New caenagnathid (Dinosauria: Theropoda) specimens from the Upper Cretaceous of North America and Asia

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New specimens of caenagnathid theropods are described from the Judith River Formation (Campanian) of southern Alberta, the Hell Creek Formation (Maastrichtian) of South Dakota, and the Bissekty Formation (Turonian) of Uzbekistan. With the exception of the Hell Creek specimen, and a vertebra from Alberta, all are from the symphysial regions of the lower jaws. Caenagnathids are rare and poorly known animals, and the described fossils preserve heretofore unknown features, including vascular grooves and foramina in the symphysial region, and the pattern of overlapping sutures between jaw elements. Most of the new specimens are different from the holotype of *Caenagnathus collinsi* Sternberg and may represent the second described species, *Caenagnathus sternbergi*. The two jaws from the Bissekty Formation are the first oviraptorosaurian jaws described from Uzbekistan and represent a new genus and species anatomically closer to *Caenagnathus* than to central Asian forms like *Oviraptor*, *Conchoraptor* and *Ingenia*. There are at least five characters that distinguish caenagnathid and oviraptorid jaws, but it is concluded that the length of the symphysial region must be used with caution. Jaw anatomy supports the idea that oviraptorids were well adapted for eating eggs, although their diet was probably not restricted to one food type.

De nouveaux spécimens de théropodes caenagnathidés sont décrits, ils proviennent de la Formation de Judith River (Campanien) de l'Alberta méridional, de la Formation de Hell Creek (Maastrichtien) du Dakota Sud, et de la Formation de Bissekty (Turonien) de l'Uzbekistan. À part le spécimen de Hell Creek, et une vertèbre de l'Alberta, ils appartiennent tous à des régions symphysiales de mâchoires inférieures. Les caenagnathidés sont des animaux rares et mal connus, et les fossiles décrits exposent des particularités inconnues jusqu'à présent, incluant des cannelures vasculaires et des foramina dans la région symphysiale, et la disposition des sutures chevauchantes localisées entre les éléments de la mâchoire. La majorité des nouveaux spécimens sont différents de l'holotype de *Caenagnathus collinsi* Sternberg, et pourraient représenter la deuxième espèce décrite, *Caenagnathus sternbergi*. Les deux mâchoires provenant de la Formation de Bissekty sont les premières mâchoires d'oviraptorosaurien décrites provenant de l'Uzbekistan, et elles représentent un nouveau genre et espèce qui est du point de vue anatomique plus proche parent avec *Caenagnathus* qu'avec les formes de l'Asie centrale telles *Oviraptor*, *Conchoraptor* et *Ingenia*. Il y a au moins cinq caractères qui permettent de distinguer les mâchoires de caenagnathidés et de celles d'oviraptidés, mais la conclusion est que la longueur de la région symphysiale ne doit être utilisée qu'avec prudence. L'anatomie des mâchoires renforce l'idée que les oviraptoridés étaient bien adaptés pour manger des oeufs, bien que leur alimentation n'était pas limitée à ce type de nourriture.

[Traduit par la rédaction]

本文描述了兽脚类中新颌龙类（caenagnathids）的新标本；它们产自加拿大阿尔伯塔省南部坎佩尼阶（Campanian）的 Judith River 组、美国南达可塔州麦斯里希特阶（Maastrichtian）的 Hell Creek 组、以及乌兹别克土仑阶（Turonian）的 Bissekty 组。除了 Hell Creek 的标本和阿尔伯塔的一块椎骨例外，几乎所有标本都属于下颌联合部分。新颌龙类属于罕见动物，至今所知甚少。本文描述的标本保存了前所未知的特征，包括下颌联合部的血管沟孔以及下颌诸骨之间的重迭方式。本文描述的大部分标本与 Caenagnathus collinsi Sternberg 的正型标本不同，但可能属于本属中已知的第二个种，Caenagnathus sternbergi。Bissekty 组所产的两具下颌骨是食蛋龙类（oviraptorosaurian）在乌兹别克的第一次发现和描述，是一新属新种。它的解剖特征与 Caenagnathus 的关系比与中亚的 Oviraptor，Conchoraptor，以及 Ingenia 更为接近。至少有五个特征可以把新颌龙类和食蛋龙类的下颌骨区别开来，但是在分类中使用下颌联合的长度时必须

谨慎。食蛋龙类的下颌骨解剖特征支持它们非常适应于食蛋的观点，虽然它们的食谱可能不限于这一种食物。

Дается описание новых экземпляров теропод caenagnathid из отложений формации Джудит Ривер (кампан) южной части штата Альберта, формации Хелл Крик (маастрихт) южной Дакоты и формации Биссекти (турон) Узбекистана. За исключением экземпляра из Хелл Крик и позвонка из Альберты, все остальные представляют собой симфизальные отделы нижних челюстей. Caenagnathids - редкие и малоизученные животные, а описанные ископаемые остатки сохранили доселе неизвестные характеристики, в том числе васкулярные борозды и отверстия в симфизальном отделе, а также характер перекрывающих друг друга швов между элементами челюсти. Большинство новых экземпляров отличаются от голотипа Caenagnathus collinsi Sternberg и, возможно, представляют собой второй описанный вид Caenagnathus sternbergi. Две челюсти из формации Биссекти представляют собой первые экземпляры челюстей овираплорозавров, описанных в Узбекистане и являющихся новым родом и видом, с анатомической точки зрения более близким к Caenagnathus, чем к центральноазиатским формам, таким как Oviraptor, Conchoraptor и Ingenia. Существует по крайней мере пять различий в челюстях Caenagnathidae и Oviraptorid, но авторы пришли к выводу, что использовать длину симфизального отдела надо осторожно. Анатомия челюстей подтверждает предположение о хорошей приспособленности авирапторид к поеданию яиц, хотя их рацион, возможно, не был ограничен одним видом пищи.

[Перевод выполнен для редакции Научно-Исследовательские Журналы]

Introduction

In 1940, R.M. Sternberg described the lower jaws (Canadian Museum of Nature CMN 8776) of an unusual animal from quarry 112 (see map in Danis 1988) in an area now known as Dinosaur Provincial Park, southern Alberta. The specimen (Fig. 1) came from a relatively high level in the Judith River Formation. The edentulous dentaries are inextricably fused along a long symphysis, and the articular region is unusual. These avian characters led Sternberg to establish a new species of bird, *Caenagnathus collinsi*, for which he had to erect a new family (Caenagnathidae) and a new order (Caenagnathiformes).

The avian status of *Caenagnathus* was reviewed by Cracraft (1971), and a second species (*Caenagnathus sternbergi*) was established on the basis of CMN 2690, the posterior end of the right ramus of a mandible. The provenance of this specimen is unknown, although it is probably from the Judith River Formation of Dinosaur Provincial Park.

Although many believed that *Caenagnathus* was a theropod rather than a bird, convincing evidence was not presented until 1976, when Osmólska noted its striking similarities to the jaws of an oviraptorid. *Oviraptor* is known from complete skeletons from the Upper Cretaceous of Mongolia (Osborn 1924), and this animal is unquestionably a theropod.

Barsbold (1976) feels that *Oviraptor* is different enough from *Caenagnathus* to merit distinction at the family level, and the Oviraptoridae is further subdivided into two subfamilies (Barsbold et al. 1990). All of these animals share a number of derived characters that unite them in the infraorder Oviraptorosauria.

Numerous specimens of oviraptorids have been recovered in China and Mongolia in recent years, and papers by Barsbold (1976, 1977, 1981, 1983a, 1983b, 1986), Barsbold et al. (1990), Osmólska (1976), and Smith (1992) have done much to expand our understanding of their morphology. The acquisition of knowledge on caenagnathids has not kept pace, despite intensive collecting programs in the Upper Cretaceous beds of North America. Nevertheless, new specimens have been found in recent years, some of which are better preserved than the holotypes of *C. collinsi* and *C. sternbergi*. Two small specimens found in Uzbekistan appear to be the first records of caenagnathids from Asia and extend the temporal range of the family back to late Turonian times. A large specimen from South Dakota shows that caenagnathids were still alive in North America during Maastrichtian times.

Although the recently discovered specimens are isolated and fragmentary, they provide hitherto unknown anatomical information on these enigmatic theropods, and some insight into their habits and relationships.

Abbreviations

AMNH, American Museum of Natural History, New York; BHM, Black Hills Museum of Natural History, Hill City, South Dakota; CMN, Canadian Museum of Nature, Ottawa; CMGP, Central Museum of Geological Prospecting, St. Petersburg, Russia; GI SPS, Geological Institute, Section of Palaeontology and Stratigraphy, Academy of Sciences of the Mongolian People's Republic, Ulan Bator, Mongolia; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; PIN, Paleontological Institute, Moscow;
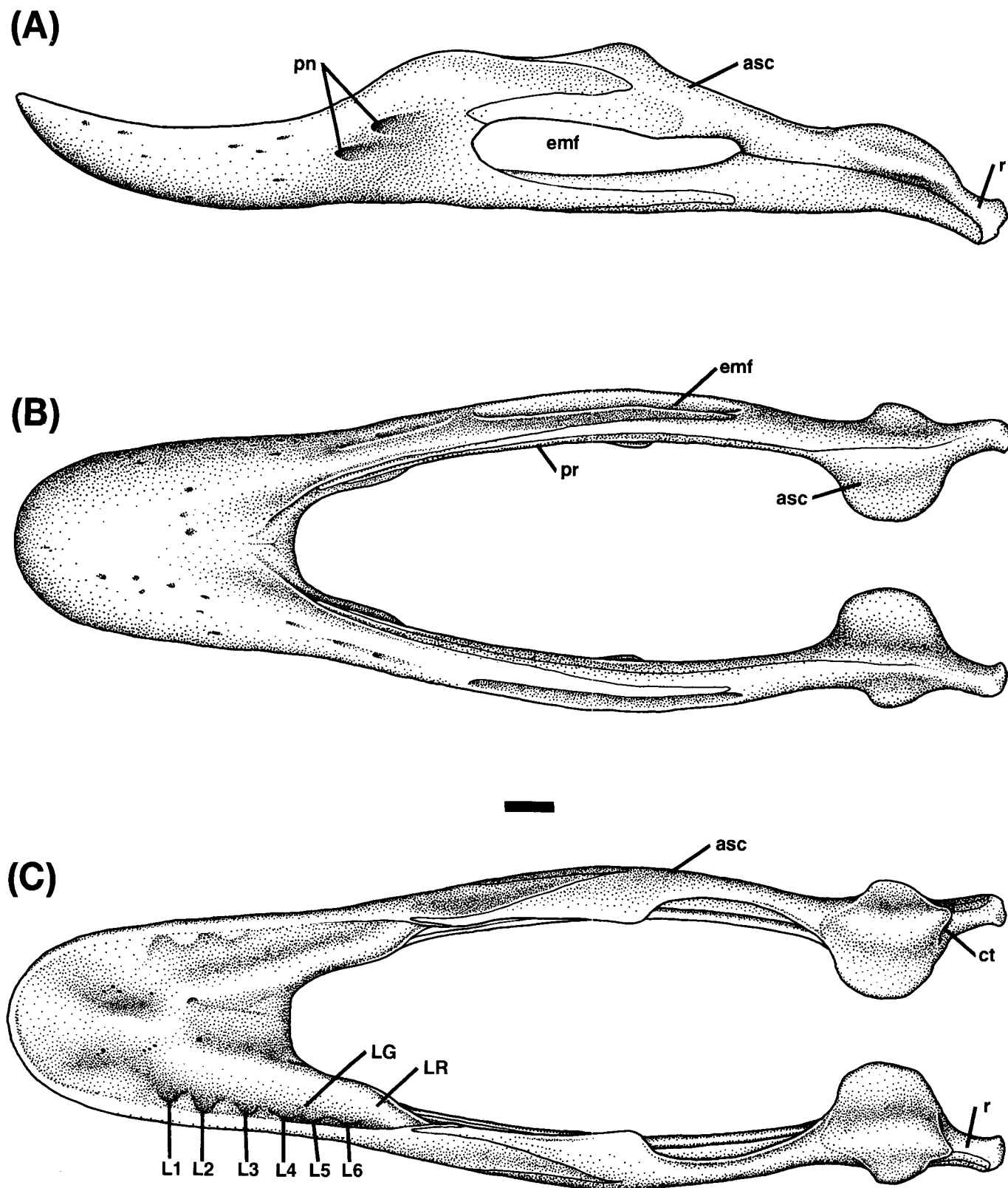
(A)

(B)

(C)

FIG. 1. *Caenagnathus collinsi*, CMN 8776, holotype. Partially reconstructed mandible in (A) lateral, (B) ventral, and (C) dorsal aspects. A1 and A2, anterior occlusal grooves; aln, foramen for the inferior alveolar nerve and internal mandibular artery; an, angular; as, sutural surface on dentary for angular complex; asc, articular–surangular–coronoid complex; ascs, sutural surface on dentary for articular–surangular–coronoid complex; ct, chorda tympani foramen; ds, dentary suture; emf, external mandibular fenestra; idf, infradiapophysial fossa; ipf, infraprezygapophysial fossa; L1–L6, lateral occlusal grooves; LG, lateral groove; lvg, longitudinal vascular groove; LR, lingual ridge; Mc, contact surface on dentary for Meckel's cartilage; Mg, Meckelian groove; nf, nutrient foramen; pn, pneumatopore; pr, prearticular; pra, articular facet on dentary for prearticular; pz, postzygapophysis; r, retroarticular process; t, tubercles; vg1 and vg2, vascular grooves. Scale bar = 10 mm.

RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta.

Systematic palaeontology

Archosauromorpha Huene, 1946
Dinosauria Owen, 1842
Saurischia Seeley, 1888
Theropoda Marsh, 1881
Oviraptorosauria Barsbold, 1976
FAMILY Caenagnathidae Sternberg, 1940

Material

BHM 2033, left articular—surangular—coronoid complex. Hell Creek Formation, South Dakota.

CMGP 401/12457, anterior region of fused dentaries collected in 1979 from Dzhyrakuduk locality (site CDZh-17a), north of Bukhara in the central Kyzylkum Desert, Uzbekistan. Lower part of Bissekty Formation (upper Turonian), 26 m above base of formation.

CMGP 402/12457, most of a right dentary collected from same site as CMGP 401/12457.

CMN 2690, posterior end of right mandibular ramus. Probably Judith River Formation, Dinosaur Provincial Park, Alberta. Holotype of *C. sternbergi.*

CMN 8776, complete lower jaws. Collected from quarry 112 (L.S.D. 15, Sec. 31, Tp. 20, Rge. 11, W. of 4th Mer.) by R.M. Sternberg, 1936. Judith River Formation, Dinosaur Provincial Park, Alberta. Holotype of *C. collinsi.*

RTMP 79.8.622, anterior portion of fused dentaries collected by Hope Johnson in Dinosaur Provincial Park (Sec. 32, Tp. 20, Rge. 11, W. of 4th Mer.).

RTMP 90.56.6, almost complete pair of fused dentaries collected from bonebed 75 in Dinosaur Provincial Park (L.S.D. 7, Sec. 32, Tp. 20, Rge. 11, W. of 4th Mer.) by M. Marsovsky.

RTMP 91.144.1, most of a pair of fused dentaries collected from the Judith River Formation on the south side of the Bow River (L.S.D. 11, Sec. 34, Tp. 13, Rge. 13, W. of 4th Mer.) near Hays (Alberta) by Wendy Sloboda.

RTMP 92.36.53, anterior caudal vertebra collected from the Judith River Formation of Dinosaur Provincial Park (L.S.D. 10, Sec. 32, Tp. 20, Rge. 11, W. of 4th Mer.) by Susan Currie.

RTMP 92.36.390, almost complete pair of fused dentaries collected from the Judith River Formation of bonebed 47 in Dinosaur Provincial Park (L.S.D. 2, Sec. 31, Tp. 20, Rge. 11, W. of 4th Mer.) by Wendy Sloboda.

RTMP 92.40.44, anterior region of fused dentaries collected from the Judith River Formation at Sandy Point (Tp. 21, Rge. 1, W. of 4th Mer.) by Wayne Marshall (East Coulee, Alberta).

Description

The holotype of *C. collinsi* (Fig. 1) is an almost complete mandible, lacking only the bar of bone below the external mandibular fenestra on the right side. It remains the best-known, most complete specimen of any recognized caenagnathid. It has been well described previously (Sternberg 1940, Cracraft 1971), and few comments are necessary. The jaw rami are parallel only in the sense that the width of the jaws is the same across the articular area as it is at the back of the symphysial area. The jaws are not as straight as originally reconstructed, however, but bow outward at midlength as in

oviraptorids (Osmólska 1976; Barsbold et al. 1990). As pointed out by Sternberg (1940), the articular and surangular had fused into a single unit. Although this is a single bone with no sutures, it occupied the position and function of three bones (articular, surangular, and coronoid) in other theropod jaws. It is more logical to assume that the three bones have coossified than to conclude that any of the three were lost in the history of the group. The unit will be referred to in this paper as the articular—surangular—coronoid (ASC) complex. The angular described by Sternberg extends forward to the symphysial region, where it covers the medial surface of the Meckelian canal and in part occupies the position of a theropod splenial. This region is not well preserved in the specimen, and there probably is a separate splenial. In oviraptorids, the angular inserts into the floor of the Meckelian canal between the dentary and splenial, as it does in other theropods (Barsbold 1977). The angular and splenial will be treated as separate units in this paper, even though the separation has not been identified and it is possible that they have become fused into a single unit in caenagnathids. The prearticular has developed an anterior, rodlike extension that crosses the medial surface of the splenial and runs along its dorsal margin to plug into a socket above the Meckelian groove behind the symphysial shelf.

RTMP 79.8.622 (Fig. 2) is the smallest known specimen of *Caenagnathus.* The symphysis is relatively shorter (Table 1) than that of the holotype of *C. collinsi.* Despite its smaller size, RTMP 79.8.622 has more pronounced vascular furrows and more numerous foramina on the dorsal surface of the symphysial shelf, and the sutures for the splenial and prearticular are better defined. Although the lingual surface of the symphysis in RTMP 79.8.622 exhibits a complex configuration, it is not rugose as in CMN 8776 (Sternberg 1940).

Another small, well-ossified specimen, RTMP 90.144.1 (Fig. 3), also has a relatively shorter jaw symphysis than that of CMN 8776. The ventral surface of this specimen was destroyed by erosion, exposing the pneumatic interior of the symphysial region.

RTMP 92.36.390 (Fig. 4), is the best-preserved pair of dentaries known and has not suffered from any postdepositional deformation. The posterior rami of the dentary were broken off before burial and were not recovered with the specimen.

RTMP 90.56.6 (Figs. 5 and 6) is a nearly complete pair of fused dentaries, and only a short segment of the right ramus has been restored in plaster. The specimen experienced some postmortem distortion, which reduced its height and exaggerated its width. RTMP 90.56.6 is somewhat larger than the type specimen of *C. collinsi,* but the symphysis is not as long (Table 1). The symphysis (Fig. 5) is deeper than in CMN 8776 (Fig. 1A), and the jaw margin is higher than the level of the dorsal border of the external mandibular fenestra. The lingual surface of the pars symphysis has been crushed, obscuring most details.

A fragmentary but well-preserved symphysial region, RTMP 92.40.44 (not figured), is from another individual with a short, deep symphysis.

Dentary

The dorsal (occlusal) margin of a *Caenagnathus* dentary is concave in lateral aspect (Figs. 1A and 6A) and ends anteriorly in a sharp, beaklike prominence (Fig. 4B). The anteromedial portion of the beak rises well above the lateral occlusal edge in RTMP 92.36.390 (Fig. 4) and RTMP 92.40.44, and

FIG. 3. *Caenagnathus* cf. *sternbergi*. RTMP 91.144.1 in dorsal view. For explanation of abbreviations, see Fig. 1. Scale bar = 10 mm.
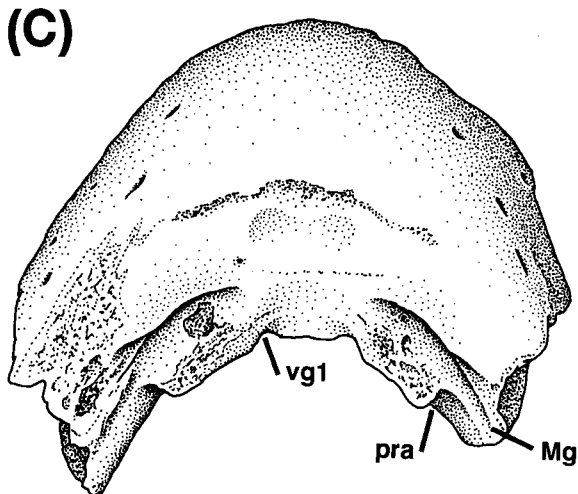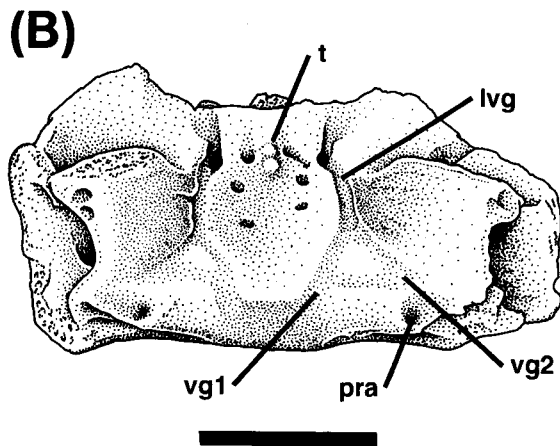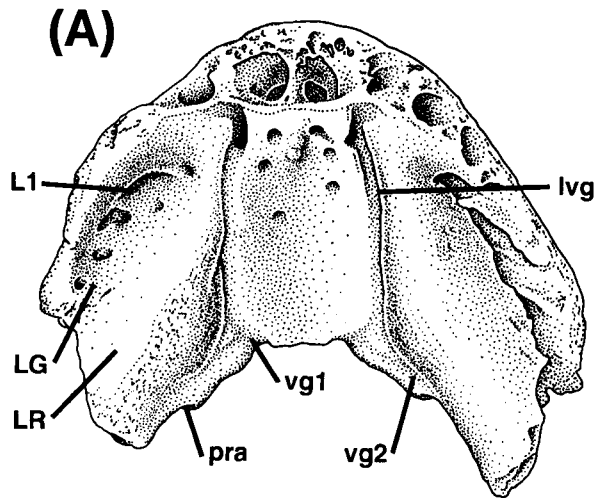

FIG. 2. *Caenagnathus* cf. *sternbergi*. Specimen drawing of RTMP 79.8.622 in (A) dorsal, (B) posterior, and (C) ventral views. Note that the entire dorsal and posterolateral margins of this element are incomplete. For explanation of abbreviations, see Fig. 1. Scale bar = 10 mm.

presumably would have done the same in the other specimens if they had not been crushed. The dentaries are fused together anteriorly, and the contacts are strengthened by a distinct symphysial shelf. The ventral margin is almost uniformly convex
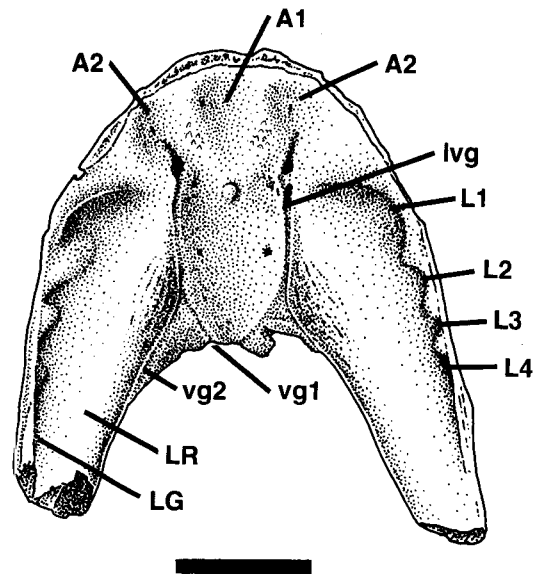
in CMN 8776 (Fig. 1A), but there is a distinct "chin" at the back of the symphysis in other specimens (Figs. 4A, 5A and 6A). Posteriorly, the dentary bifurcates where it forms the anterior border of the external mandibular fenestra and contacts the articular–surangular–coronoid complex and angular. The prearticular extends far forward, its anterior contact with the dentary being a distinct facet close to the symphysis.

The outer surface of RTMP 79.8.622 (Fig. 2) is generally smooth except for two roughly linear series of foramina. On RTMP 92.36.390 (Fig. 4B) and the left side of RTMP 90.56.6 (Figs. 5A and 5C), the foramina parallel the upper and lower margins of the mandible in the symphysial region. There are a dozen openings in the upper series, compared with eight anterior and lower foramina. The largest foramen is generally the most anterior one and was probably used by the alveolar ramus of the inferior alveolar nerve to innervate the beak at the tip of the jaw. Behind it, the upper foramina open onto the occlusal edge close to the jaw margin anteriorly, and several millimetres lower posteriorly (Figs. 4B and 5). The lower row diverges from the upper, attaining its greatest separation where the jaw deepens into the chin. The two rows converge behind this point (Figs. 5C and 6). Minute foramina pit the surface of the bone within the area bound by the larger foramina. The midline of the fused mandible is smooth and free of openings anteriorly, demonstrating the bilateral distribution of blood vessels and nerves. The foramina originate from the hollow interior of the dentaries and would have carried branches of the internal mandibular artery and the inferior alveolar nerve. Upper foramina emerge dorsolaterally onto the outer surface of the dentary, and most of the lower openings are oriented posterolaterally. In dorsal view, the broken peripheral rim of RTMP 79.8.622 exposes the courses of the upper foramina (Fig. 2A). The enlarged size of the canals beneath the surface of the bone may indicate the presence of pneumatic diverticula that followed the blood vessels.

