsal margin. By contrast, the acetabulum of the arboscansorial models has a relatively narrow articular facet, and is relatively shallower in *Arctictis* than in other taxa. In *Arctictis* and *Ursus* the femoral head is hemispherical. This shape and orientation of the head, protruding more proximally than laterally, provide for a great mobility of the hip joint. In comparison, in *Neofelis* and *Thylacinus* the femoral neck is shorter and more massive, and the femoral head is less prominent proximally, a morphology that may reflect reduced mobility at the hip joint. The articular surface of the acetabulum in *Prothylacinus* suggests a greater range of movement for the femur than in *Borhyaena*, but the femoral head is still less hemispherical than in extant arboreal taxa.

Knee joint (Text-fig. 19). The distal extremity of the femur exhibits a morphological gradient that coincides with the behavioural gradient (arboreal and slow moving forms versus terrestrial and cursorial forms). In *Arctictis* and *Ursus*, the distal epiphysis is wider than high. In *Gulo*, *Neofelis*, and especially *Thylacinus*, this rectangular shape is less marked (Text-fig. 19A–E). The femoral trochlea is very shallow in *Gulo* and delimited by low ridges (Text-fig. 19C), which suggests that the knee joint was not strongly constrained by an agile, swift locomotion. By contrast, the femoral trochlea of *Neofelis* is relatively deeper and narrower, and is delimited by more prominent ridges (Text-fig. 19B). In *Hyaena* (Text-fig. 19D) and especially in *Canis* (Text-fig. 19E) the distal femoral epiphysis is higher than wide. The femoral trochlea is particularly deep and narrow in *Canis*, where it reaches a maximum anteroposterior and proximodistal development. This condition reflects the great range of excursion of the patella in cursorial forms. Similarly, the morphology of the femoral trochlea of *Hyaena* reflects its running capabilities more than that of the proximal part of the femur. The anterior tibial crest is much sharper and more prominent anteriorly along the proximal third of the diaphysis in terrestrial than in arboscansorial models (Text-fig. 19F–G).

Both femoral condyles are approximately equal in size in all the taxa examined, except *Ursus*. In the latter the condyles are asymmetrical in relation to the distal protrusion of the medial condyle, while the articular facet of the lateral condyle faces slightly internally and is narrower than the medial condyle. A similar morphology is also observed in *Ailuropoda* (Davis 1964). In *Gulo* the femoral condyles are morphologically quite similar to those of *Ursus*, although the medial condyle is relatively narrower. This condition suggests a medial displacement of the load line, but the relation of this morphology to the posture of the leg is not clear. In *Gulo* and *Ursus*, the difference between the tibial facets (the medial one concave and the lateral one flat) is particularly marked, and may provide for a slight rotational capability. The medial femoral condyle of *Borhyaena*, wider than the lateral one, differs from the morphology seen in living didelphids and most metatherians, in which the medial condyle is narrower than the lateral one (Szalay and Sargis 2001; Argot 2002). This suggests a medial displacement of the load in *Borhyaena*, perhaps reflecting a less abducted position of the femur in an obligate terrestrial animal. In fully cursorial extant taxa however, the femoral condyles are more prominent posteriorly and they are equivalent in width. The origin of the gastrocnemius externus is also more marked above the lateral condyle in the terrestrial models, in relation to the propulsive role of this extensor of the foot.

Morphology of the tibia and fibula (Text-fig. 19H–I). The lateral shaft of the tibia is straight to concave as seen in anterior view in arboscansorial forms, the anterior tibial crest is thick and convex, and the insertion of the hamstring muscles is well defined and positioned relatively distally. In contrast, in placental cursors and especially *Canis*, the tibial shaft is more sigmoid due to a proximal lateral concavity (M. tibialis anterior origin), and a distal lateral convexity (where the tibia forms a syndesmosis with the fibula). The short, sharp anterior crest is particularly prominent at the insertion of the hamstring muscles, especially M. biceps femoris (Miller *et al.* 1964). This proximal insertion provides for fast extension of the thigh and flexion of the crus. In lateral view, the shaft of the tibia is also straighter in arboscansorial models, whereas that of cursors is proximally more concave posteriorly. Cursorial forms
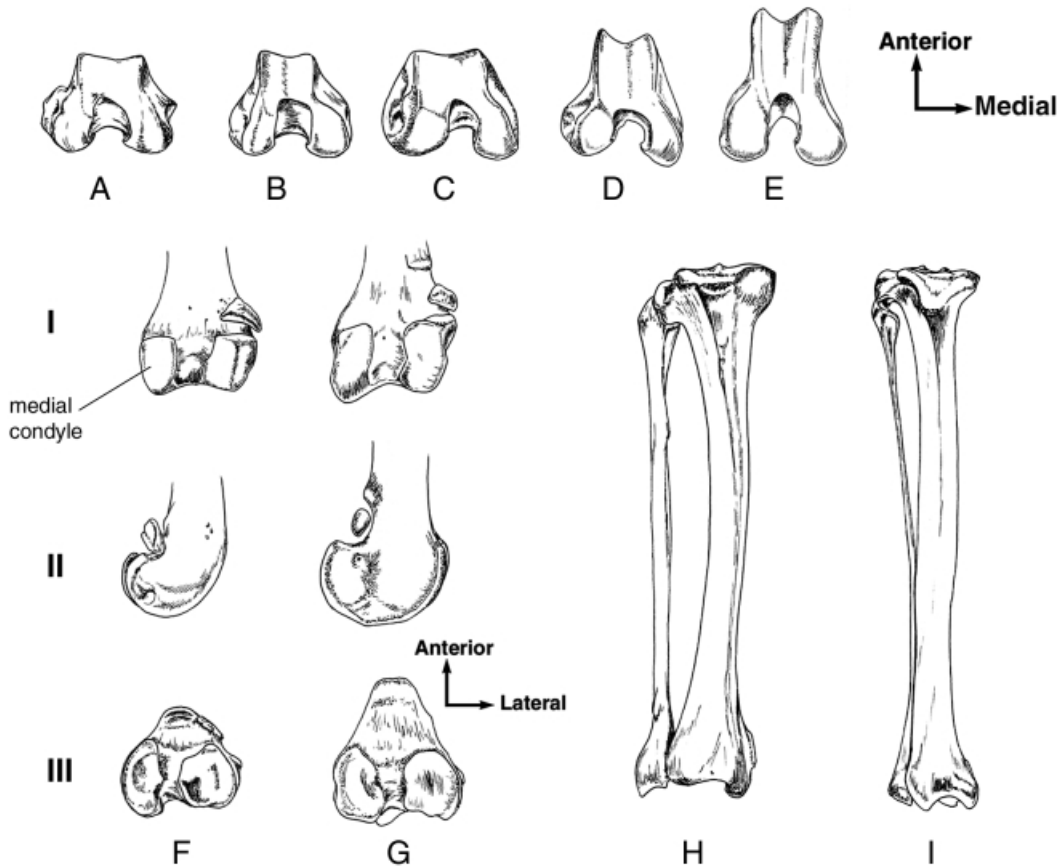
TEXT-FIG. 19. A–E, distal epiphysis of the right femur in distal view. A, *Arctictis binturong* MNHN 1975–78. B, *Neofelis nebulosa* MNHN 1961–101. C, *Gulo gulo* MNHN 1935–3. D, *Hyaena hyaena* MNHN 1910–90. E, *Canis lupus* MNHN 1984–08. F–G, knee joint. I–II, distal epiphysis of the right femur in I, posterior and II, lateral views. III, proximal epiphysis of the right tibia in proximal view. H–I, right tibia and fibula in anterior view. F, H, *Gulo gulo* MNHN 1935–3; G, I, *Hyaena hyaena* MNHN 1910–90. Not to scale.

are characterized by strong plantar flexors of the tarsus, the gastrocnemii. In canids the forces exerted by these muscles are increased by the formation of a strong common tendon that originates from the caudal border of the Mm. semitendinosus, gracilis, and biceps femoris (Miller *et al*. 1964) and inserts on the tuber calcanei. According to Lanyon (1980), the final shape of the tibia is reached when a trend towards greater curvature, induced by muscular pressure, is stopped as the increased curvature engenders excessive functional bone strain. The anterior convexity of the proximal part of the tibia of cursorial forms may represent such a compromise and might be partly related to the loads generated by these strong plantar flexors of the foot. The broad fibular facet for parafibula in *Prothylacinus* probably relates to a well-developed gastrocnemius externus, although its origin is not well marked on the femur, unlike living cursors. The parafibula is extremely well-developed and hook-like in *Thylacinus*.

