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OCCIPITAL CONDYLE IN THE CERATOPSIAN DINOSAUR *TRICERATOPS*, WITH COMMENTS ON BODY SIZE VARIATION

BY

JASON S. ANDERSON¹

Abstract — Study of a previously unidentified dinosaur basicranium shows that it belongs to *Triceratops* sp., probably *Triceratops horridus*. The occipital condyle can be used to predict body size and skull size in extant reptiles, as illustrated here by study of *Basiliscus vittatus* and *Alligator mississippiensis*. Occipital condyle size is now known for 35 *Triceratops* specimens, and these can also be used to predict body and skull size. Comparison based on the size of the occipital condyle shows that there is no significant increase in size of *Triceratops* with increasing latitude. Previously postulated allocations of *Triceratops* specimens to sex or species groupings involve no significant differences in size. Finally, variability of occipital condyle size in *Triceratops* is no greater than that observed in growth series of adults of other species.

INTRODUCTION

In the summer of 1938, E. C. Case led a University of Michigan expedition to Montana to collect a specimen of *Edmontosaurus* for exhibition. Case had learned of the *Edmontosaurus* from Major Will Harris of nearby Fort Peck. After a five-day journey they arrived at Fort Peck, set up camp at a government hotel with “decent rooms and good food,” and proceeded into the field (Case, 1938). *Triceratops* is common here, and before starting work Major Harris showed Case a *Triceratops* too weathered and brittle to be of use.

During the first day of excavation at the *Edmontosaurus* site parts of a different dinosaur were found. In Case’s words (Case, 1938):

Tuesday, 21 [June]. Out to Bear Creek to work on *Trachodon* [*Edmontosaurus*]. Uncovered left half of pelvis with bones going in, but not in excellent shape. Collected ribs of another specimen of *Triceratops* and a basicranium of ?

With study, the queried basicranium, now University of Michigan specimen UM 17062 described here, has proven to be of *Triceratops* too. Comparison with other specimens shows the new basicranium to represent a large individual. The occipital condyle is well preserved. Size of

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the occipital condyle is a useful measure of skull size in other reptiles (*Basiliscus*, *Alligator*), and size of the occipital condyle in *Triceratops* facilitates study of size in relation to latitude and study of size in other contexts.

INSTITUTIONAL ABBREVIATIONS

AMNH	— American Museum of Natural History, New York
BSP	— Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich
CM	— Carnegie Museum, Pittsburgh
FMNH	— Field Museum of Natural History, Chicago
LACM	— Los Angeles County Museum, Los Angeles
MPM	— Milwaukee Public Museum, Milwaukee
NMC	— Canadian Museum of Nature, Ottawa
RM	— Redpath Museum, McGill University, Montréal
SMM	— Science Museum of Minnesota, St. Paul
UCMP	— University of California Museum of Paleontology, Berkeley
UM	— University of Michigan Museum of Paleontology, Ann Arbor
UMMZ	— University of Michigan Museum of Zoology, Ann Arbor
USNM	— United States National Museum, Washington
YPM	— Yale Peabody Museum, New Haven

NEW BASICRANIUM (UM 17062)

UM 17062 is a basicranium, consisting of the occipital condyle, most of the basioccipital, portions of the exoccipital, and the basisphenoid (Fig. 1). All bones are fully coossified with no remnants of sutures. The specimen is slightly distorted obliquely. It was apparently buried upside-down, as there is a distinct area of different color surrounding the base of the specimen, with the highest degree of weathering on the ventral surface of the basioccipital-basisphenoid. The dorsal margins display relatively freshly fractured surfaces and there was evidently once more to the specimen than remains now.

Case described the discovery locality as being in the Upper Cretaceous "Lance" Formation, along Bear Creek, about 28-30 miles south and east of Fort Peck, Montana. The area described above falls within the Hell Creek Formation (Lance equivalent) near the boundary with the overlying Paleocene Fort Union Formation (Renfro and Feray, 1972). More precise stratigraphic information is unavailable, but inference can be made regarding the relative placement within the Hell Creek Formation by comparison with other *Triceratops*-bearing strata. The upper-most member of the Lance Formation of Niobrara County, Wyoming (Torrington member of Schlaikjer, 1935) was the interval in which J. B. Hatcher found the exquisite collection of *Triceratops* that he recovered for O. C. Marsh (Lull, 1933; Schlaikjer, 1935). According to Knowlton (1909), the fossiliferous part of Hatcher's area was the upper 100-150 feet, just below the overlying Fort Union.

Description. — The well preserved occipital condyle occupies the end of a long neck, or peduncle, that widens anteriorly. In dorsal view (Fig. 1C), a foramen perforates the peduncle dorsoventrally, one half of the way down and slightly to the left of the midline. This feature, previously unnoted in a braincase of *Triceratops*, is probably a nutrient foramen, but it may have served some other function. A similar structure has been figured on the articular surface of the condyle in the sauropod *Camarasaurus* (Madsen et al., 1995). There is slight weathering on the lateral edges of the articular surface of the occipital condyle, meaning that a transverse measurement may under represent width slightly. The articular surface is hemispherical in shape, with a slight concavity on the dorsal surface that continues into the braincase (Fig. 1A).

