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FEATURED ARTICLE

GERROTHORAX PULCHERRIMUS FROM THE UPPER TRIASSIC FLEMING FJORD FORMATION OF EAST GREENLAND AND A REASSESSMENT OF HEAD LIFTING IN TEMNOSPONDYL FEEDING

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ABSTRACT—The plagiosaurine *Gerrothorax pulcherrimus*, a ubiquitous faunal component of the Fleming Fjord Formation, is recognized by tubercular ornamentation, contact between the postfrontal and supratemporal, at least two tooth rows on the posterior coronoid, and a posttemporal fenestra that is small or absent. *Gerrothorax pulcherrimus* also possesses a derived pectoral morphology that includes an interlocking claviculocleithral complex and an interclavicle with paired posterolateral projections and a transversely truncated posterior margin. *Gerrothorax pustuloglomeratus* is a junior synonym of *G. pulcherrimus*; other *Gerrothorax* species cannot be differentiated from *G. pulcherrimus*. Flat-headed temnospondyls have been interpreted as having achieved a large gape by raising the skull rather than by lowering the jaw. No detailed, corroborating anatomical evidence from the atlanto-occipital joint, however, has ever been adduced. In *G. pulcherrimus* the widths of the atlantal and condylar facets are comparable, but dorsoventrally the condylar facets are 45% longer than the comparable dimension of the atlantal facets. Elevation of the skull occurred by atlanto-occipital rotation, and was facilitated by a radius of curvature of the dorsal part of the condylar facets that is shorter than that of the inferior part. From a resting, closed mouth position, *G. pulcherrimus* was capable of elevating the skull through an excursion of approximately 50°, a movement that rotated the quadrate forward and protruded the lower jaw. An elongate, broadly open neural canal in the atlanto-occipital region, and dorsal displacement of the occipital condyles, are related to relieving the spinal medulla of the sharp angular deformation that head lifting might entail.

INTRODUCTION

Plagiosauridae, a family of Triassic temnospondyls first recognized on the basis of scanty material from western Europe, are distinguished by highly specialized cranial and vertebral structure. The substantially foreshortened skull (breadth about twice length) is dorsoventrally compressed and semilunar in outline. The preorbital rostrum is extremely short. The orbits are large and the circumorbital bones reduced. The posterior end of the quadratojugal forms a short, posterolaterally directed projection. The hyobranchial elements are well ossified and robust. Vertebral centra (putatively intercentra) are spool-shaped. In the posterior dorsal region, the pedicles of the neural arches are intervertebral in position and are thus borne by two adjacent centra, as are the ribs. The limbs are short. The trunk of plagiosaurids is armored with a densely packed array of scutes. The ornamentation on the dermal bones of the skull, shoulder girdle and body armor is variously tubercular ('pustular') or reticular.

Recent collections have increased known materials of plagiosaurids many fold. Jenkins et al. (1994) reported plagiosaurids to be the most commonly found taxon in the Late Triassic Fleming Fjord Formation of Jameson Land, East Greenland, and tentatively assigned the extensive materials to *Gerrothorax* cf. *pulcherrimus*, an interpretation formally confirmed by the present study. Hellrung (2003) described well preserved plagiosaurids from the Lower Keuper (Upper Ladinian) of Kupferzell-Bauersbach, southern Germany, including the most complete *Gerrothorax* specimen known.

Hellrung (2003) briefly reviewed two plagiosaurid subfamilies (Plagiosaurinae, Plagiosterninae) and erected another (Plagiosuchinae). Plagiosternines include Russian taxa (*Plagiosternum danilovi*, *P. paraboliceps*, *Melanopelta antiqua*, and *Arenetsia improvisa*) as well as two German taxa (*Plagiosternum granulosum* and *P. nanum*). Plagiosuchinae includes one German (*Plagiosuchus pustuliferus*) and two Russian taxa (*Plagioscutum ochevi* and *P. caspiense*). Plagiosaurinae includes *Plagiosaurus depressus* and five species of the genus *Gerrothorax*; prior to the Greenlandic discoveries, plagiosaurines were known only from Germany, Scandinavia, and possibly Thailand (Suteethorn et al., 1988). *Gerrothorax* is a long-lived genus, appearing first in the Ladinian (Middle Triassic) of Kupferzell and surviving until the 'Rhaetic' in Sweden.

We regard the Fleming Fjord plagiosaurids as representing the plagiosaurine *Gerrothorax*—versus plagiosuchines or plagiosternines—on the basis of a suite of distinctive features. All Fleming Fjord plagiosaurids exhibit a tubercular dermal ornamentation that is characteristic of all known plagiosaurids except the plagiosternines, which have reticular ornamentation. Fleming Fjord plagiosaurids have a marginal tooth row on the dentary

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that occupies over half the length of the mandible, in contrast to plagiosuchines in which the dentary tooth row is approximately one third of mandibular length (Hellrung, 2003). Additional plagiosaurine features present in the Greenlandic skulls are the nature of the posttemporal fenestra on the occiput, which is slit-like or absent, and the presence of one or more rows of teeth on all three coronoids of the lower jaw, with the posterior coronoid, at least, possessing at least two rows. Furthermore, the plagiosaurine *Gerrothorax* is distinguished from plagiosuchines on the basis of features of the pectoral girdle (Hellrung, 2003). The lateral margin of the interclavicle in plagiosaurines bears two processes, and the posterior margin is relatively broad and straight, in contrast to plagiosuchines in which there is only a single lateral process and the posterior margin is relatively narrow and rounded. Additionally, in plagiosaurines the clavicle and cleithrum articulate not only by the primitive temnospondyl arrangement wherein the dorsal process of the clavicle lies anteriorly on the ventral process of the cleithrum, but also by the development of a dorsally projecting, ornamented lamina of the clavicle that meets a descending, ornamented cleithral process (forming an interlocking claviculocleithral complex). The cleithrum is also ornamented dorsally. In plagiosuchines no extensive overlap of cleithrum and clavicle is developed, and neither bone bears a substantial area of ornamentation on its lateral aspect.

Gerrothorax from the Fleming Fjord Formation is represented by several nearly complete, three dimensionally preserved skulls; the postcranial material, however, is less complete than that from Kupferzell. Nevertheless the Greenlandic collection presents an opportunity to further explore the seemingly bizarre anatomy of *Gerrothorax*. In this paper we first aim to place the Fleming Fjord *Gerrothorax* in a taxonomic context, a problematical undertaking given the multiplicity of taxa based on fragmentary specimens. Second, we elucidate various distinctive morphological features of *Gerrothorax*. Finally, we examine the hypothesis, first advanced by Watson (1919) for *Mastodonsaurus* and later extended by Panchen (1959) to brachyopids and plagiosaurids, that flat-headed temnospondyls raised the cranium to achieve a large gape in feeding.

Institutional Abbreviations—**FMNH**, Field Museum of Natural History, Chicago, IL; **MGUH** and **GM**, Geological Museum, University of Copenhagen, Copenhagen, Denmark; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, MA; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany.

MATERIAL AND METHODS

The collection of *Gerrothorax* from the Fleming Fjord Formation comprises sixty-four specimens, which are deposited in the Geological Museum of the University of Copenhagen (GM-V-2008-4–GM-V-2008-25, inclusive; and MGUH 28916–28925, inclusive) and the Museum of Comparative Zoology (MCZ 9487–9518, inclusive), Harvard University. The majority of specimens (49) were collected from a quarry on the southern side of Macknight Bjerg (71° 22.277′ N, 22° 33.341′ W). Three specimens (GM-V-2008-24, GM-V-2008-25, MCZ 9513) were found at localities at the southern end of the exposures of the Fleming Fjord Formation on the west side of Carlsbjerg Fjord (71° 15–16′ N, 22° 31–33′ W). Two skulls (MGUH 28923, MGUH 28925) were discovered in skree derived from the northern end of Fleming Fjord exposures at Sydkronen (71° 49.975′ N, 22° 36.370′ W). The remaining eleven specimens were recovered as isolated finds in the vicinity of Klit Dal, Macknight Bjerg and Tait Bjerg.

For comparative purposes, European specimens of *Gerrothorax* were examined during the course of this study. AW reviewed the *Gerrothorax* collection from Kupferzell-Bauersbach, southern Germany, housed in the Staatliches Museum für Naturkunde, Stuttgart. Postcranial material from Kupferzell-Bauersbach was made available by the Field Museum of Natural History (FMNH PR 1679, PR 1680, and PR 1685). A. W.'s personal collection of isolated elements of the Kupferzell *Gerrothorax* was also employed, and deposited in the Museum of Comparative Zoology (MCZ 9519–9532, inclusive).

To obtain accurate representations of the curvature of exoccipital condyles, molds of both condyles on several specimens were made from MOLD A^{2}Z SOLUTIONS silicone putty 40, and casts produced with POR-A-KAST™ liquid urethane. Each condylar cast, mounted on a Buehler ISOMET™ low speed saw, was fixed in a position relative to the diamond blade (0.32 mm width) so as to bisect the condyle in a plane normal to the facet surface. Graphic reproductions of the silhouettes of the hemisected facets were produced by utilizing a stamp pad to ink the cut surfaces, which were then applied to paper.

Reconstructions of the skull and shoulder girdle in *Gerrothorax pulcherrimus* required composite morphological data from four specimens: MGUH 28925, a large skull; MGUH 28918, a dorsal and lateral surface of a skull (lacking a mandible) and pectoral girdle with articulated claviculocleithral complex; MGUH 28919, a complete skull prepared in ventral aspect, with mandible, branchial arches and clavicles; GM-V-2008-24, a very small partial skull (without mandible) with an incomplete but three-dimensionally preserved pectoral girdle. The cranium is reconstructed primarily on the basis of MGUH 28925, which is a relatively undeformed skull. The relative size of the skull and pectoral girdle, and in particular the relative depth of the pectoral girdle, was first determined by scaling up the claviculocleithral complex of MGUH 28918 by a factor representing the difference in skull width between MGUH 28918 and MGUH 28925. The proportional relationship was then verified with GM-V-2008-24, in which both skull width and pectoral girdle depth could be determined.

SYSTEMATIC PALEONTOLOGY

Order TEMNOSPONDYLI Zittel, 1887–1890
Family PLAGIOSAURIDAE Abel, 1919
Subfamily PLAGIOSAURINAE Abel, 1919

Revised Diagnosis—Differing from plagiosternines in: tubercular ornament on the dermal bones of the skull, mandible and pectoral girdle. Differing from plagiosuchines in: marginal tooth row on the dentary over half mandibular length; at least two tooth rows on the posterior coronoid, and one or more rows on the middle and anterior coronoids; posttemporal fenestra reduced to a slit or absent; interclavicle with paired posterolateral projections and an almost transverse posterior margin; interlocking claviculocleithral complex.

GERROTHORAX Nilsson, 1934
Figs. 1–10

Revised Diagnosis—Plagiosaurine in which the postfrontal and supratemporal bones are in contact (primitive condition). Differs from the only other known plagiosaurine, *Plagiosaurus depressus*, which lacks a postfrontal-supratemporal contact.

Type Species—*Gerrothorax pulcherrimus* (Fraas, 1913) by combination.