In RTMP 90.56.6, several larger foramina open posterolaterally onto the lateral surface of the dentary 17 mm ahead of the anterior margin of the mandibular fossa (Fig. 6A). A
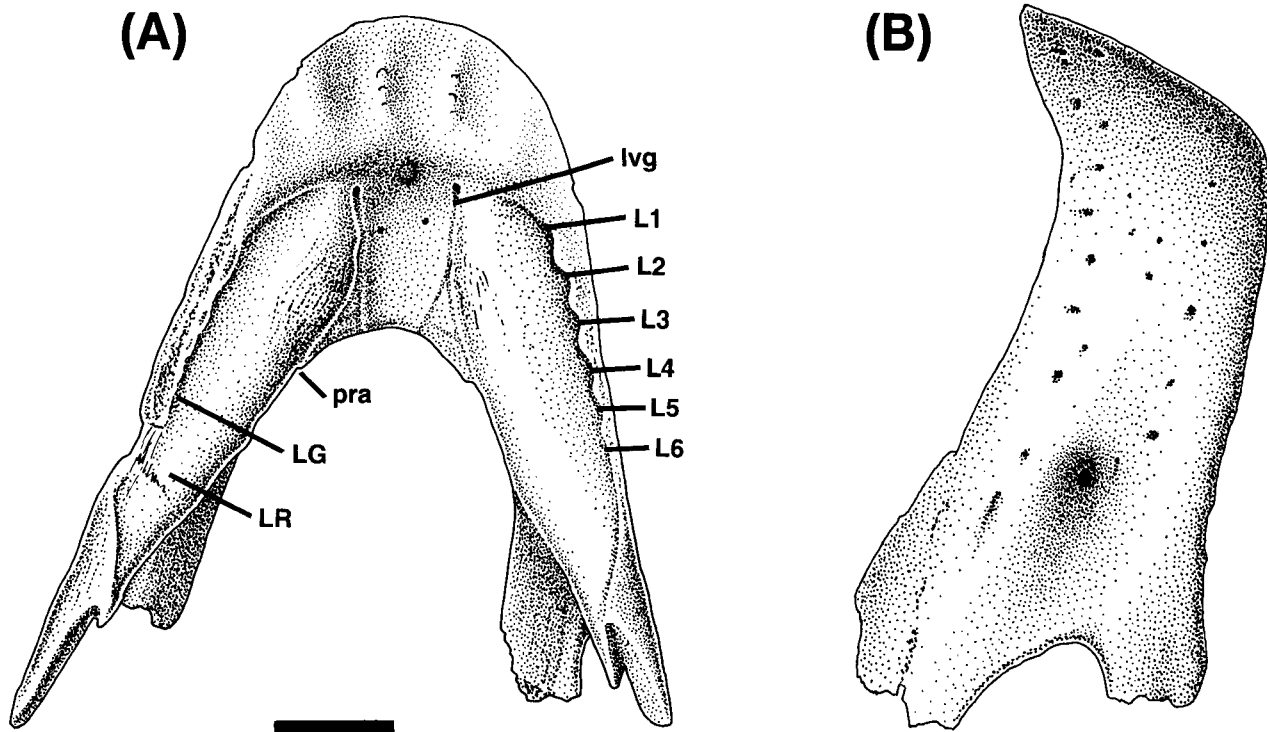
Fig. 4. *Caenagnathus* cf. *sternbergi*. RTMP 92.36.390 in (A) dorsal and (B) lateral aspects. For explanation of abbreviations, see Fig. 1. Scale bar = 10 mm.

TABLE 1. *Caenagnathus* jaw measurements

Specimen	Measurements (mm)						
	1	2	3	4	5	6	7
CMN 8776	61.9	159	70.9	17.4	48	23	104
CMGP 401/12457	11.2	—	18	8.3	15+	7.5	—
CMGP 402/12457	—	—	—	9	—	—	24.3+
RTMP 79.8.622	21+	—	26+	13+	32e	15	—
RTMP 90.56.6	46.5	120	55	25	57e	21	79.5
RTMP 91.144.1	27.2	—	31.6	12.3+	34.5	17e	—
RTMP 92.36.390	29.6	—	38.5	18.4	34	18	51.5
RTMP 92.40.44	32	—	42.7	21.7	—	—	—

NOTES: 1, shortest symphysial length; 2, total dentary length; 3, symphysial length along curve; 4, height behind symphysis; 5, width behind symphysis; 6, intermeckelian width behind symphysial shelf; 7, length from symphysis to external mandibular fenestra. e, estimate.

pair of openings occupy a more anterior position in CMN 8776 (Fig. 1A). This area is better preserved in RTMP 92.36.390 (Fig. 4B), and on each side there is a single, relatively large opening with a diameter of more than 1.5 mm. It is located in a distinct, smooth-surfaced depression in front of the mandibular fenestra. The opening passes anteromedially into the dentary, which is hollow from this point forward. This strongly suggests that the opening is a pneumatopore.

The most ventral portion of the symphysial area is marked by a shallow but distinct, hourglass- or dumbbell-shaped depression in RTMP 79.8.622 (Fig. 2C), RTMP 92.36.390, and RTMP 92.40.44. The depressions of these specimens differ in shape and degree of expression from that of RTMP 90.56.6 (Figs. 5A and 6B). In the latter specimen, the depression is not constricted on the midline, although rugosities on the floor of the depression still exhibit bilateral symmetry. The

depression probably marks the insertion of the genioglossus muscle. The surface of the bone anterior to the depression is smoothly convex. The smooth region behind is pierced by a pair of minute foramina (Fig. 5A). On each side, a shallow trough extends posterolaterally into the Meckelian groove (Fig. 5A).

Behind the depression and immediately anterior to the posteromedian margin of the symphysis, deep but narrow troughs, the Meckelian grooves, diverge posterolaterally along the ventromedial margins of the dentaries (Figs. 1B, 2C, 5A, 6B, and 9D). The Meckelian groove is narrower and deeper than it is in most other theropods. A foramen, presumably for Meckel's cartilage, passes anteriorly into the hollow interior of the symphysial region near the front of the Meckelian groove in RTMP 91.144.1, RTMP 92.36.390, and RTMP 92.40.44, and probably all of the other specimens.
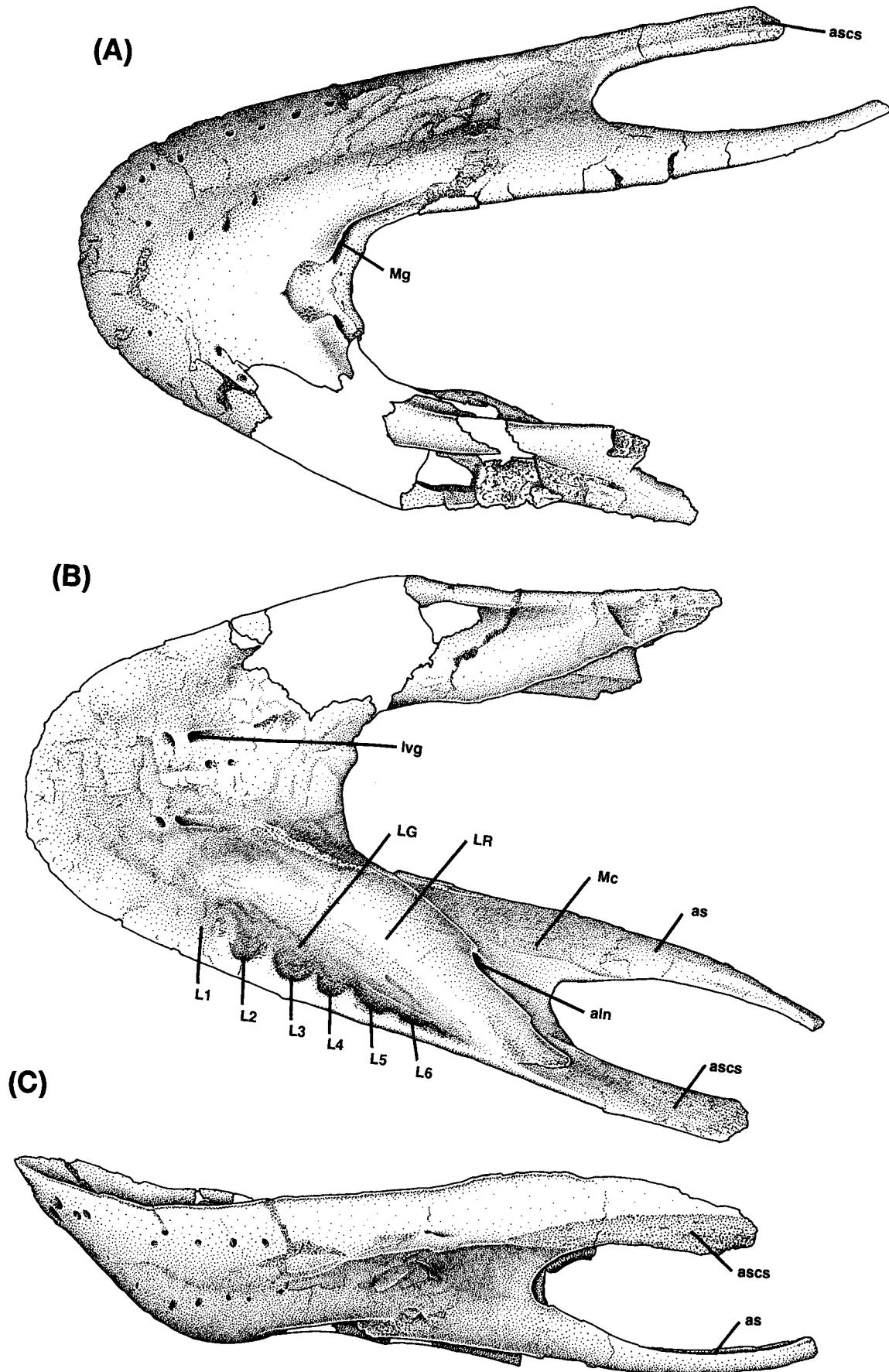
FIG. 5. *Caenagnathus* cf. *sternbergi*. Specimen drawing of RTMP 90.56.6 in (A) ventral, (B) dorsal, and (C) lateral views. For explanation of abbreviations, see Fig. 1. Scale bar = 10 mm.
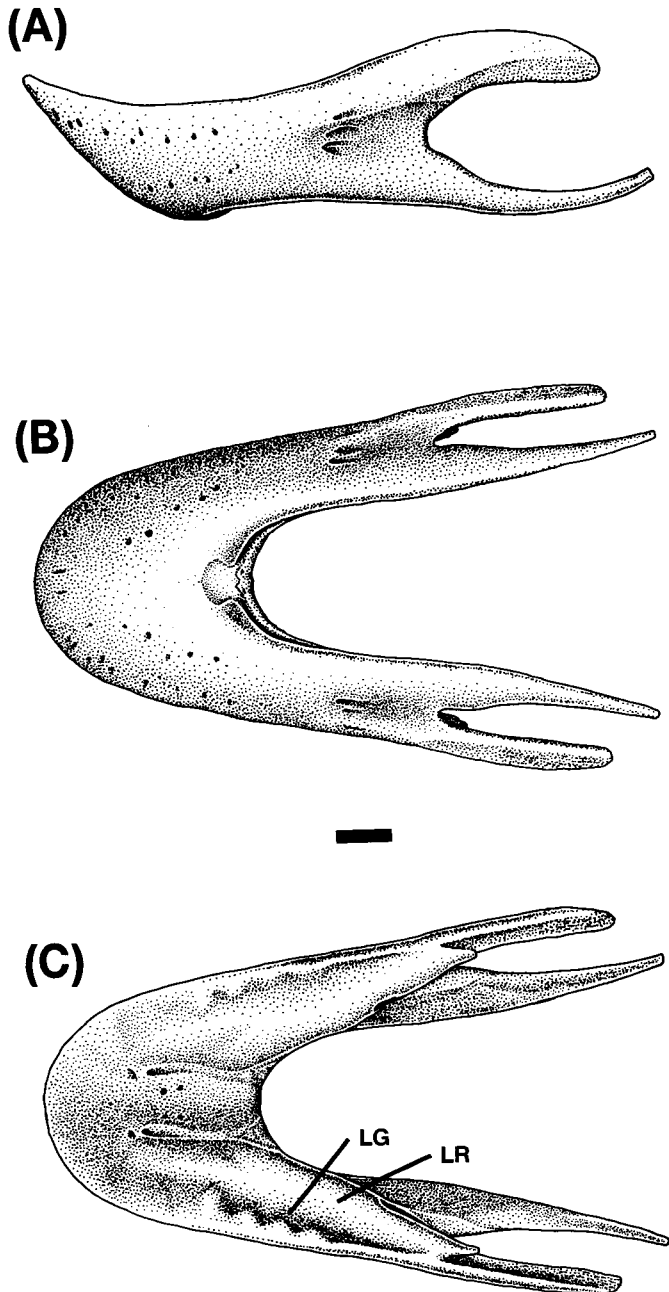
(A)

(B)

(C)

LG
LR

Fig. 6. *Caenagnathus* cf. *sternbergi*. Restoration of dentaries, based mainly on RTMP 90.56.6 in (A) lateral, (B) ventral, and (C) dorsal views. For explanation of abbreviations, see Fig. 1. Scale bar = 10 mm.