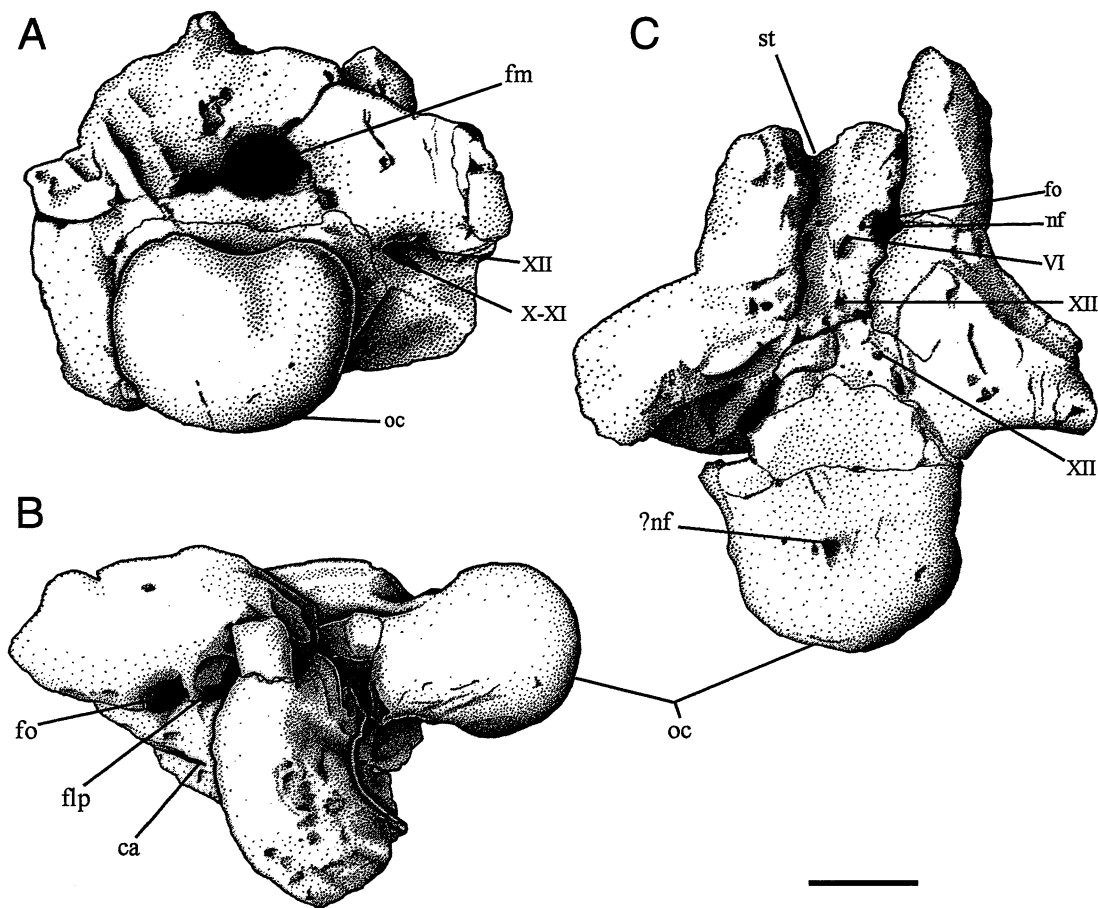


FIG. 1 — Basicranium of *Triceratops* sp. (UM 17062) from the Hell Creek Formation near Fort Peck, Montana. Specimen is shown in occipital (A), left lateral (B), and dorsal (C) views. Abbreviations: *ca*, foramen for the carotid artery; *flp*, foramen lacerum posterius; *fm*, foramen magnum; *fo*, foramen ovale; *nf*, nutritive foramina; *oc*, occipital condyle; *st*, sella tursica (pituitary fossa). Roman numerals represent corresponding cranial nerves. Scale bar equals 50 mm.

Exoccipital processes terminate just lateral to the condylar peduncle. The foramen magnum is horizontally oval, due to distortion. Piercing the exoccipital lateral to the condyle are two foramina that are separated by a horizontal septum. The upper portion conducts the hypoglossal nerve from the brain case, exiting just within the foramen magnum (Forster, 1996a), and the lower, larger foramen is for the joint passage of X-XI (Hatcher et al., 1907; Forster, 1996a). The latter branches into two passages, one enters the brain case anterior to the entrance of XII (according to Hatcher et al., 1907), and is probably for transmission of the accessory nerve. The other branch enters into the foramen lacerum posterius and is interpreted as being for the vagus nerve.

Two large foramina exit the lateral wall anterior to the exoccipital-basioccipital buttress (Fig. 1B). The more posterior opening was identified by Hatcher et al. (1907) as the foramen lacerum posterius for passage of cranial nerves X and XI, and the more anterior opening was identified as the foramen ovale (for passage of nerve V). Forster (1996a) added the glossopharyngeal nerve (IX) to the posterior passage. A plane drawn through these large foramina runs parallel to another that bisects the condyle peduncle horizontally. Between these they describe an internal auditory meatus. Although poor preservation obscures the morphology externally, its position can be

established internally. Ventral to the foramen ovale on either side can be seen two large foramina that converge anteriorly into the pituitary fossa. These are interpreted as foramina for the carotid arteries. Anterior to these foramina are two additional foramina that enter the braincase just posterior to the pituitary fossa. Weathering obscures most additional fenestration.

The braincase is not preserved anterior to the pituitary fossa, although the posterior margins of the fossa remain. Nevertheless, foramina for cranial nerves XII, XI, X (foramen lacerum posterius), VIII (internal auditory meatus), VI, V (foramen ovale) and several vesicular foramina can be identified on the floor of the braincase (Fig. 1C). Three foramina identified by Hatcher et al. (1907) as auditory cavities in the otic capsule are present in the braincase roof. Forster (1996a) identified only two: the anteriormost for the passage of cranial nerve VIII, and the other either for a branch of the vestibulocochlear nerve or the vestibular aqueduct. In total, about one-half of the braincase is preserved, or about three-fourths of the post-olfactory lobe region.

The occipital condyle of UM 17062 measures 101.1 mm in width and 85.7 mm in height. The foramen magnum measures 44.4 mm in width and 31.0 mm in height. The distance from the posterior margin of the pituitary fossa to the occipital condyle is 231 mm.

Ribs. — Two complete ribs were found with the basicranium, as were several portions of rib shafts and rib heads and a few pieces of vertebrae, including a prezygapophysis and postzygapophysis identified by Case as belonging to *Triceratops*. These specimens are collectively cataloged as UM 20716.

One rib, probably a right eighth cervical rib, based upon the description of *Triceratops "brevicornus"* of Ostrom and Wellnhofer (1986), is long and triangular. The capitulum is long, and it projects from the main shaft at an 80° angle. The tuberculum is broad and well defined. Both articular surfaces are oval. From the broad, flat head, the shaft becomes thin quickly and ends in a sharp point. There is little medial curvature. Along the posterior surface of the shaft runs a groove that becomes less pronounced distally. The shaft is oval in cross-section.

The other rib, probably left thoracic rib 1 or 2, is longer, stouter, and curved. The tuberculum is much less pronounced. The capitulum is strongly defined, triangular in shape and projects from the shaft almost orthogonally. The articular surface of the tuberculum is oval in shape; the head of the capitulum is missing. Along the midline of the posterior surface runs a sulcus, and along the lateral margin of the anterior surface runs a ridge. The shaft remains robust along its length, only tapering gently. The shaft terminates in a vesicular knob, where it attached to the sternum.

Measurements of UM 20716, ribs identified as *Triceratops* by Case (1938), follow. Cervical rib 8 has a maximum length of 666 mm; the capitulum is 227 mm long; the angle of the capitulum is 80°; and the width of the rib from capitulum to tuberculum is 274 mm. Dorsal rib 1, lacking the capitulum, has a maximum length estimated at 618 mm; the length of the capitulum is estimated at 214 mm; the angle of the capitulum is estimated at 89°; and the width from the capitulum to tuberculum is estimated at 243 mm. All details of morphology are consistent with previously described ribs of *Triceratops*.

Discussion — The occipital condyle peduncle is diagnostic of neoceratopsians (Dodson and Currie, 1990). There is no condylar peduncle in *Tyrannosaurus rex* (Osborn, 1912). The distribution of foramina differs from genus to genus within Ceratopsia (Hatcher et al., 1907; Lull, 1933; Dodson and Currie, 1990; Lehman, 1993; Godfrey and Holmes, 1995). The arrangement of foramina in this braincase exactly matches several previously figured *Triceratops* (Hatcher et al., 1907; Lull, 1933; Forster 1996a). In *Torosaurus*, there is a greater separation between the foramina in the exoccipitals lateral to the condyle (pers. obs.). Also, *Torosaurus* is relatively rare and, on average, smaller than *Triceratops* (measured by occipital condyle diameter; Hatcher et al., 1907; Lull, 1933—but sample size is very small). For these reasons, UM 17062 is identified as *Triceratops* sp.