Discussion—Hellrung (2003) provided a new description of *Plagiosaurus depressus*, and distinguished this taxon from all *Gerrothorax* spp. on the interpretation that the postfrontal and supratemporal bones are separated by the intervening parietal and postorbital. Other characters employed by Hellrung to differentiate *Gerrothorax* from *Plagiosaurus* were based on relative size and shape, and cannot be applied confidently in determining the generic assignment of the Greenlandic material.

Currently the most complete, well-preserved *Gerrothorax* ma-

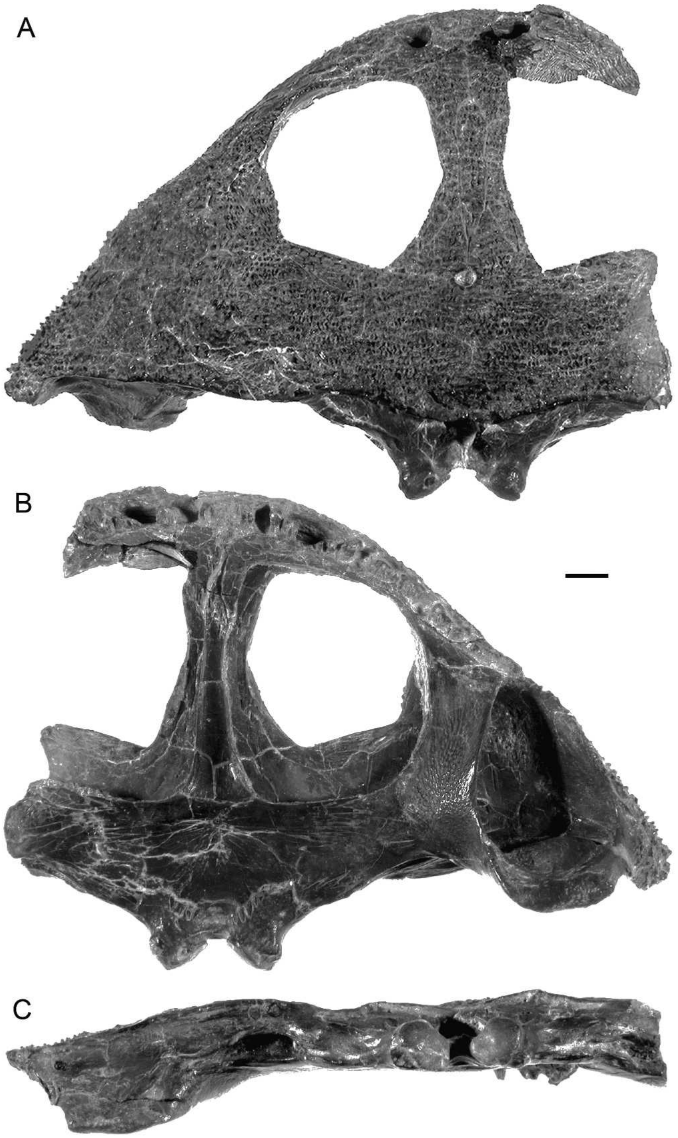

FIGURE 1. *Gerrothorax pulcherrimus* partial skull (MGUH 28925) in **A**, dorsal, **B**, ventral and **C**, occipital views. Scale bar equals 1 cm.

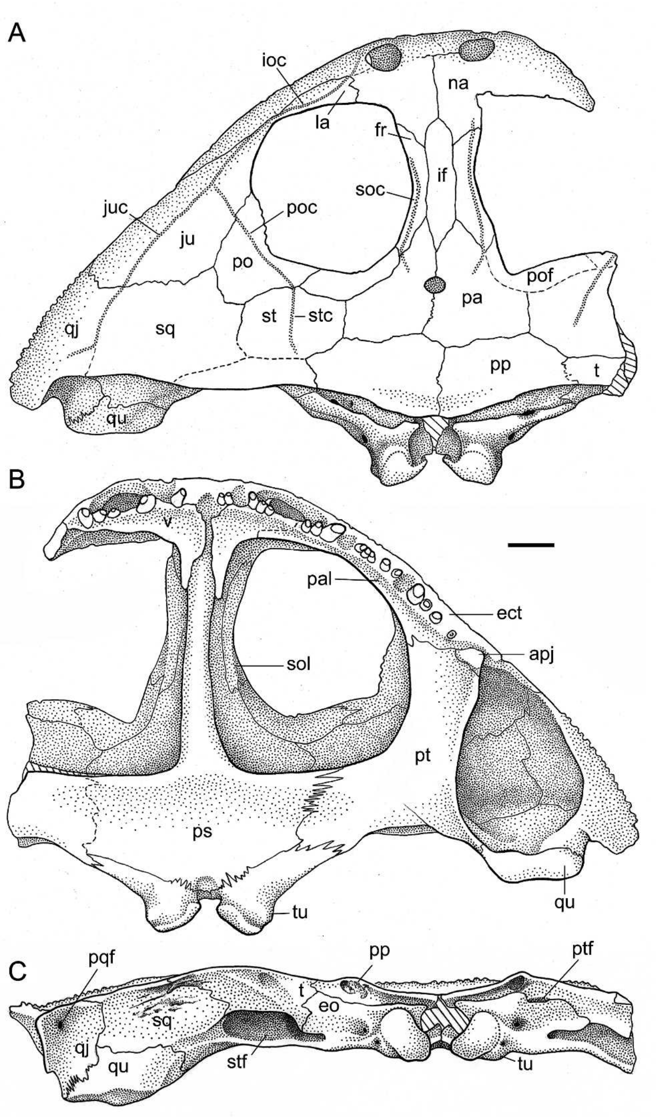

FIGURE 2. *Gerrothorax pulcherrimus* partial skull (MGUH 28925) in **A**, dorsal, **B**, ventral and **C**, occipital views. **Abbreviations**: **apj**, alary process of the jugal; **ect**, ectopterygoid; **eo**, exoccipital; **fr**, frontal; **if**, interfrontal; **ioc**, infraorbital canal; **ju**, jugal; **juc**, jugal canal; **la**, lacrimal; **na**, nasal; **pa**, parietal; **pal**, palatine; **pof**, postfrontal; **po**, postorbital; **poc**, postorbital canal; **pp**, postparietal; **pqf**, paraquadrate foramen; **ps**, parasphenoid; **pt**, pterygoid; **ptf**, posttemporal fenestra; **qu**, quadrate; **qj**, quadratojugal; **soc**, supraorbital canal; **sol**, suborbital lamella, **sq**, squamosal; **st**, supratemporal; **stc**, supratemporal canal; **stf**, subtympanic fossa; **t**, tabular; **tu**, tubercle of the condylar process; **v**, vomer. Scale bar equals 1 cm.

terial is represented by a comprehensive collection from the Lower Keuper of Kupferzell. Hellrung (2003) referred all of this material to *G. pustuloglomeratus* on the basis of similarity between the Kupferzell clavicles and the single clavicle that constitutes the type of *G. pustuloglomeratus* (Huene, 1922); the Grenzbonebed of southern Germany, from which the type was derived, is the uppermost member of the Muschelkalk sequence (Schoch, 1999), not Lower Keuper (contra Hellrung, 2003). In particular Hellrung considered that the smaller size of the Kupferzell material should exclude an assignment to *Gerrothorax pulcherrimus*; the cleithra of the Kupferzell *Gerrothorax* range from about 12 mm to 83 mm in length, whereas the cleithrum of *G. pulcherrimus* from Pfaffenhofen measures 100 mm. Additionally the cranium of *G. pulcherrimus* is an estimated 340 mm in maximum width compared with 240 mm in SMNS 84786, the larger of the two skulls illustrated by Hellrung (2003:fig. 12). Other differences found were that the tubercular sculpture of *G. pulcherrimus* is more prominent than in *G. pustuloglomeratus*, and that sensory canals on the skull table were clearly visible in *G. pustuloglomeratus* but not in *G. pulcherrimus*.

Considerable variation in size is evident in *Gerrothorax* from Greenland. Two isolated skulls of large size (MGUH 28923, MGUH 28925; estimated skull widths 290 mm, 240 mm, respectively; Figs. 1–3) were recovered from the Sydkronen locality. In other localities where *Gerrothorax* is more abundant, skull widths range from 60 mm (GM-V2008-24) to 250 mm (MCZ 9493), and postcranial elements from much larger individuals (e.g., MGUH 28917, GM-V-2008-25) are known from the Macknight Bjerg quarry as well as the Carlsbjerg Fjord locality. We find no justification for making any taxonomic distinctions on size or other variables (development of the tubercles, apparent distribution of sensory canals, and other features described below). We thus interpret the material as a continuum reflecting