The straight tibia of *Prothylacinus* is probably related to the similar width of the two femoral condyles, which therefore bear an equal part of the body weight in contrast to most of metatherians (Szalay and Sargis 2001). The long insertion of the gracilis and semitendinosus caput ventrale increases the mechanical advantage of these muscles that extend and adduct the thigh and flex the knee, an action that provides for powerful extension during the first phase of propulsion. This suggests short bursts of speed, consistent with an ambush hunting mode. The poorly defined insertion of the medial collateral ligament suggests reduced rotational constraints at the knee joint compared to highly arboreal didelphids like *Caluromys*. In *Prothylacinus*, the well-developed medial fibular crest (insertion of peroneotibialis) and the distal area for the strong distal ligament between tibia and fibula probably contributed to the firm connection

between the two bones, increasing the stability of the crus. Similarly, the fibula of *Arctictis* has a strong medial crest developed towards the tibia. In contrast, the fibula is reduced and a large syndesmosis extends along at least one-third of the length of the crus in *Canis* and *Hyaena*, so that the two bones act as a single unit. This loss of movement may be related to the disappearance of the deeper interosseal musculature (Haines 1942).

As a marsupial, *Thylacinus* is the only extant taxon of the series that has a large fibular head that articulates with the femur via a cartilaginous disc (Haines 1942; Barnett and Napier 1953*a*, *b*). Barnett and Napier (1953*b*) did not find significant differences between the form and the mobility of the fibula in ecologically distinct marsupial species like the yapok (*Chironectes minimus*), the koala (*Phascolarctos cinereus*), and *Thylacinus cynocephalus*, although distinctive adaptations were observed in Macropodinae, Peramelidae, and other taxa such as the kultarr (*Antechinomys laniger*), the tree kangaroo (*Dendrolagus ursinus*), the murine opossum (*Marmosa murina*), and the marsupial mole (*Notoryctes typhlops*). It appears that the tibio-femoro-fibular relationship found in the majority of marsupials probably approximates the ancestral pattern. Although the fibular head is not preserved in *Mayulestes*, the lateral protrusion of the femoral condyle suggests a femoro-fibular contact, unlike the fibular head and lateral femoral condyle of *Prothylacinus*, which would therefore illustrate a derived condition. In *Thylacinus*, the morphology of the tibia and fibula, despite the historical constraints, exhibits a general trend towards cursoriality with a distally sigmoid tibia, its lateral convexity reducing the interosseous space. However, the tibia and fibula are not as closely appressed as in cursorial placental taxa, and they probably did not act as a single unit.

In eutherians the distal articulation between the tibia and fibula forms a deep socket for the astragalus, and movements between the two bones of the crus become minimal. Nevertheless, Barnett and Napier (1953*a*) reported that felids and ursids have a mobile fibula compared to that of canids. The mobile phase occurs in bears when the foot is dorsiflexed from the neutral position, whereas in felids fibular rotation is limited to the plantar-flexion phase. This difference is due to the difference in the position of greatest stability in plantigrade versus digitigrade animals. Such mobility would be an adaptation to move on uneven, rocky or partly arboreal substrates. On the tibia of *Prothylacinus*, the anteroposterior extension of the distal fibular facet indicates the preservation of a mobile articulation between the tibia and fibula, permitting anteroposterior gliding movements, as shown in another Santacrucian borhyaenoid, *Sipalocyon gracilis* (Szalay 1994, p. 207).

Tarsal joints (Text-fig. 9). This part of the study will not detail the astragalus and calcaneum of the seven extant taxa examined, as it does not contribute to the understanding of the functional adaptations of borhyaenoids. The shape of the astragalus and calcaneum, more than any other part of the postcranial skeleton, is known to reflect phylogenetic affinity rather than function (Szalay 1994). Even the marsupial model of the series, *Thylacinus* (Szalay 1994, fig. 7.39), provides no useful comparison since Australidelphia exhibit tarsal specializations very distinct from those of Borhyaenoidea. Therefore, the atragalus of *Prothylacinus* and calcaneum of *Borhyaena* are here compared to those of other known borhyaenoids, *Mayulestes* (Muizon 1998; Argot 2002), *Pharsophorus* (pers. obs.), and *Sipalocyon* (Szalay 1994).

According to Szalay (1994, pp. 207–208), the posterior extension of the lateral astragalotibial facet observed in *Sipalocyon* may be related to peak loading during the dorsiflexed and abducted position of the foot in borhyaenoids, and may represent a primitive climbing adaptation in ameridelphian metatherians, still preserved in small borhyaenoids. It may also be preserved in large borhyaenoids like *Prothylacinus* where its presence is consistent with climbing capabilities.

The distal astragalar tuber of *Sipalocyon* indicates that astragalonavicular contact was most extensive during dorsiflexion of the distal part of the foot and distal tarsals (Szalay 1994, p. 209). There is no distal astragalar tuber in *Prothylacinus*, unlike *Sipalocyon*, while *Pharsophorus* is intermediate. The absence of this tuber in *Prothylacinus*, as well as the oblique upper margin of the astragalar head (seen in anterior view), suggest a greater mobility of its transverse tarsal joint. On the cuboid, above the peroneal groove, a prominent posterior tuberosity reflects the strength of the calcaneocuboid ligament stabilizing the mid-tarsal joint, and therefore the need to resist loads due to slight rotations of the distal part of the foot. This tuberosity also suggests frequent contacts with the ground, which is consistent with a semiplantigrade posture.

In *Prothylacinus* the anteroposterior axis of the distal malleolus is perpendicular to the transverse axis of the distal epiphysis, whereas in *Mayulestes*, both axes are oriented at an angle of 135 degrees. This morphology suggests that plantarflexion was associated with a slight inversion of the foot in the Paleocene borhyaenoid (Muizon 1998, p. 119), unlike *Prothylacinus*. Therefore, although the pes of *Prothylacinus* was probably able to accommodate differently orientated substrates because of transverse tarsal mobility, it appears to have been less specialized than that of *Mayulestes*.