Ostrom and Wellnhofer (1986, 1990) noted that type specimens of 11 of the 16 named species of *Triceratops* came from a small part of one county, Niobrara County, Wyoming, and questioned whether it was likely that 11 species of similarly large herbivores (live weight estimated to be 6-9 tons; Colbert, 1962; Alexander, 1985) could have lived within such a small area. They found that

variation in horn shape within species of modern bovids was greater than that distinguishing 'species' of *Triceratops*, and concluded that all of the specific distinctions proposed to date could be explained by normal variation found within a single biological population. Hence all species were subsumed within *Triceratops horridus*. If Ostrom and Wellnhofer are correct, then UM 17062 is undoubtedly *T. horridus* too.

DIMENSIONS OF THE OCCIPITAL CONDYLE AS A PROXY FOR BODY SIZE

J. F. Anderson et al. (1985) studied long-bone dimensions in mammals extended this to estimate dinosaur body masses, which yielded lower masses than previous estimates based on dinosaur models (Colbert, 1962; Alexander, 1985). However, unfortunately, ceratopsian postcrania are rare. Where postcranial remains have been found, they are conservative with few (if any) diagnostic apomorphies (Dodson and Currie, 1990; Forster 1996b), meaning that specific identification is impossible without an associated skull. Ceratopsian postcrania are rarely complete, and all reconstructions published to date have been composites (Dodson and Currie, 1990). Since all systematically-important information comes from the skull, and since only cranial material has been collected in large enough samples to make statistical analysis meaningful, characteristics used to predict body size are necessarily cranial as well.

Martin (1980) correlated body weight in mammals to dimensions of the occipital condyle, and I here explore the relationship of body weight to occipital condyle size in two extant reptiles, *Basiliscus vittatus* and *Alligator mississippiensis*, as well as extinct *Triceratops* sp.

Condyle in *Basiliscus vittatus*

Basiliscus vittatus, commonly known as the brown basilisk, is a small to medium-sized iguanid lizard. Its range extends throughout Central America, with a recent introduction into Florida (R. W. VanDevender, pers. comm., 1996). The species is dimorphic, based on size of a head crest, dorsal crest, caudal crest, and color patterns (Maturana, 1962; Hirth, 1963). Males grow faster and reach larger sizes (Hirth, 1963). There can be regional variation in size as well (VanDevender, pers. comm., 1996). Males begin to produce sperm at a snout-vent length (SVL) of 70 to 80 mm in southern Mexico (Glidewell, 1974), and in Costa Rica at 80-90 mm, with the most active breeding population averaging 90 mm (Hirth, 1963). Females have been found with yolked ovarian follicles at a SVL of between 90-100 mm in southern Mexico (Glidewell, 1974), but as low as 83 mm in Costa Rica, where the average SVL of the most actively breeding females is 92 mm (Hirth, 1963).

Two samples, one of 34 individuals (16 male, 18 female) and the other of 14 individuals, were selected from a large collection of *B. vittatus* in the University of Michigan's Museum of Zoology. These animals were collected from the same population in Panama between July and September 1962, and some were skeletonized before preservation. The first of my samples was drawn to be representative of the range of sizes of adults, and juveniles with unsutured skulls were excluded from the sample. The smallest of the remainder are all above the minimum size indicative of adulthood (as measured by SVL at capture). Body weight was not recorded at capture, so here body size means snout-vent length, and SVL is the dependent variable of interest. The second of my samples of *B. vittatus* was drawn to study basal skull length (BSL) in relation to occipital condyle area.

The occipital condyle borders the foramen magnum ventrally, and it is much wider than it is high. Measurements reported here are maximum width and height of the occipital condyle, and snout-vent length (SVL; Table 1); and maximum width and height of the occipital condyle, and

TABLE 1 — Specimens and measurements of *Basiliscus vittatus* used in study of relationship of snout-vent length (SVL) to occipital condyle size (Fig. 2).

UMMZ specimen	Sex	Condyle width (mm)	Condyle height (mm)	SVL (mm)	UMMZ specimen	Sex	Condyle width (mm)	Condyle height (mm)	SVL (mm)
150225	f	2.33	1.86	98	150366	f	2.90	2.19	111
150235	f	2.68	2.10	110	150214	m	3.28	2.44	126
150242	f	2.62	1.76	96	150218	m	3.23	2.33	119
150244	f	2.85	1.90	100	150248	m	2.66	2.14	98
150251	f	2.92	2.14	109	150275	m	3.30	2.69	118
150261	f	2.88	2.35	118	150279	m	3.50	2.62	126
150262	f	3.10	2.12	112	150295	m	2.83	2.06	106
150267	f	2.66	1.50	89	150301	m	3.15	2.24	110
150282	f	2.65	1.80	114	150304	m	3.06	2.50	119
150317	f	2.82	1.96	109	150310	m	3.30	2.63	128
150320	f	2.40	1.66	92	150315	m	2.78	2.34	102
150328	f	2.64	2.04	107	150332	m	3.15	2.50	119
150330	f	2.65	1.94	102	150334	m	3.16	2.56	121
150331	f	2.50	1.95	99	150340	m	3.51	2.16	130
150333	f	2.66	2.09	105	150342	m	2.84	2.45	111
150354	f	2.81	2.23	116	150362	m	3.16	2.22	124
150360	f	2.75	2.24	106	150365	m	3.14	2.45	120

TABLE 2 — Specimens and measurements of *Basiliscus vittatus* used in study of relationship of basal skull length (BSL) to occipital condyle size (Fig. 3).

UMMZ specimen	Sex	Condyle width (mm)	Condyle height (mm)	BSL (mm)	UMMZ specimen	Sex	Condyle width (mm)	Condyle height (mm)	BSL (mm)
150215	f	2.65	1.85	20	150293	m	3.20	2.15	31
150219	f	2.75	1.80	22	150319	m	3.01	1.98	27
150229	f	2.46	1.60	22	150326	m	2.66	1.77	23
150266	f	2.66	1.90	26	150339	m	3.23	2.21	31
150207	m	3.10	2.25	31	150348	m	3.14	2.12	31
150234	m	3.15	2.25	30	150350	m	3.05	2.05	29
150292	m	2.84	2.10	27	154433	m	2.95	2.00	27

basal skull length (BSL; Table 2). Measurements of condyles were made using dial calipers under a 10× dissecting microscope, and were recorded to the nearest 0.01 millimeter. Condyle area is taken throughout as the simple product of condyle width and height.

