

THE TEMNOSPONDYL AMPHIBIAN *CYCLOTOSAURUS* FROM THE UPPER TRIASSIC OF POLAND

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Abstract: A gap in the Late Triassic fossil record of the capitosaur amphibian *Cyclotosaurus* is filled by new material from lacustrine deposits at Krasiejów, Poland, corresponding in age to the Lehrberg Beds (late Carnian) of Germany. The skull of the Polish cyclotosaur is intermediate in several respects between that of *Cyclotosaurus robustus* from the middle Carnian Schilfsandstein of Germany and the younger *C. mordax* from the early Norian Stubensandstein. It shows a decrease in the width of the skull and in the degree of con-

cavity of the posterior margin of the skull roof. The differences are significant enough to warrant erection of a novel species, the name *Cyclotosaurus intermedius* sp. nov. being proposed. The pectoral girdle, identified for the first time in *Cyclotosaurus*, suggests the genus was more fully adapted to an aquatic mode of life than was *Paracyclotosaurus*.

Key words: temnospondyls, capitosaur, cyclotosaur, Late Triassic.

THE capitosaur is among the best known groups of Mesozoic temnospondyl amphibians. They are almost ubiquitous in vertebrate-bearing sediments of Triassic age (Damiani 2001a) and have been reported from all continents, including such regions as Greenland and Spitsbergen (Schoch 2000a). The taxonomy of Capitosauroida is still debated (Ochev 1966; Shishkin 1980; Schoch 2000a; Damiani 2001a). In the review of stereospondyls by Schoch and Milner (2000), the Capitosauroida includes five families: Paratosuchidae, Eryosuchidae, Mastodonsauroidae, Paracyclotosauroidae and Cyclotosauroidae. The skull of capitosauroids is very conservative: the orbits are well posterior, the jugals are usually broad and the orbital margin is raised above the skull table. The skull outline is parabolic in primitive forms, whereas more derived taxa may have slender or triangular skulls (Schoch and Milner 2000).

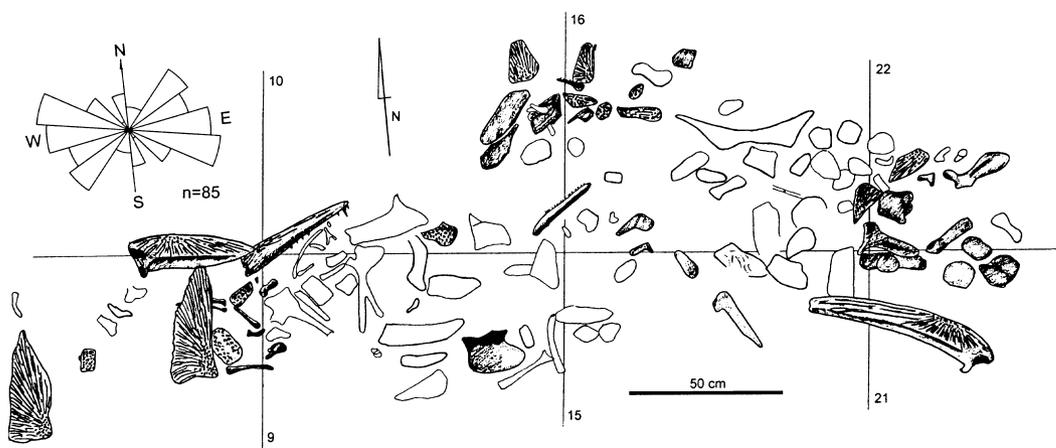
Several aspects of capitosauroid anatomy and evolution still await clarification, including the relationships between species of *Cyclotosaurus*. This genus has been reported from East Greenland (Jenkins *et al.* 1994) and Thailand (Ingavat and Janvier 1981), but is most widely known from various horizons of the German Basin in Europe: *C. robustus* Meyer and Plieninger, 1844; *C. mordax* Fraas, 1913; *C. posthumus* Fraas, 1913; *C. hemprichi* Kuhn, 1942 and *C. ebrachensis* Kuhn, 1932.

The new cyclotosaurid material from Poland comes from the Krasiejów in the Opole Silesian Region (Dzik *et al.* 2000). Most of the fossils from this locality occur in one of two horizons. In the lower horizon, bones of the amphibian *Metoposaurus* (Sulej 2002a) and the phytosaur

Paleorhinus (Dzik *et al.* 2000) predominate followed by bones of the aetosaur *Stagonolepis* (Dzik 2001) and *Cyclotosaurus* (Majer 2002). The upper horizon is dominated by *Stagonolepis* and the dinosauriform *Silesaurus* (Dzik 2003). Between these horizons, a small accumulation of bones of the rauisuchian *Teratosaurus* (Sulej 2002b, in press) and *Silesaurus* have also been found. Bones belonging to *Cyclotosaurus* have been collected from both the lower and the upper horizons. These include elements of the shoulder girdle. Some of these elements, such as the scapulocoracoid and cleithrum, were previously unknown in *Cyclotosaurus*, and remain poorly known in capitosaur generally. In the present paper preliminary results of our study on the *Cyclotosaurus* material from Krasiejów and its suggested evolutionary interpretation are presented.