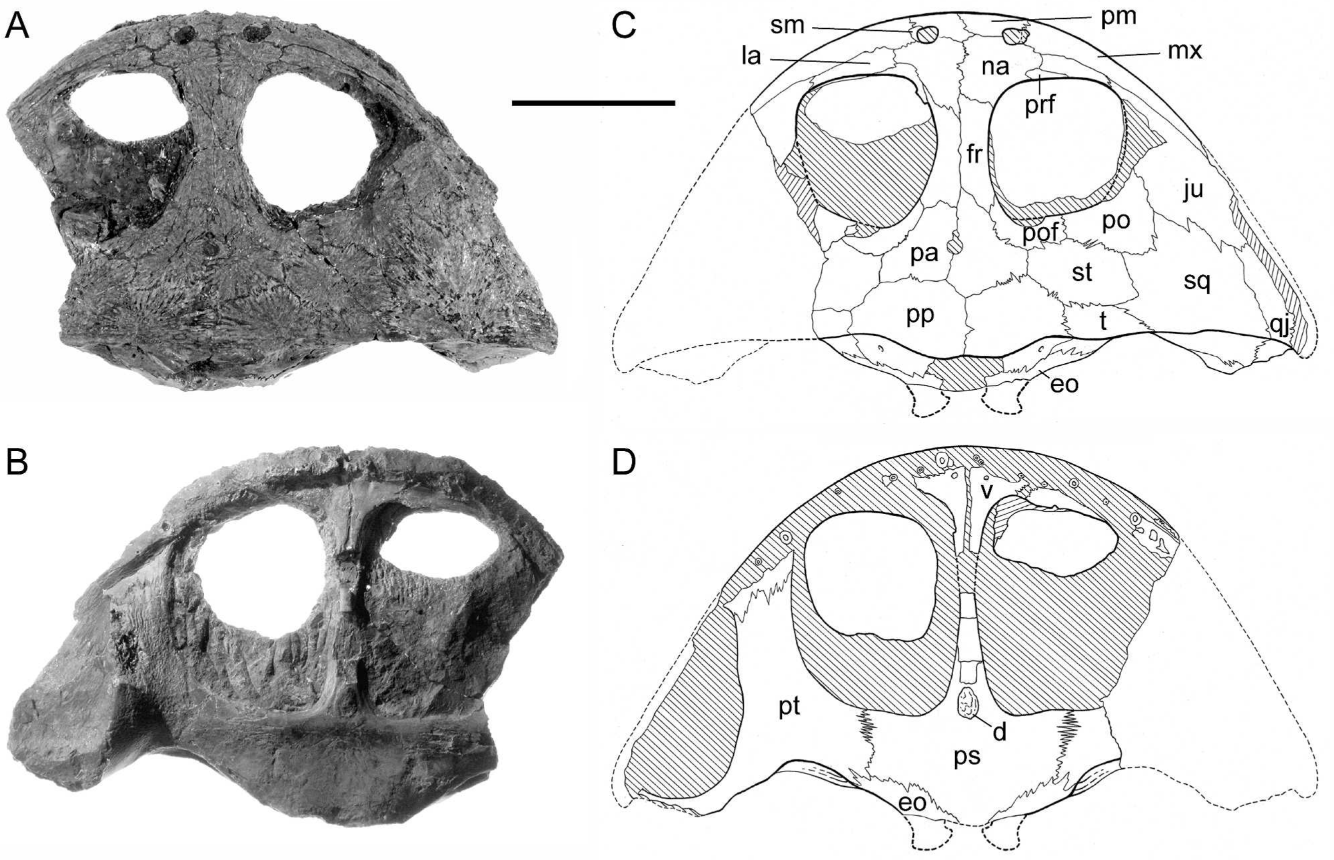

FIGURE 3. *Gerrothorax pulcherrimus* partial skull (MGUH 28923) in dorsal (**A**, **C**) and ventral (**B**, **D**) views. At the base of the cultriform process of the parasphenoid is a raised, oval area (**d**) that may have borne denticles. **Abbreviations**: **eo**, exoccipital; **fr**, frontal; **ju**, jugal; **la**, lacrimal; **mx**, maxilla; **na**, nasal; **pa**, parietal; **pof**, postfrontal; **po**, postorbital; **pp**, postparietal; **prf**, prefrontal; **pm,** premaxilla; **ps**, parasphenoid; **pt**, pterygoid; **qu**, quadrate; **qj**, quadratojugal; **sm**, septomaxilla; **sq**, squamosal; **st**, supratemporal; **t**, tabular; **v**, vomer. Scale bar equals 5 cm.

intraspecific variation and different ontogenetic stages, and assign all specimens to the same taxon as the Kupferzell *Gerrothorax*. Additionally, as the size difference that was used by Hellrung (2003) to separate *Gerrothorax pustuloglomeratus* (Huene, 1922) from *G. pulcherrimus* (Fraas, 1913) is present within the Greenlandic *Gerrothorax* population, we synonymise these taxa.

Other species of *Gerrothorax* are known from only limited materials. Nilsson (1934) erected *Gerrothorax rhaeticus* on the basis of an incomplete postcranium, to which he later referred more extensive postcranial material and a partial skull (Nilsson, 1937, 1946a). The type of *Gerrothorax franconicus* is an interclavicle only (Kuhn, 1932), and is now lost; Hellrung (2003) regarded this species as a nomen dubium. *Gerrothorax striopustulatus* rests on fragmentary shoulder girdle and vertebral elements (Huene, 1922). Hellrung (2003:111) suggested that *G. striopustulatus* and *G. pustuloglomeratus* are subjective synonyms. Given the limited nature of the types of these *Gerrothorax* species, we have been unable to identify characters that reliably distinguish any of them.

With the diagnosis of Plagiosaurinae resting largely on characters of the pectoral girdle, and as comparable girdle material is present in the type species of the genus, *Gerrothorax pulcherrimus*, we suggest that all known *Gerrothorax* material be assigned to *G. pulcherrimus*. The abundant *Gerrothorax* from Kupferzell (Hellrung, 2003) and the Greenlandic material described below add to our understanding of the cranial and mandibular structure of the genus, details of which are less complete in the type of *G. pulcherrimus*.

The status of the only other known plagiosaurine, *Plagiosaurus depressus*, remains uncertain. The lectotype is only distinguishable from *Gerrothorax* by the contact between the parietal and postorbital (Hellrung, 2003:fig. 35); this region of the skull roof is not represented in *G. rhaeticus*, *G. franconicus*, *G. striopustulatus* or the originally described material of *G. pustuloglomeratus*. Until more complete material becomes available, the plagiosaurines comprise two monospecific genera: *Gerrothorax* in which the postfrontal has a sutural contact with the supratemporal, and *Plagiosaurus* in which these bones are separated by a suture between the parietal and the postorbital. Noteworthy is the difference between Nilsson's (1937:fig. 13) representation of the sutural topology of *P. depressus*, which is comparable to that in *Gerrothorax*, and Hellrung's (2003:fig. 35) interpretation.

GERROTHORAX PULCHERRIMUS (Fraas, 1913)

Gerrothorax franconicus (Kuhn, 1932:121)
Gerrothorax pustuloglomeratus (Huene, 1922:425)
Gerrothorax rhaeticus Nilsson, 1934:440
Gerrothorax striopustulatus (Huene, 1922:439)

Revised Diagnosis—As for the genus.

Referred Material—MGUH 28923, MGUH 28925, isolated, incomplete skulls. GM-V-2008-12, a mandibular ramus; MGUH 28917, a large clavicle; MGUH 28918, a skull, mandible and the anterior part of the postcranial skeleton; MGUH 28919, a skull, mandible, clavicles and branchial skeleton; MGUH 28921, a partial skull lacking the right subtemporal fossa and quadratojugal;

MCZ 9511, a skull and mandible; MGUH 28922, articulated ventral scutes and gastralia; MGUH 28924, two specimens including a vertebral series with articulated cleithroclavicular complex, a skull roof and atlas attached to dorsal scutes, and an interclavicle with articulated ventral scutes; GM-V-2008-24, a small skull, pectoral girdle, vertebrae and scutes; MGUH 28916, a small, partial skull.

Localities and Horizons—71° 49.979′ N, 22° 36.370′ W, Sydkronen, Jameson Land, East Greenland; Middle Malmros Klint Member, Fleming Fjord Formation, Scoresby Land Group, Upper Triassic. 71° 22.277′ N, 22° 33.341′ W, a quarry on the southeast flank of Macknight Bjerg, Jameson Land, East Greenland; Lower Carlsbjerg Fjord beds, Ørsted Dal Member, Fleming Fjord Formation, Scoresby Land Group, Upper Triassic.

Referred Material Described Elsewhere—*Gerrothorax* material from Kupferzell, Germany, referred to *G. pustuloglomeratus* by Hellrung (2003). All other material from Germany previously described as *G. striopustulatus* Huene, 1922, *G. pustuloglomeratus* Huene, 1922, and *G. franconicus* Kuhn, 1932, and the Swedish material described as *G. rhaeticus* (Nilsson, 1934, 1937, 1946a, b).

DESCRIPTION

Skull

Tubercular Ornamentation—Tubercles of dermal ornamentation are commonly embedded deeply in and adherent to the matrix. As a consequence, skulls often split in a manner that separates the dorsal skull roof from the palate (likewise, the dorsal body armor and cleithra usually cleave from the ventral body armor, clavicles and interclavicle). Many cranial specimens are thus presented in internal view only. Where external surfaces of skulls have been exposed through laborious preparation, the tubercles in some specimens appear to have been arranged in rows radiating from the center of individual bones, particularly the squamosal. Such rows are found in MGUH 28923 (Fig. 3A) and MGUH 28921 (Fig. 4A). In most other skulls, such as MGUH 28925 (Fig. 1A), rows of tubercles are relatively short; elsewhere on these skulls the tubercles are more or less evenly scattered.

Skull Roof—Large, subcircular orbits are the dominant feature of the flat skull roof, occupying about one fifth of the total surface area (20% in MGUH 28921; 22% in MGUH 28925). The posterolateral orbital rim protrudes into the orbital space as a slightly convex margin, but the degree of convexity varies in both the Fleming Fjord and Kupferzell material. The orbital margins are thin except anterolaterally where the margin is prolonged ventrally as a vertically descending lamina. In MGUH 28925 narrow infraorbital and jugal canals form a triple junction on the jugal with a postorbital canal (Fig. 2A). A supraorbital canal is discernable along the medial orbital margin, but its continuity with the postorbital canal is not evident. A supratemporal canal arises from the postorbital canal and traverses the entire supratemporal. With the possible exception of an infraorbital canal, represented as a shallow sulcus, sensory canals are not preserved on MGUH 28923 (Fig. 3).

Septomaxillae are known in the Kupferzell *Gerrothorax* (Hellrung, 2003) and are variably present or absent in Greenlandic specimens. A septomaxilla forms the lateral edge of the left naris in MGUH 28923 (Fig. 3A, C) and meets both the premaxillary-maxillary and maxillary-nasal sutures; the right septomaxilla is missing. In MCZ 9511 both left and right septomaxillae are present, but the left element is dislodged and rotated ventrally within the naris, suggesting that the sutural attachments of the septomaxilla were not strong. The diminutive, rounded naris in MGUH 28923, in which the septomaxilla is present, contrasts with the more oval nares of specimens in which a septomaxilla is absent, evidence that the bone was lost post mortem.

A small prefrontal bone forms a suture with the medial edge of the lacrimal in MGUH 28923 (Fig. 3C). Left and right prefrontals are asymmetric in size and shape. On the left the crescentic prefrontal forms the anteromedial border of the orbit and overlaps the frontal to exclude the nasal from the orbital margin. On the right the medial part of the prefrontal is reduced so that there is an extensive exposure of the nasal bone in the orbit. In contrast to MGUH 28923, sutures delineating a prefrontal could not be found in MGUH 28925, nor could the presence of prefrontals be confirmed in other Greenlandic skulls where sutural structure is not as evident as in MGUH 28923.

A lacrimal is present along the anterolateral orbital margin and extends to a narrow contact with an anterior process of the jugal, thus excluding the maxilla from the orbital margin. On the ventral surface of the frontals and postfrontals is an elongate flange of bone, the suborbital lamella, which parallels the orbital margin and is especially evident in MGUH 28919 (Fig. 5B; see also Figs. 1A, 2B). In MGUH 28925 an accessory median element (an interfrontal, or the interfrontoparietal of Hellrung, 2003) occurs in the midline between the orbits (Fig. 1A, 2A).

Prominent quadratojugal horns, ornamented both dorsally and ventrally, form the posterolateral corners of the skull and extend posterior to the occipital border of the skull roof. In MGUH 28925 and MGUH 28921 the centers of the tabulars and squamosals are raised above the level of the surrounding bones with the squamosal forming the highest point of the skull roof. An ornamented triangle of bone formed from the posteromedial part of the postparietals extends onto the occipital surface in the midline.

Palate—An anterior palatal vacuity is absent in MGUH 28923; the area is not well preserved in other specimens. A dorsal process from the palatine is sutured to the ventral surface of the lacrimal and prefrontal. The jugal is exposed on the palate at the anterior margin of the subtemporal fossa as an alary process (Fig. 2B). The elongate suture between the exoccipitals and pterygoids is preserved. At the base of the cultriform process of the parasphenoid is a clearly defined raised oval area with a roughened surface (Fig. 3B, D); although no denticles are preserved, a probable denticle appears to be preserved on MGUH 28921 but most of the cultriform process is missing. An oval denticular area was noted by Hellrung (2003:fig. 11) in several specimens from Kupferzell.

Upper Dentition—Small teeth and tooth loci, estimated at 38 in MCZ 9511 and 44 in MGUH 28921, are present as an external row on the maxilla, and slightly larger teeth as an internal row on the ectopterygoid, palatine and vomer; the last three bones also bear a small number of hypertrophied teeth (commonly referred to in the literature as ‘tusks’). The inner row of teeth in MCZ 9511 and MGUH 28919 extends anteriorly along the medial margin of the choana.