The Meckelian groove is covered posteromedially by the anteriormost section of the splenial.

A shallow groove dorsomedial to the Meckelian groove ends anteriorly in a distinct circular pit (Fig. 2B) or notch (Fig. 4A), marking the anterior limit of the prearticular.

The lingual surface of the sharp occlusal edge is vertically fluted in all specimens. The vertical ridges and grooves are found in two distinct areas. They are strongest anteriorly (A1 in Figs. 3 and 4; RTMP 92.40.44), where there is a vertically oriented concavity on the midline bound laterally by occlusal ridges that converge ventrally (Fig. 3). There is a distinct patch of rugosities near the base of each of these occlusal

ridges, perhaps attachments for the epidermal beak. Below the rugosities, the ridges are less pronounced but converge and meet on the midline. At this point, there is a small but distinct, pointed tubercle in RTMP 91.144.1 (Fig. 3), RTMP 92.36.390 (Fig. 4A), and RTMP 92.40.44 and a pair of tubercles in RTMP 79.8.622 (Fig. 2A). There is a second anterior occlusal groove lateral to the first occlusal ridge (Figs. 3 and 4A).

The second region of fluting is on the inside of the occlusal margin beside the longitudinal depression that Sternberg (1940) referred to as the lateral groove (Figs. 1C, 3, 4A, and 6C). The most prominent occlusal groove is the anterior one, which is continuous with a relatively deep pit at the front of the lateral groove. The more posterior ridges and grooves decrease in their vertical and mesial expression. Four occlusal grooves rise up the inside of the occlusal edge from the longitudinal groove in RTMP 91.144.1 (Fig. 3), whereas there are six in RTMP 92.36.390 (Fig 4A), RTMP 90.56.6 (Fig. 5B), and probably CMN 8776. This suggests the number of vertical grooves increases with size, in contrast with other theropods where the number of tooth rows remains constant regardless of ontogenetic stage, confirming the conclusion of Sternberg (1940) that these are not alveolar grooves. In RTMP 90.56.6, the mesially directed apex of each ridge is separated from the next by about 6 mm. The same measurement is 5 mm in RTMP 91.144.1 and RTMP 92.36.390. In all specimens the posterior apices are closer together. This suggests that antero-posterior length of the occlusal grooves increased ontogenetically. The apical protuberances of the occlusal ridges have rugose surfaces, and may be homologous to the toothlike process in the area of fusion between the vomers and maxilla on the palate in oviraptorids (Osmólska 1976). As suggested by Cracraft (1971), there would have been a rhamphothecal covering over the occlusal edge, possibly with toothlike tubercles over the protuberances on the occlusal ridges. Vascular grooves originate from foramina in the lateral groove and extend dorsolaterally up the surface of the occlusal grooves.

The lateral groove, homologous to the alveolar channel of toothed theropods, separates the sharply upturned jaw margin from a lower, rounded ridge. This elongate oval pocket encompasses five foramina on the left side (the right side is damaged) of RTMP 79.8.622 (Fig. 2A) and at least seven foramina in RTMP 92.36.390 (Fig. 4). These foramina would have formed exits for branches of the internal mandibular artery and inferior alveolar nerve.

Medial to the longitudinal groove is a low, rounded, longitudinal ridge (Figs. 1C, 2A, 3, 4A, 5B, 6C, and 7B), referred to subsequently as the lingual ridge. The lingual ridges in all of the new dentaries converge anteriorly, but do not join into a single longitudinal median ridge as in CMN 8776 (Sternberg 1940). Posteriorly, the lingual ridge ascends to meet the peripheral rim of the beak, squeezing out the lateral groove.

The posteromedian margin of the symphysis is a thick, well-defined horizontal shelf of bone. Laterally, this shelf is emarginated by a shallow vascular groove (one per side) that continues anteriorly and slightly laterally onto the dorsal (lingual) surface of the dentary (Figs. 2A, 2B, 4A, and 6C). This groove, which is parallel to the midline, becomes more pronounced anteriorly where it is joined by two branches of a second shallow vascular groove originating above the socket for the prearticular (Figs. 2B, 4A, and 5B). Anteriorly, the blood vessel divided, sending one branch anterodorsally in a groove that entered the base of the second anterior occlusal

groove (Fig. 3), while the second branch turned anteriorly, ventrally, and medially to pass through a foramen into the highly pneumatic spongiosa. In RTMP 90.56.6, a bridge of bone covers the region where the vessel divides (Fig. 5B). The bridge of bone separating the groove from the latter foramen is an ontogenetically mature expression of the incipient mesially directed flange of bone seen in this area in RTMP 79.8.622 (Fig. 2A).

A medial concavity between the longitudinal vascular grooves on the dorsal surface of the symphysial region is pierced by additional foramina, six in RTMP 79.8.622 (Fig. 2A), four in RTMP 91.144.1, two in RTMP 92.36.390, and at least three in RTMP 92.40.44. Crushing of the symphysis between the vascular grooves has obscured some of the median foramina in this area of RTMP 90.56.6. At least two are preserved on the right side of the symphysis. The more anterior of these foramina pass posteriorly, ventrally, and medially into the bone and are therefore not directly connected to the more distinct longitudinal vascular grooves on either side. The anterior pair of medial foramina are separated by the small pustulate or tuberculate ridge at the base of the converging first colateral pair of vertical occlusal ridges.

Large internal and external facets in RTMP 90.56.6 (Fig. 5) show the dorsal prong of the dentary was wedged deeply within the Y-shaped anterior end of the articular—surangular—coronoid complex (ASC). The surfaces of this rather complicated contact are smooth and may have permitted some movement, as postulated by Barsbold (1977) for oviraptorids. Externally, the dorsal prong of the dentary presents a narrow longitudinal straplike area immediately above the upper rim of the mandibular fossa against which the ASC lay (Fig. 5A). Internally, most of the posterodorsal prong of the dentary exhibits a lightly striated area where it was medially overlapped by the ASC (Fig. 5B). At the anterior end of this area, the ASC was overlapped mesially by a posterodorsally directed tongue-shaped flange of the dentary (Figs. 4A and 5B) as in CMN 8776. The flanges are not as well developed posteriorly in RTMP 90.56.6 and RTMP 92.36.390 as they are in CMN 8776 (Sternberg 1940). The flange is the most posterior expression of the lingual ridge.

A shallow anteroventrally directed groove marks the posteroventral edge of the lingual ridge (Figs. 4A and 5B), setting it off from the posteroventral prong of the dentary. Midway along the posteroventral edge of the ridge, a foramen passes anteroventrally and slightly laterally into the body of the bone. This foramen lies near the anterior apex of a triangular patch of smooth periosteal bone anterior to the mandibular fossa (Fig. 5B) and opens into the hollow interior of the lingual ridge and symphysial region. The position is equivalent to a pair of foramina for the inferior alveolar nerve and internal mandibular artery of *Allosaurus* (Madsen 1976) and other theropods. The foramen is opposite but slightly posterior to the apparent pneumatopore on the lateral surface of the jaw. The position and relatively large size of the foramen suggest that it may also have served as a pneumatopore.

As in CMN 8776, the lower prong of the dentary of RTMP 90.56.6 is longer and more gracile than the dorsal. At the anterior end of the mandibular fenestra, the lower prong approximates the dorsoventral depth of the dorsal ramus (1.1 cm in RTMP 90.56.6). Posteriorly, the prong curves slightly ventrally, then turns posterodorsally, tapering to a slender rod. A transverse section at any point along the posterior half is a triangle in outline, the apex of which points ventrally. This lower
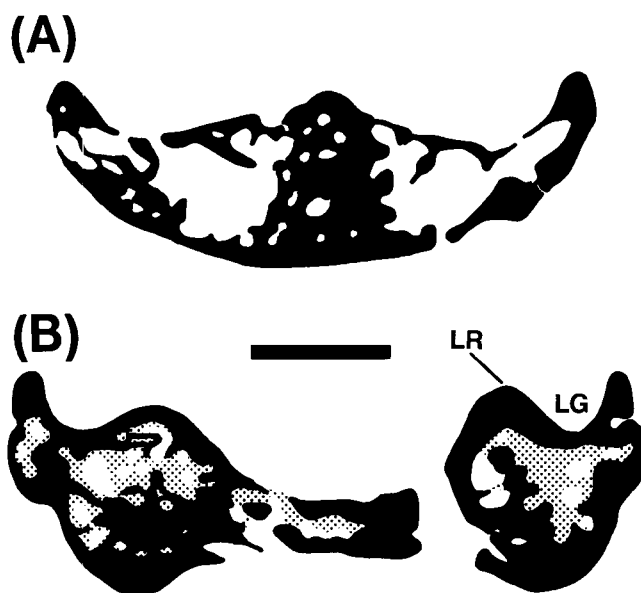

FIG. 7. CT scan sections of *Caenagnathus* mandible (CMN 8776). (A) Cross section through front of symphysial region showing midline ridge and its supporting pillar of bone. (B) Cross section through back of symphysial region. For explanation of abbreviations, see Fig. 1. Scale bar = 10 mm.

prong has smooth periosteal bone laterally. The inflection between the dorsal and mesial surfaces is more clearly expressed posteriorly (Fig. 5B). As in CMN 8776, both surfaces contact the angular in a tongue-and-groove arrangement. A low but clearly defined ridge in RTMP 90.56.6 (Fig. 5B) and RTMP 92.36.390 outlines a relatively large area anteroventral to the mandibular fenestra which would have been covered mesially by the angular and splenial ventrally, and Meckel's cartilage dorsally. This surface is finely textured with minute longitudinal ridges. It lies entirely below the broad lingual ridge, tapering to an acuminate point anteroventrally where the splenial would have covered the Meckelian groove medially.

The dentary is hollow beneath the lingual ridges and symphysis in all specimens. Although blood vessels and nerves passed through this space, the openness (Fig. 7) suggests that it was pneumatic. The bone surrounding the hollow interior is dense, but is pierced by channels for blood vessels and nerves passing directly or obliquely through to the outer surface. No sign of a suture is evident between the right and left dentaries, which must have coossified early ontogenetically. There is no midline bony constriction between the hollow spaces of the right and left dentaries in any specimen except CMN 8776. In this specimen a bar of bone between the dorsal and ventral surfaces supports the midline ridge on the lingual surface of the symphysial shelf (Fig. 7A). The posterior prongs of the dentary above the external mandibular fenestra are densely cancellous internally, and clearly were not pneumatic.