The dorsal orientation of the calcaneoastragalar facet of *Borhyaena* precludes it from inverting the foot. This is in contrast to *Mayulestes* where this facet is oriented medially, a morphology that indicates a plantar sole facing medially in a neutral stance, improving the contact with curved supports. Unfortunately, the calcaneum of *Prothylacinus* is
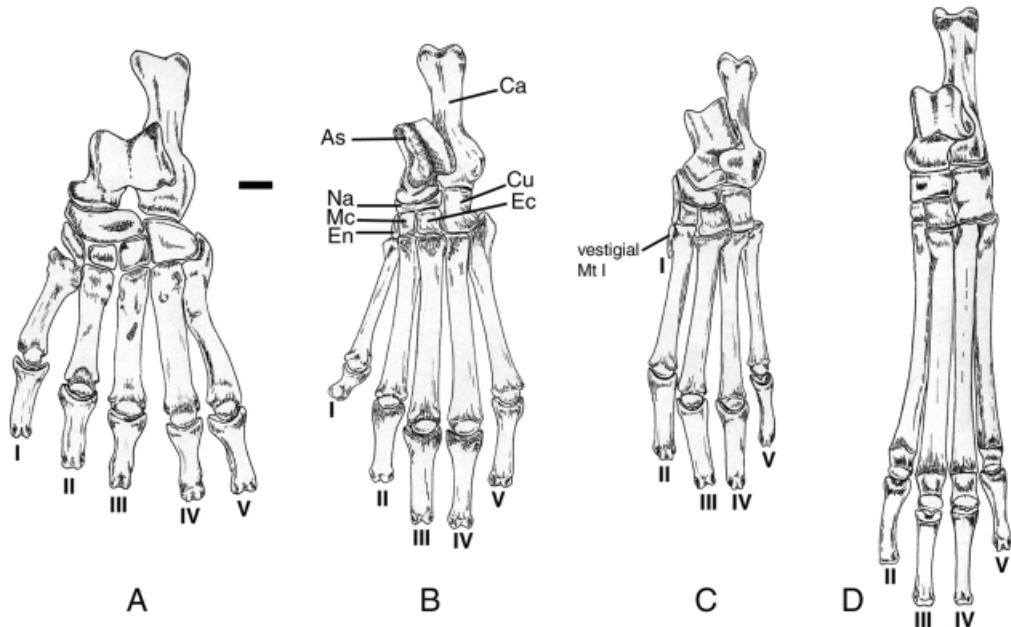
TEXT-FIG. 20. General morphology of the left pes in dorsal view. A, *Ursus malayanus* MNHN 1913–505. B, *Gulo gulo* MNHN 1935–3. C, *Neofelis nebulosa* MNHN 1961–101. D, *Canis lupus* MNHN 1946–1. Compare the development of the hallux and the width of the pes in the various taxa. Abbreviations: As, astragalus; Ca, calcaneum; Cu, cuboid; Ec, ectocuneiform; En, entocuneiform; Mc, mesocuneiform; Na, navicular. Scale bar represents 10 mm.

unknown. The orientation of the astragalar facets of the calcaneum of *Borhyaena* certainly facilitated parasagittal movements between the two proximal tarsal bones. Their orientation is consistent with that of the facets observed on the astragalus of *Pharsophorus*.

In *Borhyaena*, the absence of the peroneal process indicates a reduced mechanical advantage (and probably a reduced development) of the Mm. peronei. The peroneal process is absent in cursorial extant taxa, but it protrudes laterally in the arboscansorial forms, increasing the mechanical advantage of the peroneus longus. However, the presence of this process is also related to historical constraints as it is prominent in all Palaeocene metatherians (Szalay 1994), including *Mayulestes*. In contrast to living arboreal marsupials, the fibular head of *Prothylacinus* is not extended anteroposteriorly. This condition is consistent with the small groove observed on the cuboid for the passage of the tendon of the peroneus longus and with the vestigial Mt I, all features suggesting a reduced peroneus longus.

Form and function of the pes (Text-fig. 20). In highly arboreal and plantigrade forms like *Arctictis* or *Ursus* (Text-fig. 20A), the metatarsals are robust and widely spaced, and the fourth metatarsal is the longest. Mt V is as long and robust as Mt III and exhibits a well-developed lateral process for the insertion of M. peroneus brevis, an adductor of the pes. The calcaneal facet of the cuboid is more helical than that of other taxa, promoting rotation in the calcaneocuboid joint. Mt I is as robust as the other metatarsals but it is not opposable. In the other taxa, the metatarsals are relatively longer, more slender, and less widely spaced, especially in the two cursors. In *Canis* and *Neofelis* (Text-fig. 20C–D) the vestigial Mt I articulates with an elongated entocuneiform, while *Hyaena* and *Thylacinus* have no hallux. *Gulo* is characterized by relatively long metatarsals and a well-developed hallux (Text-fig. 20B). As noted above, the enlargement of the robust, widely spaced metapodials, is related to walking on soft snow, which necessitates large paws for creating a large surface area to travel easily (Van Valkenburgh 1985). Because the feet are large, they spread the load of the body, increasing the advantage to the predator by contrast to ungulates with long, thin legs (MacDonald 1984).

The metapodials represent approximately 10 per cent of their respective limb length in the arboreal-plantigrade taxa, against 17 per cent in cursorial-digitigrade taxa, and *Prothylacinus* clearly falls in the first category (Table 4). In the digitigrade but arboscansorial *Neofelis* the third metacarpal and metatarsal are 13–14 per cent of their respective limb length. *Thylacinus* lacks the lengthening of the metapodials found in placental cursors. As in *Neofelis*, Mt III

represents 14 per cent of the hind limb length, and 33 per cent of the femoral length. Keast (1982, table 1) noted that the ratio of Mt IV to the total hindlimb length is similar and relatively low in *Thylacinus* and the smaller dasyurids, *Antechinus* and *Dasyurus* (13·7–15·7 per cent), whereas it is higher in the placentals examined (17·3–18·8 per cent). The relative length of the metapodials may therefore be partly phylogenetically constrained. The Mt I of *Prothylacinus*, also vestigial, is relatively long and was therefore capable of supporting a well-developed plantar pad which would have allowed the pes to conform to curved arboreal surfaces even if not able to grasp branches.

PROPORTIONS OF THE LIMBS AND RESTORATIONS

A few indices that quantify the proportions of the limbs of fossils are listed in Table 4. The brachial index divides the models into two groups according to their primary locomotor category: arboscansorial or terrestrial. The significance of this index was described by Iwaniuk *et al*. (1999) for extant North American carnivorans, but these authors tested this index against a group that contains only moderately arboreal species. In the present study the four arboscansorial models, including the digitigrade *Neofelis*, have low brachial indices, between 0·79 and 0·85. Shorter forearms probably increase stability by enabling the animal to maintain its centre of gravity closer to the support (Taylor 1970). In contrast, the terrestrial taxa have a brachial index equal or higher than 1·00, indicating longer distal segments related to cursorial locomotion. With an index of 0·84, *Prothylacinus* clearly falls within the arboscansorial group.

The indices for the hindlimb are less easy to interpret. The crural index is particularly low in *Ursus malayanus* which has a very short tibia, a feature noted in bears by Davis (1964). Davis concluded that the short distal segments of *Ursus sp*. would result in relatively powerful but slow movements in the distal parts of the limb, precluding them from fast pursuit-related predation. In *Prothylacinus*, the crural index is also low, but not as low as in *Ursus*. In *Arctictis* and *Hyaena*, the crural index is about 0·90, whereas it is equal or higher than 1·00 in *Canis*, *Gulo*, and *Thylacinus*. *Neofelis* falls between the two groups.

Davis (1964) found some morphological disharmonies in the postcranial skeleton of the giant panda and noted that 'the persistence of such disharmonies in a natural population is unusual but not unique, and might in fact be anticipated in highly specialized forms' (p. 123). Davis further noted that similar disharmonies are found in hyaenas which, like *Ailuropoda*, are specialized masticators that do not rely on speed or agility either to escape or to capture prey. The results found underline the brevity of the hindlimb of *Hyaena* (see also Spoor, 1985), although morphologically, the tibia and fibula are very similar to those of *Canis*.