Quadrate Condyle—Two specimens exhibit slight differences in the geometry of the articular facet of the quadrate. In MGUH 28921 the anteroposterior curvature of the facet is a full hemicircle (Fig. 4B), spanning from the anterior to the posterior aspects of the quadrate. In MGUH 28925 the anteroposterior curvature is not as extensive, with the anterior and posterior margins of the facet extending only slightly onto the anterior and posterior surfaces of the quadrate. In both specimens the articular facet is transversely wide, with medial and lateral ends that are more convex than the central region of the facet.

Occiput—The occipital surface lacks a posttemporal fenestra in MGUH 28923 but a small, slit-like fenestra is preserved on the right side in MGUH 28925 (Fig. 2C). Small foramina, especially marked on MGUH 28923, pass into the occipital flange of the postparietals; a paraquadrate foramen is preserved in MGUH 28925. The largest opening, the subtympanic fossa, is bounded by the tabular, pterygoid, exoccipital and cartilaginous wall of the

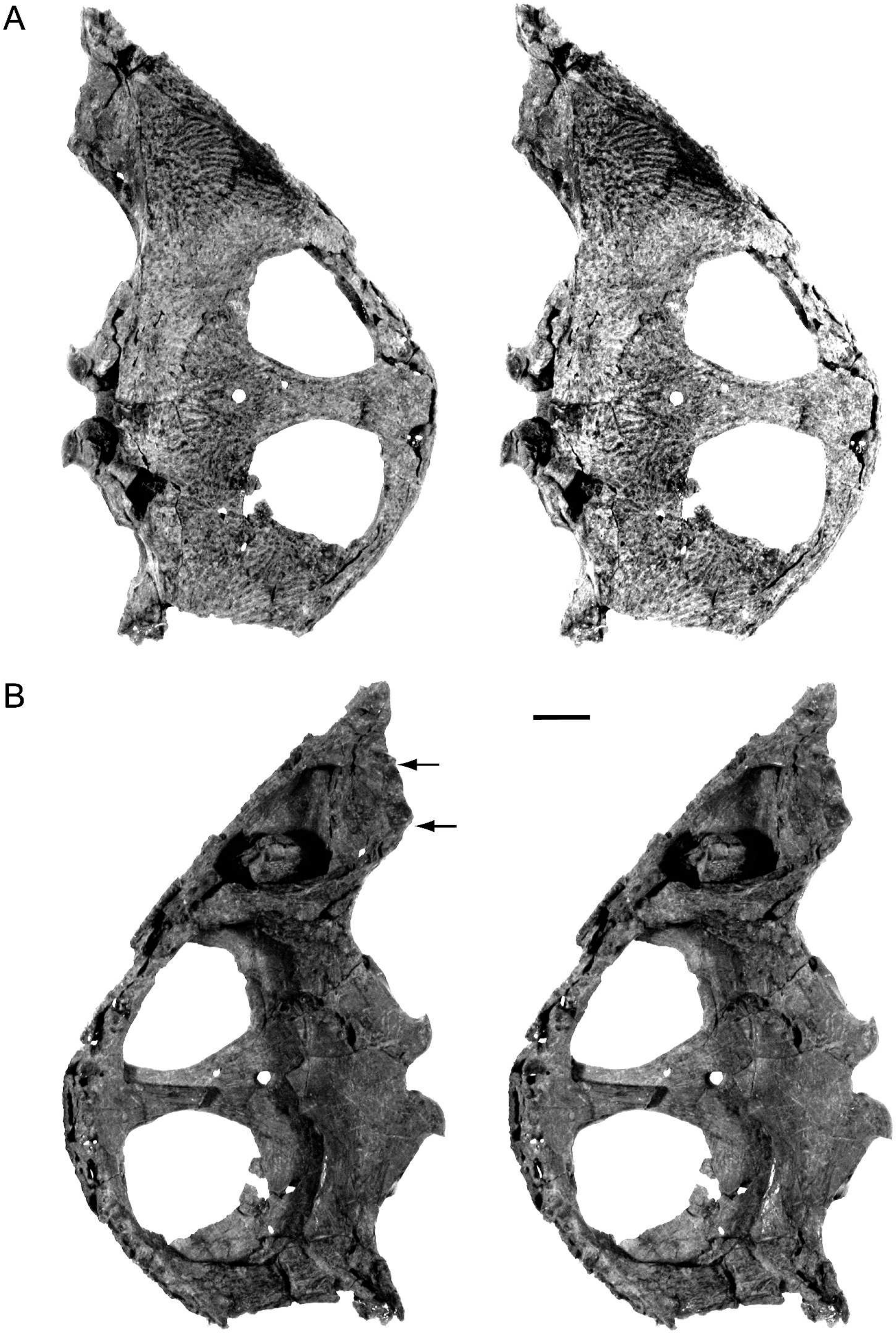

FIGURE 4. *Gerrothorax pulcherrimus* skull (MGUH 28921) in **A**, dorsal, and **B**, ventral stereographic views. In **A**, note the radiating ornamentation on the left squamosal. In **B**, the arrows indicate the medial and lateral extent of the quadrate condyle. Scale bar equals 1 cm.

braincase, and is made more pronounced by the absence of an otic notch. A bony fragment in this fossa in MGUH 28923 may be part of a stapes, an interpretation supported by the presence of a fragment in a similar position in MGUH 28921. A stapes is present in one *Gerrothorax* specimen from Kupferzell (R. Schoch, pers. comm., 2004).

An ovate, rugose area of the squamosal just below the dorsal skull roof of MGUH 28923 is similar in position and extent to that described by Shishkin (1987:fig. 8a) in plagiosuchines and identified as the insertion area for the depressor mandibulae; a comparable feature occurs in the Kupferzell material (Hellrung, 2003:fig. 14). In MGUH 28925 this feature is expressed as a series of fine transverse ridges and delicate rugosities associated with the suture between the squamosal and tabular (Fig. 2C).

Exoccipital condyles, well preserved on several specimens

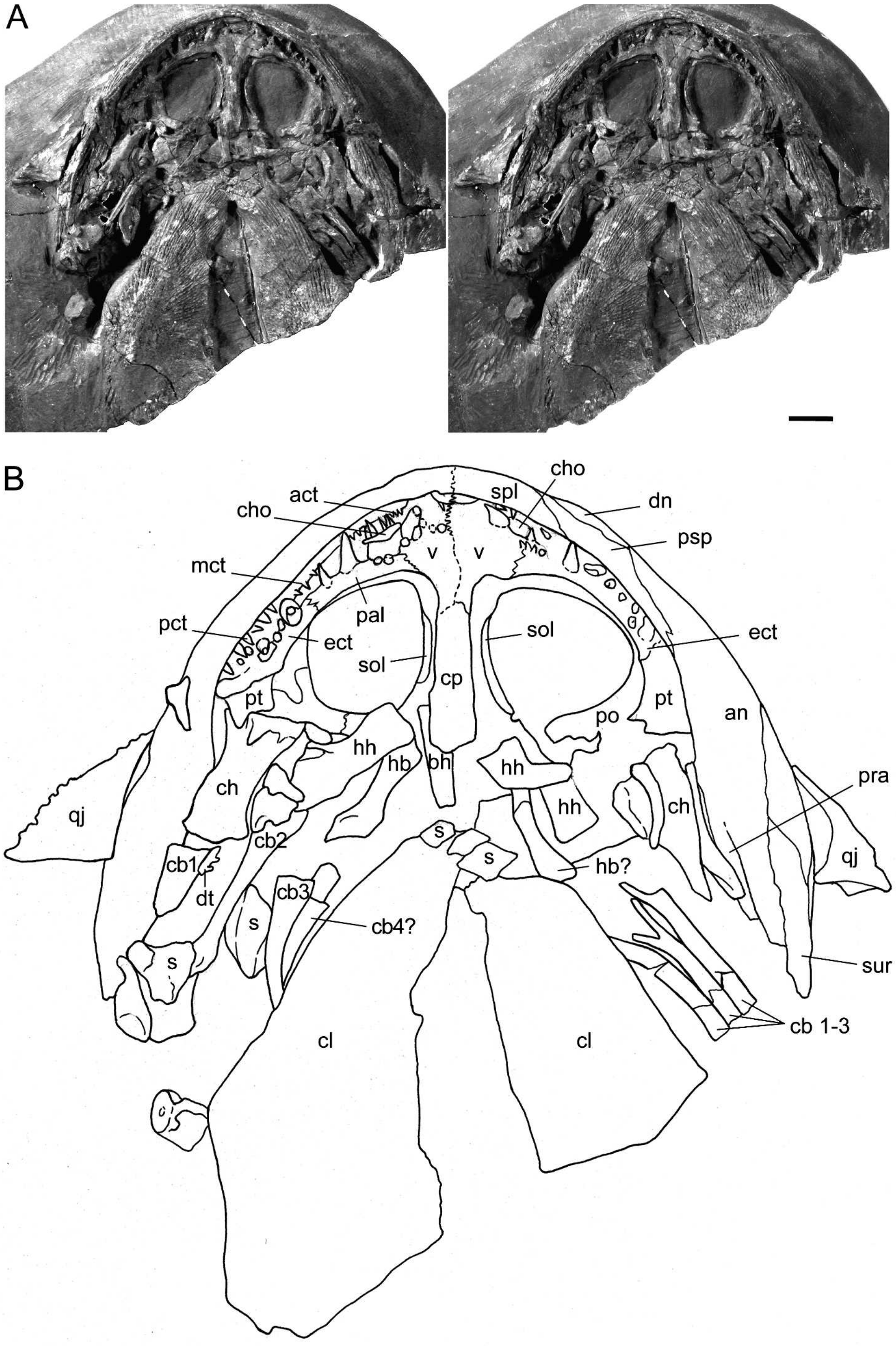

FIGURE 5. *Gerrothorax pulcherrimus* (MGUH 28919). **A**, ventral stereographic view to show the branchial skeleton and distribution of teeth on the coronoid bones of the lower jaw and palate; **B**, interpretive drawing. **Abbreviations**: **act**, anterior coronoid teeth; **an**, angular; **bh**, basihyal; **cb**, ceratobranchial; **ch**, ceratohyal; **cho**, choana; **cl**, clavicle; **cp**, cultriform process of the parasphenoid; **dn**, dentary; **dt**, denticles; **ect**, ectopterygoid; **hb**, hypobranchial; **hh**, hypohyal; **mct**, middle coronoid teeth; **pal**, palatine; **pct**, posterior coronoid teeth; **po**, postorbital; **pra**, prearticular; **psp**, postsplenial; **pt**, pterygoid; **qj**, quadratojugal; **s**, scute; **sol**, suborbital lamella; **spl**, splenial; **sur**, surangular; **v**, vomer. Scale bar equals 1 cm.

(MGUH 28916, MGUH 28921, MCZ 9511, MGUH 28925), are developed on robust, posteriorly projecting processes. The articular facets are piriform in outline, tapering towards the midline. Although the facets face primarily posteriorly, they are turned inward to face slightly medially. The radius of curvature is greater ventrally than dorsally. On MGUH 28925, a pronounced tubercle is situated on the ventrolateral aspect of each condylar process; the tubercle, which lies at the level of the surface of the parasphenoid, is most completely preserved on the right side (Fig. 2B, C).

