群馬県立自然史博物館研究報告(15)：1－17, 2011
Bull.Gunma Mus.Natu.Hist.(15)：1－17, 2011

Original Article

A sub-adult growth stage indicated in the degree of suture co-ossification in *Triceratops*

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Abstract：A *Triceratops* specimen, GMNH-PV 124, excavated from the Hell Creek Formation, South Dakota, is composed of nearly complete skull elements, axial skeleton, and partial limb elements. Co-ossification of the skull elements and the scapula-coracoid contact are not finished and hence the specimen is sub-adult. However, co-ossification has been started or finished among the occipitals, supraorbital horn cores, and parietal, between the rostrum and premaxillae, between the epinasal and nasals contacts, the first to third cervical vertebrae, and sacral vertebrae.

Key Words：Hell Creek Formation, South Dakota, Ceratopsia, *Triceratops*

Introduction

Triceratops（Ceratopsia: Ceratopsidae）is known for its rich fossil record from fluvial plain deposits of western North America, from Alberta and Saskachewan in the north to Colorado in the south, adjacent to the Western Interior Seaway during the Maastrichtian（Hatcher et al., 1907; Dodson, 1996）. More than 50 skulls and a number of postcranial skeletons have been excavated from this region（Dodson, 1996）. In *Triceratops,* several parts of th;keletal elements co-ossify during ontogeny such as skull elements, syncervicals（co-ossified cervicals）, synsacrum（co-ossified dorsals, sacrals, and caudals）, and scapulocoracoid（Hatcher et al, 1907; Horner and Goodwin, 2008; Tsuihiji and Makovicky, 2007）.

Several ontogenetic stages from infant to adult have been recognized in this animal based on the deformation and timing of co-ossification of the cranial elements（Horner and Goodwin, 2006, 2008; Scannella and Horner, 2010）. Although abundant fossil records are present, little information on postcranial associated with cranial elements is available, and thus, the timing of co-ossification of the postcranial elements during the growth stage is yet to be investigated（e.g., Marsh, 1891, 1898; Hatcher et al., 1907; Ostrom and Wellnhofer, 1986; Fujiwara, 2005, 2009）. The complete growth process of this animal is understood when the co-ossification patterns and timings of postcranial elements are understood as well as those of associated cranial elements.

In 1992, a new *Triceratops* specimen, GMNH-PV 124, containing cranial and postcranial elements was excavated from the Hell Creek Formation in Harding County, South Dakota（45°50’N 103°54’W）by Michael Triebold（Triebold Paleontology Inc.: Fig. 1B-D）. The specimen was subsequently purchased by the Gunma Museum of Natural History in 1996.

The skeletal elements were spread approximately 18 m long in the northeast-southwest direction（Fig. 1A）. Bite marks were seen on some ribs and the left coracoid. Theropod and crocodilian teeth were scattered around the ribs.

The specimen is considered as a sub-adult, since co-ossification of the cranial and postcranial elements is incomplete. This study describes GMNH-PV 124, emphasizing its co-ossification patterns. Since many detailed descriptions of this genus are present（e.g., Hatcher et al., 1907; Forster, 1996a, b）, we only provide the detailed descriptions of skeletal elements which has been co-ossfied or may co-ossify in the growth process with the adjacent skeletal elements. Measurements shown in the figures were taken by caliper（< 200 mm; Mitutoyo Co., Ltd.）and tape measure（> 200 mm）.

Co-ossification pattern of GMNH-PV 124 was compared with that of other sub-adult and adult *Triceratops* specimens that contained both cranial and postcranial elements: YPM 1821 and 1822（Hatcher et al., 1907）, and NSM PV 20379（Garstka and Burnham, 1997; Fujiwara, 2005, 2009）,

Abbreviations

BSP; Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany
GMNH; Gunma Museum of Natural History, Gunma, Japan
NMNH; Smithsonian Institution, National Museum of Natural History, Washington, D.C., U.S.
NSM; National Museum of Nature and Science, Tokyo, Japan（formerly National Science Museum）
YPM; Peabody Museum of Natural History, Yale University, New Haven, U.S.

受付：2010年12月20日，受理：2011年2月10日

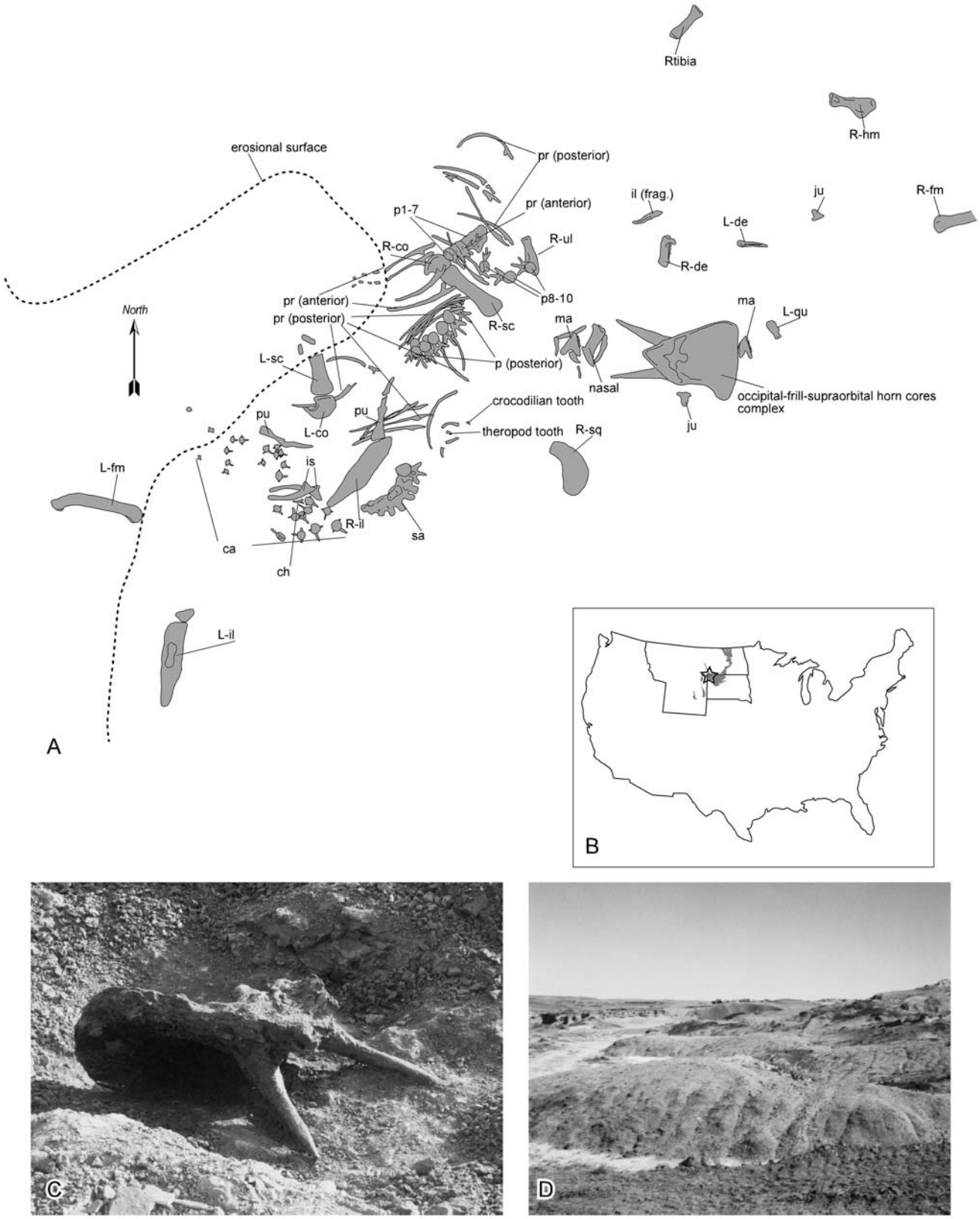


Fig. 1. A) Site map of GMNH-PV 124, B) the locality map of the site shown in asterisk, and C) photographs of the occipital-frill-supraorbital horn cores complex and D) locality during the excavation taken by M. Triebold (Triebold Paleontology Inc.). Grey area in B indicates the distribution of the Hell Creek Formation. R- and L- before the following abbreviations indicate the right and left, respectively. Abbreviations: ca, caudal; ch, chevron; co, coracoid; de, dentary; fm, femur; hm, humerus; il, ilium; is, ischium; ju, jugal; ma, maxilla; p*n*, *n*th presacral; pr, presacral rib; pu, pubis; qu, quadrate; sa, sacrum; sc, scapula; sq, squamosal; ul, ulna.

Description

Order Ornithischia Seeley, 1888
Suborder Ceratopsia Marsh, 1890
Family Ceratopsidae Marsh, 1888
Subfamily Chasmosaurinae Lambe, 1915
Genus *Triceratops* Marsh, 1889
Triceratops sp.
(GMNH-PV 124)

The specimen includes an incomplete skull (rostrum, premaxillae, maxillae, nasals, epinasal, jugals, orbital elements with two supraorbital horncores, occipitals, and frill), an incomplete mandible (dentaries), axial skeletal elements (20 of 21 presacrals, complete synsacrum, 12 caudals, 29 presacral ribs, and two chevrons), partial right (scapula, coracoid, humerus, and ulna) and left (scapula and coracoid) forelimbs, right and left pelvic girdles, and right (tibia) and left (femur) hindlimbs (Fig. 1A). Although most of the skeletal elements were disarticulated, they are assumed to be of the same individual because the skeletal elements were concentrated in a small area (approximately 18 m long and 6 m wide), no other skeletal elements of ceratopsids were found in this locality, no overlaps of skeletal elements except for a fragment of the right ilium, and the size of each elements are agreeable to be from the one individual.

The specimen was identified to belong to *Triceratops* on the basis of the following characteristics (Ostrom and Wellnhofer, 1986; Dodson and Currie, 1990; Forster, 1990; Sampson, 1995; Forster, 1996a, b; Lehman, 1996; Chinnery and Weishampel, 1998; Holmes et al., 2001; Makovicky, 2001; Dodson et al, 2004; Sampson et al., 2010). It possesses three horn cores–a relatively short core on the rostral end of the nasals and a pair of relatively long cores above the orbits. It has a broad frill consisting of parietals and squamosals extending caudally from the skull roof, with the squamosals extending to the posterior frill margin. The parietal fenestrae are absent. Large external nares and an edentulous beak are formed by the rostrum and premaxillae at the rostral end of the upper jaw. The jugals extend ventrally and overlap the quadrate, and the dentary is massive with a strong laterally placed coronoid process. The synsacrum comprises 10 vertebrae including caudal dorsals and cranial caudals as described in Ostrom and Wellnhofer (1986), and the first three cervicals are co-ossified as in Tsuihiji and Makovicky (2007).

