



Theropods of the Judith River Formation of Dinosaur Provincial Park, Alberta, Canada. P.J. Currie (Drumheller, Alberta).

The dinosaur fauna of the Judith River Formation of Dinosaur Provincial Park and vicinity is the richest known in terms of numbers of specimens (Beland and Russell 1978), quality of the specimens collected, and overall diversity. Thirty-five species of dinosaurs are currently recognized from this area (Currie 1986, 1987b), of which almost a third are theropods. In spite of the large number of articulated skeletons recovered from the park however, reasonably complete skeletons are only known for Gorgosaurus libratus and Daspletosaurus torosus (Russell, 1970). The remaining theropods are known from isolated bones and teeth, and partial skeletons (Currie 1987a; Currie and Russell, in preparation). In most cases, isolated bones and teeth can be associated with each other by comparison with articulated specimens of closely related genera from Mongolia. However, this is not true for four species (Caenagnathus collinsi, C. sternbergi, Chirostenotes pergracilis, Elmisaurus sp.) and the discovery of more complete material will almost certainly lead to one or two synonymies.

The frontal is one of the more useful isolated bones of theropods as there is only a single pair in any individual, they tend to be found relatively frequently and they are diagnostic at the species level. In fact, frontals are so diagnostic that they give some indication of the inter-relationships of the Theropoda.

Fourteen species of theropods are currently recognized in Dinosaur Provincial Park (Table 1), whereas only eight different types of frontals have been identified (Fig. 1). The frontals of Ornithomimus edmontonicus, caenagnathids and elmisaurids still have not been found in this region.

Troodon (Currie 1985, 1987a) has an elongate, triangular frontal with a long orbital rim (Figs. 1a, 2). A prefrontal has not been identified with certainty in troodontids, although a small, slender bone along the orbital rim

of the frontal may be that bone (Currie, 1985). The lacrimal suture encroaches onto the dorsal surface of the frontal, and ends caudally in a wall of bone. The dorsal surface of the frontal is concave in cross-section in the interorbital region, raised on both the midline and the orbital rim. A well defined ridge running from the medial edge of the frontoparietal suture to the deep, pit-like suture for the postorbital marks the anterior boundary of the supratemporal fenestra. As in ornithomimids, NMC 12355 and dromaeosaurids, the frontal provides very little area of bone for muscle attachment within the supratemporal fenestra.

Ornithomimid frontals are very rare. Cranial bones in these animals are much lighter than those of other theropods both in terms of relative thickness, and the density of the spongy bone layer. Consequently, they may have been preserved less frequently because of their fragility. As in troodontids, the frontal of Dromiceiomimus is long and triangular (Fig. 1b). There is a distinct but shallow sutural surface for the prefrontal rostrorodorsally. The lacrimal contact is unusual in that it is a long tapering suture on the rostralateral surface of the frontal. Unlike most other theropods, there is a simple process of the nasal overlapping the frontal. The dorsal surface of the frontal is almost flat in the interorbital region, but caudally curves posteroventrally in an almost bulbous fashion to meet the parietal. The anterior margin of the supratemporal fenestra is not marked by a well-defined rim.

The frontals of Struthiomimus altus (AMNH 5355) and Ornithomimus edmontonicus (ROM 851, Horseshoe Canyon Formation) are essentially identical to that of Dromiceiomimus samueli.

Sues (1978) briefly described an indeterminate frontal in the collections of the National Museum of Canada (NMC 12355, Fig. 1C) and referred it to the Theropoda. However, comparison with Mongolian specimens suggests that it may represent Erlicosaur (Currie, in preparation), a genus that is currently regarded as a Late Cretaceous prosauropod (Paul 1984). The frontal suture of an isolated caenagnathid parietal (TMP 81.19.252, Currie, in preparation) shows that NMC 12355 is not a caenagnathid, but it still may turn out to be an elmsaurid or other theropod. This frontal is an elongate triangle, like those of troodontids and ornithomimids. A shallow, rostrorodorsal sutural surface suggests that the prefrontal was present and in the same position as in ornithomimids. The caudolateral margin of the ventral suture of the lacrimal is a transverse wall of bone similar to that of Troodon. A longitudinal trough runs along the dorsal surface of the frontal between the midline and the orbital rim. A poorly defined ridge marks the rostral boundary of the supratemporal fenestra.