Mandible—The following description is based on three specimens. In MGUH 28919 (Fig. 5) and MCZ 9511, the mandibles are preserved in articulation with the skull and are presented in ventral aspect. GM-V-2008-12 is an isolated mandible primarily exposed in medial aspect, but prepared posteriorly in both medial and lateral aspects. An outstanding feature of the mandible in *Gerrothorax* is the sharp curvature formed by the anterior, tooth bearing halves of the mandibular rami (Fig. 5), which is a structural accommodation for an extremely foreshortened rostrum. In contrast, the posterior halves of the rami, which include the adductor fossa and retroarticular process (the postglenoid area of Jupp and Warren, l986), are only slightly arcuate (cf. Hellrung, 2003:figs. 4b, 15). The development of different curvatures by the anterior and posterior mandibular halves, although present in *Hadrokkosaurus* (*Taphrognathus*) (Welles, 1947), is not a feature found in other temnospondyls. Tubercular ornamentation is present along the ventral surface of the mandible, as well as the lateral surface behind the dentary. Ornamentation is absent from all but the most anterior part of the dentary and from the dorsolateral part of the retroarticular process. In no specimen is the articular ossified, but this condition is not necessarily a relevant feature because so few specimens preserve the articular region. The retroarticular process is elongate (Fig 5A). The surangular, which forms the external surface of the process, is exposed as a shelf along the dorsolateral surface beside the trough that would have been filled by the articular. The posterior end of the angular laps onto the internal surface of the retroarticular process, rather than occupying its ventral surface (Fig. 5B). Dorsal to the angular is a posterior tongue of the prearticular that ends about half way along the retroarticular process. Anterior to the level of the glenoid fossa the prearticular flares as a lingually directed flange.

Lower Dentition—Dentary teeth are larger and fewer in number than maxillary teeth. In GM-V-2008-12 there are 15 large and four somewhat smaller anterior teeth, and an estimated 12 unoccupied tooth loci, comprising approximately 31 tooth positions in all. A smaller specimen, MCZ 9511, exhibits 38 teeth/tooth loci in the maxilla, whereas the associated mandible has 29 dentary teeth/tooth loci on either side (it is possible that additional teeth were present posteriorly). A short row of at least three symphyseal teeth is present inside the dentary tooth row of MCZ 9511; the outer symphyseal teeth are the same size as coronoid teeth, the inner tooth is smaller. Teeth are present on all three coronoids, with an irregular alignment that is suggestive of multiple rows. Hellrung (2003) described the coronoid dentition in the Kupferzell *Gerrothorax* as consisting of numerous shagreen-like teeth, ranging from being ordered in multiple rows to a completely irregular pattern; her illustration (Hellrung, 2003:fig.15) depicts two rows on the posterior coronoid and single rows on the middle and anterior coronoids. Coronoid teeth are about the same size as maxillary teeth, and a little smaller than dentary teeth. Hellrung (2003) estimated the number of teeth in the maxilla and dentary of the Kupferzell *Gerrothorax* to be about 60 and more than 50, respectively, but did not specify the size of the specimen(s) on which these estimates were made.

Branchial Arches—The branchial arches of MGUH 28919 are preserved with most of the elements close to their natural positions (Fig. 5). The ends of these bones are crushed, an indication of incomplete ossification, but their shafts are well preserved. On the left their arrangement is similar to that in the Kupferzell *Gerrothorax* (Hellrung, 2003:fig. 17). The three curved ceratobranchials, which are aligned between the clavicle and mandible, bear longitudinal vascular sulci, a feature rarely reported in temnospondyls but which were also noted in the Kupferzell *Gerrothorax* (Hellrung, 2003). The ceratobranchials lie posteromedial to a larger, subrectangular ceratohyal. Two hypobranchials (one broad and the other more slender) and a rectangular hypohyal are situated anteromedially to a large ceratohyal; a median basihyal (copula), not found by Hellrung, lies beneath the parasphenoid. On the disrupted right side four ceratobranchials may have been present as in *G. rhaeticus* described by Nilsson (1946a). Two slender elements preserved on the palate of MCZ 9511 may represent a copula and ceratobranchial.

Vertebral Column

Atlas and Axis—We devote particular attention to the atlas, which is less well known than the axis (Hellrung, 2003), and include, for descriptive purposes, two almost complete atlas-axis pairs of *Gerrothorax* from Kupferzell (MCZ 9519; FMNH PR 1685). An atlas is represented in only one specimen from Greenland (MGUH 28924; associated with a partial skull roof, the axis centrum, and the centra of the following three vertebrae). Although the neural arch is missing and the bone appears to have been subjected to some post mortem deformation, the specimen does provide evidence of the distinctive geometry of the atlantal facets for the occipital condyles.

Structural details of the atlas in *Gerrothorax* are best represented in MCZ 9519 (Fig. 6A, B) and FMNH PR 1685. Huene (1922) and Nilsson (1934) first noted in various plagiosaurs that presacral neural arches are not fused to centra and furthermore are intercentral in position. This condition, however, is not present in anterior cervical vertebrae of Kupferzell *Gerrothorax*. Neural arches are synostosed to the centra on the axis and 3rd cervical vertebra (Hellrung, 2003:figs. 19, 21) as well as on the atlas (Fig. 6B). The pedicle bases extend for nearly the length of the centra. Traces of the suture between pedicle and centrum are not evident except on the axis of FMNH PR 1685 where there is a faint, linear ridge. Comparable features were reported for *Gerrothorax* sp. by Shishkin (2000). The atlantal arch is low and inclined posteriorly at 30° to horizontal. The laminae exhibit a rugose, median sulcus; no neural spine is developed. The articular facets for the exoccipital condyles (Fig. 6A) are ovoid, with the long axis of the articular surface oriented mediolaterally; medially, the dorsal and ventral margins of the facets converge to an attenuated juncture. The facets are directed primarily anteriorly, but also slightly dorsolaterally. Posteriorly the centrum exhibits a shallow notochordal fossa, flanked on either side by extensive areas of rugosity. The atlas exhibits no indication that it bore a rib; the axis bears a pair of costal facets vertically aligned in the middle of the centrum.

Presacral Vertebrae—MGUH 28924 is a composite of several specimens. One vertebral series, exposed in ventral aspect, comprises 21 centra in articulation that decrease in size posteriorly (Fig. 7A). We interpret this series as a complete (or nearly complete) presacral column; 19 were figured previously (Nilsson, 1946a; Hellrung, 2003). The dorsal surface of the neural spine is constructed of finished bone in at least one specimen (unlike most stereospondyl neural spines). The neural spines have rugose lateral processes with strongly developed scars anteriorly and posteriorly, short transverse processes and small zygapophyses, as in other plagiosaurids.

The centra are essentially platycoelous with only a shallow central notochordal depression. Centra in the posterior presacral region bear the neural arches in an intervertebral position, as indicated by the recessed facets on both the anterior and posterior ends of centra (GM-V-2008-8); costal articulations in the posterior presacral region are likewise shared by adjacent centra. Towards the anterior end of the series of 21 centra (MGUH 28924), however, ribs shift from an intervertebral to a single vertebral articulation, a modification that probably coincides with a comparable displacement of neural arches to single centra (as is the case for the atlas and axis).

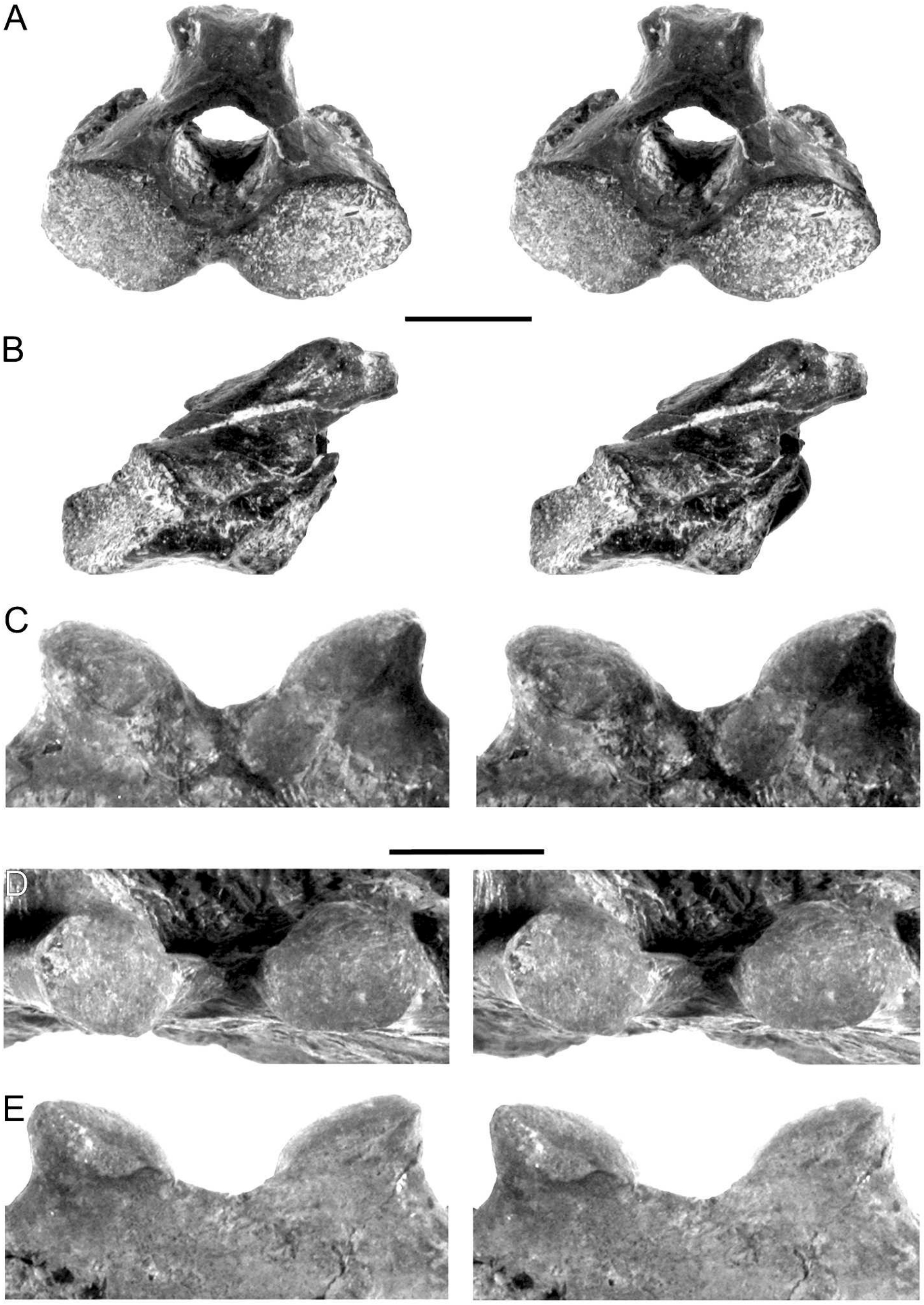

FIGURE 6. Stereophotographs of atlanto-occipital joint geometry in *Gerrothorax pulcherrimus*. **A**, anterodorsal and **B**, lateral views of an atlas of *Gerrothorax* from Kupferzell (MCZ 9519). The occipital condyles of a Fleming Fjord *G. pulcherrimus* (MGUH 28916) in **C**, dorsal; **D**, posterior; **E**, ventral views. Scale bars equal 1 cm.