The forelimb of the Hyaenidae is characterized by a short humerus, a long radius, and long metacarpals. This morphology, together with the long and powerful neck, underlines the fact that hyaenas are particularly well adapted to carry large, heavy prey. The aardwolf (*Proteles cristatus*), a more insectivorous form, also has a long neck and well-developed forelimbs, but the hindlimbs are longer than in the spotted and striped hyaenas (*Crocruta* and *Hyaena*), with proportions more similar to those of canids (Spoor 1985). Mustelids have a forelimb that becomes proportionately longer with increasing body mass (Heinrich and Biknevicius 1998). *Gulo gulo* has an intermembral index of 0·88, representing the largest intermembral index among four mustelid species, *Martes americana*, *M. pennanti*, *Eira barbara*, and *Gulo* itself. The smallest form, *Martes americana*, has the smallest intermembral index (0·767, Heinrich and Biknevicius 1998). The intermembral index is particularly large (> 1·00) in *Hyaena* and *Ursus*, marking their short hindlimb, whereas it is about 0·90 in *Arctictis*, *Canis*, and *Gulo*. *Prothylacinus* exhibits a low intermembral index (0·78), consistent with an arboreal mode of life. The similarity between the intermembral and tibio-radial indices of *Neofelis* and *Prothylacinus* is informative with respect to locomotor habits and relative agility. It is worth noting that the intermembral index of *Prothylacinus* is also quite similar to that found in living carnivorous marsupials, the dasyuromorphs (*Thylacinus*, but also *Antechinus* and *Dasyurus*; Keast 1982).

The comparison between *Prothylacinus* and *Arctictis*, a skilful living arboreal plantigrade animal with prehensile hands, that moves relatively slowly, is particularly informative. The low intermembral index of *Prothylacinus* suggests a complex use of the limbs, with the relatively short forelimbs adapted to an arboreal mode of locomotion, and a relatively elongated hindlimb, used as an efficient propulsor, consistent with active predatory habits. Spoor (1985) related the long femur and strong musculature of the thigh to an increased stability of the hindquarters in the Hyaenidae. This would appear necessary in an

animal carrying a heavy load in its mouth, and was perhaps the strategy followed by *Prothylacinus* given its carnivorous habits and powerful neck musculature.

The length of Mc III and Mt III in *Prothylacinus*, relative to the length of the corresponding limbs, clearly falls within the arboreal-plantigrade category. Despite the relatively long femur and vestigial hallux that suggest a trend towards incipient cursorial habits, Mt III is relatively short. In *Prothylacinus* the McIII/MtIII and MtIII/F ratios are quite similar to those of *Arctictis* and *Ursus*, suggesting exploitation of an arboreal environment. The MtIII/F ratio must be considered with caution, as this ratio alone cannot provide precise information on maximal running speed, nor determine whether an extinct carnivore was capable of fast pursuit (Garland and Janis 1993). However, this ratio may shed light on general changes in locomotor abilities within lineages. In the present study, this ratio clearly divides the arboreal-plantigrade forms from the digitigrade-cursorial ones (with exception of the special case of *Gulo*). The ratio in *Prothylacinus*, therefore, leaves little doubt with respect to the habitual postures of the foot, especially when combined with the detailed morphological study of the tarsals and metatarsals. The proximal phalanges represent 51 per cent of metacarpal length in *Prothylacinus*, a relatively low value compared to 65–66 per cent in *Arctictis* and *Neofelis*, and 100 per cent in arboreal didelphids (Argot 2001). However, allometry may play a part: Van Valkenburgh (1987, fig. 1) compared the manus of a striped hyaena (*Hyaena hyaena*) and of a kinkajou (*Potos flavus*) drawn to the same overall length. The difference in proportions appears to be exaggerated because phalanx length scales with negative allometry against metacarpal length. Based on a regression line using the measurements of 61 species of Recent mammals (among them 53 carnivorans), Van Valkenburgh predicted that an arboreal animal the size of a hyaena would have metacarpals about twice the length of its phalanges, a prediction that fits perfectly in the case of *Prothylacinus*. In the case of *Borhyaena* the value of 38 per cent is consistent with a digitigrade posture.

The life and skeletal restorations of both taxa (Text-figs 21–22) call for comments. Because the scapulae, radii and ulnae of *Borhyaena* (PU 015701) and *Prothylacinus* (PU 015700) are of the same length, I hypothesized that the humeri also had an equivalent length (in the absence of any reliable estimation) although the morphological study and the brachial index suggest that *Prothylacinus* was more arboreal than *Borhyaena*. These restorations shed light on the fact that *Prothylacinus* was certainly semiplantigrade, whereas *Borhyaena* was digitigrade with longer metacarpals and shorter phalanges. The pollex is unknown in both taxa. Its reduction in *Borhyaena* is assumed on the basis of its inferred digitigrade posture and the brevity of digit V. The restored morphology of the pollex of *Prothylacinus* is based on the preserved pollex of other borhyaenoids: the Santacrucian *Cladosictis patagonica* and *Sipalocyon gracilis* (Argot in press), and the Laventan *Lycopsis longirostris* (pers. obs.). The shoulder height of *Borhyaena*, estimated to be approximately 50 cm in a neutral stance, was certainly slightly greater than that of *Prothylacinus*, given its digitigrade posture. The restoration of the hindlimb of *Borhyaena* is tentative, since the only well-preserved bone is the left femur, and that is significantly shorter than in *Prothylacinus*.

This short femur provides for three possibilities regarding the restoration of the hindlimb. The first was suggested by Sinclair (1906) who considered that the hip and shoulder of *Borhyaena* were of equal height and that the animal was semiplantigrade. The tibia and fibula, therefore, were necessarily elongated relative to those of *Prothylacinus*, also regarded as semiplantigrade but with a longer femur. However, based on the living models an elongated crus is not compatible with a semiplantigrade posture, but is usually related to a curso-saltatorial mode of life, and to elongated metapodials.

The second possibility is that *Borhyaena* was actually semiplantigrade, but with a crural index similar to that of *Prothylacinus*, so that the back sloped downward from the shoulders, an alternative rejected by Sinclair. Considering that *Borhyaena* had a semi-digitigrade or fully digitigrade forelimb, adapted to an incipiently cursorial mode of locomotion, it does not seem possible that it also had a short, semiplantigrade hindlimb coupled with a low hip joint relative to the height of the shoulder.

The last alternative is shown in the present restoration. It gives *Borhyaena* a digitigrade hindlimb, with relatively elongated metatarsals, and a slightly higher crural index than that of *Prothylacinus*, to account for a reduced slope of the back. Based on the Mt III/F ratio calculated for the living models and *Prothylacinus*, this ratio was estimated at approximately 0·35 for *Borhyaena*, with the length of Mt III at approximately 60–70 mm. This estimated length gives a value *c*. 0·65 for Mc IV/Mt III. This is close to