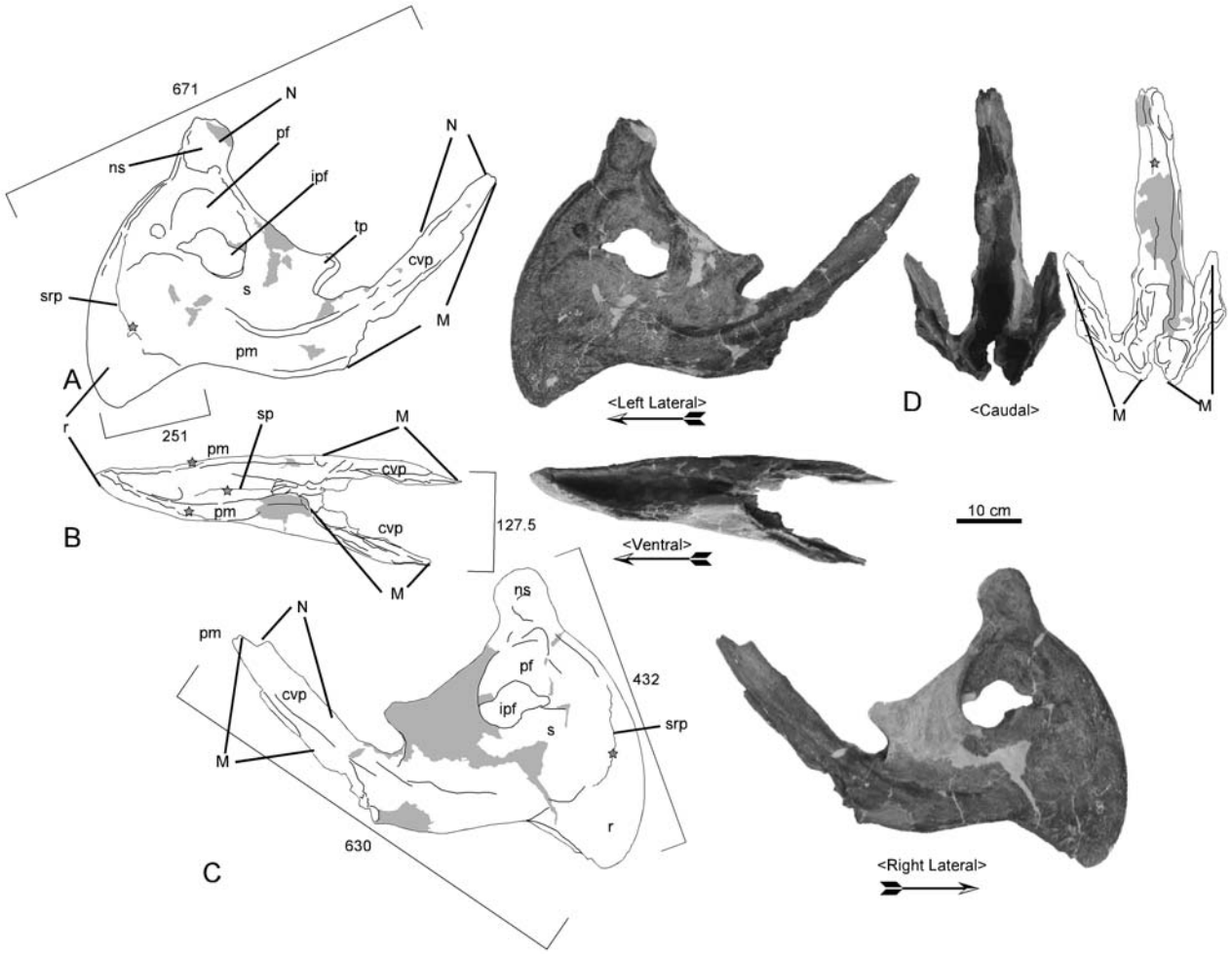


Fig. 2. Premaxillae-rostrum complex of GMNH-PV 124 in A) left lateral, B) ventral, C) right lateral, and D) caudal views. Arrows indicate the rostral orientations. Gray area indicates the restored part. Abbreviations: cvp, caudoventral process; ipf, interpremaxillary fenestra; M, maxillar contact; N, nasal contact; ns, nasal strut; pf, premaxillary fossa; pm, premaxilla; r, rostrum; s, septum; sp, suture between premaxillae; srp, suture between rostrum and premaxilla; tp, triangular process. Gray asterisks indicate fused suture.

Cranial skeleton

The cranial element is separated into more than eleven portions: the rostrum-premaxillary complex; a pair of maxillae; the nasals-epinasal complex; the distal portions of the jugals; the left quadrate; the left squamosal; a complex of the supraorbital horn cores, frill, and occipitals; and a pair of dentaries.

The rostrum and premaxillae are well preserved (Fig. 2). The rostrum is a triangular bone in both lateral and ventral views and articulates with the premaxillae at the caudal surface (Fig. 2A,C). The premaxillae are compressed laterally to form a broad septum, and a straight caudoventral process extends posteriorly and dorsally from the caudoventral edge of the oral margin (Figs. 2A,C). A triangular process extends caudally from the caudoventral margin of the septum (Fig. 2A). A depression is present in the septum, and a fossa (interpremaxillary fossa) with an accessory strut on its rostral edge opens between the premaxillae in the ventral half of the septum (Fig. 2A,C). The premaxillae are co-ossified with each other at the medial surfaces (Fig. 2B). The entire rostral margin of the premaxillary complex is convex and co-ossifies with the rostrum; sutures between the premaxillae and rostrum are completely closed. A short tenon-like process extends dorsally from the summit of the septum forms a non-rugose facet, which inserts into a mortise-like facet at the anterior extremity of the nasals (Fig. 2A,C). The ventral and dorsal margins of the caudoventral process possess grooved facets for the rostral margins of the maxillae and the caudoventral process of the nasals, respectively. The facets did not show any signs of co-ossification to the maxillae or to the nasals (Fig. 2).

Laterally, maxillae are triangular bones that are well preserved (Fig. 3). Caudally, each maxilla produces three branches–dorsolateral, dorsomedial, and caudal branches. A facet for the ventral margin of the premaxillary caudoventral process extends from the rostrodorsal margins of both the dorsolateral and dorsomedial branches (Fig. 3B). A deep maxillary cavity opens between these two branches (Fig. 3A,E,F). In the lateral view, facets for the rostral extensions of the jugals are concave at the end of the dorsolateral branches (Fig. 3B). The caudolateral margins of the dorsomedial branches are articular facets for the lacrimals and nasals (Fig. 3B). The medial aspects of the dorsolateral branches form facets for the palatine (Fig. 3E). The caudomedial end of the dorsomedial branches and the medial side of the end of the caudal branches are flattened to form facets for the pterygoid (Fig. 3E). None of these facets are

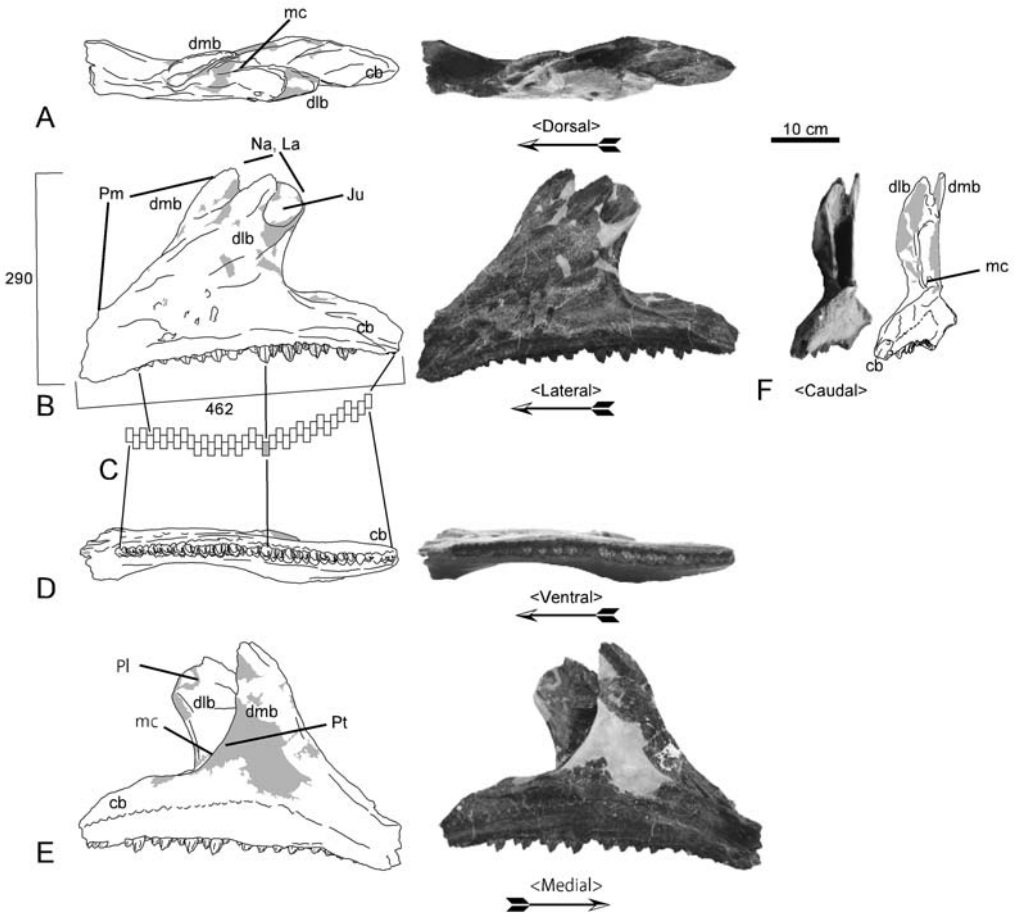


Fig. 3. Left maxilla of GMNH-PV 124 in A) dorsal, B) lateral, D) ventral, E) medial, and F) caudal views. Arrows indicate the rostral orientations. Gray area indicates the restored part. C) The stepwise alignment of the tooth row is also shown in a simplified diagram of a row of boxes, correlated with the illustrations of the left maxilla in lateral and ventral views. Each box indicates the superficial teeth. The more emerged teeth are shown below, and the more receded teeth are shown above. The box filled with gray indicates the worn teeth, and the non-filled box indicates unworn teeth. Abbreviations: cb, caudal branch; dmb, dorso-medial branch; dlb, dorso-lateral branch; Ju, jugal contact; La, lacrimal contact; mc, maxillary cavity; Na, nasal contact; Pl, palatine contact; Pm, premaxilla contact; Pt, pterygoid contact. The maxilla is not fused to any other elements.

co-ossified with the adjacent bones. The alveolar (oral) margin is nearly straight. Thirty-six teeth are closely packed together and aligned in a longitudinal direction (Fig. 3B,C). The teeth align stepwise: the tooth emerges (or recedes) half above (or below) the adjacent tooth. Some teeth show attrition at their tips, while the remaining teeth are unworn, suggesting that most of the functioning teeth are not preserved (Fig. 3C). As in other ceratopsids, replacement teeth are embedded beneath each superficial tooth and, as a whole, forms a dental battery.