Forelimb

Pectoral Girdle—Articulated dermal pectoral girdles present an overall massive appearance, and range in width from about 60 mm (GM-V-2008-24) to 240 mm (GM-V-2008-25); isolated elements are known from even larger girdles (e.g., MGUH 28917; Fig. 8A). Interclavicles (MGUH 28918, MCZ 9498, MGUH 28924, MCZ 9517, GM-V-2008-25) vary in the size and shape of the anterior process and the two paired lateral processes, as in the Kupferzell interclavicles (Hellrung, 2003:figs. 24, 25). The anterior two thirds of the medial margins of articulated clavicles (MGUH 28918, MCZ 9517, GM-V-2008-25) are straight overall, and the two bones abut anteriorly in the midline for approximately one quarter of total clavicular length. The clavicle is widest posteriorly where the bone ventrally overlaps the interclavicle between the two lateral processes. The lateral side of the clavicle is upturned, presenting a tuberculated lateral surface ventrally and a short process for articulation with the cleithrum

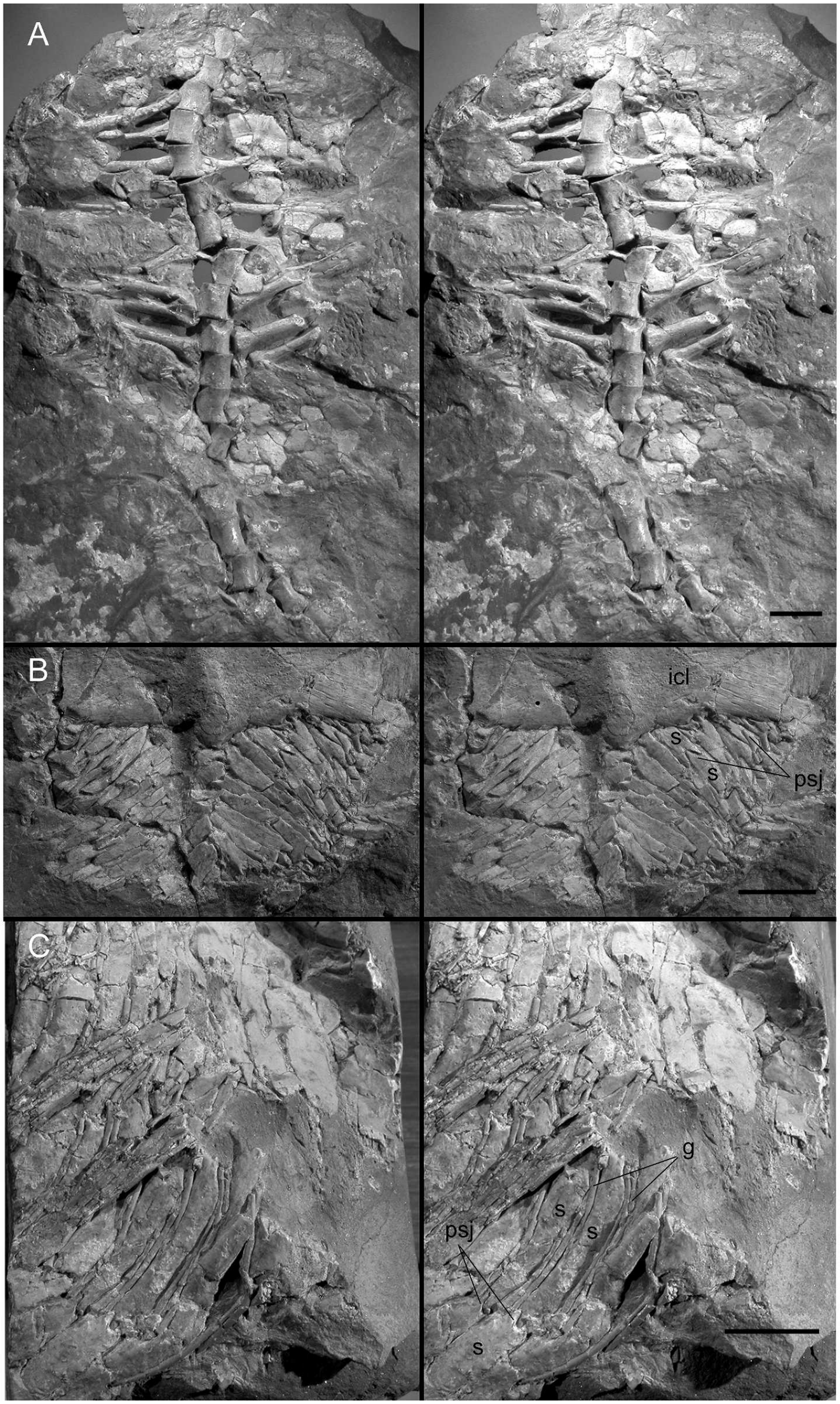

FIGURE 7. Vertebrocostal structure and armor in *Gerrothorax pulcherrimus*. **A**, ventral view of centra, ribs, and dorsal and ventral scutes (MGUH 28924, in part); anterior end of the vertebral series is at the top. **B**, dorsal view of ventral body scutes just posterior to the interclavicle (MGUH 28924, in part). Ventral scutes are in overlapping rows with peg and socket joints between scutes in the same row. **C**, dorsal view of ventral scutes and gastralia (MGUH 28922). Gastralia, which usually occur in triads, lie in grooves between the scute rows, taper at both ends and overlap one another. **Abbreviations**: **g**, gastralia; **icl**, interclavicle; **psj**, peg and socket joint; **s**, scute. Scale bars equal 1 cm.

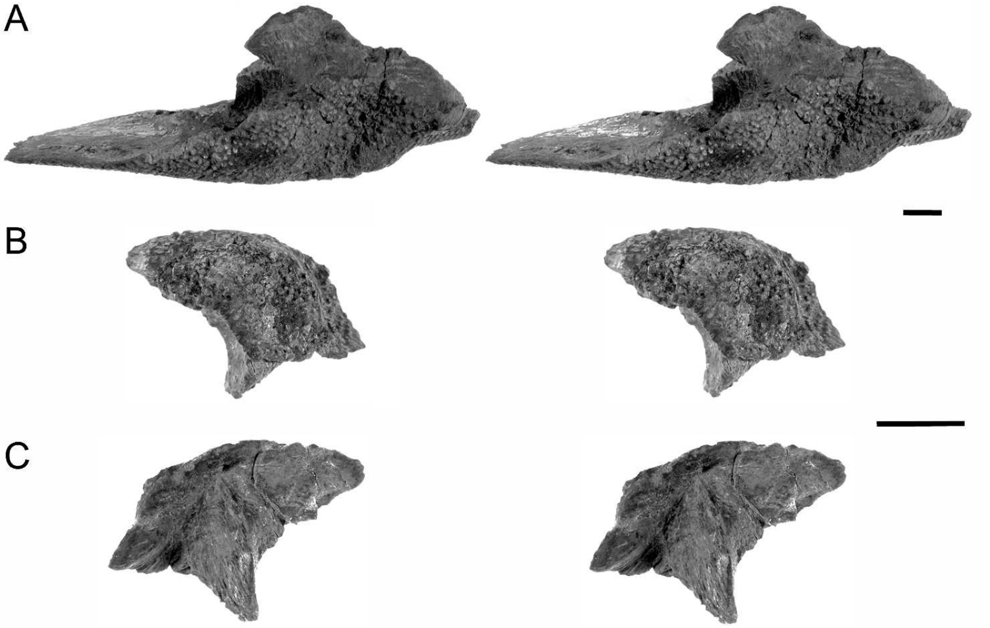

FIGURE 8. Stereophotographs of the cleithrum and clavicle of *Gerrothorax pulcherrimus*. **A**, right clavicle in lateral view (MGUH 28917). Cleithrum (MGUH 28918) in **B**, lateral, and **C**, medial views; the specimen is from the left side, but the image has been reversed to depict a right cleithrum that can be compared to the right clavicle. Scale bars equal 1 cm.

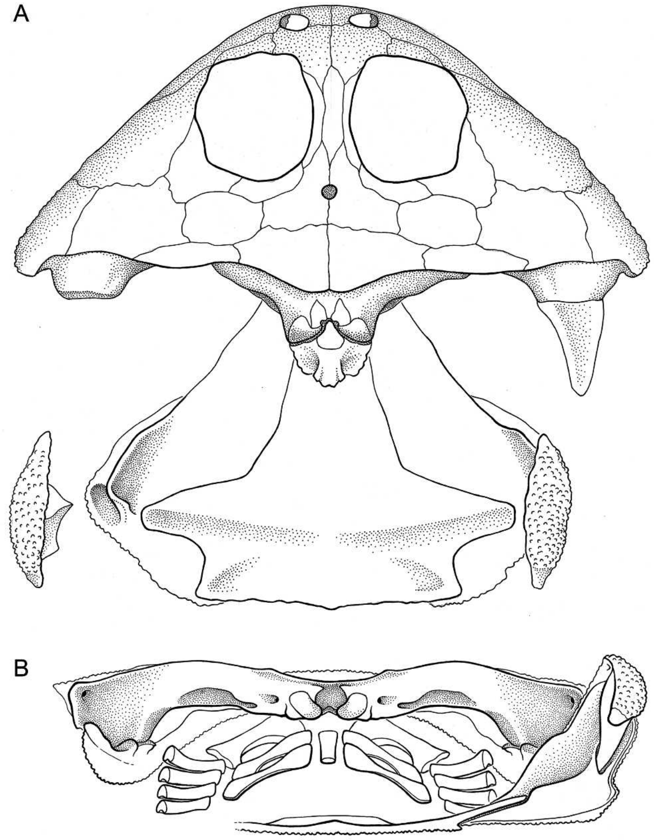

FIGURE 9. Reconstruction of the skull, branchial skeleton and shoulder girdle of *Gerrothorax pulcherrimus*. **A**, dorsal view; the atlas is also shown, and the left cleithrum has been elevated from the recess in the interclavicle with which it articulates. **B**, posterior view; the atlas is not shown, and the left shoulder girdle omitted to reveal the branchial skeleton.

dorsally. The dorsal process forms the anterior wall of a recess that receives the short ventral process of the cleithrum (Fig. 8A). Anteriorly the dosal process is continuous with the upturned margin of the clavicle, which in this region is transversely swollen and devoid of ornamentation. Two cleithra preserved in articulation (MGUH 28918, Fig. 8B, C; MGUH 28924) reveal the cleithral head as a thick, tubercle-covered cap that extends anteroposteriorly. Thus, the pectoral girdle possesses a continuously ornamented surface from the interclavicle ventrally, to the clavicle ventrally and laterally, and to the cleithrum laterally and dorsally. Overall cleithral structure is similar to that described by Nilsson (1946b).

Humerus—The right humerus associated with GM-V-2008-25 is 45 mm in length, and thus only 19% of the estimated breadth of the shoulder girdle. The bone is similar to that of *Plagiosaurus depressus* figured by Nilsson (1939:fig. 3), and confirms Nilsson's (1946a:fig 13; 1946b:fig. 6) reconstruction of relatively small forelimbs in *Gerrothorax*.