TEXT-FIG. 21. Skeletal and life restorations of *Prothylacinus patagonicus*; *c.* ×0·13. The darkened parts represent the preserved postcranial elements used in the present study.
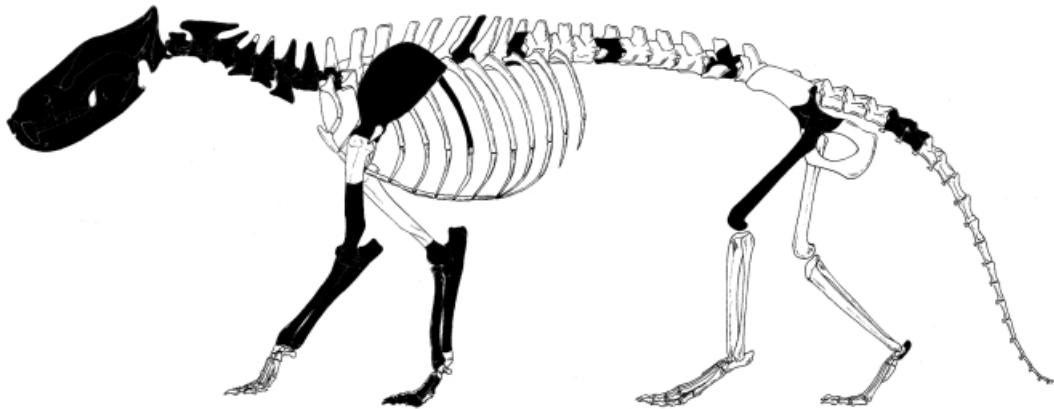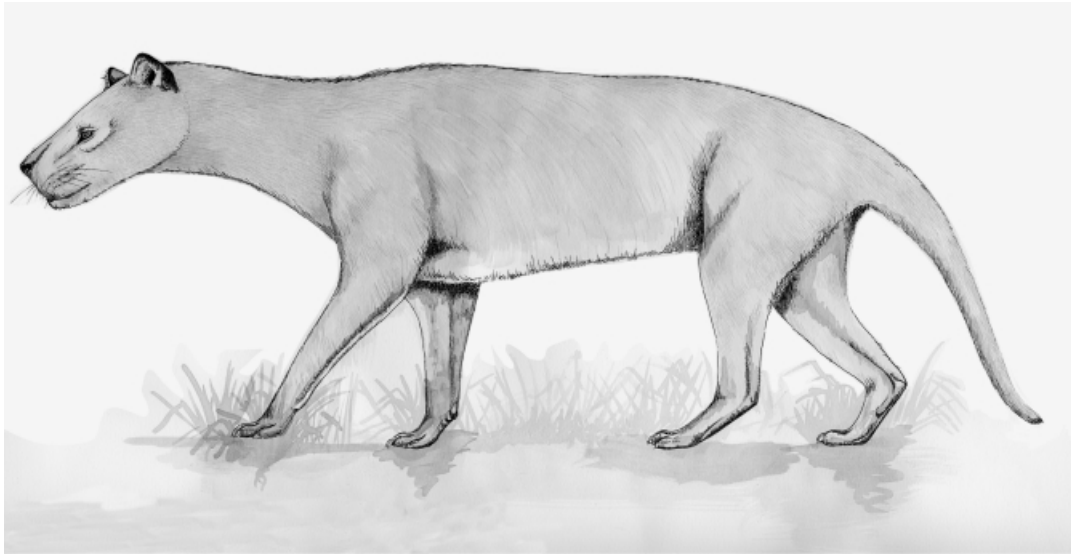
TEXT-FIG. 22. Skeletal and life restorations of *Borhyaena tuberata*; *c*. ×0·13. The darkened parts represent the preserved postcranial elements used in the present study.

that of *Thylacinus*, and supports the conclusions based on the rest of the skeleton. However, this hypothesis obviously requires more complete postcranial remains for confirmation. The length of the thoracolumbar region was estimated from existing vertebrae. It is largely hypothetical for *Borhyaena*, since only two vertebra are known for PU 015701. Sinclair's restoration (1906, pl. 61, fig. 3, based on a thylacinid model) makes the thoracolumbar length longer than represented here. The length of the tail is also largely hypothetical. Its external aspect, more flexible than in *Prothylacinus*, is related to the morphology of the anterior caudals.

The last point concerns the relative length of the limbs. Sinclair (1906) considered borhyaenoids to be short-legged, based on the relative length of the femur compared to the skull. However, one of the main characteristics of borhyaenoids seems to be skull elongation (see below). Therefore, the relative length of the limbs cannot be reliably evaluated using the skull as a point of reference, while the axial skeleton, especially in *Borhyaena*, is too poorly known to provide an alternative. Seven thoracolumbar vertebrae are

known for *Prothylacinus*, and the restoration does not emphasize the shortness of the limbs. Its reconstructed shoulder height (45–50 cm) is quite similar to that of *Gulo* (Table 2). Savage (1977) estimated that the forelimbs of *Prothylacinus* measured approximately 50 per cent of the total presacral length, and the hindlimb 64 per cent. This is similar to *Gulo* (respectively 55 and 64 per cent), but does not take into account the relative development of the neck in the fossil form.

ESTIMATED WEIGHT

The weight of *Borhyaena tuberata* (PU 015701) and *Prothylacinus patagonicus* (PU 015700) is estimated using regression equations based on the relationship between mass and femoral measurements. The equations used were established by Anyonge (1993), based on a sample of 28 species of extant carnivores (14 felids, 7 canids, 4 ursids, and 3 hyaenids). Among the femoral measurements chosen by Anyonge, three are available for the fossils: the proximodistal length of the femur (F), the circumference of the femur at the midshaft (f), and the distal articular area, calculated as the sum of the areas (length × width) of the two femoral condyles (DAA). The equations obtained by Anyonge (1993) for the regressions performed on the total sample are:

1. Log Body Weight = $2.92 \times$ Log (F) $- 5.27$; r (the correlation coefficient) is 0.95, and PE (the percentage prediction error, an indicator of the percentage difference between the actual weight and that predicted by the regression) is 25 per cent.

2. Log Body Weight = $2.88 \times$ Log (f) $- 3.40$; r is 0.98, and PE is 22 per cent.

3. Log Body Weight = $1.31 \times$ Log (DAA) $- 2.12$; r is 0.99, and PE is 22 per cent.

Based on these equations, the mean estimated weights obtained were: 23 kg for *Borhyaena* (19–29 kg according to the equation used), and 33 kg for *Prothylacinus* (27–37 kg) (Table 5). The equations tested against the extant taxa used in this study give coherent results for almost all the species, the variation in the results obtained with the three different equations falling in the range of 3–7 kg. The only exception is *Ursus malayanus* in which the equation using femoral circumference gives a result that is very different from the others. However, according to Anyonge (1993), femoral circumference is the best predictor of weight for Ursidae. This study clearly shows that *Prothylacinus* was heavier than *Borhyaena*, in spite of its more arboreal habits. The weight of *Prothylacinus* is not incompatible with this lifestyle. The highest value recorded for *Gulo* is 32 kg, whereas the lowest value recorded for *Ursus malayanus* is 27 kg (Nowak and Paradiso 1983). In *Prothylacinus*, this weight is partly related to the increased muscle masses in the distal part of the limbs as in living arboreal species. In contrast, the limbs of *Borhyaena* were lighter, with the muscle masses located more proximally. The estimated weight of *Borhyaena* corresponds to that of a small hyaena or wolf, or to that of a large thylacine.

The very massive skull of *Borhyaena*, with large zygomatic arches, reflects powerful jaw muscles. This parallels the large zygomatic arches of hyaenas, and the proportions of the skull in *Borhyaena* PU 15701 fall close to that of the sample of striped hyaenas recorded by Rieger (1979, fig. 2). The development of the borhyaenoid skull relative to the rest of the skeleton is particularly obvious when the weight of the animal is estimated from the greatest skull length (SKL, in millimeters). Van Valkenburgh (1985, 1987) used an equation derived from regressions of body weight against skull length for 70 species of extant fissiped carnivores: Log BW = $3.13 \times$ Log SKL + Log 0.003 (correlation coefficient r = 0.895). This equation, with a SKL of 230 mm for *Borhyaena* (PU 15701, Sinclair's measurement), and an estimate of 215 mm for the restored skull of *Prothylacinus* (PU 15700) gave 74 kg for *Borhyaena* and 60 kg for *Prothylacinus*. Van Valkenburgh (1987) also obtained aberrant weights for fossil carnivores like *Hoplophoneus* (Nimravidae) and *Hyaenodon* (Creodonta), which have relatively large skulls relative to their body size. She thus proposed that this type of estimate is not appropriate for archaic fossil predators with proportions that are very different from extant carnivorans.