Nearly complete nasals and epinasal are preserved (Fig. 4). These three elements are completely co-ossified with each other and together form a semicylindrical bone. An internasal suture is visible only from the internal aspect (Fig. 4D). The epinasal with numerous vessel grooves on its surface is fused at the rostrodorsal end of the nasals, and the suture is indistinguishable on the external surface (Fig. 4A,B,C,E). The rostral and caudal processes extend ventrally from the nasals across the broad and convex dorsal margin of the external nares (Fig. 4A,C,D). A pair of the rostroventral process forms a mortise-like facet which overlaps the dorsal process of the rostrum-premaxillary complex (Fig. 4A,C). The caudoventral processes are relatively long. The rostral margins of the process form the caudal margins of the external nares, and the caudal margins form facets for the caudoventral process of the premaxillae (Fig. 4A,C,D). The nasals are not co-ossified with the premaxillae at these processes. In the dorsal view, the dorsal roof of the nasal complex forms a caudal extension to form a facet for the lacrimals, prefrontals, and frontals. Most of the caudal extension is broken. However, the preserved suture of the articular facet indicates that the nasals are not co-ossified with the adjacent bones in GMNH-PV 124 (Fig. 4B).

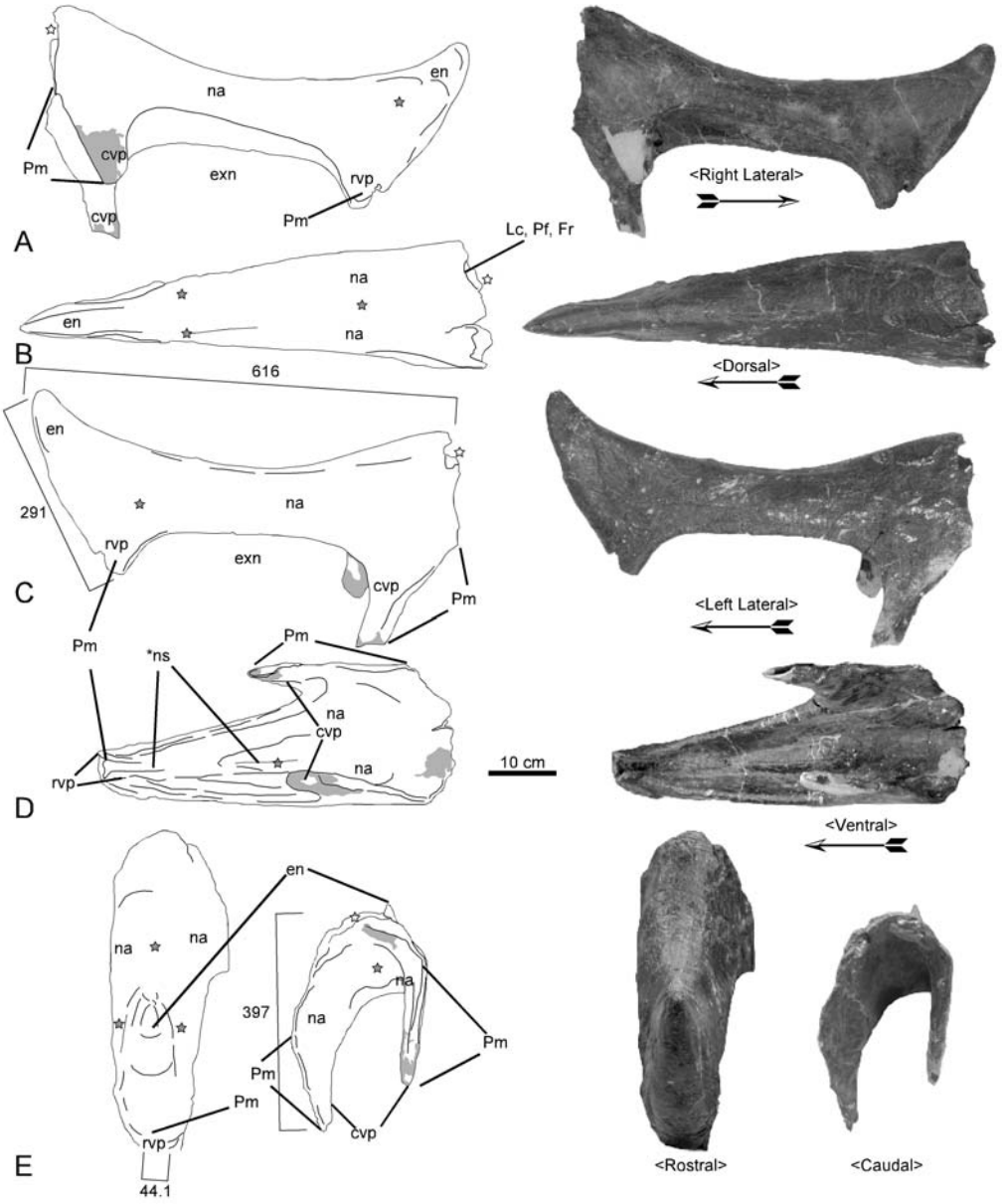
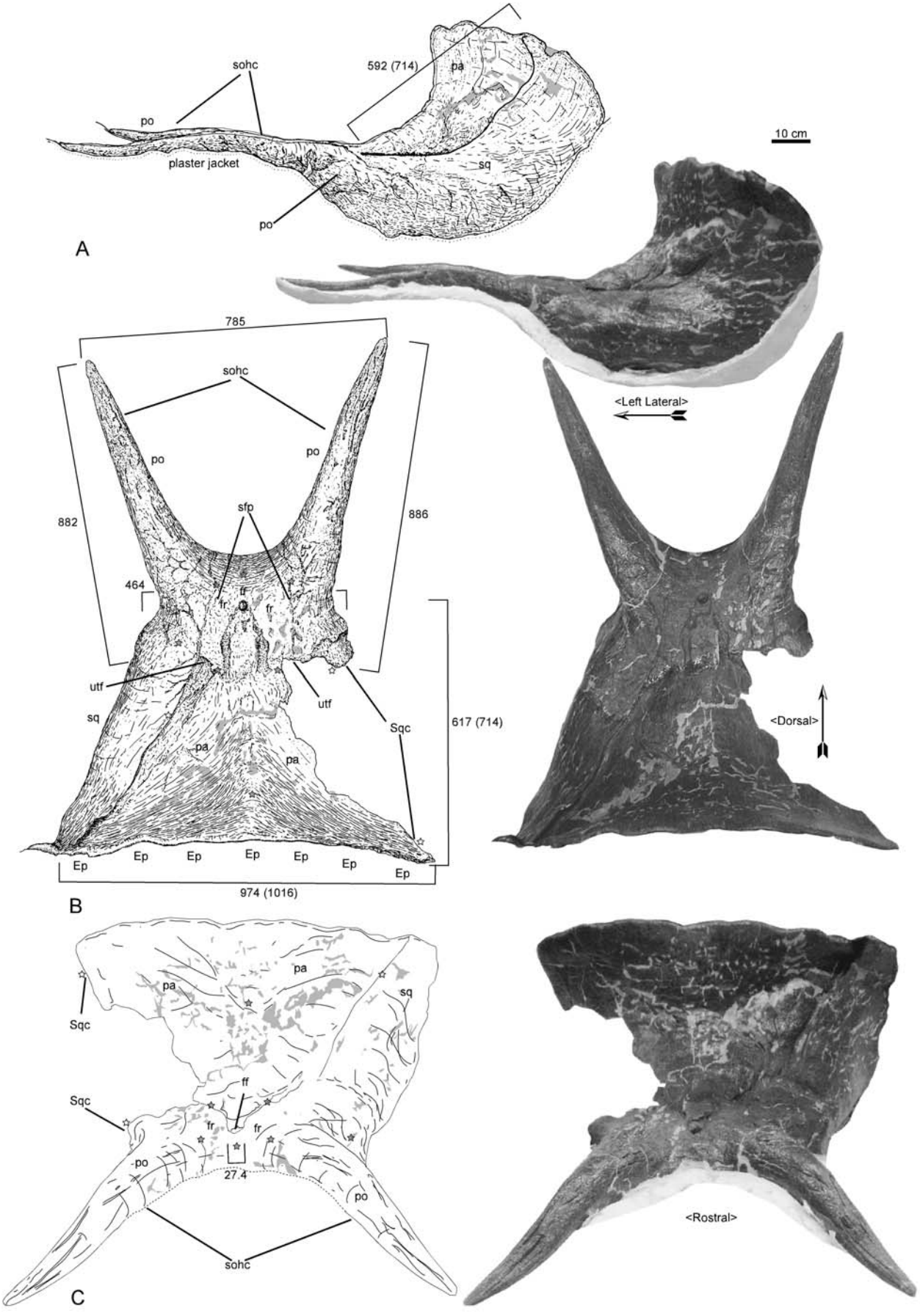