MATERIAL AND GEOLOGICAL SETTING

At the Krasiejów locality, marly clays are exposed to a depth of 14 m. The tetrapod fossils are mostly disarticulated and occur mainly in two fossil-bearing horizons, both of which probably correspond to the subsurface Drawno Beds and the Lehrberg Beds of Baden-Württemberg (Dzik 2001). Some regularity in the arrangement of cyclotosaur bones in the upper horizon seems to be the result of deposition on a riverbed. The direction of the long axes of the bones suggests that the river flowed from north-west or south-east (Text-fig. 1). A large Late Trias-



TEXT-FIG. 1. Orientation of bones of *Cyclotosaurus intermedius* sp. nov. in the upper horizon at Krasiejów. Rose diagram of the long bones indicates the current direction.

sic lake basin was located to the north of the locality (Ziegler 1990), whereas the newly formed Variscan Mountains (the Sudetes) lay to the south. The *Cyclotosaurus* specimens collected from the lower horizon include a complete skull with associated mandible (ZPAL Ab III 1173), an isolated mandibular ramus (ZPAL Ab III 680) and several postcranial bones: humerus (ZPAL Ab III 887/3), scapulocoracoid (ZPAL Ab III 887/2) and interclavicle (ZPAL Ab III 887/1). The specimens from the upper horizon include: disarticulated skull bones (lacrimal, ZPAL Ab III 471/25; jugal, ZPAL Ab III 471/20; palatine, ZPAL Ab III 471/16; pterygoids: ZPAL Ab III 471/8, 471/19, 471/31, 471/45), incomplete mandibular rami (ZPAL Ab III 471/113, 472/28), and an almost complete clavicle (ZPAL Ab III 397), cleithrum (ZPAL Ab III 471/51) and interclavicle (ZPAL Ab III 367).

Institutional abbreviations. ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

SYSTEMATIC PALAEOLOGY

Superfamily CAPITOSAUROIDEA Watson, 1919

Family CYCLOTOSAURIDAE Shishkin, 1964

Genus CYCLOTOSAURUS Fraas, 1889

Cyclotosaurus intermedius sp. nov.

Text-figures 1–8

Derivation of name. The species name was chosen in order to emphasize that it is intermediate between the older *Cyclotosaurus robustus* Meyer and Plieninger, 1844 and younger *C. mordax* Fraas, 1913.

Holotype. ZPAL Ab III 1173, Text-figures 2–3. The specimen is held in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