Dromaeosaurid frontals (Figs. 1d, 1e, 3) are readily distinguished from those of other theropods. They are relatively shorter and broader than troodontid and ornithomimid frontals. In ventral view, the orbital rim is split rostralaterally, and the lacrimal passes through this slot onto the dorsal surface of the bone. This is very different from the broad lacrimal suture on ventral surface of the frontals of Troodon and NMC 12355, but is comparable with this part of the frontolacrimal suture of tyrannosaurids. Rostrorodorsally, the dromaeosaurid frontal has a squamose sutural surface for the nasal and prefrontal bones. In dorsal view, the postorbital process of the frontal diverges strongly from the rest of the orbital rim. The postorbital suture extends onto the caudodorsal surface of the postorbital process, and is not well defined. The frontal is only shallowly dishd out in the interorbital region.

Saurornitholestes langstoni (Figs. 1d, 3) is the most common small theropod in the Judith River Formation of Dinosaur Provincial Park, judging from the number of frontals (Table 1) and teeth (Currie, Rigby and Sloan, in preparation) recovered. In contrast with Dromaeosaurus, the medial prong of the nasal does not extend as far caudally over the frontal as the more lateral prong. The slot that the lacrimal passes through the frontal to contact the prefrontal is relatively small (Fig. 1d). The frontal is somewhat bulbous caudally where it curves posteroventrally to meet the parietal. A faint, sigmoidally curved ridge runs rostrolaterally onto the front margin of the postorbital process, and marks the anterior limit of the supratemporal fenestra. Unlike Dromaeosaurus, the portion of the frontal within the supratemporal fenestra is posterodorsally concave, and even forms a deep pit in some specimens (TMP 86.77.57, Fig. 1d).

Dromaeosaurus is a more robust animal than Saurornitholestes langstoni, and is much rarer (Table 1). The lacrimal slot (Fig. 1e) is well developed. In both AMNH 5356 and NMC 12349, the orbital rim is squared off and rugose, suggesting the presence of an additional bone on the orbital rim, similar to that of Troodon. If this is the case, it may be a palpebral. An examination of Dromaeosaurus teeth from Dinosaur Provincial Park suggests that more than one species was present in Judithian times (Currie, Rigby and Sloan, in preparation). It may be significant then that NMC 12349 is more robust than AMNH 5356, and that the ridge marking the anterior limit of the supratemporal fenestra is more strongly curved. As in tyrannosaurids, the posterodorsal surfaces of the paired frontals separate on the midline for an anteromedial process of the fused parietals (Fig. 1e) in NMC 12349.

Tyrannosaurid frontals are very distinctive in their relationships with the bones they contact. Two or three prongs of the nasal overlap the rostral end of the frontal. The prefrontal is always present, although in some species it may be fused to either the nasal or lacrimal, and in others it is covered by the lacrimal. The prefrontal sits in a pit on the dorsolateral surface of the frontal. Primitively (Figs. 1f, g), the pit is overlapped posteriorly by the dorsal surface of the frontal, so that the caudal end of the prefrontal actually inserts into a socket in the frontal, and is completely surrounded by that bone. In more progressive forms (Molnar 1980; Bakker, Williams and Currie, in preparation), the socket is lost, and one suspects that this is the case in Daspletosaurus torosus (Fig. 1h). The orbital rim of the frontal is very short, and in some species is reduced to a slot passing between the lacrimal and postorbital (Fig. 1g). The frontal-postorbital suture is expanded in all tyrannosaurids (Figs. 1f, g, h). At the rostral end of the contact, the frontal develops a pronounced buttress with a posterolaterally oriented suture (Fig. 1f), behind which the frontal is broadly overlapped by the postorbital. The relationship between the frontal and postorbital changes both ontogenetically and in more progressive tyrannosaurids however, and the contact becomes more elongate rostrocaudally and more vertical. A rostradorsal process of the parietals separates the frontals posteriorly, and the sagittal crest extends onto the frontals. Tyrannosaurid frontals are essentially flat dorsally between the orbits. The temporal musculature extends far onto the dorsal surface of the frontal, its anterior boundary being a low sinuous ridge between the sagittal crest and the postorbital buttress.