Fig. 4. Nasals-epinasal complex of GMNH-PV 124 in A) right lateral, B) dorsal, C) left lateral, D) ventral, E) rostral and caudal views. Arrows indicate the rostral orientations. Gray area indicates the restored part. Abbreviations: cvp, caudoventral process; en, epinasal; exn, external nares; Lc, Pf, Fr, lacrimal, prefrontal, and frontal contacts; ns, suture between nasals; Pm, premaxillar contact; rvp, rostroventral process. Gray and white asterisks indicate fused and unfused suture or contact, respectively.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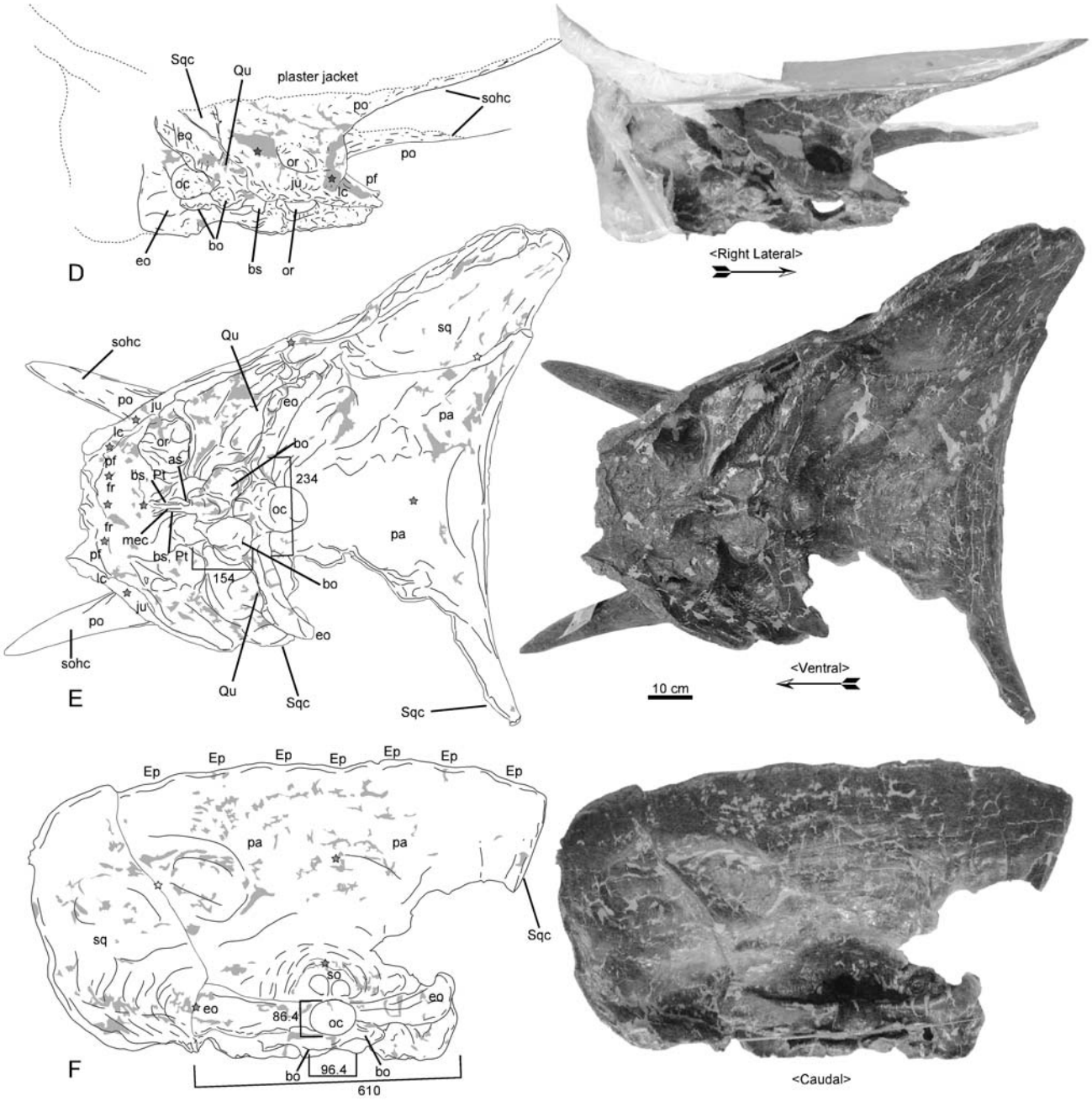

Fig. 5. Occipital-frill-supraorbital horn cores complex of GMNH-PV 124 in A) left lateral, B) dorsal, C) rostral, D) right lateral, E) ventral, and F) caudal views. Arrows indicate the rostral orientations. Gray area indicates the restored part. Non-parenthetical numbers are the lengths in straight lines, and parenthetical numbers are the lengths along the curvatures. Abbreviations: as, alisphenoid; bo, basioccipital; bs, basisphenoid; eo, exoccipital; Ep, epiparietal contact; ff, frontal fontanelle; fr, frontal; ju, dorsal half of the broken jugal; lc, lacrimal; mec, median eustachian canal; oc, occipital condyle; or, orbit; pa, parietal; pf, prefrontal; po, postorbital; Pt, pterygoid contact; Qu, quadrate contact; sfp, suture between frontal and postorbital; so, supraoccipital; sohc, supraorbital horn core; sq, squamosal; Sqc, squamosal contact; utf, upper temporal fenestra. Gray and white asterisks indicate fused and unfused suture or contact, respectively.

Co-ossification is observed in lacrymals, prefrontals, frontals, dorsal portions of the jugals, postorbitals, parietals, left squamosal, and occipital elements (Fig. 5). The occipital elements are compressed dorsoventrally (Fig. 5F). Among the occipital bones, the exoccipitals, basioccipitals, supraoccipital, basisphenoids, and alisphenoids (laterosphenoids) are identifiable (Fig. 5D-F). These occipital bones are co-ossified with each other and no sutures are seen even on the occipital condyle. The occipital complex is co-ossified with the parietals at the dorsal margins of the supraoccipital and exoccipitals, and with the left squamosal at the left lateral margin of the exoccipital (Fig. 5E,F). In the ventral view, the basisphenoids form a pair of ridges across the median eustachian canal (Fig. 5E). A facet for the pterygoid is formed on each ridge, but the pterygoids are not ossified to the occipital complex.

A broad and very flat frill extends caudodorsally above the occipitals (Fig. 5A,B). The frill is composed of the parietals in the middle and squamosals at the sides; the right squamosal is disarticulated from the rest of the frill (Figs. 5B–F and 6). The parietals are co-ossified with each other in the median line and no sutures are observed (Fig. 5B,E,F). In the dorsal view, the parietal complex is triangular and curves dorsally. The caudal margin of the parietals complex is not straight but undulating: seven concavities align in equal intervals along the caudal margin (Fig. 5B,C,F). Locations of these concavities at the margin may correspond to the locations of contacts with the epiparietals (Horner and Goodwin, 2008). No epiparietals are preserved in GMNH-PV 124. The squamosals are long triangular bones, and exceed to the caudal margin of the frill (Figs. 5A,B,E and 6B,C). Each squamosal curves dorsally along its length. In the rostral half, the lateral margins of the squamosals are folded ventrally (Figs. 5A–C,F and 6A,C). The frill, as a whole, forms a

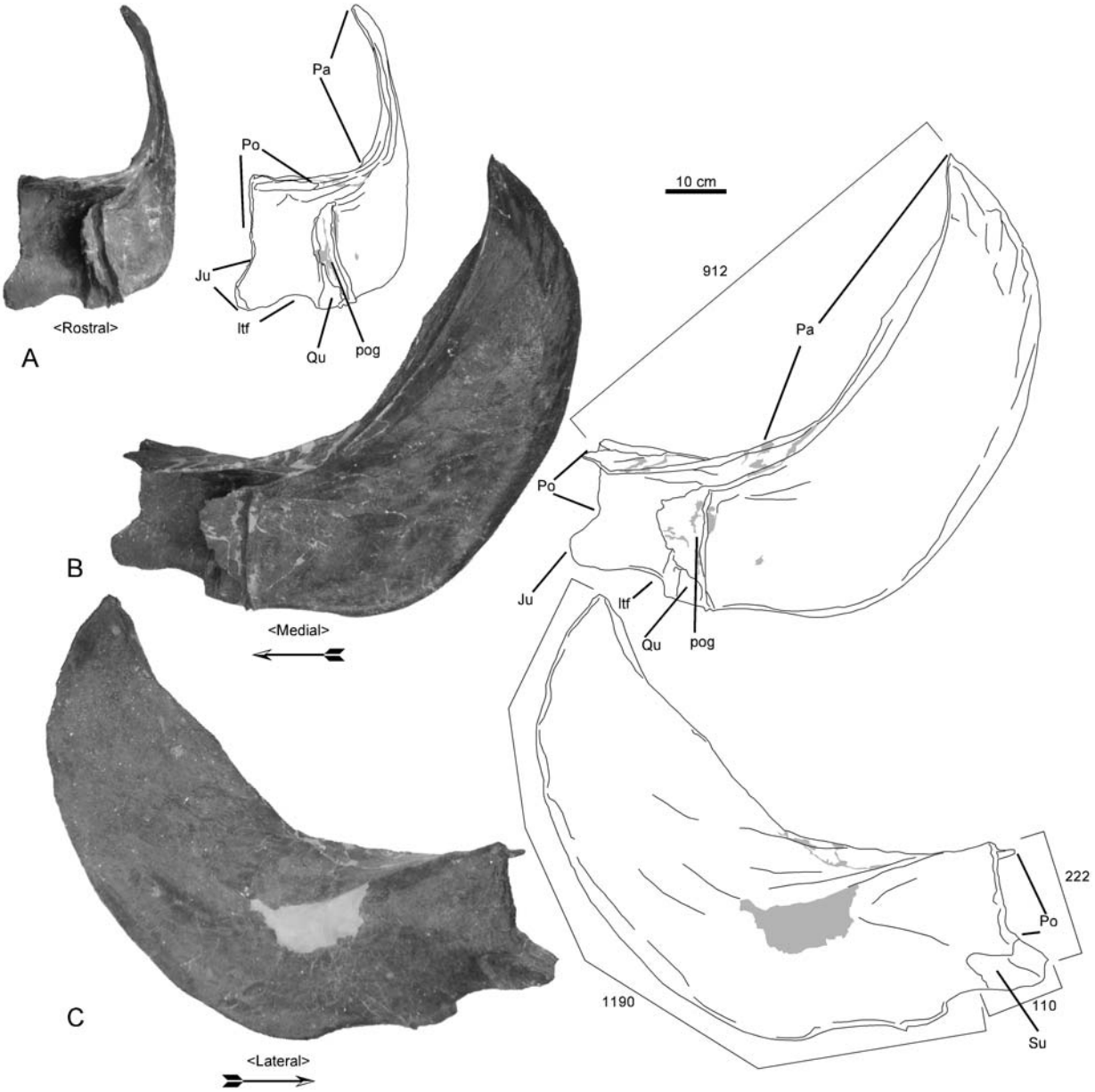

Fig. 6. Right squamosal of GMNH-PV 124 in A) rostral, B) medial, and C) lateral views. Arrows indicate the rostral orientations. Gray area indicates the restored part. Abbreviations: Ju, jugal contact; ltf, lower temporal fenestra; Pa, parietal contact; Po, postorbital contact; pog, paraoccipital groove; Qu, quadrate contact. The right squamosal is not fused to any other elements.

saddle shape (Fig. 5A–C). The co-ossification between the parietals and squamosals is not complete. The squamosal is detached on the right side but attached with the parietal on the left side; the two bones are not co-ossified at least along the caudal half of the suture (Fig. 5B,C,F). The upper temporal fenestrae open rostroventrally at the boundaries of the squamosals, parietals, and frontals (Fig. 5B). The fenestrae continue caudally to the mid portion of the frill as grooves between the parietals and squamosals. The episquamosals are neither preserved nor co-ossified with the squamosals. In the dorsal view, the rostral margins of the parietals are co-ossified with the frontals across grooves extending caudolaterally from frontal fontanelles, which open at the midline of caudal end of the frontals (Fig. 5B,C). The rostral margin of the left squamosal is in contact with the frontal on the medial side and with the postorbital on the lateral side. The contact of the left squamosal with the postorbital and frontal are visible but fused. Two long horns extend rostrolaterally on the postorbitals (Fig. 5A–E). The barrels of the horns are continuous from the lateral folds of the squamosals (Fig. 5A–C). Numerous vessel canals reticulate on the surfaces of the horn cores (Fig. 5A,B). At the base of the supraorbital horns, the postorbital is in contact with the frontal on the medial side. The sutures are observable on the caudal half of the margin, but are completely closed on the rostral half (Fig. 5B,C). In addition, sutures between the frontals are completely closed. Relatively small orbits open laterally beneath the base of each horn core (Fig. 5A,D). The bones surrounding the orbits–lacrimals, prefrontals, frontals, postorbitals, and jugals–are completely co-ossfied with each other at the orbital margin. The rostral margins of the lacrimals, prefrontals, and frontals are more or less broken, and their original sutures are not preserved (Fig. 5D,E). The ventral halves of each jugals are broken (Fig. 5A,B).