Articular—surangular—coronoid complex

The back of a caenagnathid jaw was recovered from the Hell Creek Formation of South Dakota. The coronoid process, part of the jaw articulation, and the back of the retroarticular process were abraded, and only the base (Fig. 8) remains of the anterolateral process that excludes the dentary from the dorsal margin of the external mandibular fenestra. BHM 2033
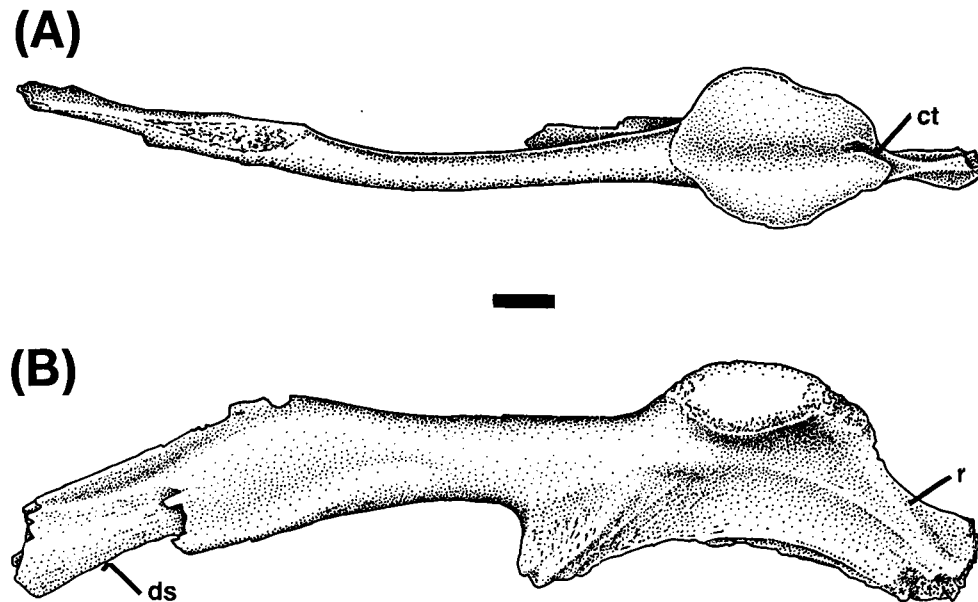
FIG. 8. *Caenagnathus* sp. BHM 2033. Left articular—surangular—coronoid complex in (A) dorsal and (B) lateral views. For explanation of abbreviations, see Fig. 1. Scale bar = 10 mm.

represents the largest caenagnathid individual presently known. The distance between the back of the dentary suture and retroarticular process is almost 50% greater than the same measurement in CMN 8776 (Fig. 9). A barely discernable line on the medial surface might represent the remnant of a line of fusion between the surangular and coronoid.

The articular—surangular—coronoid complex (ASC) is unusual in a number of ways (Sternberg 1940; Cracraft 1971). The elongate jaw articulation protrudes conspicuously above the dorsal margin of the complex and is convex in lateral view (Figs. 1A and 8B). The ridge that separates the glenoid concavities of most reptilian jaws has become the dominant articular surface in oviraptorosaurs and has assumed a more anteroposterior alignment. The medial glenoid is almost as long as the ridge, convex in medial view, and shallowly concave in cross section. The retroarticular process is relatively long for a theropod, and is oriented posteriorly, ventrally, and laterally. The process is formed laterally by the ASC complex, . ventrally by the angular, and medially by the prearticular. The top of the retroarticular process is concave in transverse section proximally, and the articular surface of the jaw is emarginated posteriorly (Fig. 8A). The chorda tympani foramen is located in this slot and served as a passage for the chorda tympani of nervus facialis and the posterior condylar artery. These emerged on the medial surface anteroventral to the jaw articulation through a slit in the ASC complex. The short process medial to the slit was sutured to the lateral surface of the prearticular, which medially covered most of the ASC complex behind this point. Below the jaw articulation, there is a concave depression on the lateral surface that may be homologous with a relatively larger and more anteriorly positioned depression found in oviraptorids. Barsbold (1977) feels the depression marked the insertion region for the external mandibular adductors, although the position and orientation suggests it may have been the insertion point of the muscle (M.) pterygomandibularis. That this latter muscle is well developed in oviraptorids is indicated by the well-developed origin on the pterygoid (Barsbold 1977). The lower part of the ASC is over-

lapped laterally by the angular (Fig. 8B), which may also cover the contribution of the complex to the posterior margin of the external mandibular fenestra. The ASC complex bows anterolaterally from the jaw articulation. Anteriorly, it splits into two vertical plates of bone. The medial one forms the dorsal margin of the jaw, but is largely covered laterally by the dentary. Anteriorly it is covered medially by the tonguelike process at the back of the dentary's lingual ridge. The lateral division of the ASC complex, most of which was lost in BHM 2033, covered the dorsal prong of the dentary and excluded it from the dorsal margin of the external mandibular fenestra (Fig. 1A).

The coronoid process has a pronounced medial inflection. There is a longitudinal depression along the lateral surface of the upper margin of the ASC complex anterior to the coronoid process, possibly marking the insertion of the M. pseudotemporalis superficialis. A roughened oval of bone on the medial surface ventral to the coronoid process was described by Sternberg (1940) in *C. collinsi*. This region, bounded posteriorly by a well-defined groove (which may be the surangular—coronoid suture) in CMN 8776 and BHM 2033, probably marks the insertion of the M. adductor mandibularis externus medius (Oelrich 1956). There is no evidence of either anterior or posterior surangular foramina, both of which were presumably incorporated into the enlarged external mandibular fenestra.

Caudal vertebra

An isolated proximal (probably the first or second) caudal vertebra (RTMP 92.36.53, Fig. 10) may be from a caenagnathid. The transverse processes, anterior zygapophyses, and the tip of the neural spine were broken when discovered. Like the caudals of other theropods, there is a pair of longitudinal ridges on the ventral surface of the centrum, the intervertebral articulation on the posterior surface of the centrum is bevelled for contact with the haemal arch, and the posterior zygapophyses are oriented more laterally than ventrally (about 55 – 60° from horizontal). The centrum is 31.4 mm long, has a
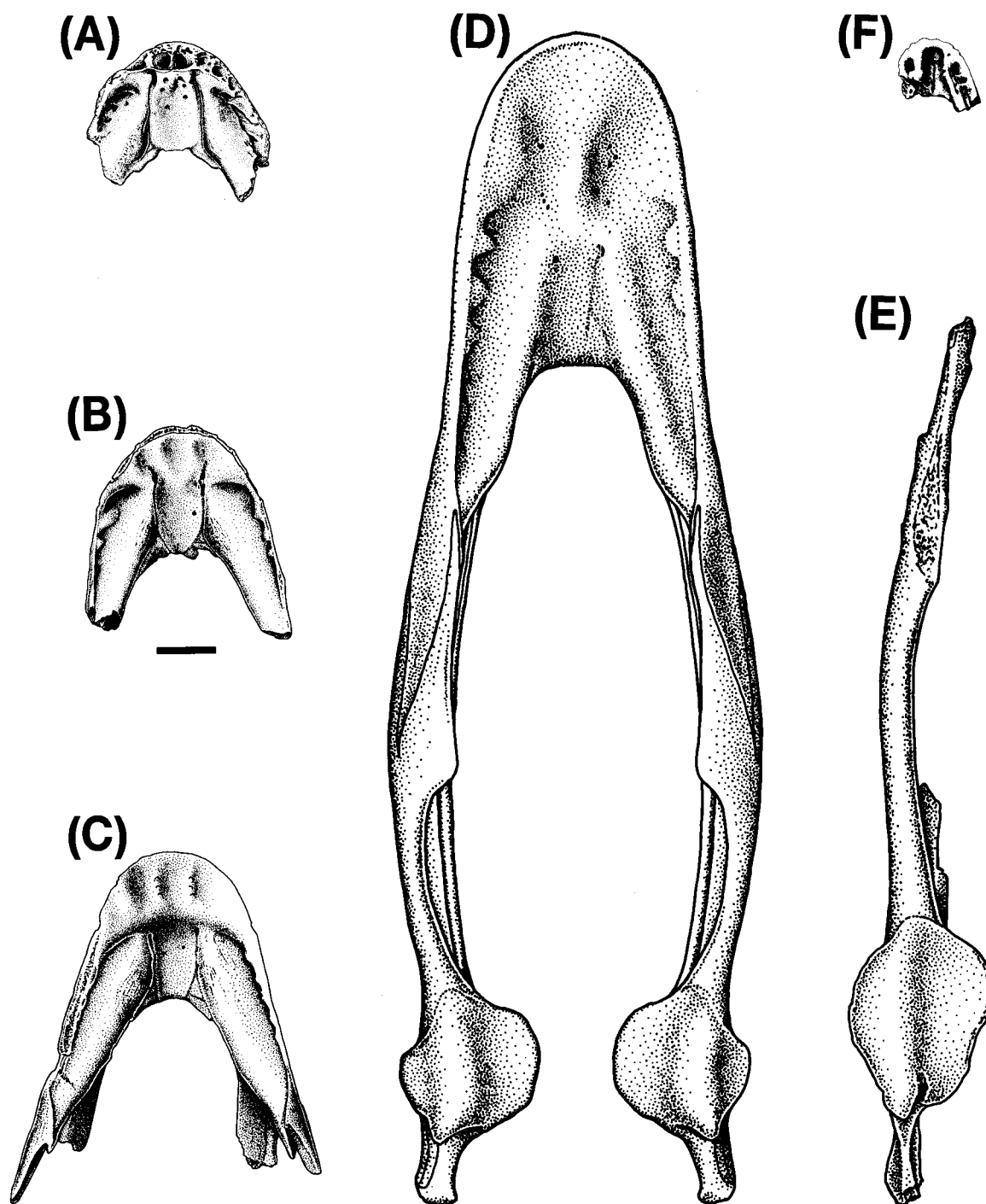
FIG. 9. Comparison of caenagnathid mandibular elements in dorsal view. (A) RTMP 79.8.622. (B) RTMP 91.144.1. (C) RTMP 90.56.6, (D) CMN 9776. (E) BHM 2033. (F) CMGP 401/12457. Scale bar = 10 mm and applies to all specimens.

maximum posterior width of 25.5 mm, a maximum posterior height of 23.8, and a midlength width of 21.0 mm.

The centrum is biconcave, although the margins of both intervertebral surfaces have been eroded slightly to expose a highly cancellous internal structure (Fig. 10B). It is unknown whether all of the interior of the bone was cancellous, or whether the central region was hollow. The neural arch is fused to the centrum, so it is difficult to determine whether some of the lateral pneumatopores are invading the centrum or the base of the neural arch. A relatively large opening with a

diameter of 2 mm is found between the two longitudinal ridges on the ventral surface of the centrum near the posterior margin. This may have been a vascular foramen, a pneumatopore, or both. A small foramen on each side at midlength and midheight of the centrum appears to have been vascular. High on the lateral surface of the centrum there is a smooth-walled depression that could be referred to as a shallow pleurocoel, with at least two pneumatopores entering the body of the centrum (Fig. 10A). Above the pleurocoel is a deep pneumatic infradiapophysial fossa, pierced ventrally by at least two pneu-
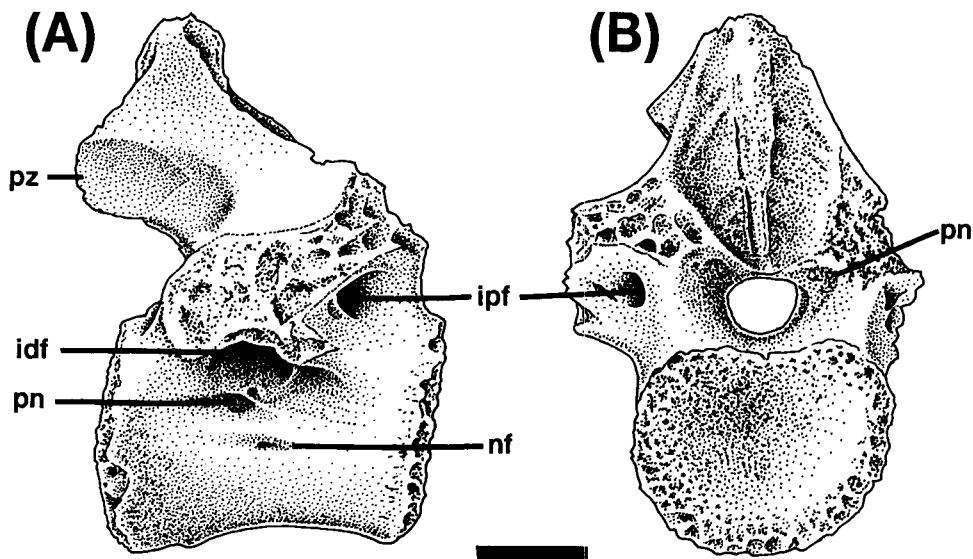
FIG. 10. *Caenagnathus* sp. RTMP 92.36.53. Anterior caudal vertebra in (A) lateral and (B) anterior views. For explanation of abbreviations, see Fig. 1. Scale bar = 10 mm.

matopores that enter the interior of the neural arch, and dorsomedially by several more. There is a shallow infraprezygapophysial fossa on the right side (Fig. 10B) pierced by a pneumatopore with a maximum diameter of 6 mm. A smaller pneumatopore is posteroventral to the larger one, the inner wall of which is pierced by even smaller foramina. As expected with pneumatic invasion of bone, the distribution of pneumatopores is not symmetrical. The main pneumatopore in the left infraprezygapophysial fossa is only half the size, but the second one is considerably larger than that of the right side. There is an additional pneumatopore anterodorsal to the main pneumatopore. Infrapostzygapophysial fossae, such as characterize the dorsal vertebrae of most theropods, are not present in this caudal. Between the postzygapophysial facet and the transverse process there is a shallow depression, the floor of which is pierced by several pneumatopores. A horizontal lamina of bone connects the bases of the prezygapophyses, arching over the neural canal (Fig. 10B). Two pneumatopores invade the vertebra in the concavity between the lamina, neural arch pedicel, and neural canal on the left side, whereas there are six pneumatopores on the right side (Fig. 10B). The neural spine is lateromedially wider than it is anteroposteriorly long and has well-defined scars anteriorly and posteriorly for attachment of the interspinous ligaments. Grooves on either side of the anterior and posterior scars are invaded by numerous pneumatopores as in the dorsals of tyrannosaurids (B. Britt, personal communication, 1993). There appear to have been pneumatopores around the dorsal margin of the posterior zygapophysial facet. The broken surfaces of the neural arch show that the posterior zygapophysis had a hollow interior and that most of the interior was coarsely cancellous, and presumably pneumatic.