At least three species of Tyrannosauridae seem to have lived in the area now known as Dinosaur Provincial Park. The first is a gracile tyrannosaurid (Fig. 1f) with a relatively long, narrow frontal. Isolated teeth identified as Aublysodon are the premaxillary teeth of a small tyrannosaurid. They are relatively common, and can be distinguished from the teeth of juvenile

specimens of large tyrannosaurids by their lack of serrations and more gracile appearance. Gracile, small maxillary and dentary teeth with serrations have also been identified as a small, Judithian tyrannosaurid. It would appear that a Lancian theropod described by Molnar (1978) is in fact a small tyrannosaurid, and that this animal is the same as the tooth genus Aublysodon (K. Carpenter and R.E. Molnar, personal communication, 1986). It seems possible then that TMP 80.16.485 (Fig. 1f) is Aublysodon or a closely related genus. It is conceivable that further preparation and study of the type specimen of Gorgosaurus sternbergi (AMNH 5664, Matthew and Brown 1923) will reveal that this is a valid species, and that this is the source of the aublysodont teeth.

Gorgosaurus libratus frontals are characterized by the presence of a prefrontal socket, the reduction of the orbital rim to a notch, and the retention of a relatively short (rostromedially), overlapping suture for the postorbital (Fig. 1g). Immature frontals of Gorgosaurus libratus can be distinguished from that of cf. Aublysodon by their relatively greater thickness and width for a given length. In Daspletosaurus torosus, the shape of the frontal has been changed by the enlargement of the lacrimal and postorbital, causing an increase in the posterior width of the frontal (Fig. 1h), and a lengthening of the postorbital suture.

Although frontals of caenagnathids are currently unknown from Dinosaur Provincial Park, one can predict that they will be bulbous and lightly built, like those of Oviraptor. The isolated parietal (TMP 81.19.252) shows that the frontals are separated from each other caudally by a rostral process of the fused parietals, and that the frontal broadly overlaps the parietal posterolaterally.

There is no cranial material known for elmisaurids from either Mongolia or Alberta. Currie and Russell (in preparation) have expressed an opinion that the elmisaurid Chiostenos is congeneric with Caenagnathus, and therefore that the taxon Elmisauridae is invalid. Unfortunately, there is no way of solving this dilemma until better specimens are recovered.

A lower jaw described by Gilmore (1924) was tentatively assigned to "Chiostenos". If Chiostenos and the toothless Caenagnathus are congeneric, then NMC 343 represents another theropod that can be characterized by long, slender jaws bearing teeth with extremely fine serrations. It is possible that this animal is the one that had the frontal that has been assigned to Erlicosaurus.

A minimum of twelve species of theropods have been recovered from the Judith River Formation of Dinosaur Provincial Park. This includes one troodontid, three ornithomimids, two dromaeosaurids, two caenagnathids, three tyrannosaurids and one indeterminate form (NMC 343). However, on the basis of available evidence, it seems more likely to me that there was in addition a second species of Dromaeosaurus and a fourth species of tyrannosaurid.