Pair of the ventral halves of the jugals, which are isolated from the dorsal halves, are preserved. These two bones are broken horizontally above the line connecting the facets of maxillary and squamosal contacts (Fig. 7). The ventral portion extends

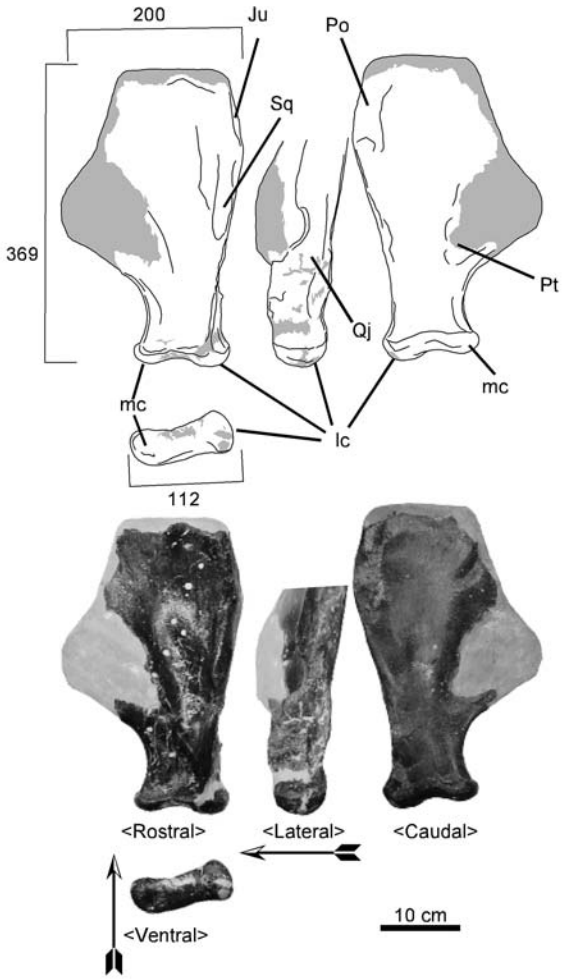

Fig. 8. Left quadrate of GMNH-PV 124. Arrows indicate the rostral orientations. Gray area indicates the restored part. Abbreviations: Ju, jugal contact; lc, lateral condyle; mc, medial condyle; Po, paroccipital contact; Pt, pterygoid contact; Qj, quadratojugal contact; Sq, squamosal contact. The left quadrate is not fused to any other elements.

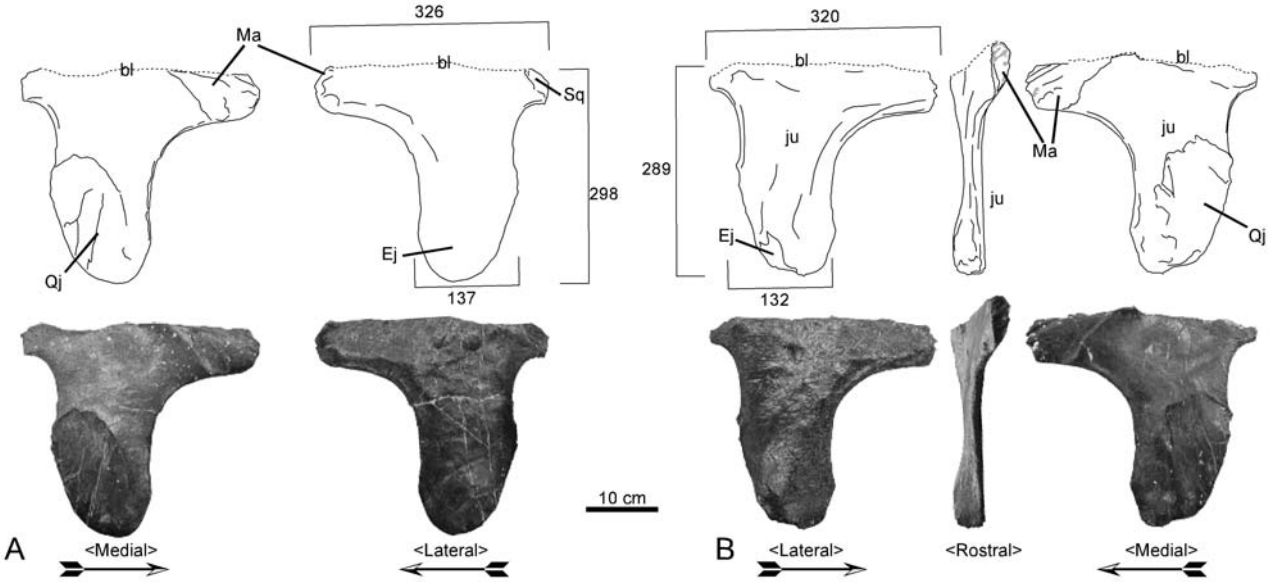

Fig. 7. Ventral portion of A) left and B) right jugals of GMNH-PV 124. Arrows indicate the rostral orientations. Abbreviations: bl, broken line between dorsal and ventral portions; Ej, epijugal contact; ju, jugal; Ma, maxilla contact; Sq, squamosal contact; Qj, quadratojugal contact.

ventrally. A facet for the quadratojugal is present at the medial side of the caudoventral half of the jugal process; the jugal and the quadratojugal are not fused to each other. The epijugals are not preserved. The rostral and caudal processes bear facets for the maxillae and squamosals, respectively. Clear articular surfaces are preserved on both facets.

When complete, a quadrate is a thin plate-like bone with a broad flange extending on its medial side. However, the flange is broken in GMNH-PV 124. The quadrate is in contact with the quadratojugal at the lateroventral edge, with the squamosal at the dorsal margin, and with the pterygoid at the medial surface of the flange (Fig. 8).

The left dentary is completely preserved (Fig. 9). However, the rostral end of the body and the distal end of the coronoid process are not preserved on the right side. The coronoid process extends from the lateral side of the tooth row and protrudes high above the row (Fig. 9A,C,E). The dentary articulates with the angular, surangular, and articular on the caudal margin and with the splenial on the ventral margin (Fig. 9C–F). Articular facets for the predentary and the opposite side of the dentary are located at the rostral and rostroventral margins, respectively (Fig. 9A,C–E). However, both dentaries are not co-ossfied with other mandibular bones. The number of the teeth expressed on the superficial row is 36, the same as in the upper jaw (Fig. 9A,B). The teeth are closely packed together to form a dental battery with two or more replacement teeth beneath each tooth position. The teeth align stepwise as those of the upper jaw. The most expressed teeth project above the alveolar margin. Attrition of the teeth starts after the entire crown emerges above the alveolar margin (Fig. 9B).

Axial Skeleton

Twenty of the 21 presacrals (cervicals and dorsals), a complete synsacrum, 12 caudals, 29 presacral ribs, and one chevron are preserved. The centrums of these vertebrae are completely co-ossified with the associated neural arches.

Parapophyses, facets for capitulums of the associated ribs, appear on the lateral surface of the centrum in the cranial nine of the 21 presacrals (cervicals). Toward the caudal cervicals, the transverse processes increases in length, as the centrums increase in size. The first three cervicals are co-ossified to form a syncervical (Fig. 10: Tsuihiji and Makovicky, 2007). These three vertebrae co-ossify with each other between the adjacent centrum, neural spines, and pre- and postzygapophyses. In GMNH-PV 124, the left interzygapophyseal and intercentral joints between the third and fourth cervicals are clearly detached (Fig. 10C,E). However, the right prezygapophysis of the fourth cervical is closely attached to the postzygapophysis of

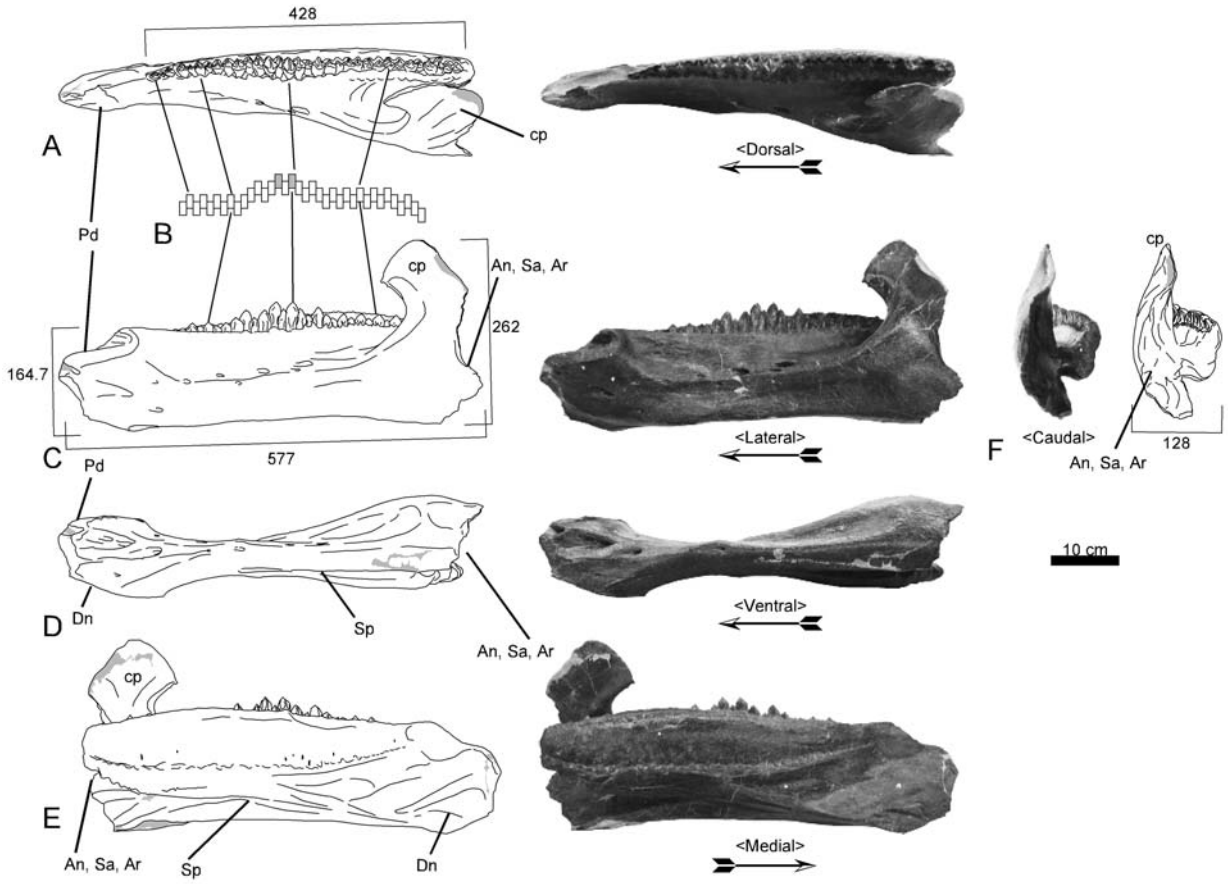

Fig. 9. Left dentary of GMNH-PV 124 in A) dorsal, C) lateral, D) ventral, E) medial, and F) caudal views. Arrows indicate the rostral orientations. Gray area indicates the restored part. B) The stepwise alignment of the tooth row is also shown in a simplified diagram of a row of boxes, correlated with the illustrations of the left dentary in dorsal and lateral views. Each box indicates the superficial teeth. The more emerged teeth are shown above, and the more receded teeth are shown below. The box filled with gray indicates the worn teeth, and the non-filled box indicates unworn teeth. Abbreviations: An, angular contact; Ar, articular contact; cp, coronoid process; Dn, dentary contact; Sa, surangular contact; Sp, splenial contact. The left dentary is not fused to any other elements.

the third, and there is no gap between these zygapophyses (Fig. 10E), although the co-ossification between the zygapophyses is not determined yet. The remaining cervicals do not co-ossify with each other. The diapophyses face caudally in the cranial cervicals, but ventrally in the caudal cervicals.