Dermal Armor and Associated Ossifications

Scutes—An imbricate series of six dorsal scutes (MGUH 28924), exposed in ventral aspect, is preserved in close approximation to a partial skull roof and is aligned with the midline suture between the postparietals; the position and orientation thus indicate that these are nuchal scutes from the dorsal midline. The scutes are broad (approximately half the width between the outer edges of the exoccipital condyles). The outline of most scutes is obscured by breakage, but the fifth is nearly complete; the convex anterolateral margins converge on an anterior process that contributes to the overall lanceolate appearance of the scute. The posterior margin is oriented transversely and appears to be more or less straight. Median linear rugosities occupy the anterior half of the ventral surface. The posterior half of the ventral surface bears a median sulcus. Each anterior process articulates within the sulcus developed on the posterior half of the ventral surface of the preceding scute. The scutes thus imbricate, with the ventral sulcus of each scute overlapping the dorsal surface of the anterior process of the following scute. As preserved, the series of nuchal scutes of MGUH 28924 lie in a single plane, and the anterior processes do not appear to extend into the most anterior parts of the sulci. The unoccupied sulcal space, however, would accommodate an increase in overlap of the nuchal series that would occur upon head lifting, as is postulated below.

The presence of large, midline scutes differs from the reconstruction by Hellrung (2003:fig. 32) that depicts midline and lateral body wall scutes as approximately the same size. More lateral scutes are oval to polygonal in outline and smaller than midline scutes (Fig. 7A). In GM-V-2008-24 an area of dorsal scutes that includes midline and lateral members confirms that the lateral scutes are smaller.

MGUH 28922 is a fragment of a lateral body wall that has split, showing internal surfaces of the dorsal and ventral scutes, and some lateral scutes. Scutes medial to the lateral scutes have a large pit, as noted previously by Nilsson (1937, 1946a) and Hellrung (2003:fig. 32), which may have transmitted a sensory canal system.

In addition to MGUH 28922, MCZ 9501 and MGUH 28924 preserve ventral scutes in dorsal aspect. Ventral scutes differ from dorsal scutes in being narrow rectangles arranged in rows. The rows are oriented more posteriorly than the ribs, which are positioned nearly transversely. In MGUH 28924, left and right series of ventral scutes both imbricate and interdigitate at the midline (Fig. 7B). Along their short edges adjacent scutes articulate by peg and socket joints. In some cases a single, elongate peg and socket is developed, whereas in others the joint surface is a W-shaped pair of short pegs and sockets. Along their long edges anterior scutes overlap the anterior margin of posterior scutes; similar joints are present in *Gerrothorax rhaeticus* (Nilsson, 1937:pl. 2). Rows of ventral scutes increase in width distally, with the most distal scute having a rounded, rather spatulate terminus (MGUH 28922).

Gastralia—In MGUH 28922 gastralia occur as overlapping triads of delicate rods on the dorsal aspect of the ventral scutes. These bundles lie along the linear junctions of scute rows where the posterior margins of the scutes are thin and form a continuous groove on the dorsal surface of the scutes (Fig. 7C). Cylindrical in cross section, the gastralia taper at both ends. Nilsson's (1937:fig.9; 1946a:figs. 10, 11) reconstructions of the gastralia of *Gerrothorax rhaeticus* depict the distal ends with a blunt, almost bulbous terminus, and thus appear to have been confounded with gastralia and the spatulate ends of ventral scutes; the labels on Nilsson's (1937:pl. I, II; 1946a:pl. III) photographs, however, correctly differentiate between scutes and gastralia. Gastralia have also been reported in the Kupferzell *Gerrothorax* (Hellrung, 2003). *Gerrothorax* gastralia are unlike gastralia of archosaurs (Claessens, 2004) in that they do not imbricate in the midline and are not expanded proximally. Robust ventral scutes have been referred to as gastralia in *Greererpeton* (Godfrey, 1989) and basal tetrapods (Lebedev and Coates, 1995). Inasmuch as both ventral scutes and gastralia are present in *Gerrothorax*, we recommend that the imbricating series of ventral dermal scutes commonly present in early tetrapods be referred to as ventral scutes, and restrict the term gastralia to elements found internal to the scutes or within abdominal wall musculature.

DISCUSSION

Analysis of Craniomandibular Mechanics

Review of Previous Interpretations—The distinctive cranial features of plagiosaurids, which include an extremely depressed, foreshortened skull, protruding exoccipital condyles, and elongate retroarticular processes, have been accorded diverse interpretations. Watson (1919) was the first to raise the possibility that aquatic temnospondyls, especially those with flattened skulls, achieved a large gape by elevating the skull rather than by depressing the mandible, and suggested mechanical roles for the elongate retroarticular process and depressor mandibulae muscle in effecting this movement. Watson (1951,1958) later proposed that the skull of *Paracyclotosaurus* was lifted by the action of neck muscles and also by contraction of the depressor mandibulae while the lower jaw rested on the ground. Panchen (1959) extended Watson's interpretation to brachyopids and plagiosaurids, but noted that differences in skull configuration would have yielded dissimilar effects in terms of gape width and mandibular protrusion.

Howie (1970) identified a number of mechanical improbabilities in Watson's hypothesis of head lifting by the depressor mandibulae, and instead proposed that a muscle from the shoulder girdle, the cleidomastoideus, may have served this function. Shishkin (1987), in reconstructing craniomandibular mechanics in *Plagiosternum*, agreed with Howie that the skull was held in a more or less horizontal position and that the cleidomastoideus initiated skull elevation, but that neck muscles played a major role in raising the skull. Shishkin (1987:fig. 14b) portrayed a dorsal rotation of about 30° upon jaw opening. Yet Shishkin (1987:53) also suggested that "the maximum amplitude of mouth opening in *Plagiosternum* is determined by the structure of the joint surface on the quadrate, in which the inferior and anterior divisions form a bend of approximately 90° (it is usually lower in labyrinthodonts). Apparently, the jaws could open almost at a right angle, which made the lower jaw protrude strongly forward." With reference to Shiskin's illustration (1987:fig. 14b) of craniomandibular movements in *Plagiosternum*, we note that a 50° depression of the lower jaw would bring the retroarticular process into contact with the occiput, with the area between them, presumably occupied by a depressor mandibulae muscle, having been entirely occluded. The extreme gape proposed by Shishkin thus appears improbable. Hellrung (2003) interpreted the "dorsal orientation" of the exoccipital facets in *Gerrothorax* from Kupferzell as evidence that the head was held at an elevated posture of about 30°.

No detailed anatomical evidence has been adduced by any previous study that would corroborate the unusual skull raising that has been postulated for plagiosaurids and other temnospondyls. Of prime relevance is the geometry of the atlanto-occipital joint.

Atlanto-occipital Joint Structure and Function—Although no specimen preserves a complete atlanto-occipital joint, the relations of the apposing condylar and atlantal facets in *Gerrothorax* may be reconstructed from various specimens in which either the condyles or atlantal facets are intact. Three atlases were used for this purpose; MGUH 28924 and FMNH PR 1685 have been subjected to some post mortem distortion but MCZ 9519 appears undeformed. The concave facets of MCZ 9519 are approximately oval with an attenuated medial margin, and are oriented rostrally and somewhat dorsolaterally (Fig. 6A, B). From the standpoint of atlanto-occipital joint function, the most important feature is difference between the facet's breadth, measured from lateral to medial margins along the articular plane, and the facet's height, measured in a coronal (transverse vertical) plane from dorsal to ventral margins. In all three specimens facet height is about 55% of facet width.

The geometry of the exoccipital condylar facets was determined from MGUH 28916, MCZ 9511, and MGUH 28925. The convex facets of the condyles face caudomedially to appose the anterolaterally facing facets of the atlas. Condylar facets differ significantly from those of the atlas in having height/width ratios close to 1 (measured by the same method used for atlantal facet heights and widths). On the condyles of MGUH 28925, for example, facet height is 95% of width; on both condyles of MGUH 28916 and on the left condyle of MGUH 28921 the ratios of height to width are 90%. In an articulated condition, the insertion of the wedge-like facets of the atlas into the embrasure between the exoccipital condyles precludes lateral flexure. Whereas the widths of atlantal and condylar facets in an articulated specimen thus may be expected to be comparable, the height of a condylar facet will exceed that of a corresponding atlantal facet by 40-45%. The apposition of two facets of very unequal heights is evidence that dorsoventral movements of the head took place at the atlanto-occipital joint. Articular contact of atlantal facets with the ventral part of condylar facets aligns the skull with the vertebral axis in a more or less horizontal resting position (Fig. 10A, B). Elevation of the head occurs through an atlanto-occipital rotation that brings the dorsal part of the condylar facets into articular contact with the atlantal facets (Fig. 10C, D). Elevation of the skull is further facilitated by the fact