The number of frontals recovered can be used as a means of assessing the relative numbers of individuals living in the area during Judithian times, although preservational biases have to be accounted for. It has already been noted that ornithomimid frontals are under-represented because of their fragility, and the same would apply for caenagnathids. Nevertheless, when the information on the number of frontals (Table 1) is correlated with other data (numbers of articulated skeletons, numbers of identifiable teeth, numbers of identifiable claws, etc.), it appears that the most common theropods were Gorgosaurus libratus, Saurornitholestes langstoni and Troodon formosus.

Frontal morphology suggests that dromaeosaurids are more closely related to tyrannosaurids than to any other theropod family, and that troodontids and ornithomimids may be sister groups.

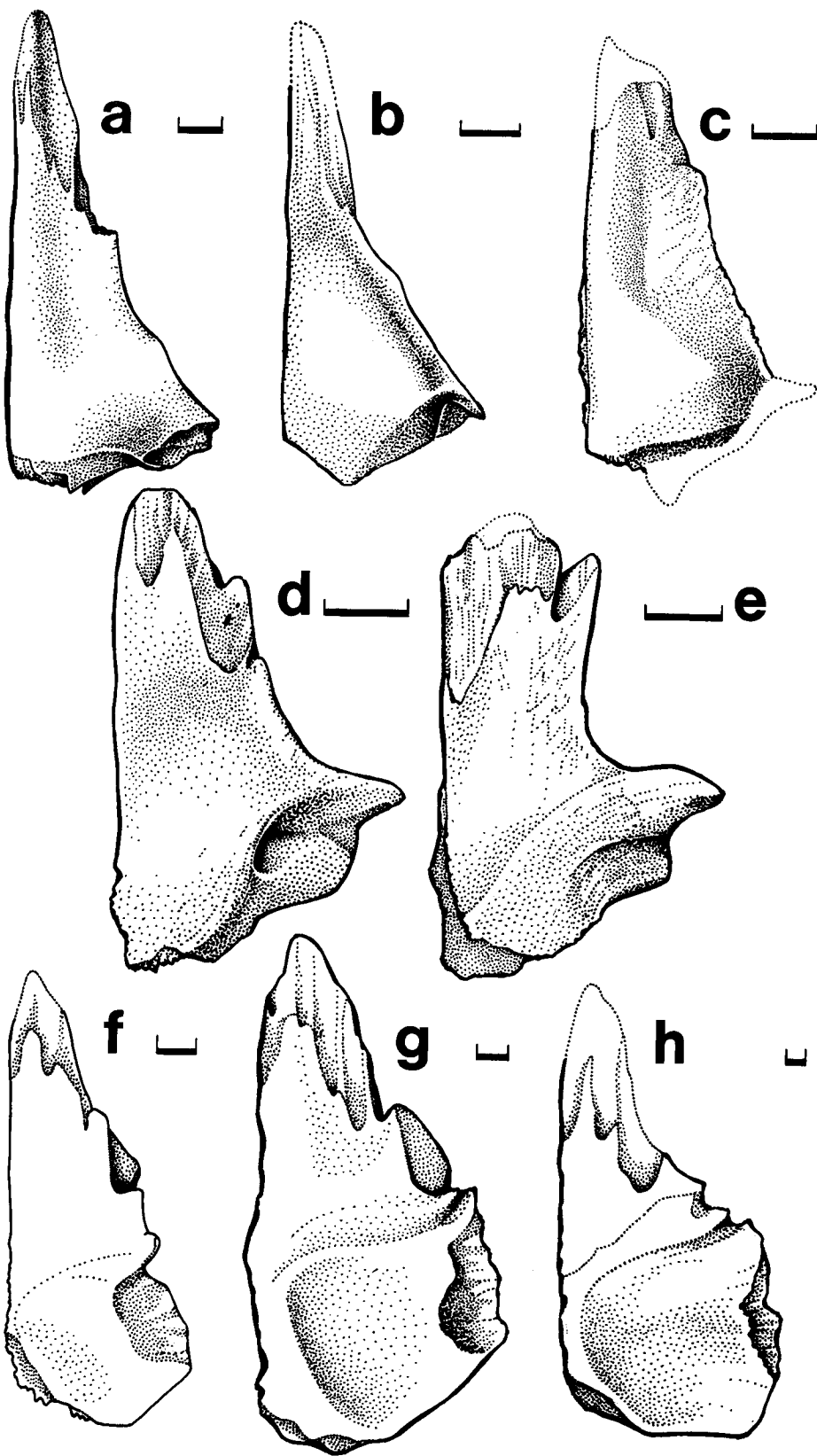


FIG. 1 Theropod frontals from Dinosaur Provincial Park. (a) Troodon formosus, TMP 86.49.10; (b) Dromiceiomimus samueli, TMP 85.56.62; (c) cf. Erlicosaurius sp., NMC 12355; (d) Saurornitholestes langstoni, TMP 86.77.57; (e) Dromaeosaurus albertensis, NMC 12349, AMNH 5356; (f) cf. Aublysodon sp., TMP 80.16.485; (g) cf. Gorgosaurus libratus, TMP 80.16.924; (h) Daspletosaurus torosus (after Russell, 1970).

(1) Caudal limit of dorsolateral exposure of the lacrimal; (2) caudal limit of orbital rim; (3) caudal limit of postorbital suture; (4) lacrimal slot; (5) postorbital buttress. Scale = 1cm.