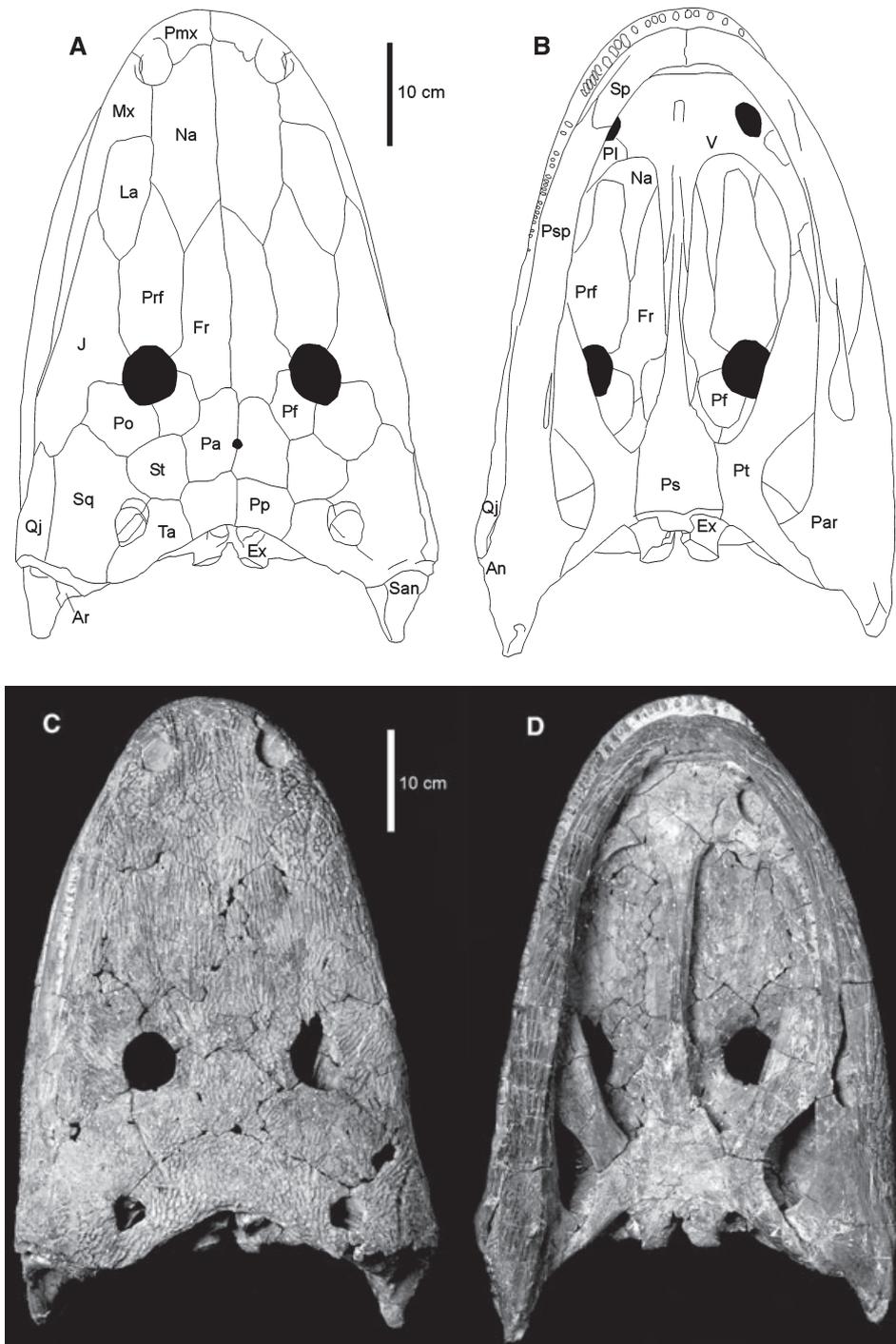
Type locality and horizon. Krasiejów, Opole Silesia, Poland; Upper Carnian, probably Drawno Beds, coeval with the Lehrberg Beds of Germany.

Diagnosis. Distinguished from related species by the projection of the quadrate behind the posterior margin of the skull roof, and the presence of a shagreen of denticles on the palate.

Remarks. *C. intermedius* differs from *C. mordax* in that the posterior border of the skull is more concave, though less so than in *C. robustus*. The orbits are in a more lateral position than in *C. robustus*, and the sides of the postorbital skull are more vertical. The interchoanal tooth row differs from that of *C. robustus* in being gently curved posteriorly (straight in *C. robustus*), while the para- and interchoanal teeth are broadly separated (single arcade in *C. robustus*). *C. intermedius* differs from *C. posthumus* Fraas, 1913, in that the lateral borders of the skull are straight rather than concave, while the choanae are oval (round in *C. posthumus*). The snout is broad in *C. intermedius* but slender in *C. hemprichi* Kuhn, 1942, while the anterior palatal vacuity is reniform, not oval as in *C. ebrachensis* Kuhn, 1932.

Description

In ZPAL Ab III 1173, both the skull and the mandible (Text-fig. 2) are well preserved, with only the posterior margins of the right tabular and squamosal slightly damaged, and the mandible displaced somewhat to the left. The skull has straight lateral bor-