CONCLUSIONS

The detailed study of the postcranial skeleton of *Borhyaena* and *Prothylacinus* has revealed adaptive features reflecting their ecology and lifestyle. The well-preserved cervical vertebrae of both taxa suggest a

TABLE 5. Estimated body weight of *Prothylacinus patagonicus* and *Borhyaena tuberata*. As a comparison, the weight of specimens of extant models used in this study is also estimated using the same method. These estimates are calculated for a single specimen in each case, and they may be compared with the weight range of each species given in Table 2, obtained from the literature. All the estimates of weight are given in kilograms.

Specimens	F (mm)	f (mm)	DAA (mm^2)	Estimation using equation 1	Estimation using equation 2	Estimation using equation 3	Mean weight (kg)
Prothylacinus patagonicus PU 015700	198	53	619·4	27·3	36·8	34·5	33
Borhyaena tuberata PU 015701	174·5	49	413·6	18·9	29·3	20·3	23
Arctictis binturong MNHN 1975–78	157	43	290·7	13·8	20·1	12·8	15·5
Gulo gulo MNHN 1935–3	151	39	346·1	12·4	15·2	16·1	14·5
Neofelis nebulosa MNHN 1961–101	163	41	322·0	15·5	17·6	14·6	16
Ursus malayanus MNHN 1913–505	245	68	898·5	50·8	75·4	56·1	60·7
Thylacinus cynocephalus MNHN 1891–61	173	39	291·9	18·4	15·2	12·9	15·5
Canis lupus MNHN 1984–08	210	50	545·3	32·4	31·1	29·2	31
Hyaena hyaena MNHN 1910–90	203	49	439·2	29·4	29·4	21·9	27

strong development of the neck musculature. The force exerted by the flexors of the neck, reflected in the development of the ventral processes on the cervical vertebrae, suggests predaceous habits for both taxa. The posterior extension of the neural process of the axis is consistent with a mode of killing using violent shaking of the head, as is usual among extant carnivores (Pellis and Officer 1987). The long cervical neural processes of the cervical vertebrae (well preserved only in *Borhyaena*) indicate well-developed neck extensors, related to the weight of the skull. The neck musculature has to resist a force equal to the weight of the head multiplied by the length of the neck (Slijper 1946). The large head and neck of *Borhyaena*, therefore, accounts for the enlargement of the cervical neural processes (and probably also those of the anterior thoracic vertebrae as suggested by T?7). As in living hyaenas, the size of the borhyaenoid skull and the long and powerful neck would enable the carnivorous marsupials to both lift and carry relatively large prey. This is consistent with the width of the zygomatic arches in *Borhyaena* (see Sinclair 1906, pls 40–42), which reflects the development of powerful jaw muscles.

In *Prothylacinus*, the position of the anticlinal vertebra (located in the posterior thoracic region) and the morphology of the lumbar transverse processes suggest a flexible axial skeleton. The anterior position of the anticlinal vertebra is a feature shared by all living active carnivoran predators (Hildebrand 1959; Taylor 1970; Gambaryan 1974; Savage 1977) that strongly flex and extend the spine when running. Therefore, the axial skeleton of *Prothylacinus* reflects a relatively active predatory mode. In *Borhyaena*, the few poorly preserved lumbars suggest that the anticlinal vertebra was located more posteriorly. The general morphology of the thoracolumbar region of *Prothylacinus* (position of the anticlinal vertebra, shape and orientation of lumbar neural and transverse processes) is consistent with enhanced flexibility of the lumbar spine compared to *Borhyaena*. A relatively reduced flexibility of the axial skeleton of the latter is not incompatible with terrestrial predatory habits as reflected in the skeleton of extant canids and hyaenids. The morphology of the few preserved caudal vertebrae suggests that *Borhyaena* had a tail lighter and more flexible at its base than that of *Prothylacinus*. Based on the length and robustness of the ninth

caudal, *Prothylacinus* probably had twenty to thirty caudal vertebrae, tapering gradually to the tip. Such a long, robust tail suggests that it was probably used as a balancing organ.

The forelimb is the best preserved part of the postcranial skeleton in both taxa. It is also the part of the postcranial skeleton that best reflects the substrate preference. Comparison of the scapula of both fossils clearly indicates the constraints exerted on the powerfully built scapula of *Prothylacinus* to resist tensile forces. The scapula is characterized by thick borders, a large, massive neck, and a relatively large infraspinous fossa. The development of the greater tubercle of the humerus reflects the role of the spinati muscles, as well as the constraints exerted at the shoulder joint. These are functionally more similar to those in a felid like *Neofelis* than to *Gulo*. By comparison, the scapula of *Borhyaena* is more lightly built. In both cases however, lack of ribs and thus of information on the shape of the thorax and the presence or absence of a clavicle makes it difficult to reconstruct detailed scapular movements.

The length and prominence of the deltopectoral crest of *Prothylacinus* reflects the development of the pectoralis group and the role played by the forelimb adductors. Among nonprimate quadrupedal mammals, between 55 and 65 per cent of body weight is supported by the forelimbs (Heinrich and Rose 1997). Therefore, the robustness of the borhyaenoid humerus, as reflected in *Prothylacinus*, but especially in the Colhuehuapian *Arctodictis sinclairi* (A. Forasiepi, pers. comm. 1999), could be related to the weight of the anterior part of the body. This suggests a different response to similar biological problems by comparison with living hyaenas, reflecting different historical constraints.

The distal extremity of the humerus demonstrates important differences between *Borhyaena* and *Prothylacinus*. It is markedly asymmetrical in *Prothylacinus*, with a lateral epicondylar crest that is well-expanded proximally, and a medial epicondyle that is more prominent. Moreover, the humerus of *Prothylacinus* has an entepicondylar foramen, which is absent in *Borhyaena*. The humeral trochlea is wider in *Prothylacinus*, less concave posteriorly, and less developed anteriorly. Compared with *Prothylacinus*, the distal part of the humerus of *Borhyaena* suggests a restriction of movements in the forearm to a more parasagittal plane.

The long bones of the forearm particularly reflect locomotor differences between the two borhyaenoids. The features characterizing *Prothylacinus* are similar to those observed in living arboreal didelphids. These include: the anterior orientation of the olecranon, the posterior convexity of the ulnar diaphysis, the long, deep fossae for the origin of flexor digitorum profundus and abductor pollicis longus, the postero-lateral extension of the radial diaphysis, and the robustness of the bicipital and supraglenoid tuberosities. These features especially reflect the role of powerful flexors. Moreover, the anterior convexity of the radial shaft, the orientation and relative enlargement of its head, and the enlargement of the proximal articular facet for the ulna, reflect an increased ability for pronation-supination, ensuring that the forefeet make adequate contact with the substrate. In contrast, in *Borhyaena* the robustness and orientation of the olecranon, the straight proximal part of the ulnar shaft, the reduction of the lateral and medial fossae on the ulna, and the reduced bicipital and supraglenoid tuberosities reflect the reduced role of the flexors, and the enlarged triceps acting from more extended positions of the arm. Moreover, the morphology of the radius, appressed against the ulna, straighter than in *Prothylacinus*, and with a relatively smaller head and a smaller ulnar articular facet, reflects a reduced capacity for pronation-supination.