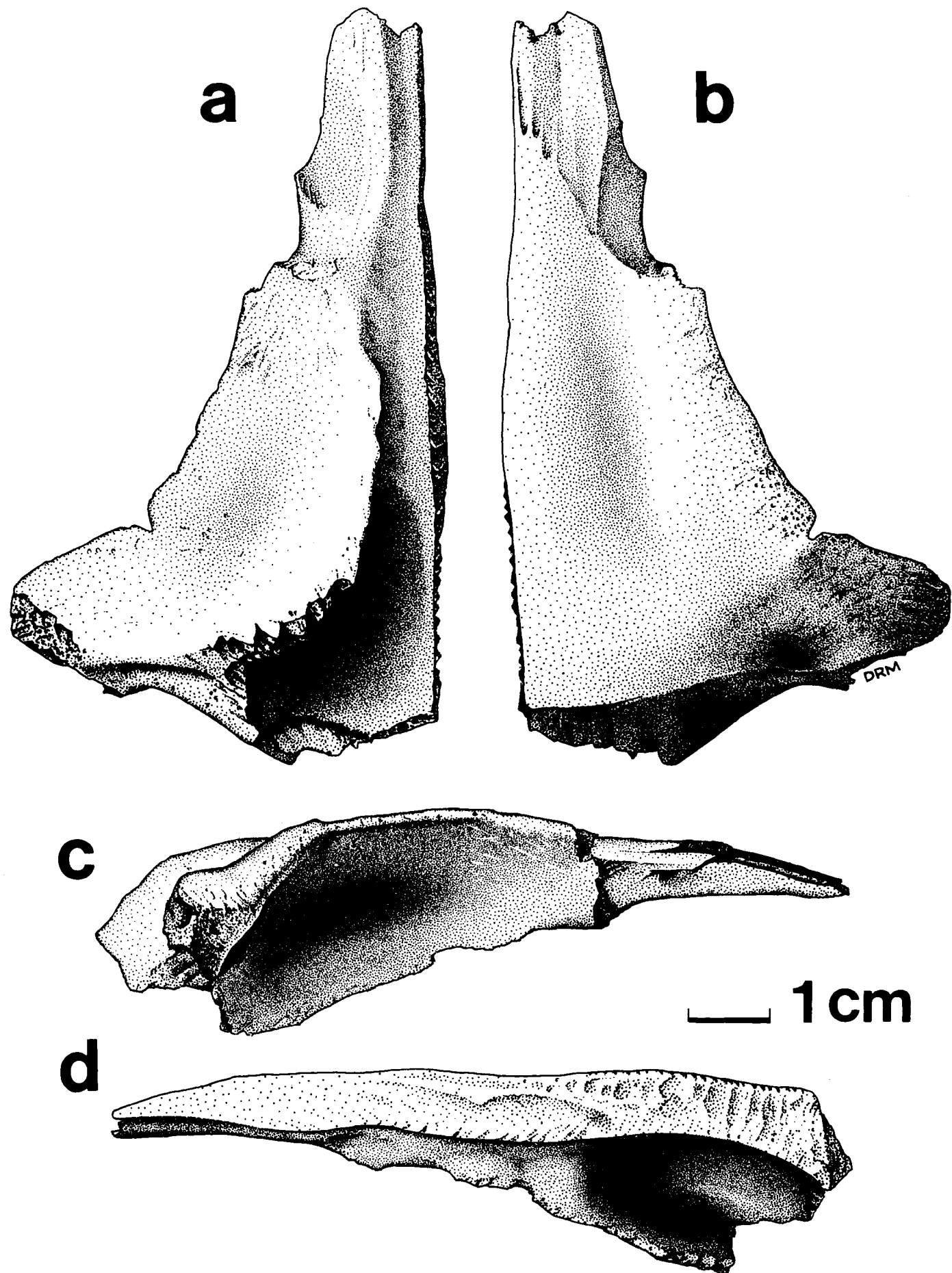


FIG. 2 *Troodon formosus* (TMP 86.49.10). Right frontal in (a) ventral, (b) dorsal, (c) lateral and (d) medial views. Scale = 1 cm.