Snout-vent length in *Basiliscus vittatus* is positively correlated with both occipital condyle width (Fig. 2A) and occipital condyle area (Fig. 2B). Coefficients of determination, r^2 , representing the proportion of variation in Y due to variation in X , are 0.725 and 0.769, respectively, and both correlations are highly significant ($p < 0.001$). Sexes generally group toward opposite ends of each plot, but there is much overlap (Fig. 2). This can be explained in part by the non-determinant growth of squamates. Males at any stage in life are larger than females (Hirth, 1963). Older females overlap the male sizes; the oldest females overlap the most. A similar pattern is seen in the

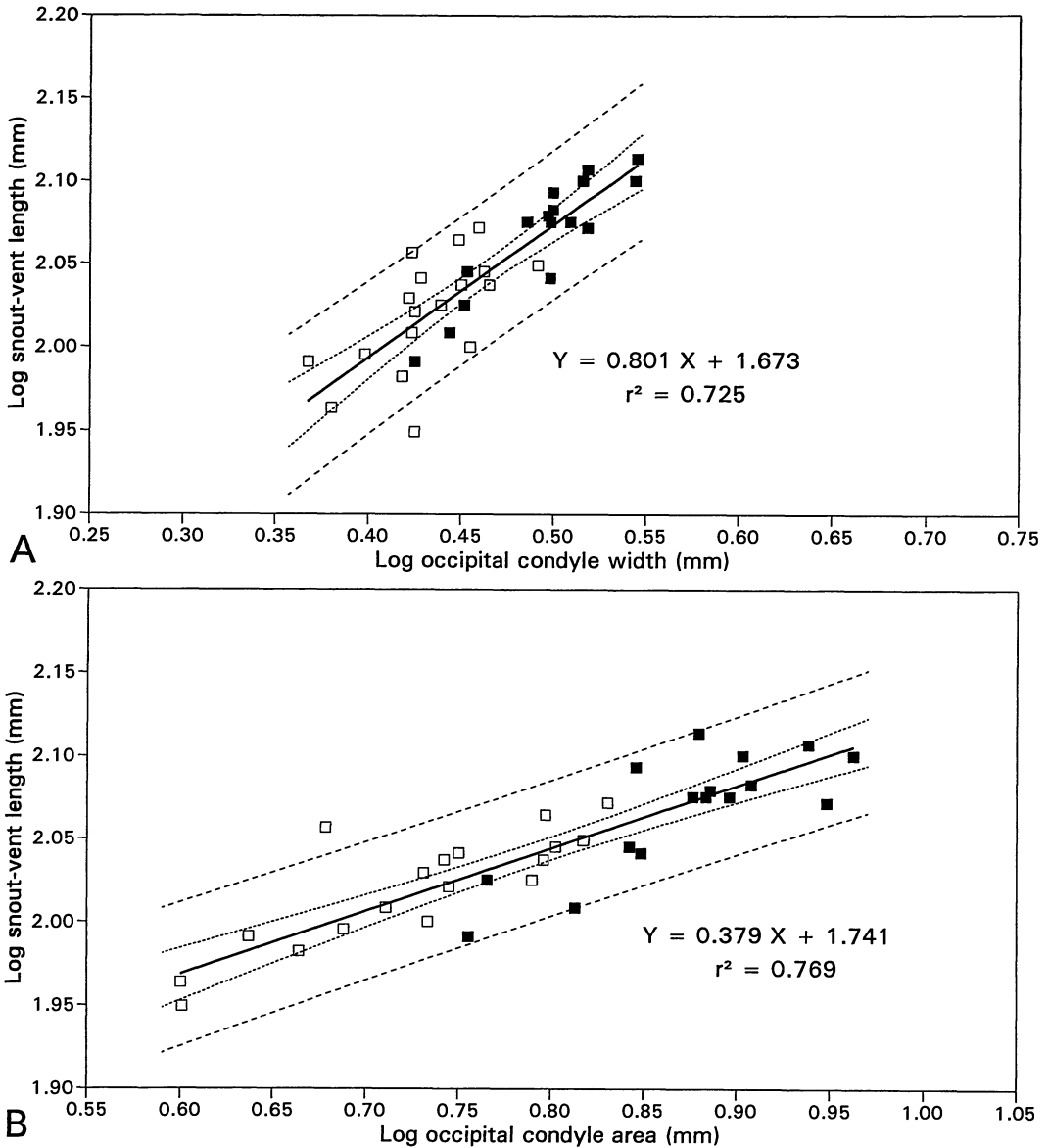
Basiliscus vittatus

FIG. 2 — Regression of snout-vent length on occipital condyle width (A) and occipital condyle area (B) in *Basiliscus vittatus*. Measurements are in millimeters (Table 1) and log transformed. Area is calculated as the simple product of condyle width and height. Open squares are females, filled squares males. Dotted lines enclose 95% confidence interval for regression. Dashed lines are 95% prediction limits.

ceratopsian *Protoceratops*, where morphological divergence occurs at sexual maturity (Dodson, 1976).

Basal skull length in *Basiliscus vittatus* is positively correlated with occipital condyle area (Fig. 3). The r^2 is 0.838, which is close to those found in the SVL analyses above. Again, sexes

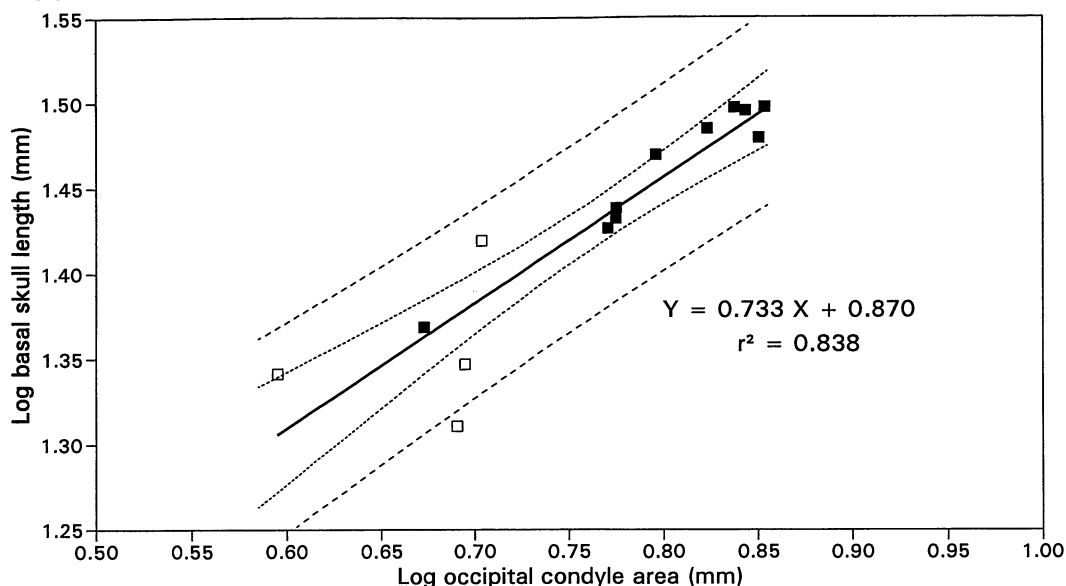
Basiliscus vittatus

FIG. 3 — Regression of basal skull length on occipital condyle area in *Basiliscus vittatus*. Measurements are in millimeters (Table 2) and log transformed. Area is calculated as the simple product of condyle width and height. Open squares are females, filled squares males. Dotted lines enclose 95% confidence interval for regression. Dashed lines are 95% prediction limits.