In *Prothylacinus*, the proximal articulation of the wrist joint, and the morphology and length of the metacarpals and phalanges clearly indicate a palmigrade manus. This certainly suggests some grasping ability considering the potential development of the flexor digitorum profundus, abductor pollicis longus, and depth of the ungual phalanges. Unfortunately the pollex is unknown. In *Borhyaena*, the manus was semi- or fully digitigrade based on the scaphoradial articulation and the length of the metacarpals. The pollex is also unknown, but digit V was reduced compared to digits III and IV, a condition absent in living carnivores. The morphology of the ungual phalanges also suggests a more terrestrial locomotion. The ungual phalanges, the digitigrade manus, and the reduced mobility of the radius suggest less manipulation of prey by *Borhyaena*. In *Prothylacinus* therefore, the mobile forearm and longer cheiridia not only allowed increased grasping of supports but also probably meant increased skill in handling prey.

The forelimb of *Prothylacinus* as a whole reflects the role of flexors and adductors, and a potential for controlled climbing ability. All the morphological features support extensive arboreality, although this is unexpected considering the size of the animal. The morphology of the forelimb in *Borhyaena* is modified

for more cursorial habits, judging from an elbow joint that indicates more parasagittal excursions of the forearm and a more erect posture (elbow more extended, digitigrade manus). However, modern highly cursorial forms are characterized by the lengthening of the distal parts of the forelimb (ulna and radius), and of the metacarpals. This is not the case in *Borhyaena*, except at the level of the metapodials. Yet the morphology of the forelimb suggests a reduced development of the distal musculature, a common modification for more cursorial habits since it reduces the moment of inertia that must be overcome during each stride. Therefore, if *Borhyaena* cannot be compared with modern pursuit-predators, it can be considered as a terrestrial predator with some cursorial ability within the Borhyaenoidea, especially compared to *Prothylacinus*.

The hindlimb is well preserved in *Prothylacinus*, but only a femur and a calcaneum are preserved in *Borhyaena*. As the main propulsive thrust is provided by the hindlimbs in all quadrupedal mammals, especially with increased specialization towards running (Gambaryan 1974), hindlimbs are usually said to be less representative of the substrate used than forelimbs. However, they are more representative of some locomotor characteristics, especially fast versus slow and cautious movements, and the morphology of the different joints can help to determine the substrate used and the locomotion practiced.

The innominate of *Prothylacinus* is difficult to interpret, but the large gluteal fossa and the tall greater trochanter suggest relatively fast extension performed by glutei. The anteroventral deflection of the ilium suggests a well-developed erector spinae, consistent with a flexible lumbar spine. The acetabulum reflects a more mobile articulation in *Prothylacinus* than in *Borhyaena*, and this is compatible with more arboreal habits. However, the poorly prominent lesser trochanter indicates that ilio-psoas was primarily used for flexion rather than rotation, as in extant terrestrial models.

At the knee joint, the equal-sized femoral condyles in *Prothylacinus* indicate that parasagittal movements were performed. This feature is more marked in *Borhyaena*, where the medial condyle is slightly larger than the lateral one. This reorientation of the limb is consistent with active predatory habits, as sagittally oriented limbs engender minimal lateral displacements of the trunk, and thus minimal movement in the prey's line of vision (Jenkins and Camazine 1977). The fibula of *Prothylacinus* did not articulate with the femur (a derived feature among metatherians) and, therefore, the fibula was not involved in movements of the knee.

The cruroastragalar articulation of borhyaenoids is specialized, with the tibia characteristically restricting the joint medially as noted by Szalay (1994). This morphology is also known for most of the other marsupial groups of the Palaeocene of Itaboraí and later in South America. In borhyaenoids, this specialization suggests a powerful propulsive phase in relation to running capabilities, and this might be the result of selective forces toward active predatory habits.

The presence of a vestigial hallux on a plantigrade foot characterized by short metatarsals is a special feature of *Prothylacinus*. The plantigrade foot is certainly related to arboreality because it is found in arboreal models like ursids, whereas the vestigial hallux of more terrestrial models is usually considered to reflect a quite fast mode of running.

The conclusions reached here differ significantly from those of Sinclair (1906) who claimed that both taxa were terrestrial. However, Sinclair did not discuss the differences between the forelimb in the two taxa, although he did note that *Prothylacinus* was more active in attacking prey than *Borhyaena*. Muizon (1998) concluded that *Borhyaena* was 'at least partially, cursorial or semi-cursorial' (1998, pp. 125–126), whereas *Prothylacinus* 'has a forelimb compatible with agility and good capacity of grasping (possibly some climbing)' (Muizon 1998, p. 126), and a knee joint compatible with some running or/and bounding ability. Nevertheless, he was cautious about the arboreal capabilities of *Prothylacinus*, concluding that these two taxa 'were terrestrial (with perhaps some arboreality in *Prothylacinus*) capable of relatively efficient running (to a greater extent in *Borhyaena*) but probably for a short distance' (1998, p. 126). It is clear from the present study that *Prothylacinus* was well-adapted for climbing, and that it was a much more active predator than living bears. As underlined by Taylor (1989), the general structure of carnivores is the result of a compromise between the ability to catch prey, and the ability to kill it. Compared to living models, *Prothylacinus* exhibits a particularly original combination of features. In *Prothylacinus*, the forelimb is particularly well-adapted toward flexion, adduction, and pronation-supination, and the manipulative manus suggests a capacity for slow, deliberate movements in moving and searching for

prey. In contrast, the hindlimb indicates a potential for fast acceleration compatible with active predation. *Borhyaena* was certainly more dependent on its teeth to bite prey, its forelimbs performing less complex movements than those of *Prothylacinus*. *Borhyaena* is less difficult to interpret compared with living models, as it initiates a cursorial adaptive trend, but one obviously less specialized than *Canis* or *Thylacinus*.

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APPENDIX

Measurements of Prothylacinus patagonicus *and* Borhyaena tuberata.

The measurements of *Prothylacinus patagonicus* were taken on two different specimens, PU 015700 for the major part of long bones, MACN 708–720 for the measurements of the manus. The measurements of *Borhyaena tuberata* were taken on five specimens, all referred to the same species by Marshall (1978). The specimen PU 015701 exhibits the most complete and best preserved postcranium. e, estimated measurements; –, measurement not available. All measurements are in millimeters.

Measurements of the scapula	*Prothylacinus patagonicus* PU 015700	*Borhyaena tuberata* PU 015701
Total length, parallel to the spine	132·0*	137·8*
Maximum width, perpendicular to the spine	–	71·8
Maximum length of the supraspinous fossa, parallel to the spine	105·0	101·0
Maximum width of the infraspinous fossa, perpendicular to the spine	48·7	41·0
Anteroposterior width of the neck	31·5*	25·0*
Anteroposterior length of the glenoid cavity	33·7	31·2
Dorsoventral height of the glenoid cavity	22·6	22·8

* measurement from Sinclair (1906)

Measurements of the humerus	*Prothylacinus patagonicus* PU 015700	*Borhyaena tuberata* MACN 2074–2078
Humerus length	155·0	–
Anteroposterior length of the humeral head	28·7	–
Transverse width of the humeral head	29·3	–
Maximum anteroposterior length of the proximal extremity	42·2	–
Length of the deltopectoral crest	99·7	–
Deltopectoral crest length expressed as a percentage of the humerus length	64·3	–
Maximum transverse width of the distal extremity	53·5	43·5
Transverse width of the distal articular surface in distal view	23·8	28e
Anteroposterior depth of the trochlea in distal view	20·4	26e
Transverse width of the capitulum in anterior view	18·0	–
Proximodistal height of the capitulum in anterior view	15·2	–
Length of the lateral epicondylar ridge	62·5	54·9
Lateral epicondylar ridge expressed as a percentage of the humerus length	40·3	–
Distance between the medial lip of the trochlea and the apex of the medial epicondyle (T-E)	18e	11e
T-E expressed as a percentage of the distal extremity width	33·6	25·3
Mid-shaft anteroposterior diameter	22·4	–
Mid-shaft transverse diameter	17·7	–