The proximal portions of the ribs associated with the cervicals branch into two processes, the capitulum and turberculum. The capitulum connects with the parapophysis on the centrum, and the turberculum connects with the diapophysis on the transverse process (Ostrom and Wellnhofer, 1986). Of these branched cervical ribs, the fourth, fifth, eighth, and ninth are identified on the right, and the third, fifth, and seventh to ninth are identified on the left (Fig. 1A). The ribs associated with the third to fifth presacrals are relatively short and extend caudally. The ribs associated with the sixth to eighth presacrals are elongated and extend uncurved in a ventral direction. The seventh and eighth ribs of the series are especially thick, long, and robust.

In the caudal 12 of the 21 presacrals (dorsals), parapophyses appear on the proximal half of the transverse processes. The positions of the parapophyses migrate distally toward the caudal dorsal vertebrae. The cranial-most dorsal is the most robust vertebra of the series and the width of the neural arches narrows toward the caudal dorsals in cranial view. Eleven of the 12 dorsals are preserved in GMNH-PV 124 (Fig. 1A). The craniocaudal relations among them are identifiable on the basis of features of the parapophyseal positions mentioned above, the articulations between the centrums and between the pre- and postzygapophyses, and the description of other Triceratops specimens (NMNH 4842 and BSP 1964 I 458; Hatcher et al., 1907; Ostrom and Wellnhofer, 1986). These dorsals are not co-ossified or articulated with each, so the exact position of the dorsals are not known. Ossified tendons are found along the caudal half of the presacral neural spines in some Triceratops specimens (e.g., BSP 1964 I 458 and NSM PV 20379; Hatcher et al., 1907; Fujiwara, 2009). However, these tendons are not preserved or yet ossified in GMNH-PV 124.

The heads of the ribs associated with the dordals are not branched. Of these ribs, those associated with cranial (anterior) dorsals are relatively straight, long, and extend ventrally, but those associated with caudal (posterior) dorsals are curved and extend laterally. In *Triceratops*, the first vertebra of synsacrum also possesses a pair of rib which extends beneath the ilia. Of these ribs, 13 right and seven left ribs are preserved (Fig. 1A). However, the vertebrae corresponding to these ribs are unidentified because the articular surfaces of these elements are not completely preserved. Some of the ribs may be composites of the other individuals.

A nearly complete synsacrum, consisting of 10 co-ossified vertebrae and four pairs of sacral ribs, is preserved (Fig. 11). However, the synsacrum was broken into two parts between the sixth and seventh vertebrae (Fig. 11B–D). These vertebrae are co-ossified with the adjacent vertebrae at the intercentrum and pre- and postzygapophseseal joints (Fig. 11B–D). The neural spines of the last three vertebrae are not co-ossified with the preceding or succeeding neural spines (Fig. 11B,D).

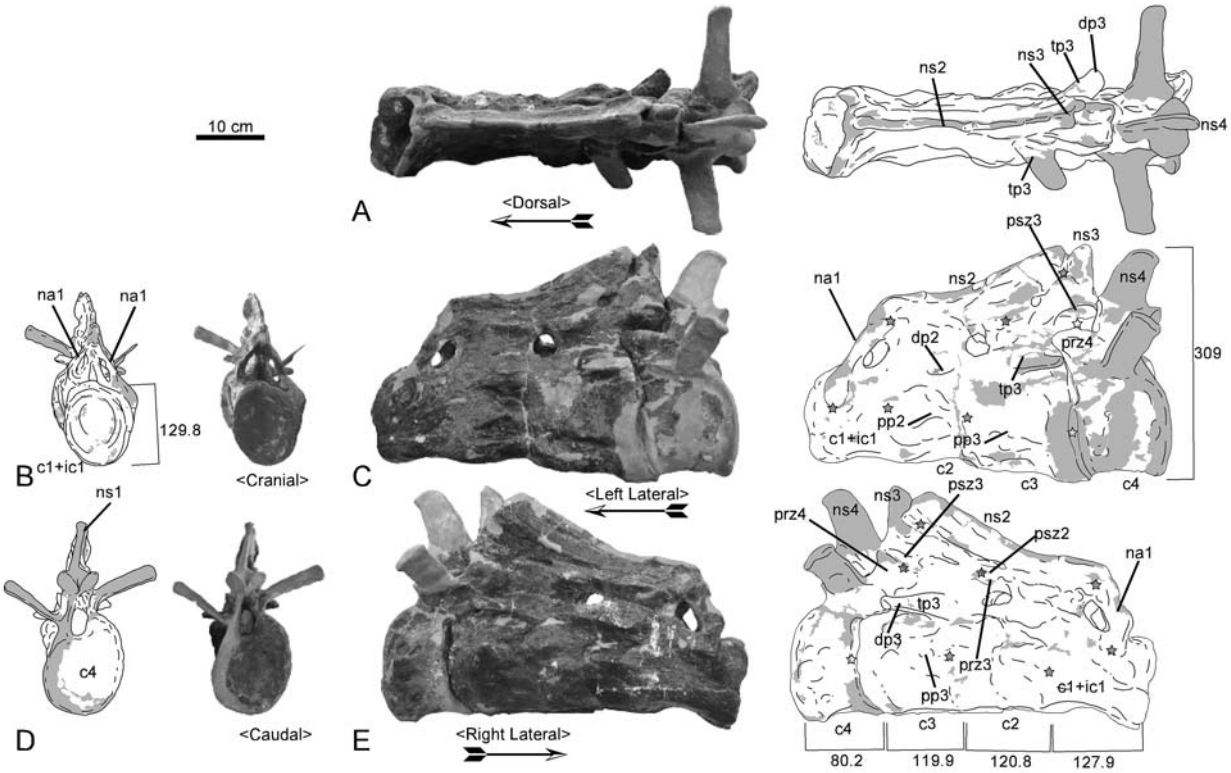

Fig.10. First to fourth presacrals of GMNH-PV 124 in A) dorsal, B) cranial, C) left lateral, D) caudal, and E) right lateral views. First three presacrals are completely co-ossified to form syncervical. Arrows indicate the cranial orientations. Gray area indicates the restored part. Abbreviations: c*n*, dp*n*, na*n*, ns*n*, pp*n*, prz*n*, psz*n*, and tp*n*, centrum, diapophysis, neural arch, neural spine, parapophysis, prezygapophysis, postzygapophysis, and transverse process of *n*th presacral, respectively. Gray and white asterisks indicate fused and unfused suture or contact, respectively.

Co-ossifications among the other neural spines are unclear because the neural spines are broken in the first seven vertebrae. The transverse processes of the first three vertebrae are fused at the distal ends (Fig. 11C). However, the transverse processes of the other vertebrae are not fused with those of either the cranial or the caudal vertebrae. Sacral ribs are associated with the third to sixth syncervical vertebrae (Fig. 11A,B,D). These sacral ribs are co-ossified with the parapophyses and diapophyses of the associated vertebrae. These ribs are also co-ossified with each other, and together form an acetabular bar on each side for connection to the pelvic girdle (Fig. 11B,D). The cranial- and caudal-most surfaces of the syncervical show no sign of