TABLE 3 — Specimens and measurements of *Alligator mississippiensis* used in study of relationship of basal skull length (BSL) to occipital condyle size (Fig. 4).

RM specimen	Sex	Condyle width (mm)	Condyle height (mm)	BSL (mm)	RM specimen	Sex	Condyle width (mm)	Condyle height (mm)	BSL (mm)
2787	—	6.15	5.20	113	2794	—	8.50	6.95	144
2791	—	6.75	5.05	124	2795	—	10.40	8.55	177
2795	—	7.60	5.45	131	2790	—	11.70	8.05	189

generally group toward opposite ends of the plot, but there is still overlap. Variation is high at the smaller end of the plot because the condyle is sometimes poorly ossified in small individuals.

Condyle in *Alligator mississippiensis*

Squamates are phylogenetically distant from dinosaurs, so it is important to test the correlation of body size with occipital condyle size in archosaurs. A sample of 13 skulls of *Alligator mississippiensis* was drawn from the teaching collection of the Redpath Museum at McGill University, and this was trimmed to six in the middle of the range (Table 3) for comparability to both *Basiliscus* and *Triceratops* samples. Snout-vent lengths are not known for these specimens (nor

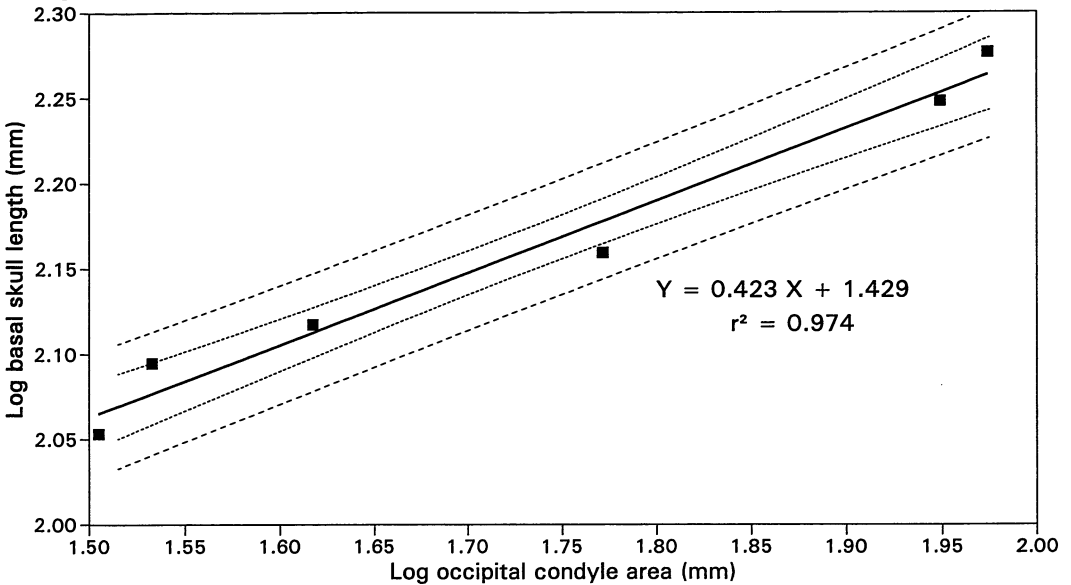
Alligator mississippiensis

FIG. 4 — Regression of basal skull length on occipital condyle area in *Alligator mississippiensis*. Regression is statistically significant ($p < 0.05$). Measurements are in millimeters (Table 3) and log transformed. Area is calculated as the simple product of condyle width and height. Dotted lines enclose 95% confidence interval for regression. Dashed lines are 95% prediction limits.

are they known for *Triceratops*), so basal skull length (BSL) is used as an indicator of body size. Sexes are not known either, so it is assumed that both males and females are represented.

Basal skull length and occipital condyle area are highly correlated in *Alligator*, even in the small trimmed sample studied here (Fig. 4) and this relationship is highly significant ($p < 0.001$). The coefficient of determination ($r^2 = 0.974$) shows that most variation of BSL is explained by area of the occipital condyle, indicating that occipital condyle area is a good predictor of body size.

Condyle in *Triceratops* sp.

Measurements of the occipital condyle for 30 individuals of *Triceratops* sp. are listed in Table 4, grouped by formation. Measurements or reasonable estimates are also given for basal skull length (BSL) and total skull length (TSL) when known. The occipital condyle of the type of *Triceratops horridus*, YPM 1820, measures 103 mm in width, contra Hatcher et al. (1907) in which width is given as 116 mm. The discrepancy is due to the presence of an off-setting crack. The type of *T. eurycephalus* was not included because it is a juvenile (Schlaikjer, 1935), and the type of *T. albertensis* does not have the condyle preserved.

Regression of basal skull length on occipital condyle area is shown in Figure 5A. The result is significant, but the coefficient of determination is lower than that of any of the previous analyses ($r^2 = 0.574$). There are several possible reasons for this. First, preservation varies some in different individuals, and weathering, described above for UM 17062, introduces error. Many skulls have been reconstructed to varying degrees. Parts are sometimes missing, requiring that lengths be estimated (five out of 12 basal skull lengths in Table 4 are estimates, a total of 42% of the

TABLE 4 — Specimens of *Triceratops* sp. preserving the occipital condyle and used in this study. Relationship of basal skull length (BSL) and total skull length (TSL) are shown graphically in Figure 5, and the distribution of condyle widths is shown graphically in Figure 8. Allocations to sex are those of Lehman (1990) and to species are those of Forster (1996b). Measurements were made by the author whenever possible, supplemented by measurements provided by Drs. B. Erickson, C. Forster and D. Russell. Other measurements came from the literature. Reconstruction of basal skull length was required on AMNH 5116; on USNM 1201, 1205, and 2100; and on YPM 1821.