Measurements of the ulna	*Prothylacinus patagonicus* *PU 015700 **MACN 706–720	*Borhyaena tuberata* PU 015701
Total length	165·0*–165·0**	165·0
Distance between the apex of the olecranon and the centre of rotation of the elbow joint (DO)	32·8*–29·3**	38·5
DO expressed as a percentage of the ulna length	19·8*–17·7**	23·3
Distance between the insertion of the Mm. biceps/ brachialis and the centre of rotation of the elbow joint (DFU)	18·4*–18·8**	18·2
DFU expressed as a percentage of the ulna length	11·2*–11·4**	11·0
Transverse width of the apex of the olecranon	14·2*	16·8
Anteroposterior depth of the apex of the olecranon	17·7*	24·8
Anteroposterior orientation of the olecranon process with respect to the ulnar shaft in lateral view	5°	20°
Transverse width of the proximal edge of the trochlear notch	20·3*–21·9**	16·8
Proximodistal length of the trochlear notch in medial view	22·7*–21·7**	25·1
Transverse width of the coronoid process	14·6*	13·9
Anteroposterior length of the coronoid process	16·8*	19·4
Anteroposterior depth of the ulnar diaphysis at the level of the coronoid process	30·9*	31·4
Transverse width of the diaphysis (mid-shaft diameter)	8·7*	10·5
Anteroposterior depth of the diaphysis (mid-shaft diameter)	17·5*	17·7

Measurements of the radius	*Prothylacinus patagonicus* PU 015700	*Borhyaena tuberata* PU 015701
Total length	130·0	126·5
Anteroposterior length of the head	15·2	11·6
Transverse width of the head	19·9	18·3
Distance between the apex and the centre of the bicipital tuberosity (DFR)	21·6	15·2
DFR expressed as a percentage of the radius length	16·6	12·0
Anteroposterior depth of the diaphysis at the level of the bicipital tuberosity	14·7	9·0
Angle between the transverse axes of the head and the distal epiphysis	55°	30°
Anteroposterior length of the distal extremity	14·3	15·9
Transverse width of the distal extremity	27·3	22·8

Measurements of the manus		*Prothylacinus patagonicus* MACN 706–720	*Borhyaena tuberata* PU 015701
Metacarpal length	Mc II	33·5	incomplete
	Mc III	35·0	incomplete
	Mc IV	–	42·6
	Mc V	26·8	24·5
Proximal phalanges length	1*	17·8	13·3
	2	18·0	15·1
	3	18·0	16·3
	4	–	15·4
Intermediate phalanges length	1	15·5	9·3
	2	15·9	10·8
	3	16·4	11·0
	4	15·1	–
Ungual phalanges length	1	20·9	16·6 (tip broken)
	2	21·2	17·5
	3	22·7	18·1
	4	20·2	14·5
Ungual phalanges dorsoventral depth	1	10·6	5·0
	2	11·0	5·0
	3	12·4	4·8
	4	11·6	4·8

* the numbers 1, 2 . . . for phalanges are arbitrary and do not refer to digit I, II . . . etc. However, the length of the ungual phalanx 1 obviously refers to the same phalanx as the dorsoventral depth of the ungual phalanx 1.

Measurements of the innominate	Prothylacinus patagonicus PU 015700	Borhyaena tuberata MACN 6203–6265
Total anteroposterior length	184e*	–
Length of the ilium, between the apex and the centre of the acetabulum	98·9	–
Iliac length expressed as a percentage of pelvic length	53·8	–
Dorsoventral breadth of iliac blade	40·7	–
Length of the origin of the rectus femoris	25·3	18e
Anteroposterior diameter of the acetabulum	26·8	24·5
Dorsoventral diameter of the acetabulum	25·8	24·0

* measurement from Sinclair (1906)

Measurements of the femur	Prothylacinus patagonicus PU 015700	Borhyaena tuberata PU 015701
Total length	198·0	174·5
Anteroposterior depth of the head in medial view	23·7	20·6
Proximodistal height of the head in medial view	21·7	18·6
Distance between the apex of the greater trochanter and the fovea capitis	40·6	36·8
Length from tip of the greater trochanter to distal end of the trochanteric fossa	35e	34e
Distance between the lesser trochanter and the fovea capitis	24e	22e
Mid-shaft anteroposterior diameter	16·9	15·3
Mid-shaft transverse diameter	16·7	15·7
Relative compression ratio of the femoral shaft (minimum diameter/maximum diameter $\times$ 100)	99	97·5
Width of the lateral condyle in posterior view	16·7	11·8
Height of the lateral condyle in posterior view	19·5	14·7
Width of the medial condyle in posterior view	15·3	15·2
Height of the medial condyle in posterior view	19·2	15·8
Width of the trochlea in anterior view	21·0	20e
Height of the trochlea in anterior view	23·0	21e
Width of the distal epiphysis in distal view	43·2	35·3
Height of the distal epiphysis in distal view	31·7	25·6

Measurements of the tibia	*Prothylacinus patagonicus* PU 015700	*Borhyaena tuberata* MACN 653–660
Total length	172·5	–
Maximum transverse width of the proximal epiphysis in proximal view	38·8	–
Maximum anteroposterior length of the proximal epiphysis in proximal view	34·7	–
Transverse width of the lateral condyle	15·6	–
Anteroposterior length of the lateral condyle	16·6	–
Transverse width of the medial condyle	14·3	–
Anteroposterior length of the medial condyle	18·6	–
Total extent of the insertion of the semitendinosus and gracilis	46·0	–
Distal extent of the semitendinosus insertion	92·5	–
Mid-shaft anteroposterior diameter	16·8	–
Mid-shaft transverse diameter	11·5	–
Total transverse width of the distal epiphysis	24·3	21·1
Total anteroposterior length of the distal epiphysis	18·7	23·7
Transverse width of the malleolus	12·2	10·6
Proximodistal length of the malleolus	9e	–

Measurements of the fibula	*Prothylacinus patagonicus* PU 015700
Total length	164·0
Anteroposterior depth of the head	19·8
Mid-shaft anteroposterior diameter	7·0
Mid-shaft transverse diameter	10·5
Transverse width of the distal epiphysis in distal view	17·5
Anteroposterior depth of the distal epiphysis in distal view	17·0

Measurements of the astragalus	*Prothylacinus patagonicus* PU 015700
Total length	26·0
Maximum transverse width	21·2
Astragalotibial lateral facet length	14e
Astragalotibial lateral facet width	8e
Astragalar head width (anterior view)	9·8
Astragalar head height (anterior view)	10·9

Measurements of the calcaneum	*Borhyaena tuberata* MACN 2074–2078
Total length (tuber calcanei incomplete)	40·0
Proximodistal length of the ectal facet	11·3
Transverse width of the ectal facet	13·6
Proximodistal length of the sustentacular facet	10·2
Transverse width of the sustentacular facet	6·0
Dorsoplantar length of calcaneocuboid facet	13·6
Transverse width of calcaneocuboid facet	16·5

Measurements of the metatarsals	*Prothylacinus patagonicus* PU 015700
Mt I length	24·1
Mt III length	37·1
Mt III proximal epiphysis depth	11·0
Mt III proximal epiphysis width	7·1
Mt III distal epiphysis depth	8·7
Mt III distal epiphysis width	11·1