The identification as a caenagnathid is based on the presence of pleurocoels in the centrum and pneumatopores in the neural arch. Pneumatic diverticula are associated with the vertebral columns of most, if not all, theropods. However, caudal vertebrae are rarely pneumatized. Pneumatic tracks extended along the caudal neural arches of *Acrocanthosaurus* (B. Britt, personal communication, 1993). Sacral vertebrae of *Chiroste-*

notes have small pneumatopores (Currie and Russell 1988), so it is possible that elmisaurid caudals were pneumatic. But the most spectacular examples of pneumatic caudals are found in oviraptorids from Mongolia (Barsbold et al. 1990). The first nine caudals of GI SPS 100/30 (*Ingenia yanshani*) have pleurocoels, whereas the anterior 19 caudals of GI SPS 100/42 (*Oviraptor philoceratops*) are pneumatic. The pleurocoels are slightly larger in GI SPS 100/42 and 100/30 than in those of RTMP 92.36.53, but the height and anteroposterior length of the neural spines and the degree of rugosity for the intervertebral ligament scars are comparable.

The same type of vertebrae were previously reported by Gilmore (1924). CMN 8504 consists of a dorsal and three caudal centra from Maastrichtian beds of southern Saskatchewan. Although the dorsal cannot be distinguished with certainty from those of *Saurornitholestes*, the caudals are anatomically similar to RTMP 92.36.53 and clearly come from the same type of animal. They are smaller (22−25 mm in length), but display the same remarkable pneumatic features. The figured caudal (Gilmore 1924) has a well-developed pleurocoel in the centrum, and the ventral surface is pierced by two pleurocoels between the paired longitudinal ridges. There is a deep infradiapophysial fossa, and the transverse process is hollow.

Caenagnathid dentaries from Uzbekistan

A pair of fused dentaries (Figs. 9F and 11) and a right dentary (Fig. 12) from Uzbekistan are both much smaller than any specimens from Alberta (Table 1). The dentaries are completely fused to each other. There is a longitudinal groove on the midline of one specimen (Fig. 11A) which may be a remnant of the line of fusion. The isolated right dentary (Fig. 12) was fused to the left when the animal was alive, but was separated by breakage after death. The break did not occur along the division between the right and left dentaries, but to the right of the symphysis.

In overall shape, the Asian jaws are very similar to those of *Caenagnathus*. The front of the jaw slopes steeply back to a distinct chin, and the occlusal margin of the jaw is higher at the front than it is laterally (Fig. 11D). Foramina on the out-
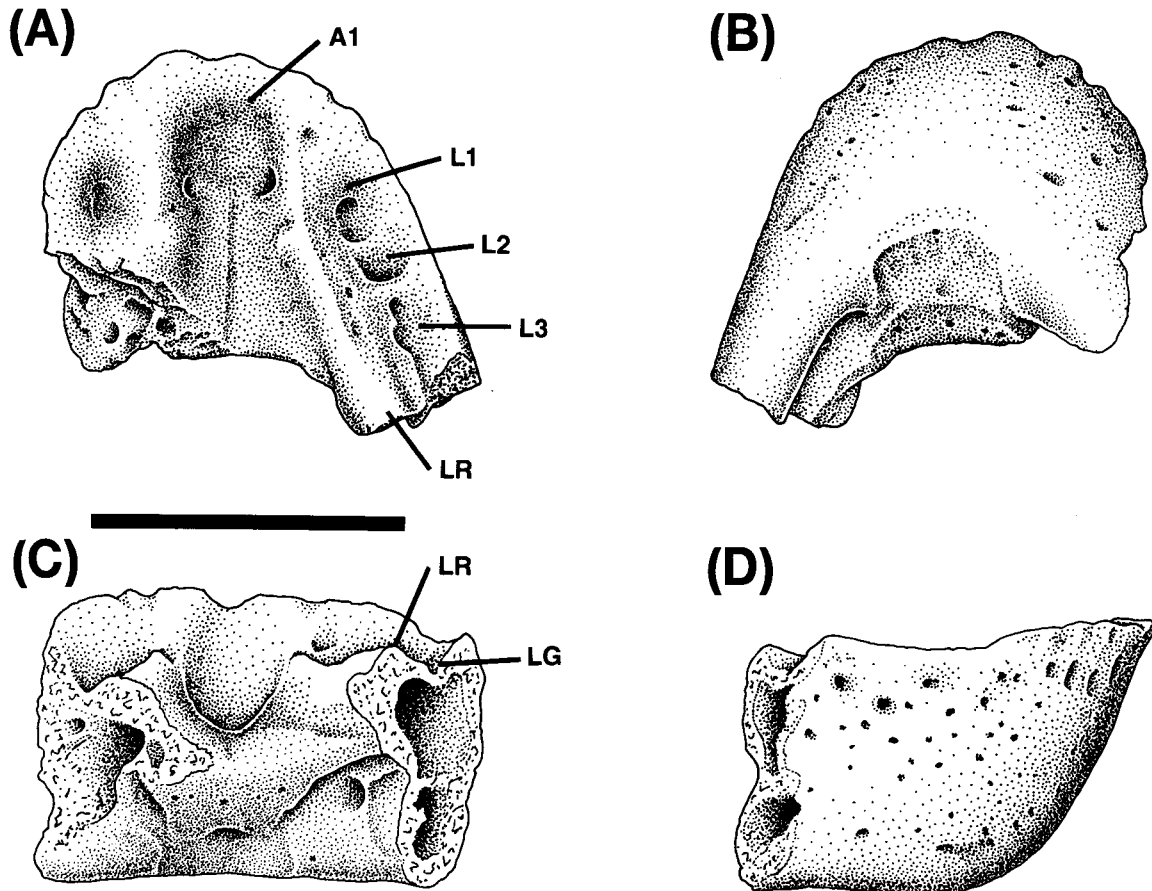
FIG. 11. *Caenagnathasia martinsoni*, holotype (CMGP 401/12457). Dentaries in (A) dorsal, (B) ventral, (C) posterior, and (D) right lateral aspects. For explanation of abbreviations, see Fig. 1. Scale bar = 10 mm.

side of the jaw are arranged in two rows that converge and meet at the front. The larger foramina encircle smaller ones that are scattered across the lateral surface of the dentary. No foramina emerge from the anterior surface of the mandible along the midline (Fig. 11B). At the back of the lateral surface of the dentary is a smooth-walled depression pierced by a relatively large anteromedially directed foramen (Fig. 12B). There is a well-defined depression on the symphysis for insertion of the genioglossus muscle (Fig. 11B), from which a shallow trough passes posterolaterally to join the Meckelian groove. The smooth bone behind the genioglossus depression is pierced by several small foramina. The lingual surface of the occlusal edge is vertically fluted, although the ridges are less pronounced than in *Caenagnathus*. The fluting is divided into an anterior, midline component and a lateral section. The lateral occlusal grooves arise in the longitudinal groove, which is widest and deepest at its anterior end. Numerous foramina pierce the floor of the lateral groove, connecting it to the hollow interior of the bone. A low rounded lingual ridge extends from the symphysial region to the posterodorsally directed, tongue-shaped flange of the dentary that medially covered part of the ASC complex. There is a symphysial shelf, the dorsal surface of which has a pair of longitudinal vascular grooves that enter foramina anteriorly and are separated by a midline depression. The Meckelian groove is a deep, slitlike trough with a foramen near its anterior terminus. There is a single foramen for the inferior alveolar nerve and internal mandibu-

lar artery (Fig. 12C). The dentaries are hollow beneath the lingual ridges (Fig. 11C), and these spaces connect anteriorly through the symphysis (Fig. 12C). These are all derived characters shared with *Caenagnathus* and presumably other oviraptorosaurs.

The dentaries from Uzbekistan are different from the specimens of *Caenagnathus* in a number of relatively trivial ways, which nevertheless show they represent a different taxon at the generic or higher level. They are hereby designated as *Caenagnathasia martinsoni* (Martinson's new jaw from Asia, named in honour of G.G. Martinson, the eminent specialist of Mesozoic freshwater and brackish-water molluscs). The more complete mandible, CMGP 401/12457, is the holotype. *Caenagnathasia* is much smaller than any other known caenagnathid, with the exception of an unnamed specimen from the Bostobe Formation (probably Santonian) of Kazakhstan figured by Nessov and Khisarova (1988). CMGP 401/12457 and 402/12457 are almost identical in size. No larger specimens of this taxon have been found in Uzbekistan, and fusion between right and left dentaries was complete. These facts suggest, but do not prove, the specimens represent mature individuals. *Caenagnathasia*, therefore, was probably much smaller than *Caenagnathus*. It was from a different continent, and lived about 5 million years earlier. The depression on the posteroventral margin of the symphysis of *Caenagnathasia* is not hourglass shaped as in some (but not all) specimens of *Caenagnathus*. There is no circular pit or notch in the dentary
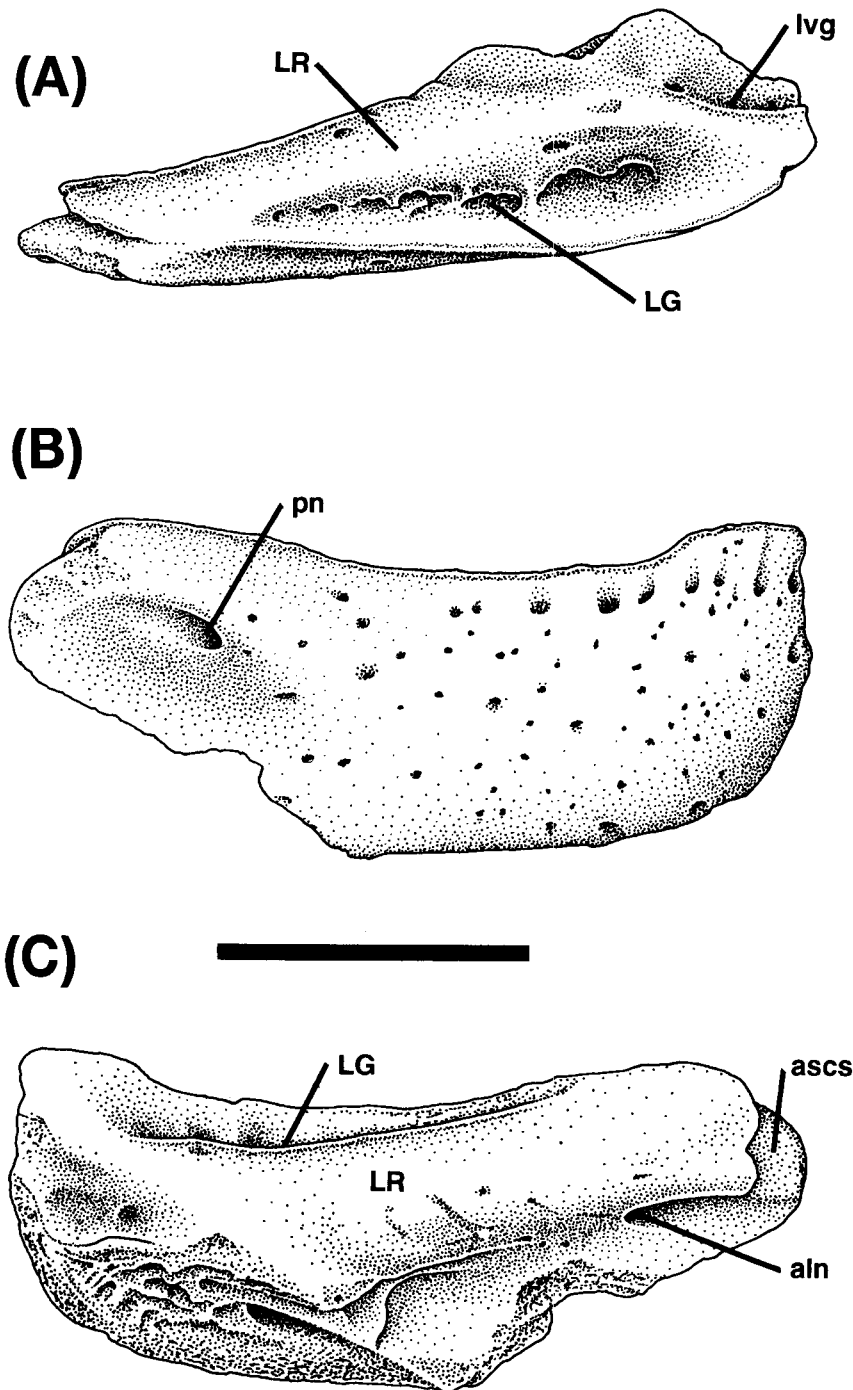
(A)

(B)

(C)

FIG. 12. *Caenagnathasia martinsoni*, CMGP 402/12457. Right dentary in (A) dorsal, (B) lateral, and (C) medial views. Scale bar = 10 mm.

for reception of the anterior tip of the prearticular. Again, this character is variable in *Caenagnathus*. The fluting on the lingual margin of the occlusal edge is not as distinct in the Asian jaws, and there are no toothlike apical projections on the ridges. The first anterior occlusal groove is relatively larger than that of *Caenagnathus*, and the first pair of lateral occlusal ridges do not meet ventrally to separate it from the concavity in the dorsal surface of the symphysial shelf. There is no second anterior occlusal groove, and there are no tubercles on the midline or at the base of the first lateral occlusal ridge. The lateral groove is narrower and deeper, and the foramina in the floor are more obvious. Vascular grooves are more conspicu-

ous on the symphysial shelf of *Caenagnathus*, and specimens of *Caenagnathasia* do not have foramina in the floor of the midline depression. Although the paired dentaries are hollow, the region underneath the anterior occlusal margin seems to be infilled with cancellous bone (Fig. 12C).