Specimen	Formation	Province or state	Sex	Species	Condyle width (mm)	Condyle height (mm)	BSL (mm)	TSL (mm)
NMC 34824	Frenchman	SK	—	—	87.4	83.0	—	—
NMC 8528	Frenchman	SK	—	—	93.8	99.0	—	—
AMNH 970	Hell Creek	MT (western)	—	horridus	111.8	111.4	—	—
AMNH 5030	Hell Creek	MT (SE Lisman)	—	—	108.0	106.2	—	—
CM 1219	Hell Creek	—	—	—	104.0	104.0	—	—
CM 1221	Hell Creek	MT (western)	female	prorsus	107.0	104.5	1160	—
FMNH P12003	Hell Creek	MT (southwest)	male	horridus	104.0	104.0	1100	—
LACM 59049	Hell Creek	—	—	—	100.0	100.0	—	—
LACM 7207	Hell Creek	MT (western)	—	prorsus	99.0	95.0	1100	—
MPM 81.426	Hell Creek	—	—	—	92.0	92.0	—	—
SMM P62.1.1	Hell Creek	MT (Garfield)	female	horridus	100.0	96.0	1270	—
SMM P64.17.3	Hell Creek	—	—	—	80.0	80.0	—	—
SMM P66.33.1	Hell Creek	MT (Garfield)	—	—	103.0	104.0	—	—
SMM P60.9.1	Hell Creek	MT (Garfield)	—	—	92.0	93.0	—	—
SMM P62.15.2	Hell Creek	MT (Garfield)	—	—	87.5	87.0	—	—
SMM P93.16.1	Hell Creek	MT (Garfield)	—	—	76.0	84.0	—	—
SMM P93.17.1	Hell Creek	MT (Garfield)	—	—	99.0	78.0	—	—
SMM P96.11.1	Hell Creek	MT (Garfield)	—	—	94.0	112.0	—	—
UCMP 113697	Hell Creek	MT (McCone)	female	horridus	108.0	108.0	—	—
UM 17062	Hell Creek	MT (McCone)	—	—	101.1	85.7	—	—
AMNH 5116	Lance	WY (Niobrara)	male	horridus	95.5	96.0	1100	—
BSP 1964.I.456	Lance	WY (Niobrara)	female	prorsus	88.0	88.0	—	1652
CM 998	Lance	WY (Niobrara)	—	—	100.0	100.0	—	—
USNM 1201	Lance	WY (Niobrara)	male	horridus	102.0	100.6	1040	1934
USNM 1205	Lance	WY (Niobrara)	—	—	78.0	75.0	890	—
USNM 2100	Lance	WY (Niobrara)	male	horridus	101.4	99.8	1100	1880
USNM 4720	Lance	WY (Niobrara)	male	horridus	85.2	86.5	—	—
USNM 4805	Lance	WY (Niobrara)	male	—	99.0	99.0	—	—
USNM 4928	Lance	WY (Niobrara)	male	horridus	97.2	97.8	1180	—
YPM 1820	Lance	WY (Niobrara)	female	horridus	103.0	101.4	—	—
YPM 1821	Lance	WY (Niobrara)	male	horridus	92.5	93.0	1060	—
YPM 1822	Lance	WY (Niobrara)	female	prorsus	86.3	85.7	880	1523
YPM 1823	Lance	WY (Niobrara)	—	horridus	83.7	84.1	1020	1710
SMM P2-A-579	Lance	WY (Niobrara)	—	—	68.0	66.0	—	—
SMM P2-A-760	Lance	WY (Niobrara)	—	—	103.0	102.0	—	—

sample). Second, there are undoubtedly systematic errors resulting from combining data from different sources that used different landmarks for measurement and instruments with slightly different calibrations.

In all of the model species, most of the skull is anterior to the condyle. Ceratopsians are different in having large frills posterior to the occiput, doubling the total length of the skull. An additional analysis was performed to examine whether the condyle captures more of the variation of

Triceratops sp.

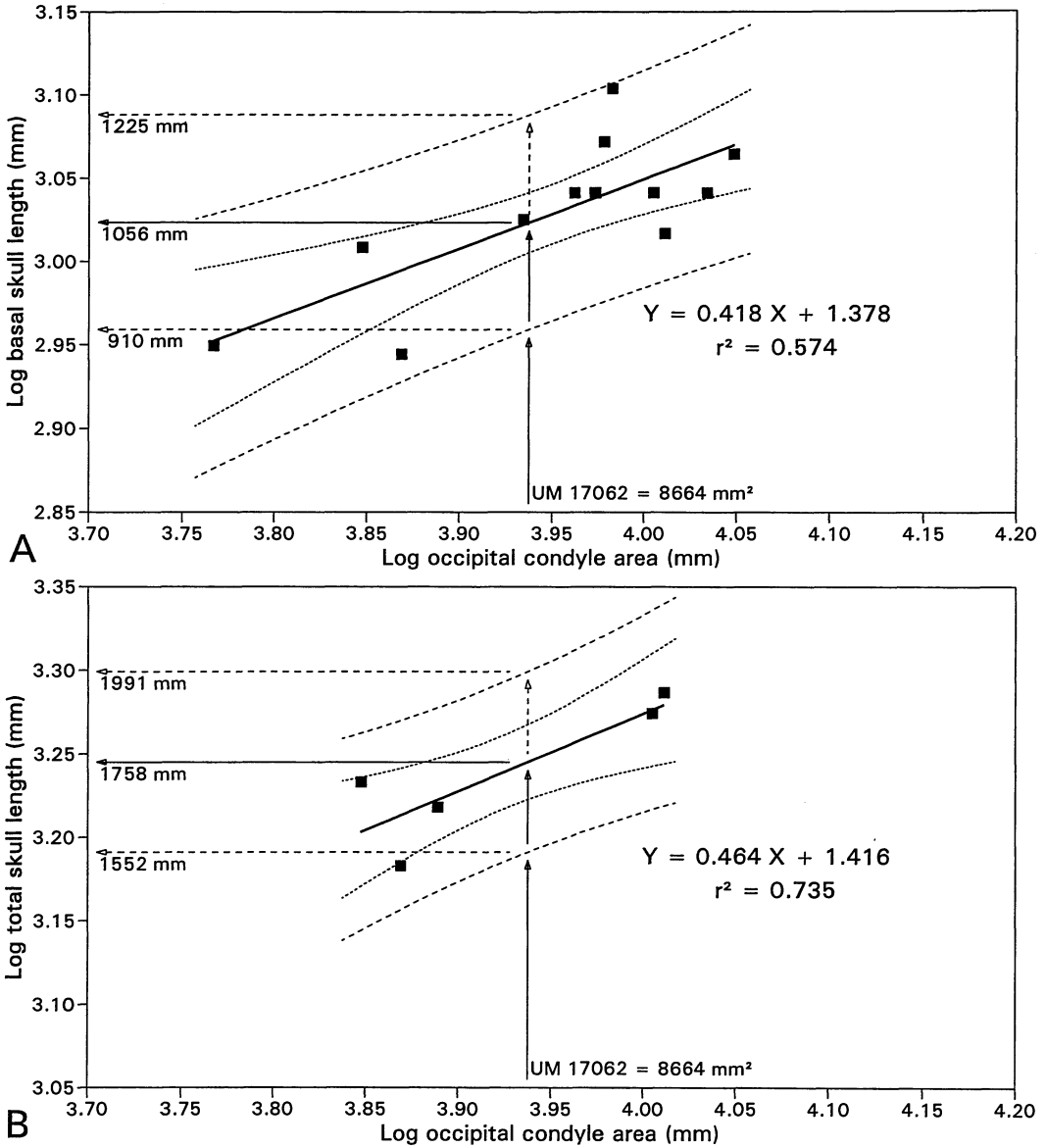


FIG. 5—Regression of basal skull length (A) and total skull length (B) on occipital condyle area in *Triceratops* sp. Measurements are in millimeters (Table 4) and log transformed. Area is calculated as the simple product of condyle width and height. Dotted lines enclose 95% confidence interval for regression. Dashed lines are 95% prediction limits. UM 17062 with an occipital condyle area of 8664 mm² probably belonged to a skull of basal length 1056 mm (\pm ca. 16%) and a skull of total length 1758 mm (\pm ca. 13%). These are well within the adult range for *Triceratops*.

total skull length. Figure 5B shows the result, and indeed the r^2 value ($r^2 = 0.732$) is increased to a level comparable to that of *B. vittatus*. However, this result must be interpreted cautiously as the sample size is small ($n = 5$) and the regression is not statistically significant ($p \sim 0.064$).