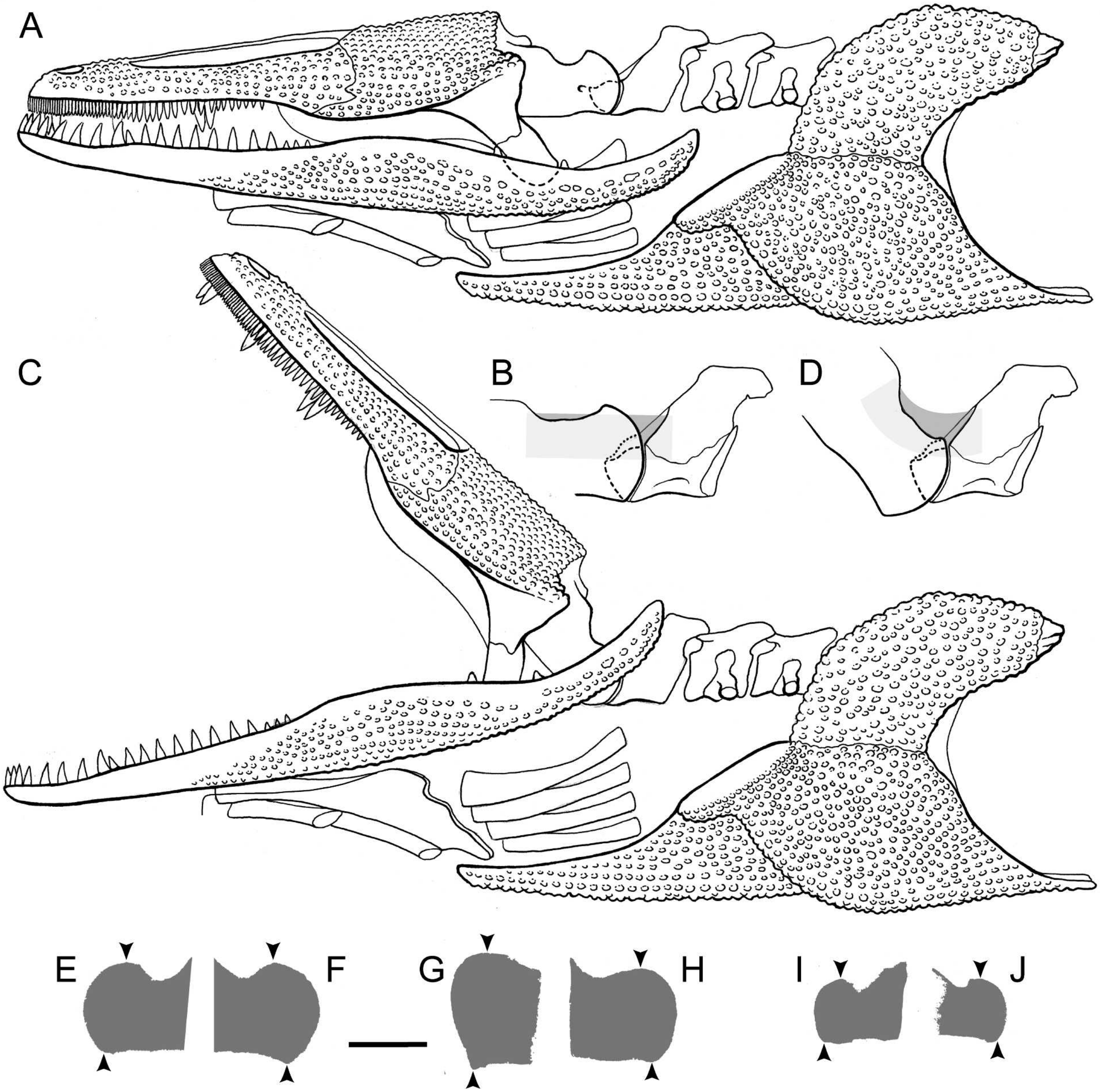

FIGURE 10. The mechanics of mouth gape in *Gerrothorax pulcherrimus*. **A**, reconstruction of the skull, mandible, anterior vertebrae, branchial arches and pectoral girdle in left lateral view. **B**, reconstruction of articular relations between the left condyle and left atlantal facet based on the proportions of MGUH 28925 and MCZ 9519; when the head rests horizontally and the mouth is closed (as in **A**), the atlantal facet contacts the ventral part of the condylar facet. **C**, a large gape is achieved by elevation of the skull through atlanto-occipital rotation; with the atlantal facets in contact with the dorsal part of the occipital facets (**D**), the skull is raised (by as much as 50°) and the lower jaw protruded. **E–J**, silhouettes of the median, dorsoventral curvature of the condylar facets in MGUH 28920 (**E**, left; **F**, right), MGUH 28925 (**G**, left, **H**, right) and MGUH 28916 (**I**, left, **J**, right). For details on how these silhouettes were produced, see Materials and Methods. Arrows indicate the dorsal and ventral margins of the articular surface. Although post mortem deformation has induced artifact asymmetries, all condyles exhibit a radius of curvature along the dorsal part of the facet that is shorter than that along the ventral part. Scale bar equals 1 cm.

that the dorsal part of the condylar facets has a shorter radius of curvature than the ventral part, a feature evident in several Greenlandic specimens (Fig. 10E-J) as well as in a Kupferzell specimen of *Gerrothorax* (SMNS 84788) figured by Hellrung (2003:fig. 8).

Features Related to Cranial Elevation—Several structural features of the atlanto-occipital region appear to be related to relieving the spinal medulla of severe angular deformation during head lifting. The neural canal between the foramen magnum and the atlantal arch is relatively elongate and open dorsally (i.e., without a bony roof). The occipital condyles are borne on prominent, posteriorly projecting processes that effectively lengthen the floor of the neural canal between the foramen magnum and the atlantal neural arch. The occiput in the region of the foramen magnum is inclined anterodorsally, with the result that the dorsal margin of the foramen magnum is recessed anteriorly. Similarly, the anterior margins of the laminae of the atlas are recessed posteriorly. As a result, both the foramen magnum and the anterior aperture of the atlantal neural arch face somewhat dorsally. Thus, bending of the medulla need not have been concentrated solely at the transverse plane of the atlanto-occipital joint, but could have been distributed along a greater length of the cord in the elongate and dorsally open neural canal between the foramen magnum and atlantal arch (Fig. 10B, D).

A second feature that reduces angular deformation of the spinal medulla during head lifting is the dorsal displacement of the exoccipital condyles. The condyles of temnospondyls commonly lie below the level of the foramen magnum. More specifically, the dorsal margins of the condyles lie at or below the floor of the foramen magnum, e.g., in *Benthosuchus* (Bystow and Efremov, 1940), *Batrachosuchus* (Watson, 1956), *Peltobatrachus* (Panchen, 1959), *Siderops* (Warren and Hutchinson, 1983), and *Konzhukovia* and *Platyoposurus* (Gubin, 1991). The mechanical axis of flexion-extension is a horizontal line approximately through the middle of the condyles, although the axis will shift slightly if the condylar radius of curvature varies. Deformation of the medulla, specifically compression upon atlanto-occipital extension and distension upon flexion, occurs in proportion to the distance of medullary tissue from the axis. Deformation of the spinal medulla is minimized if the axis is moved dorsally so as to pass through the medulla. In plagiosaurids the condyles have shifted dorsally to achieve this effect (Figs. 1C, 2C; cf. *Plagiosternum danilovi*; Shiskin, 1987:fig. 14b).

In summary, *Gerrothorax* achieved a large gape principally by raising the skull. Evidence for this movement derives from the unequal vertical extent of the condylar and atlantal facets. The angle through which the skull elevated may be estimated from the difference (Fig. 10). With the skull in a horizontal, resting position, only the lower parts of the condyles articulated with the atlantal facets. During skull elevation, the occipital condyles rotated on the atlas, bringing the dorsal part of the condylar facets into articulation with the atlantal facets. We concur with the interpretations of Panchen (1959) and Shiskin (1987) that skull elevation engenders protrusion of the lower jaw by virtue of the forward rotation of the quadrates. A modest amount of mandibular depression (on the order of 10-15°) would further enlarge the gape, but an effective gape could be achieved through head elevation alone.

The distinctive suite of plagiosaurid cranial and cervico-occipital features associated with extensive head lifting may be unique to this group. Head lifting in plagiosaurids is mechanically facilitated by the substantial foreshortening of the skull, which shifts the center of mass of the cranium close to the rotational axis of the atlanto-occipital joint. In contrast, the anteriorly displaced center of mass of the relatively elongate skulls of mastodonsauroids (sensu Damiani, 2001) engenders a relative mechanical disadvantage for atlanto-occipital rotation. Furthermore, the specific morphological specializations for head lifting, notably the differential in dorsoventral heights of the condylar and atlantal facets as well as the pronounced convexity of the condylar facets, do not appear to be developed in non-plagiosaurid temnospondyls to the extent that substantial cranial elevation was possible. Few studies provide the data to address this question directly, however. Warren and Hutchinson's (1983:figs. 4, 16) illustrations of the brachiopoid *Siderops kehli* reveal that the approximately circular condylar and atlantal facets are evenly matched in size. Watson's (1956:figs. 5–7) illustrations of the type of *Batrachosuchus watsoni*, which show a plagiosaurid-like posterior projection of the condyles and an anteroventrally directed quadrate, reveal exoccipital condylar facets that are only slightly convex. Watson (1958:237) described the exoccipital of *Paracyclotosaurus davidi* as bearing ". . . a large hemispheroidal condyle . . . viewed as a pair it is evident that the condyles allowed dorso-ventral motion of the head, perhaps through a large arc . . ." Yet Watson's (1958:figs. 3, 8) illustrations depict a peculiar geometry of the condylar facet; the dorsal half of the condyle is convex, but the ventral half is shallowly concave. Examination of a skull of *Cyclotosaurus* from the Fleming Fjord Formation (Jenkins et al., 1994:figs. 4, 5) confirms that the condylar facets are only slightly convex, as is typically the case in mastodonsauroids (e.g. *Mastodonsaurus giganteus*; Schoch, 1999:figs. 8, 13; Schoch and Milner, 2000:fig. 95).

Structure and Function of the Pectoral Girdle—*Gerrothorax* is one of two plagiosaurids with dermal armor that completely invests the trunk, extending across all surfaces from the rear of the skull to the end of the tail. Incorporated into the armor is a robust, uniquely constructed pectoral girdle that includes an intimately interlocked cleithrum and clavicle. No forelimb muscles would have originated from the external surfaces of the interclavicle, clavicle or cleithrum, as is generally the case in temnospondyls, because the surfaces are covered with dermal ornamentation. The robustness of the pectoral girdle is not matched by the development of the forelimb elements, which are short, relatively small and lack ossified ends (Hellrung, 2003:fig. 32). The scapulocoracoid is very reduced (Hellrung, 2003:fig. 28), as were probably the shoulder muscles to the proximal limb. The striking morphological divergence between the massive dermal shoulder girdle and the reduced forelimbs raises the likelihood that the shoulder girdle was specialized for functions other than its conventional roles in limb and trunk support. Rather, the claviculocleithral complex could have served as anchor for muscles that elevated the skull, an interpretation supported by the fact that the mass of the bones of the *Gerrothorax* pectoral girdle is clearly greater than that of the skull. With reference to various temnospondyls, Howie (1970) first suggested the possibility that the cleidomastoideus, a muscle linking the cleithrum and occiput, would have been suitably positioned to raise the skull. In *Gerrothorax*, such a muscle may have originated on the posterior half of the medial surface of the anteroposteriorly elongate cleithrum (Fig. 8C). A muscle arising from this area would pass to the occiput above the axis of the atlanto-occipital joint, and thus would have been positioned to elevate the skull. The interdigitation of processes that interlock the cleithrum and clavicle ensures a stable origin for the cleidomastoideus, the force from which must not only lift the skull, but do so against the resistance of water.

Nilsson (1946a) was the first to propose that *Gerrothorax*—heavily armored, dorsoventrally compressed and short limbed—was most likely an obligatorily aquatic, benthic amphibian, an interpretation that Hellrung (2003) further supported. But contra Hellrung's (2003:88) suggestion that the skull was held with 30° of elevation, we suggest that the head was held horizontally in the rest position, a posture that is typical for tetrapods and in any case in keeping with the purported benthic habits of the animal. If, as Nilsson (1946a) envisioned, *Gerrothorax* took prey through opportunistic ambush by remaining motionless on the bottom, rather than by pursuit, then the possible selective advantage of developing cranial elevation for gape and suck feeding is at least plausible. *Gerrothorax* is not unique among amphibians, however, in employing head lifting. Aquatic salamanders that suction feed lift their heads when gaping (Reilly and Lauder, 1992; Deban and Wake, 2000), although most studies do not provide the photographic documentation necessary to assess whether the displacement of the head occurs through extension of the neck or by cranial elevation at the atlanto-occipital joint. Tiger salamanders appear to employ both mechanisms, although in the larval stage only the head appears to lift (Shaffer and Lauder, 1988:pl. I, II). Schwenk and Wake (1993) provide unequivocal documentation of head lifting in the desmognathine plethodontid *Leurognathus marmoratus*, and document some of the specializations of the atlanto-occipital joint that allow both cranial elevation and depression (so-called head tucking). Inasmuch as this species employs these movements in feeding as well as for burrowing and wedging under objects, head lifting need not be considered strictly a feeding specialization. The interpretation of *Gerrothorax* as a Late Triassic fish trap, as attractive as the image may be, cannot be secure without additional evidence.

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