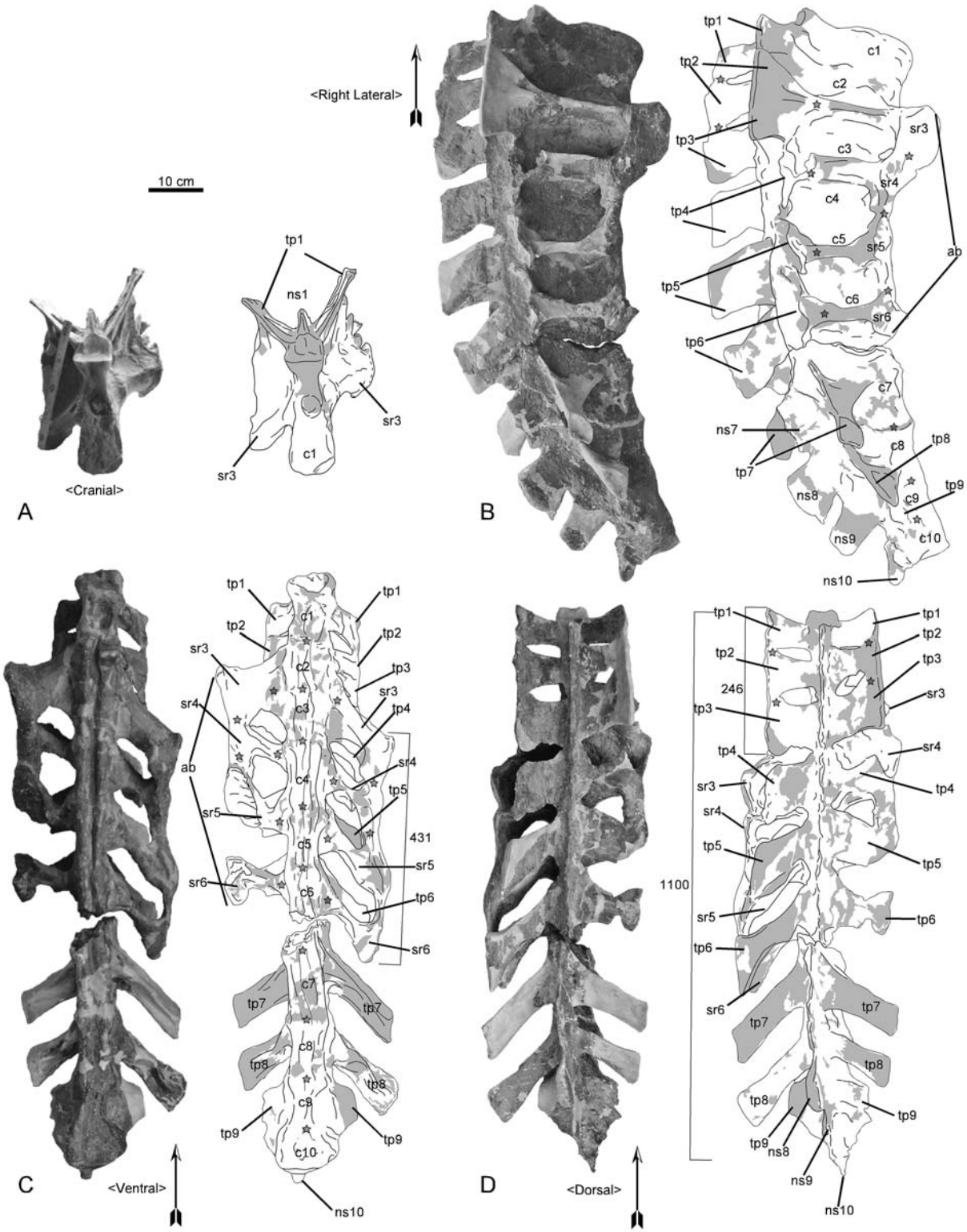

Fig.11. Synsacrum of GMNH-PV 124 in A) cranial, B) right lateral, C) ventral, and D) dorsal views. Arrows indicate the cranial orientations. Gray area indicates the restored part. Abbreviations: ab, acetabular bar; c*n*, ns*n*, sr*n*, tp*n*, centrum, neural spine, sacral rib, transverse process, of *n*th vertebra of the synsacrum, respectively. Gray asterisks indicate fused sutures.

co-ossification with the succeeding vertebrae (Fig. 11A).

Fourteen caudal vertebrae are preserved (Fig. 1A). Eleven of these 14 caudals possess transverse processes, but some of them are broken at the distal end. Co-ossifications with caudal ribs are indeterminable in these vertebrae. Only one chevron is preserved in this specimen (Fig. 1A).

Appendicular Skeleton

The scapulae of *Triceratops* are long flat bones that articulate with the coracoid, a beak-shaped bone, on the distal margin. The scapulae and the coracoids are fused during the growth process. These two bones together form a glenoid cavity. In GMNH-PV 124, both scapulae and coracoids are preserved; the proximal one-third of the left scapula is broken but the other elements are completely preserved (Fig. 12). Each scapula was very close to the adjacent coracoid when they were found (Fig. 1A). However, the scapulae and coracoids were not fused to each other (Fig. 12A,C). Among the remaining forelimb elements, only the right humerus and ulna are preserved in GMNH-PV 124 (Fig. 13 A and B). The humerus with a well developed deltopectoral crest on its lateral margin is apparently crushed and flattened dorsoventrally after deposition. The ulna possessing a prominent olecranon on its proximal end is completely preserved. Sternals, radii, and manus were not preserved.

A complete set of pelvic girdle consisting of ilia, pubes, and ischia are preserved in GMNH-PV 124 (Fig. 1A). The ilia are large flat bones. They contact the sacral vertebrae at their medial margins. Near the middle of its ventral surface, the dorsal aspect of the acetabulae lies between the pubic and ischial peduncles. The pubes articulate with the pubic peduncles. The cranioventral margin of the acetabulae lies on caudolateral side of the articular surface for the ilia. A relatively large prepubic process extends craniolaterally from the base. A narrow postpubis extends caudally from the medial aspect of the proximal end. The ischia articulate with the ilia and pubes at their proximal ends, although the articular surfaces are not preserved in either ischia of GMNH-PV 124; the ischia form the caudal margins of the acetabulae. The ischia extend caudally and curve

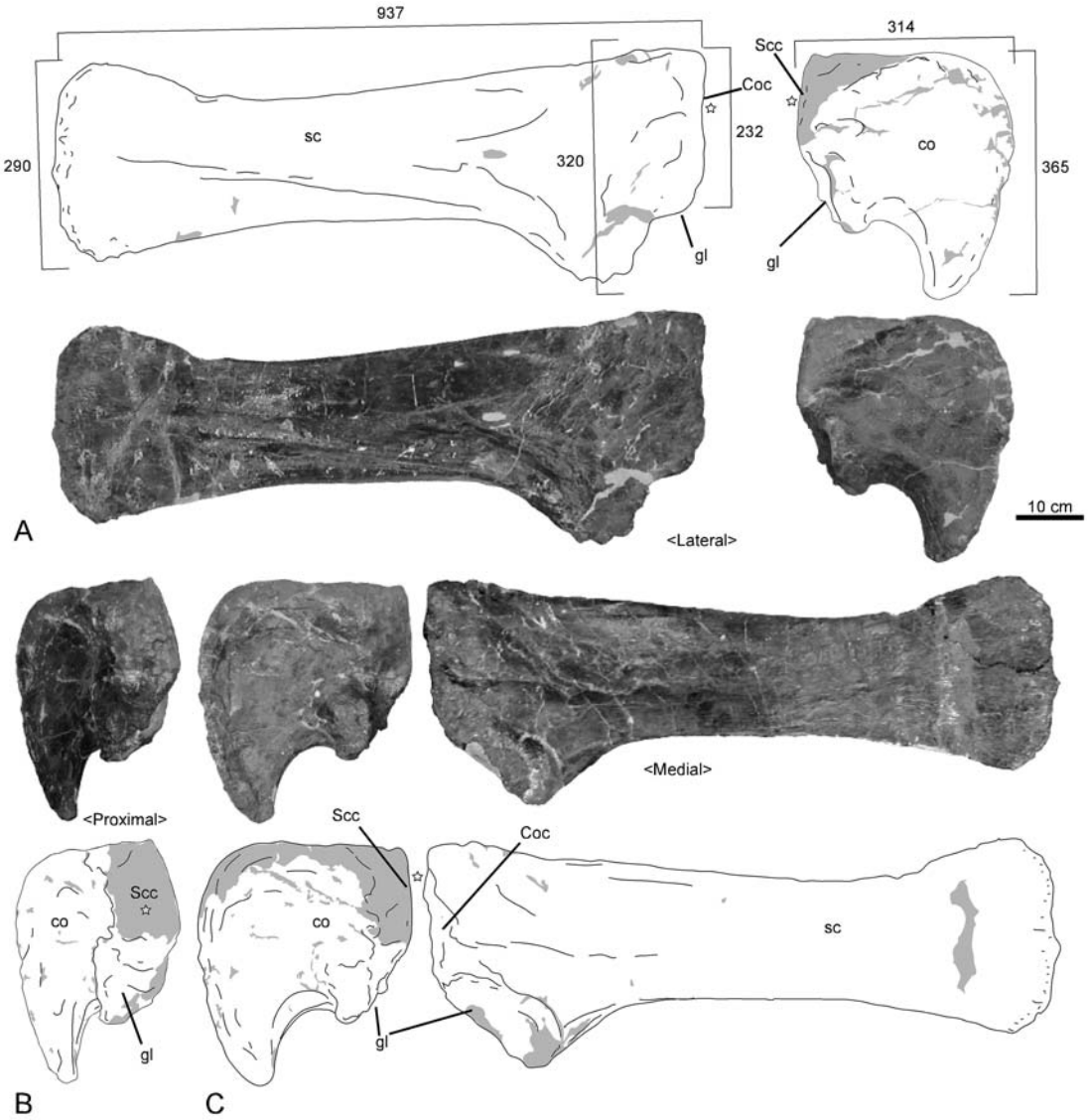

Fig.12. Right scapula and coracoid of GMNH-PV 124 in A) lateral, B) caudal, and C) medial views. Arrows indicate the cranial orientations. Gray area indicates the restored part. Abbreviations: co, coracoid; Coc, contact surface for the coracoid; gl, glenoid; sc, scapula; Scc, contact surface for the scapula. White asterisks indicate unfused contacts.

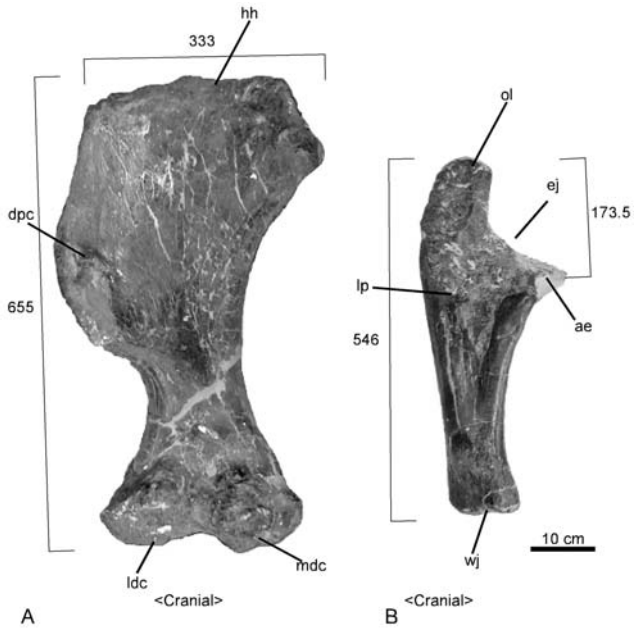

Fig.13. Cranial views of A) the right humerus and B) ulna of GMNH-PV 124. Abbreviations: ae, anterior process; dpc, deltopectoral crest; ej, elbow joint; hh, humeral head; ldc, lateral distal condyle; lp, lateral process; mdc, medial distal condyle; ol, olecranon; wj, wrist joint.

ventrally. At the distal end, the ischium connects with the contralateral ischium. According to some chasmosaurine ceratopsid specimens found in articulated positions such as *Triceratops* (NSM PV 20379; Fujiwara, 2009) and *Anchiceratops* (CMN 8547), the cranial margins of the prepubic processes reach the craniolateral tip of the ilia in the life position, and the cranial margins of the ilia and pubes contact the proximal and distal halves of the caudal-most presacral ribs, respectively. However, in GMNH-PV 124, all the bones in the pelvic girdle were not co-ossified with any other bones (Fig. 1A). The other hindlimb elements preserved in GMNH-PV 124 are the left femur and right tibia. Both are almost completely preserved.

Discussion

Co-ossification in other *Triceratops* specimens

In GMNH-PV 124, co-ossifications of bones was observed in several parts of the body: the rostrum-predentary complex; the nasal-epinasal complex; the occipital-frill-supraorbital horn core complex; the syncervicals; and the synsacrum (Fig. 14A).

A *Triceratops* specimen, YPM 1821, is considered to be a sub-adult, because its skull elements are not fully co-ossified (Hatcher et al., 1907). The specimen consists of an almost complete disarticulated skull, a mandible, a few vertebrae, ribs, partial scapulae, a pelvic girdle, a femur, and a terminal phalanx (Fig. 14C; Hatcher et al., 1907). In YPM 1821, co-ossification was observed in occipital elements. However, co-ossification of the other parts of the skeleton are less advanced than in GMNH-PV 124: the squamosals, a pair of nasals, the epinasal, a pair of premaxillae, and the rostrum are detached from the adjacent elements. The suture between the parietals is not completely closed.