Discussion

Caenagnathids were theropods that varied in size from the small (less than 5 kg of adult body weight) *Caenagnathasia* of Uzbekistan and possibly Kazakhstan to the medium-sized (50−75 kg) *Caenagnathus* from North America. The discov-

ery of caenagnathids in upper Turonian beds of Uzbekistan and in Maastrichtian rocks of South Dakota shows that this family lived throughout the Late Cretaceous. Caenagnathids, like ceratopsids (Nessov et al. 1989), lived on the western coastal plains of Asia during Turonian times and the coastal plains of North America during Campanian and Maastrichtian times, but are absent from the productive Campanian beds of China and Mongolia. It is possible caenagnathids were replaced in Asia by oviraptorids. However, the well-sampled Campanian sites of Asia represent generally drier, more inland environments, so the separation of caenagnathids and oviraptorids may have been ecological.

The new specimens bring the total number of jaws of *Caenagnathus* discovered in the Judith River Formation of Alberta to seven. An isolated parietal from the same formation has been tentatively identified as *Caenagnathus* (Currie 1992). Several vertebrae (Gilmore 1924; RTMP 92.36.53) probably belong to *Caenagnathus*. The absence of other bones identifiable as oviraptorosaur is puzzling, especially since the formation has been intensively prospected and thousands of isolated small theropod bones have been collected.

All of the new dentaries from the Judith River Formation are distinct in the symphysial region from the type of *C. collinsi*. CMN 8776 has undergone some crushing and distortion, which could explain the lack of a chin and the longer, shallower symphysis. But computerized tomography (CT) scans (Fig. 7) show that crushing was not severe enough to account for the major differences. One distinction is the presence of a midline ridge in *C. collinsi* towards the front of the symphysial shelf, and this is probably correlated with the absence of an anterior occlusal groove on the midline. The ridge is supported internally by a pillar of cancellous bone (Fig. 7A) that extends to the lower side of the dentary. The lateral grooves extend almost to the tip of the jaw, and the lingual ridges converge and join the midline symphysial ridge. All of the new dentaries from the Judith River Formation differ from the holotype of *C. collinsi* in these characters and are in fact closer to *Caenagnathasia*. Cracraft (1971) established a second species of *Caenagnathus*, *C. sternbergi*, on the basis of a fragmentary articular–surangular–coronoid complex. The holotype of *C. sternbergi* has a jaw articulation with a higher ridge. It also has a relatively shorter but wider medial glenoid, and the ramus immediately in front of the articulation is not as robust as that of *C. collinsi*. These differences might eventually prove to be attributable to individual, ontogenetic, or sexual variation when more specimens are recovered. The South Dakota specimen has a jaw articulation that is even longer and narrow than that of *C. collinsi*. Because it is the largest specimen, it does support the idea that proportions of the jaw articulation may be size related. Regardless of whether or not *C. sternbergi* is valid, however, it is clear that CMN 8776 has a dentary distinct enough from the other Judithian specimens to merit distinction at the specific, and possibly generic, level. None of the new dentaries is associated with a jaw articulation, but it is more conservative to refer them to *Caenagnathus* cf. *sternbergi* than establish a new species.

The smaller dentaries are relatively shorter and wider, suggesting that juvenile caenagnathids had shorter faces relative to the adults, a characteristic of most vertebrates. However, the new dentaries from the Judithian beds do not appear to represent a continuous growth series (Fig. 9), and it is conceivable that they represent more than one species, all of which are distinct from *C. collinsi*. Nevertheless, postmortem

deformation and individual and sexual variation can disrupt ontogenetic trends, and many more specimens would be needed to determine the source of proportional variability.

BHM 2033 is conservatively identified as *Caenagnathus* sp. It is significantly larger than any of the Judithian specimens, and the mandibular articulation is sufficiently different from CMN 2690 and 8776 to suggest that it is neither *C. collinsi* nor *C. sternbergi*.

Caenagnathasia martinsoni from the Bissekty Formation of Uzbekistan is clearly an oviraptorosaur. The front of an oviraptorid jaw, tentatively identified as *O. philoceratops* (S.M. Kurzanov, personal communication, 1990) from Khulsan (Mongolia) in the collections of the Paleontological Institute in Moscow, is considerably larger than the specimens from Uzbekistan, but is immature enough to still have a distinct symphysial suture. The smaller size of the Bissekty specimens, which lack symphysial sutures, and their greater geologic age confirm that they represent a new taxon. The posterodorsal prong of the dentary did not arch high above the level of the beak as it does in *Oviraptor*, *Ingenia* (Barsbold et al. 1990), and *Conchoraptor* (Osmólska 1976; Barsbold et al. 1990), and the overall shape is much closer to *Caenagnathus*. The ASC extended to the level of the anterior margin of the external mandibular fenestra, rather than meeting the dentary above the opening.

Caenagnathid jaws display a large number of oviraptorosaur autapomorphies. There are no teeth, but the margins of the dentaries are raised into a sharp edge, and there is a distinct beak anteriorly. The inner surface of the jaw margin is fluted with rugose, protruding apices on the ridges. The alveolar canal has become the lateral groove, and the crista dentalis has become the lingual ridge. The lateral palatal–maxillary crest (Osmólska 1976) would have opposed the lateral groove, and the more medial palatal crest would have been aligned with the medial edge of the lingual ridge. The sharp margin of the dentaries, and perhaps the symphysial shelf, lateral groove, and lingual crest, would have been covered by an epidermal beak. The dentaries are fused at the symphysis in even the smallest specimens. The articular, surangular, and coronoid coossify. The flexibility of the intramandibular joint may have been reduced by development of extensive sutural contacts on the dentary for the ASC and angular. These contacts are smooth, however, and Barsbold (1977) feels that some sliding and rotation was still possible around the anterodorsal contact between the surangular and dentary. The intramandibular joint has also been braced by the anterior extension of the prearticular. The rodlike prearticular would have prevented the dentary from rotating downward in relation to the back of the jaw, but it could still have rotated upward. Despite the trend towards solidifying the lower jaws, the external mandibular fenestra is relatively larger than it is in other theropods, and the sutures between the dentary and ASC did not fuse up. Overall, it would seem that vertical flexibility of the intramandibular joint was reduced in oviraptorids, but not lost. Although the jaw rami were bowed outward, fusion at the symphysis, coossification of the articular, surangular, and coronoid, vertically extensive contacts between the dentary and the ASC, and the rodlike anterior extension of the prearticular prevented any lateral bending at the intramandibular joint.

The mandible bows laterally midlength and is narrow between the jaw articulations. In oviraptorid, and probably caenagnathid, skulls, the head is positioned over the neck, as is evident from the down-turned orientation of the occipital

condyle. The more upright position of the head would have placed the oesophagus in a more anterior location than in other theropods, and the point of maximum width between the jaws in *Caenagnathus* and other oviraptorosaurs would have been over the entrance to the throat. The distinctive, strong insertion of the genioglossus muscle onto the lower margin of the symphysis is at least partially a reflection of the reorientation of the hyoids and throat.

Another peculiarity of the lower jaws is the jaw articulation. In most theropods, the mandibular portion of the jaw articulation is a pair of concavities separated by a ridge, and is formed by the articular and surangular. In oviraptorosaurs, the ridge is more pronounced and composes most of the articulation, and the two regions that are concave in other theropods are convex. Relative to the length of the jaw, the articulation is larger than it is in other theropods. It is also distinctively raised above the dorsal margin of the jaw. The retroarticular process is relatively long. The peculiar jaw articulation was not a simple hinge joint, but would have allowed the mandible to slide back and forth (Cracraft 1971).

Anteriorly, there is a distinct dorsomedial inflection of the coronoid region of the ASC. This is significant because it marks the anteriorly positioned insertion of the bodenaponeurosis of the adductor musculature, whereas the inflection hints at reorientation of the deep fibers of the M. intermandibularis anterior. The inflected process is positioned over the widest point of the opening between the jaws.

The highly specialized jaw apparatus of oviraptorids has stimulated considerable discussion over the years. Initially it was suggested (Osborn 1924) that oviraptorids were egg eaters because of the association of the type specimen of *O. philoceratops* with a nest of supposed *Protoceratops* eggs. The discovery of a second oviraptorid skeleton (IVPP 090790-1, site 102) on top of a nest of the same type of eggs at Bayan Mandahu (China) may support this idea, or alternatively suggests that both specimens may have been protecting their own nests.

Study of *Caenagnathus* jaws led Cracraft (1971) to conclude that this animal used its jaws for shearing herbaceous material. The bony ridges of the symphysis suggest that the rhamphothecal covering had corresponding ridges, which could have been used to cut and perhaps also crush food. Paul (1988) also concluded that oviraptorids were herbivores at least part of the time. However, oviraptorosaurs are theropods, and it is more logical to assume that they were adapted to eating meat, molluscs, or eggs than to assume that they had become herbivores.

Barsbold (1977) studied the jaw mechanics of oviraptorids, analyzing cranial and mandibular kinesis and force vectors. He concluded that when the jaws closed on food in the front of the mouth, the premaxillary unit would rotate upwards and the dentary downwards. Food bitten farther back would affect the maxillary unit, causing it to rotate up and back. Oviraptorids developed powerful compressional forces by shortening the working length of the jaw and moving the muscle insertions forward. He concluded that oviraptorids were specialized for crushing hard food, and put forward the opinion that molluscs were an appropriate food. This idea was developed further by Barsbold (1983*a*) and Barsbold et al. (1990), who stated that pelecypods are common in freshwater deposits where some of the skeletons were found. There are a number of problems with this hypothesis. Force-vector analysis was done on the basis of schematic drawings and did not take into

account the fact that the sharp-edged lower jaws do not directly oppose the lateral maxillary unit of the upper jaws. The slender posterodorsal process of the dentary above the external mandibular fenestra could not have withstood the forces imposed by biting a hard-shelled item, so the bite must have been restricted to the front of the mandible. The symphysial region of *Oviraptor* is more limited than in caenagnathids, but is still thin-walled and probably pneumatic (S.M. Kurzanov, personal communication, 1990). Animals specialized for crushing molluscs generally have flat platelike teeth or wide crushing plates in both upper and lower jaws. Finally, it is noteworthy that pelecypods are not found in the semiarid to arid depositional environments of Bayn Dzak (Mongolia) or Bayan Mandahu (China), where oviraptorids are no rarer than any other theropods.

A similar force-vector analysis by Smith (1992) concluded that the jaws behaved in a similar manner as ceratopsids, with strong shearing forces. He concluded that *Oviraptor*, despite an absence of batteries of closely spaced teeth or equivalent grinding–crushing surfaces, had a diet similar to that of *Triceratops* and was a herbivorous theropod. As in the earlier study, the force-vector analysis was conducted using two-dimensional schematic drawings and did not take into account that the only opposing jaw surfaces were between the premaxilla and the symphysial region of the lower jaw.

The fused dentaries of *Caenagnathus* formed a bilaterally narrow yet vertically deep mandible, with considerable resistance to tension and compression in the vertical plane despite the highly pneumatic interior. The long and broadly rounded lingual ridge passes from the midpoint of the symphysis posterodorsally and slightly laterally to the rim of the dentary, further strengthening the biting region of the jaw. Such a mechanical design enabled *Caenagnathus* to generate a powerful bite along the sharp shearing edges of the rhamphotheca.