Occipital condyle area of UM 17062 indicates that it belonged to a *Triceratops* with a basal skull length of about 1056 mm (Fig. 5A). A 95% confidence interval for this prediction ranges from 910 to 1225 mm or about $\pm 16\%$. Occipital condyle area of UM 17062 indicates that it belonged to a *Triceratops* with a total skull length of about 1758 mm (Fig. 5B). A 95% confidence interval for this prediction ranges from 1552 to 1991 mm or about $\pm 13\%$.

DISCUSSION

The relationship of occipital condyle size to skull size and, by inference, overall body size in *Triceratops* can be used to test several ideas about its extinction, its species-level dimorphism and diversity, and its size variability.

Latitudinal Size Gradient in *Triceratops*

Sloan (1976) found a significant increase in skull size from the Lance Formation of Wyoming to the Hell Creek Formation of Montana. This he tied into a model of late Maastrichtian climate change. Sloan cited Bergmann's Rule (Bergmann, 1847), and suggested that as North American climate at the end of the Mesozoic became more seasonal, following departure of the climate-moderating epicontinental sea, dinosaurs and mammals became more regionally varied, with a north-to-south differentiation of dominant species, and, in *Triceratops*, an increase in body size northward (see also Dodson, 1987; Ostrom and Wellnhofer, 1990).

Sloan (1976) based his idea of a northerly increase in the body size of *Triceratops* on a few measurements of basal skull length. However, results presented here (Fig. 6), based on a larger data set of occipital condyle measurements than that available for basal skull length, do not support a cline of northward increase in the body size of *Triceratops*. Samples are known from three formations, from north to south the Frenchman Formation in Saskatchewan, the Hell Creek Formation in Montana, and the Lance Formation in Wyoming. The number of occipital condyles known from each are 2, 18, and 15, respectively. The Frenchman Formation has a mean log occipital condyle width of 1.957 (standard deviation $s = 0.022$), the Hell Creek Formation has a mean of 1.990 ($s = 0.045$), and the Lance Formation has a mean of 1.962 ($s = 0.052$). These means do not form a simple cline, and the differences are not statistically significant ($t = 0.997$ with 18 degrees of freedom, $t = 1.643$ with 31 d.f., and $t = 0.131$ with 15 d.f., respectively).

Sloan et al. (1986) argued that dinosaur extinction was a gradual process, not the result of a catastrophic event like the asteroid impact proposed by Alvarez et al. (1980). Sloan et al. attributed extinction to a confluence of several factors: global temperature decrease during the late Cretaceous, lowering of sea level in the Maastrichtian with a consequent increase in seasonality and deterioration of the flora, and competition from new mammalian herbivores from Asia. Their argument is weakened by these new results to the extent that it depended on claimed clinal variation in the size of *Triceratops*.

Sexual Dimorphism of Body Size in *Triceratops*

Lehman (1990) recognized a single species of *Triceratops* and attempted to distinguish males from females. He examined the related genus *Chasmosaurus* and concluded that a subtle difference in the arrangement of the brow horn cores coupled with size differences enables one to recognize females (smaller, with horns directed forward) and distinguish them from males (larger,

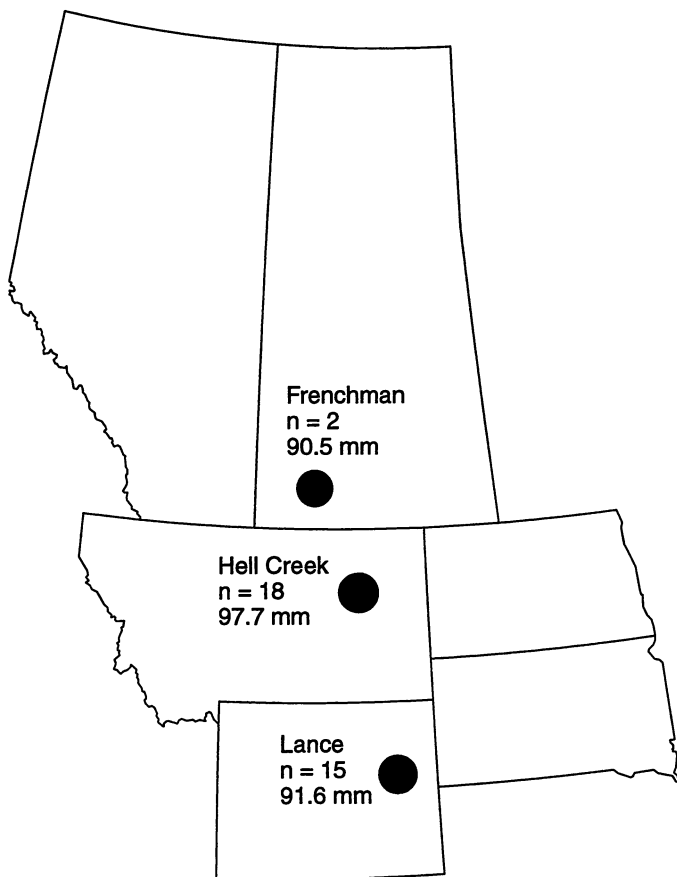


FIG. 6 — Map showing average size of *Triceratops* sp. by formation and geographic location (measurements in Table 4). Diameter of filled circle is proportional to geometric mean occipital condyle width. Differences between samples from the Frenchman Formation in Saskatchewan, the Hell Creek Formation in Montana, and the Lance Formation in Wyoming are not significant.

with horns directed dorsally and laterally). Lehman extended these criteria to all chasmosaurs, separating *Triceratops* into two ‘morphs’: *T. brevicornus*-*T. prorsus*-*T. horridus* were considered female, while *T. calicornis*-*T. elatus* were considered male (*T. obtusus*-*T. hatcheri* were described as “aged and pathologic male individuals, also referable to the same species”).

Table 4 lists specimens that are identifiable as one of the two morphs of Lehman (1990). Specimens exhibiting ‘male’ morphology are, on average, slightly smaller in log occipital condyle width than those exhibiting ‘female’ morphology, but the difference is not significant ($t = 0.333$ with 12 d.f.).

If the horn core orientation is a secondary sex characteristic, one would expect the different morphologies to segregate. Lehman (1990) included a diagram showing orientations for “males” and “females” as grouping into either “upward” or “forward” (Fig. 7A). However, these are not so much discrete groups as they are a rather arbitrarily-split continuum (Fig. 7B). Forster (1996b) found that horn cores formed a graded series inclined at 30° to 50° from vertical.