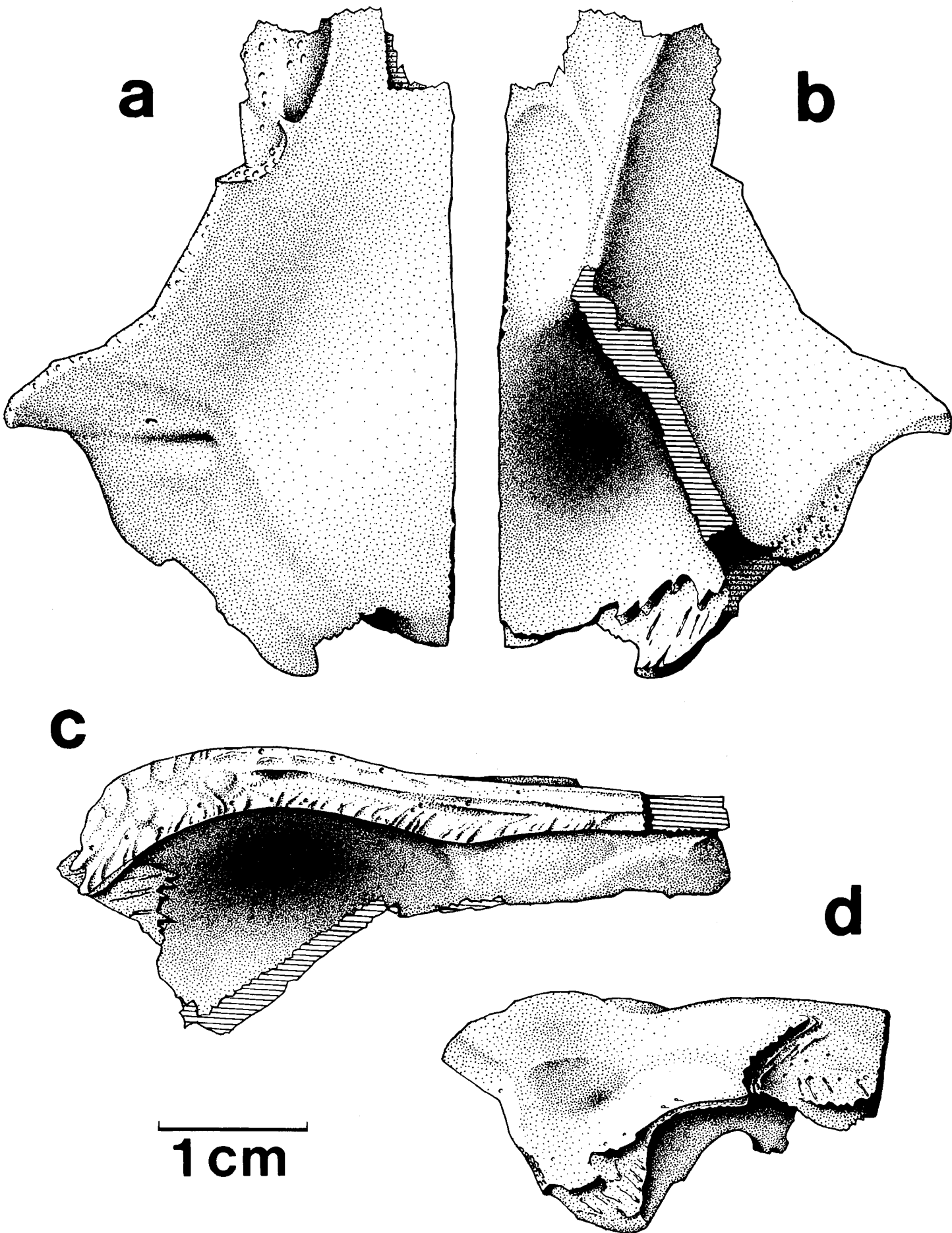


Fig. 3 *Saurornitholestes langstoni* (TMP 80.16.312). Left frontal in (a) dorsal, (b) ventral, (c) medial and (d) posterior views. Scale = 1cm.

Table 1. Theropod frontals from Dinosaur Provincial Park and vicinity. Listing includes skulls if the frontals are preserved. Abbreviations: AMNH, American Museum of Natural History; NMC, National Museum of Natural Sciences, National Museum of Canada; TMP, Tyrrell Museum of Palaeontology; UA, University of Alberta; USNM, U.S. National Museum of Natural Sciences.

Species	Specimen Numbers	Total #
<u>Troodon formosus</u>	AMNH 6174, NMC 12340, TMP 79.8.1, TMP 80.16.1478, TMP 82.16.124, TMP 82.19.23, TMP 86.36.4, TMP 86.49.10, UA 5282	9
<u>Dromiceiomimus samueli</u>	ROM 840, TMP 85.56.62	2
<u>Ornithomimus edmontonicus</u>	0	0
<u>Struthiomimus altus</u>	AMNH 5355	1
<u>Dromaeosaurus albertensis</u>	AMNH 5356, NMC 12349	2
<u>Saurornitholestes langstoni</u>	TMP 74.10.5, NMC 12343, NMC 12354, TMP 80.16.312, TMP 81.23.7, TMP 84.94.6 TMP 85.43.69, TMP 86.77.57, UA 5283	9
<u>Caenagnathus collinsi</u>	0	0
<u>C. sternbergi</u>	0	0
<u>Chirostenotes pergracilis</u>	0	0
<u>Elmisaurus sp.</u>	0	0
<u>"Chirostenotes"</u> (NMC 343)	0	0
cf. <u>Aublysodon</u>	TMP 80.16.485	
<u>Gorgosaurus libratus</u>	NMC 2120 (type), AMNH 5664, AMNH 5336, AMNH 5458, FMNH PR308, NMC 11841, cf TMP 67.14.3, cf. TMP 80.16.924, TMP 82.16.181, TMP 85.62.1, TMP 86.36.269, TMP 81.39.8, UA 10, USNM 12814	14
<u>Daspletosaurus torosus</u>	NMC 8506, NMC 11594	2

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