The sharp occlusal edge is deepest anteriorly where it opposes the premaxilla, and becomes shallower posterolaterally. The ridges on the inner margin of the edge can bear small but pronounced tuberculate projections. The keratinous beak possibly emphasized the ridges and grooves. However, it is also possible that the fluting simply strengthened the attachment of the beak and was not visible externally at all. The symphysial shelf is concave on the lingual (dorsal) surface in *Caenagnathus* cf. *sternbergi* and *Caenagnathasia*. In *C. collinsi*, there is a longitudinal midline ridge on the symphysial shelf, supported internally by a pillar of bone. Vascular canals on the medial surface of the lingual ridge of RTMP 92.36.309 and both specimens of *Caenagnathasia* suggest that the keratinous bill may have covered this surface. It appears that the occlusal edge, symphysial shelf, lateral groove, and lingual ridge may all have been contributed directly to the processing of food.

Although caenagnathid skulls are unknown, the jaws are structurally similar enough to those of oviraptorids to suggest the two groups had the same kinds of cranial specializations. The oviraptorid premaxilla is short, but very deep, and the nostrils are placed high on the head. There would have been a deep, powerful bill, which in opposition to the symphysial beak would have produced a strong nipping bite. However, the maxilla and jugal of oviraptorids are reduced (Osmólska 1976; Barsbold 1977), and there is no opposing occlusal edge laterally. A medial process of the maxilla plus the palatine, ectopterygoid, and pterygoid form a longitudinal bar of bone (Osmólska 1976) that would have inserted into the lateral

groove of the lower jaw between the lateral occlusal margin and the lingual ridge. Ridges on the palatal shelf of the pre-maxilla, maxilla, and vomer would have arched over the symphysial shelf of the dentaries. A pair of toothlike projections, the maxillary "teeth" of Osmólska (1976) and Barsbold (1981), would have extended deep into the opening between the jaws. Posteriorly, the pterygoids form broad bars that are firmly attached to both the braincase and the quadrates. Like the maxillary teeth these palatal bars would have protruded ventrally below the upper margin of the mandible.

The palatal ridges, and the opposing symphysial shelf, lateral groove, and lingual ridge of the lower jaws, possibly were used to crush food. However, the ridges are hollow tubes that would not have been well adapted to point loading, and their smooth surfaces suggest they were not adapted for grinding food either.

The shape of the mandible, bowed laterally at midlength, would prevent the jaws from anteroposterior sliding when closed. In dorsal or ventral aspect (Figs. 1 and 9), the jaws are almost as narrow at the back as they are immediately behind the symphysis. The widest point between the jaws would have marked the entrance of the throat. This is characteristic of the jaws of Caenagnathus, Conchoraptor (specimen identified in Osmólska 1976 as Oviraptor, but renamed by Barsbold in 1986), and probably all oviraptorosaurs. The skull flares laterally to produce a relatively large subtemporal fenestra (Barsbold 1977).

The upright orientation of the head, the position of the throat beneath the middle of the jaws, the high lateral margins of the lower jaws, and the insertion of the "upper jaws" between the lower jaws all suggest a mechanism whereby the food is being pushed down the throat. The pushing action would have been enhanced by the mandible sliding back and forth using the specialized jaw joints. Unlike most theropods, the jaws could not expand laterally and would have limited the size of the food being ingested. The presence of a downward-projecting tooth from the centre of the palate in Conchoraptor (Osmólska 1976; Barsbold 1986) and the reinforced ridge in the middle of the symphysis of C. collinsi are reminiscent of the "egg teeth" (specialized hypapophyses) in the throat of the egg-eating snake Dasypeltis scaber (Gans 1952). This snake lives exclusively on eggs, which it ingests whole. By breaking the shell after an egg enters the throat, none of the contents are lost. The jaws of oviraptorosaurs seem to be marvellously well adapted for processing eggs, which could have been pushed to the wide region in the centre of the jaws, where they would have been broken by the egg teeth and lateral ridges. The high margins of the jaws would have prevented loss of the contents of the eggs. The highly vascularized concavity on the postero-lingual surface of the symphysial shelf in all caenagnathid jaws might indicate the presence of a tongue that could have been used to manipulate the food and help prevent fluid loss. Eggs are common at sites in China and Mongolia where oviraptorids have been discovered, but are not found associated with caenagnathids in Asian and North American localities. These differences are the result of preservational biases, and in neither case can we be sure that eggs were available throughout the year as a steady source of food for oviraptorosaurs.

The diet of oviraptorosaurs cannot be determined with certainty at this time. The shape of the jaws, the position of the throat, and the presence of egg teeth on the palate may indicate that the jaws were adapted for eating eggs. However, that does not mean the diet was restricted to eggs. The sharp-edged rhamphotheca at the front of the jaws were capable of producing a strong nipping bite, suggesting that eggs were not the only source of food. Although the jaws were powerful, they were not well adapted for crushing molluscs or for grinding plant material. Given the close relationship to dromaeosaurids and other theropods, and the fact that an oviraptorid skeleton shows none of the adaptations of typical herbivores, it seems unlikely that they had become herbivores. The powerful nipping bite may have allowed them to cut up smaller prey, which then would have been swallowed without further processing. The rhamphotheca (which are not preserved on any specimen) may also have been adapted for tearing large pieces of flesh from other animals, although the width of the front of the jaws argues against this.

Barsbold (1981) listed six ways to distinguish caenagnathid and oviraptorid jaws. The jaws of all known oviraptorids, including Oviraptor (Barsbold et al. 1990), Conchoraptor (specimen described in Osmólska 1976), and Ingenia (Barsbold et al. 1990), are very deep when compared with Caenagnathus and Caenagnathasia. The curvature of oviraptorid jaws rises in the dentary behind the symphysial region, and with the exception of a short region near the front, the upper margin of the dentary is convex in lateral view. The external mandibular fenestra is large in both families, but it is higher and more anteriorly located in oviraptorids. Because of the difference in position of the fenestra, the coronoid process is positioned above the back of the opening in oviraptorids, and over the middle of it in caenagnathids. A prong from the ASC complex invades the external mandibular fenestra from behind in all three oviraptorid genera, but not in Caenagnathus. The dentary forms the anterodorsal, anterior, and anteroventral margins of the oviraptorid external mandibular fenestra, but is excluded from the dorsal margin by the ASC in Caenagnathus and Caenagnathasia. Barsbold (1981) also pointed out that the symphysis of caenagnathids is relatively much longer. None of the newly discovered specimens has a symphysial region as long as the holotype of C. collinsi, and the symphysis of the smallest specimen is not significantly longer than that of Oviraptor (PIN juvenile). This character should be used with caution.

Currie and Russell (1988) speculated on the basis of size, frequency of recovery, and range of variation that the North American elmisaurid Chirostenotes might be synonymous with Caenagnathus. Since the publication of their paper, additional elmisaurid and caenagnathid specimens have been recovered from Judithian and Lancian beds of North America. However, elmisaurids are still only known from postcranial material (Currie 1990), and caenagnathids from isolated cranial, mandibular, and now caudal specimens. Elmisaurid sacrals have pleurocoels, which suggests that they may have had pneumatic caudals like those of oviraptorids and, apparently, caenagnathids. However, the metatarsi of Chirostenotes and Elmisaurus (Currie 1990) are fundamentally different from those of oviraptorids (Barsbold et al. 1990) in that the flexor surface is more arched, the third metatarsal is proximally pinched, and the second to fourth metatarsals tend to coossify. Given the strong similarity between caenagnathid and oviraptorid jaws, it seems unlikely that foot structure would be as different as it is between elmisaurids and oviraptorids. There are also fundamental differences between elmisaurid and oviraptorid mani, although there are similarities too, such as the presence of a distinct "lip" on the extensor surface of each manual ungual (Currie and Russell 1988). The discovery of caenagnathids in Uzbekistan increases the probability that

elmisaurids and caenagnathids might be synonymous, because both families are now known from both continents.

Acknowledgments

Barsbold, R. 1976. On a new Late Cretaceous family of small theropods (Oviraptoridae fam.n.) of Mongolia. Doklady Akademii Nauk SSSR, **226**: 685–688. (In Russian.)

Barsbold, R. 1977. Kinetics and peculiarity of the jaw apparatus of Oviraptors (Theropoda, Saurischia). Transactions, Joint Soviet–Mongolian Geological Expedition, Vol. 4, pp. 37–47. (In Russian.)

Barsbold, R. 1981. Toothless carnivorous dinosaurs of Mongolia. Transactions, Joint Soviet–Mongolian Paleontological Expedition, Vol. 15, pp. 28–39. (In Russian.)

Barsbold, R. 1983a. Carnivorous dinosaurs from the Cretaceous of Mongolia. Transactions, Joint Soviet–Mongolian Paleontological Expedition, Vol. 19, pp. 5–120. (In Russian).

Barsbold, R. 1983b. On some avian features in the morphology of theropods. Transactions, Joint Soviet–Mongolian Paleontological Expedition, Vol. 24, pp. 96–103. (In Russian).

Barsbold, R. 1986. Theropod dinosaurs: Oviraptors. *In* Herpetological investigation in the Mongolian People's Republic. Institute of Evolutionary Morphology, U.S.S.R. Academy of Sciences, Collected Scientific Transactions, pp. 210–223. (In Russian.)

Barsbold, R., Maryanska, T., and Osmólska, H. 1990. Oviraptorosauria. *In* The Dinosauria. Edited by D.B. Weishampel, P. Dodson, and H. Osmólska. University of California Press, Berkeley, pp. 249–258.

Cracraft, J. 1971. Caenagnathiformes: Cretaceous birds convergent in jaw mechanism to dicynodont reptiles. Journal of Paleontology, **45**: 805–809.

Currie, P.J. 1990. The Elmisauridae. *In* The Dinosauria. Edited by D. Weishampel, P. Dodson, and H. Osmólska. University of California Press, Berkeley, pp. 245–248.

Currie, P.J. 1992. Saurischian dinosaurs of the Late Cretaceous of Asia and North America. *In* Aspects of Nonmarine Cretaceous Geology, Proceedings of the Conference on Nonmarine Cretaceous Correlations, Urumqi, China, 1987. Edited by N.J. Mateer and P.J. Chen. Ocean Press, Beijing, China, pp. 237–249.

Currie, P.J., and Russell, D.A. 1988. Osteology and relationships of *Chirostenotes pergracilis* (Saurischia, Theropoda) from the Judith River (Oldman) Formation of Alberta, Canada. Canadian Journal of Earth Sciences, **25**: 972–986.

Danis, J. 1988. Bibliography of vertebrate palaeontology in Dinosaur Provincial Park. Alberta: Studies in the Arts and Sciences, **1**: 225–234.

Gans, C. 1952. The functional morphology of the egg-eating adaptations in the snake genus *Dasypeltis*. Zoologica, **37**: 209–244.

Gilmore, C.W. 1924. Contributions to vertebrate palaeontology, notes on some unidentified vertebrae. Geological Survey of Canada, Bulletin 38, pp. 9–12.

Madsen, J.H., Jr. 1976. *Allosaurus fragilis*: a revised osteology. Utah Geological and Mineral Survey, Bulletin 109, pp. 1–163.

Nessov, L.A., and Khisarova, G.D. 1988. New data on vertebrates from the Late Cretaceous of Shakh-Shakh and Baybolat (northeastern Aral region). *In* Material on the history of the fauna and flora of Kazakhstan, Vol. 10. Academy of Sciences of Kazakhstan, Alma Ata, pp. 5–14. (In Russian.)

Nessov, L.A., Kaznishkina, L.F., and Cherepanov, F.O. 1989. Mesozoic ceratopsian dinosaurs and crocodiles of central Asia. *In* Theoretical and Applied Aspects of Modern Paleontology, Proceedings of the 33rd Session of the All-union Paleontological Society. Edited by T.N. Bogdanova and L.I. Khozatsky. Nauka Publishers, St. Petersburg, Russia, pp. 144–154. (In Russian.)

Oelrich, T.M. 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). Museum of Zoology, University of Michigan, Miscellaneous Publication 94.

Osborn, H.F. 1924. Three new Theropoda, *Protoceratops* zone, central Mongolia. American Museum Novitates, No. 144, pp. 1–12.

Osmólska, H. 1976. New light on the skull anatomy and systematic position of *Oviraptor*. Nature (London), **262**: 683–684.

Paul, G.S. 1988. Predatory dinosaurs of the world. Simon and Schuster, New York.

Smith, D. 1992. The type specimen of *Oviraptor philoceratops*, a theropod dinosaur from the Upper Cretaceous of Mongolia. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **186**: 365–388.

Sternberg, R.M. 1940. A toothless bird from the Cretaceous of Alberta. Journal of Paleontology, **14**: 81–85.