An almost complete postcranial and partial cranial skeleton are preserved in NSM PV 20379 (Garstka and Burnham, 1997; Fujiwara, 2007, 2009). The left side of the skeleton is eroded in this specimen. On the right side, the parietals; the rostral part of the skull including the nasal, the premaxilla, and the rostrum; the predentary; the second presacral rib; and caudals are not preserved (Fig. 14B). The occipital area of the skull is preserved, but these elements cannot be observed on the exhibit. Co-ossifications of bones in this specimen are more advanced than those in GMNH-PV 124. All the connections of bones that are co-ossified with each other in GMNH-PV 124 are co-ossified in NSM PV 20379. The parietals in NSM PV 20379 were detached or broken at the connections to the frontals, the postorbitals, and squamosals. In the skull elements, all the superficial components except the nasals, premaxillae, and parietals were united. There are no signs of co-ossification between the episquamosals and squamosals, and between the epijugals and jugals. The syncervical (the first to third cervicals) and synsacrum are completely co-ossified. The presacral vertebrae show no signs of co-ossification with the associated ribs. Although a trace of suture is present between them, the scapula and the coracoid are co-ossified with each other. The right transverse processes of the fourth to sixth vertebrae of the synsacrum are co-ossified with the right ilium. The right rib of the first vertebra and the transverse processes of the second, third, and seventh to ninth vertebrae of the synsacrum are attached to the right ilium. However, co-ossification between these appendicular elements and the ilium is unidentifiable.

In spite of its relatively small skull size compared to other *Triceratops* specimens, YPM 1822 is considered as a fully adult, because most of the sutures in the skull are closed (Hatcher et al., 1907). In YPM 1822, co-ossification is more advanced compared with GMNH-PV 124 (Fig. 14D). The specimen consists of a complete skull, a complete mandible, and the first to sixth presacrals (Hatcher et al., 1907). The sutures between the maxilla and premaxilla, between the nasal and the premaxilla, and between the quadratojugal and the jugal are still present. The episquamosals and the epiparietals are co-ossified with the squamosals and parietals, respectively. Within the syncervical, the second presacral (or cervical) rib is co-ossified with the atlas (Marsh, 1891), although the remaining ribs are not co-ossified with the associated vertebrae.

Timing of co-ossification in the postcranial elements of *Triceratops*

Comparison of the co-ossification of cranial elements in *Triceratops* specimens indicate that YPM 1821 may be in a more immature stage of growth, and NSM PV 20379 and YPM 1822 may be in a more mature stage of growth than GMNH-PV 124. This presumption of the sequence of growth stage among the specimens is consistent with a study of the epi-ossification pattern through the ontogeny of *Triceratops* based on numerous cranial specimens (Horner and Goodwin, 2008): the epinasals co-ossify first with the cranial skeleton followed by the rostral, epijugals, episquamosals, and epiparietals.

At a relatively early sub-adult stage in *Triceratops*, co-ossifications of the syncervical and the synsacrum are completed when the sutures of the occipital elements, premaxillae and rostrum contact, the nasals and epinasal contact (Horner and Goodwin, 2008), and the orbital elements (including frontals,

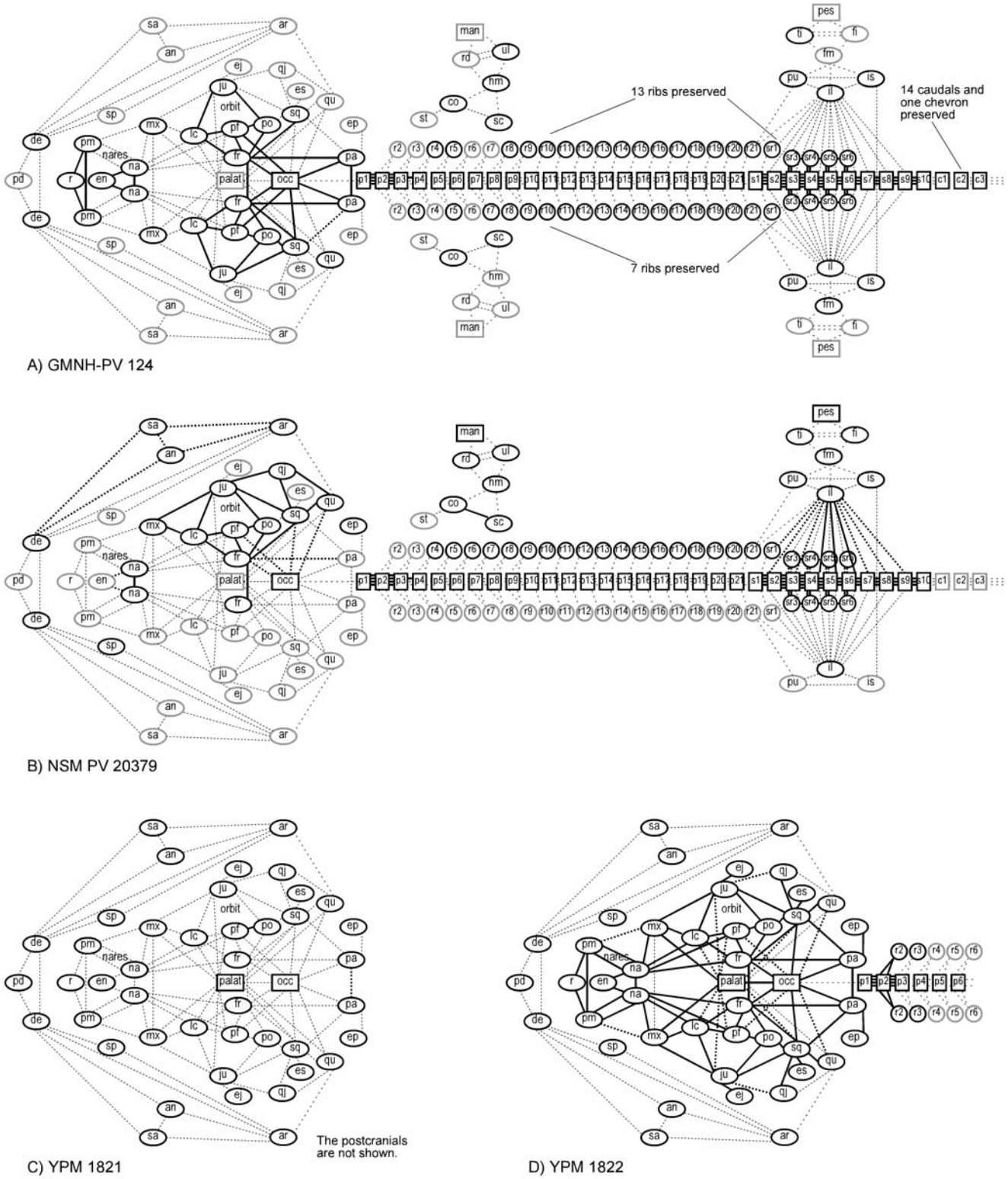

Fig.14. Co-ossification patterns of *Triceratops* specimens: A) GMNH-PV 124; B) NSM PV 20379; C) YPM 1821; and D) YPM 1822. Elements in circled in black are preserved, and elements circled in gray are not preserved or unidentified. Lines connecting between the elements indicate the joint or contact between the bones. Solid and dashed lines indicate that the contacts are co-ossified and not co-ossified/unidentified. Co-ossifications of bones in YPM 1821 and 1822 are based on Hatcher et al. (1907). Abbreviations: an, angular; ar, articular; c*n*, *n*th caudal; co, coracoid; de, dentary; ej, epijugal; en, epinasal; ep, epiparietal; es, episquamosal; fi, fibula; fm, femur; fr, frontal; hm, humerus; il, ilium; is, ischium; ju, jugal; lc, lacrimal; man, manus; mx, maxilla; na, nasal; occ, occipital bones; pa, parietal; palat, palatal bones; pd, predentary; pf, prefrontal; pm, premaxilla; p*n*, *n*th presacral; po, postorbital; pu, pubis; qj, quadratojugal; qu, quadrate; r, rostrum; rd, radius; r*n*, *n*th presacral rib; sa, surangular; sc, scapula; s*n*, *n*th vertebra of synsacrum; sp, splenial; sq, squamosal; sr*n*, rib of s*n*; st, sternum; ti, tibia; ul, ulna.

postorbitals, and jugals) are closed (e.g., GMNH-PV 124). In the next stage, the complex of the orbital elements co-ossifies with the maxillae and squamosals and the co-ossification of the scapulae and coracoids is completed (e.g., NSM PV 20379) before the remaining cranial sutures close (e.g., YPM 1822). Some of the ribs may co-ossify with the syncervical at a more advanced stage (e.g., YPM 1822).

This study described the co-ossification patterns of cranial and postcranial elements in GMNH-PV 124. Further investigations on other *Triceratops* specimens comprising both cranial and postcranial elements will reveal transition of co-ossification patterns during their growth stage.

Conclusions

1. A new sub-adult *Triceratops* specimen, GMNH-PV 124, was excavated from the Hell Creek Formation, South Dakota, US. The specimen contains most of the cranial and axial skeletons, and partial appendicular skeletons.

2. Co-ossification of the skeletal elements of GMNH-PV 124 is more advanced than a sub-adult specimen, YPM 1821, but less advanced than NSM PV 20379 and an adult specimen, YPM 1822.

Acknowledgements

The authors thank M. Triebold (Triebold Paleontology Inc.) for numerous photographs and site map during the excavation, D. Brinkman (YPM) for his great hospitality during a study, Y. Hasegawa, T. Kimura, T. Mita (GMNH), I. Takahashi (Gobi Support Japan), O. Ito (formerly belonged to GMNH), and T. Oji (The Nagoya University Museum) for support throughout this study, and T. Tsuihiji (NSM) and R. Matsumoto (University College London) for their helpful advices. We also thank M. Manabe (NSM) for his great hospitality during a study and for improving this paper.

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トリケラトプス*Triceratops*（Ceratopsia: Ceratopsidae）亜成体標本および骨格要素の癒合状態の報告

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要旨：アメリカ･サウスダコタ州のヘル･クリーク層より産出したトリケラトプス標本（GMNH-PV 124）は，ほぼ完全な頭蓋骨格，体軸骨格そして部分的な体肢骨格から構成される．本標本は脳頭蓋，フリルの一部，及び上眼窩角の癒合，吻骨と左右の前上顎骨の癒合，縁鼻骨と左右の鼻骨の癒合，第1－3頸椎の癒合，および仙椎の癒合が開始している．一方，他の頭蓋骨格要素の癒合や肩甲骨－烏口骨間の癒合は起こっていない．その癒合の状態から，亜成体であると考えられる．

キーワード：ヘルクリーク層, サウスダコタ州, *Triceratops*, Ceratopsia, 角竜