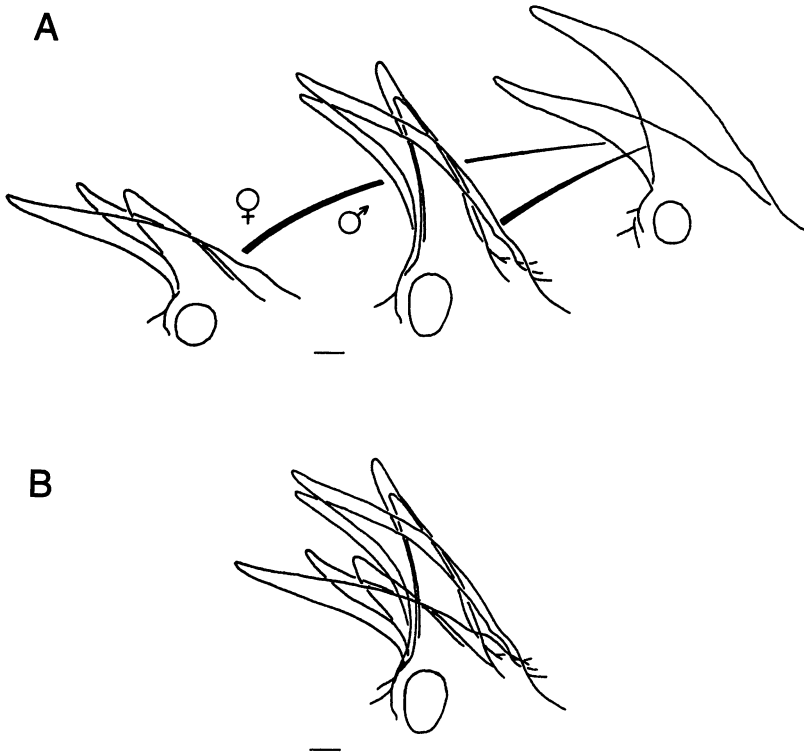


FIG. 7 — Horn core orientations in *Triceratops* sp. A, clustering by orientation into male and female morphs yields no relationship between horn core orientation and body size. B, aggregated horn cores form a graded series inclined 30°-50° from vertical (Forster, 1996b). Scale bar equals 100 mm. Modified from Lehman (1990).

Species Differences in *Triceratops*

Forster (1996b) divided *Triceratops* into two species, *T. horridus* and *T. prorsus*, based on variation in supraorbital horn height, closure of the frontal fontanel, and the shape of the rostrum. She found these characteristics to vary independently of size, as is also documented here. Species allocated to Forster's two species do not differ significantly in log occipital condyle width ($t = 0.721$ with 14 d.f.). Demonstration that Forster's two morphs do not differ significantly in size does not mean that they are necessarily the same, but size is evidently not part of the ecological partitioning that might have permitted two *Triceratops* species to coexist in the same environment.

Size Variability in *Triceratops*

Variability in the size of *Triceratops* cannot be attributed to geographic clinal variation, nor can it be attributed to sexual dimorphism, and it is reasonable to ask, finally, whether the variability of *Triceratops* is unusual for a single species.

A histogram of log occipital condyle widths is shown in Figure 8. This is left-skewed rather than right-skewed as would be expected if all individuals in a living population were being sampled. Mortality dictates that a fraction in each birth cohort die every year. Thus older and larger individuals are usually not as common as younger and smaller individuals. The left-skewing seen here

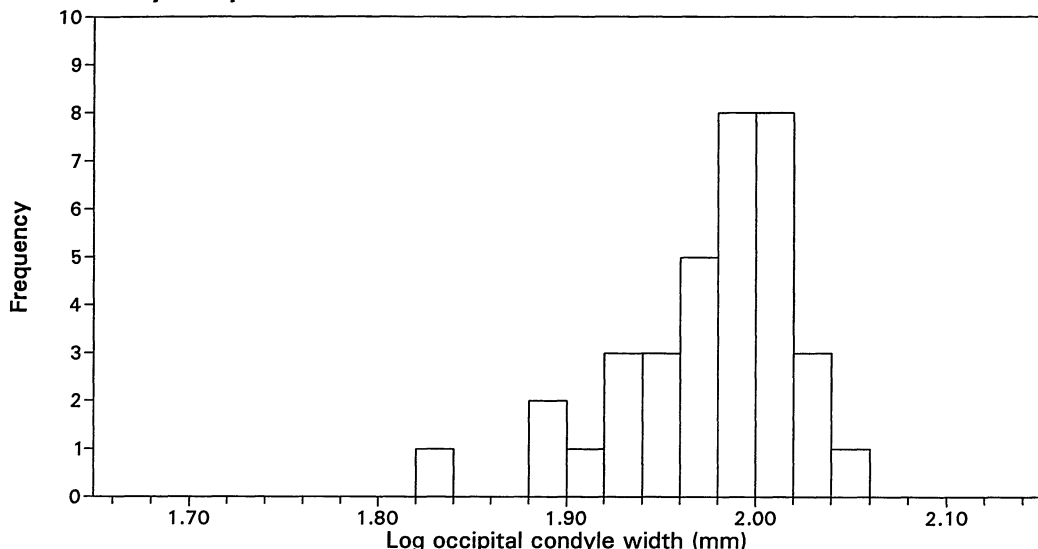
Triceratops sp.

FIG. 8 — Histogram of log occipital condyle widths in *Triceratops* sp. based on measurements in Table 4. Note the left-skewed distribution indicating a bias toward large individuals. See text for discussion.

suggesting that larger individuals are more commonly collected than smaller individuals, which is not surprising considering that older individuals have more robustly ossified skulls that are more likely to survive burial and subsequent exposure, and larger individuals make more desirable exhibit specimens and are more likely to be collected.

If we treat the histogram in Figure 8 as a normal distribution, and it is plausibly a normally-distributed sample of adult *Triceratops* specimens, we can ask how its variability compares to the variability observed in adults of other species. The coefficient of variation of occipital condyle width for all 35 individuals is 11.2. The coefficient of occipital condyle height for all 35 individuals is 11.9. These values are high for linear measurements, but not unusual for a growth series of adults. For comparison, coefficients of variation for occipital condyle width, occipital condyle height, and snout-vent length in the adult *Basiliscus vittatus* in Table 1 and Figure 2 are 10.3, 13.7, and 9.7, respectively.

CONCLUSIONS

UM 17062 is a basicranium of a large *Triceratops*. No determination of species within *Triceratops* can be made from a basicranium alone, but if Ostrom and Wellnhofer are correct there is only one species: *T. horridus*. Occipital condyle size is a reasonably good predictor of basal skull length and total skull length in *Triceratops*, with the advantage that occipital condyles are more commonly preserved in the fossil record than other cranial or postcranial elements. Occipital condyles of *Triceratops* show no significant increase in size with latitude. Occipital condyles of sexes identified by Lehman from horn cores do not differ significantly in size, nor do occipital condyles of the two species identified by Forster differ significantly in size. Variability of occipital condyle size in *Triceratops* is consistent with variability observed in growth series of adults of

other species, corroborating the idea that all *Triceratops* known to date belong to a single species (Ostrom and Wellnhofer, 1986, 1990; Dodson, 1996).

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