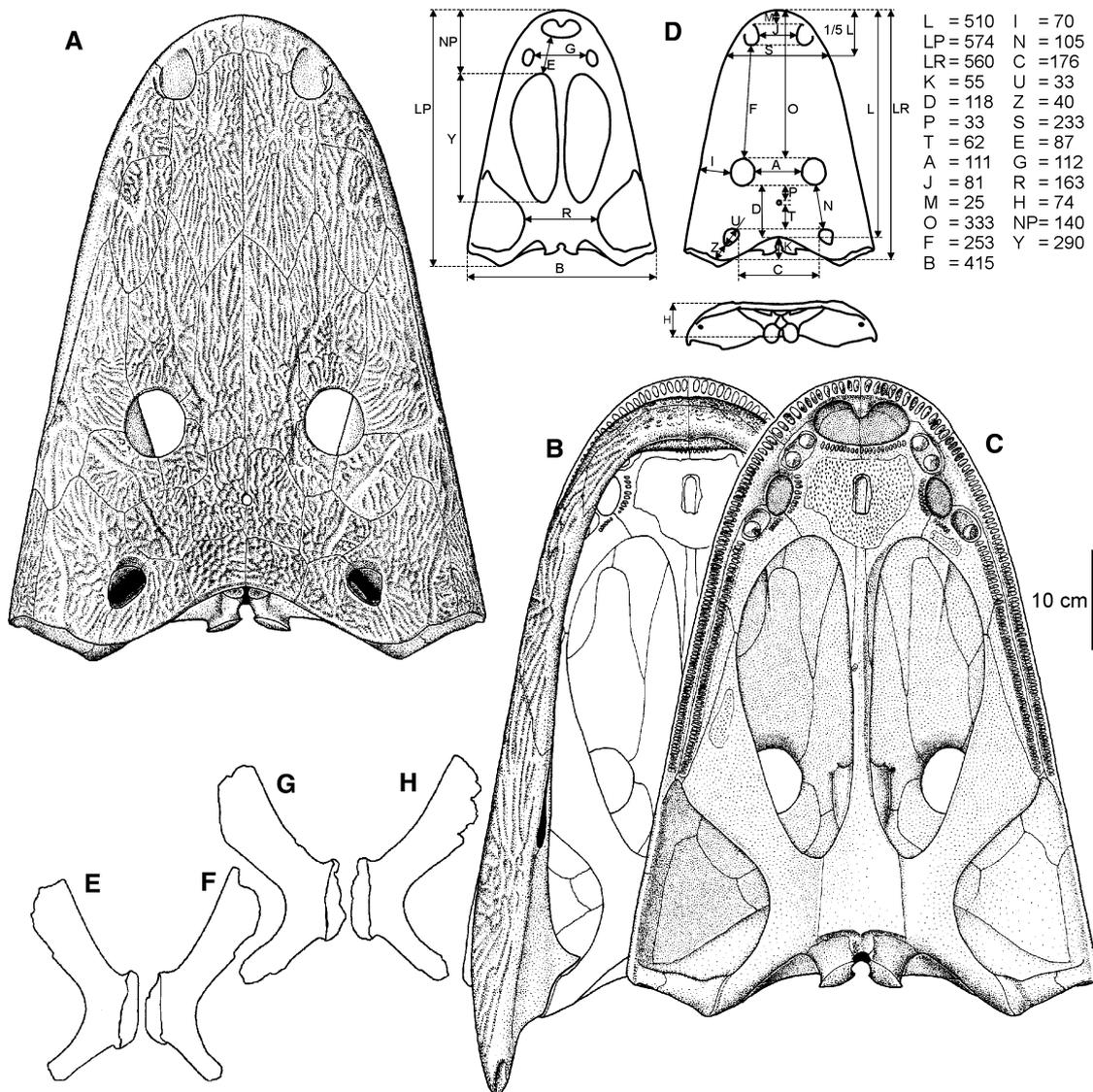


TEXT-FIG. 2. *Cyclotosaurus intermedius*. The skull and articulated mandible, holotype ZPAL Ab III 1173. A, explanatory drawing of the dorsal view. B, explanatory drawing of the ventral view. C, dorsal view. D, ventral view. For abbreviations, see Appendix.

ders and generally resembles that of typical cyclotosaurs, except that the quadrate condyles protrude posteriorly behind the skull roof and occipital condyles.

Skull roof. The bones of the skull roof are thin. Anteriorly, the nares are rather large, broad, oval and open anterolaterally, but

their anterolateral margins are not distinct. The premaxilla forms more than half of the narial margin as well as the anterior wall of the narial passage, while the nasal contributes one-third of the margin. The length of the suture between the maxilla and nasal is equal to the naris length (Text-figs 2–3A). The nasal produces a long pointed shelf that overlaps the dorsal surfaces



TEXT-FIG. 3. A–C, reconstruction of the skull and mandible of *Cyclotosaurus intermedius*. The drawings are based on ZPAL Ab III 1173 and Ab III 33. A, dorsal view. B, mandible in ventral view. C, skull in ventral view. D, skull measurements of the holotype. E–H, pterygoids from upper horizon in ventral view. E, ZPAL Ab III 471/19; F, Ab III 471/8; G, Ab III 471/31; H, Ab III 471/45. For abbreviations, see Appendix.

of the frontal and prefrontal, while a broad, more rounded shelf from the prefrontal overlaps the dorsal surface of the nasal (Text-fig. 3A–C; compare dorsal and ventral view of the skull).

The frontals form a flat area between the orbits and make a small contribution to the orbital margins. Posterior to the orbit, the skull roof is elevated. Ventrally each frontal directs a small longitudinal process toward the sphenethmoid. The jugal forms more than half of the lateral margin of the orbit, extending anteriorly to the same transverse level as the frontal and prefrontal. Dorsal to it, the anterior border of the postorbital is transverse. A round parietal foramen is situated slightly behind the mid-point of the parietal suture. The postparietal is rhomboid. Together with the tabular, it forms a deep embayment along the posterior border of the skull roof. The tabular is convex dorsally

and curved posteroventrally. Laterally, it has a suture with the squamosal behind the otic notch. This suture is as long as the otic fenestra. The squamosal is the largest bone in the postorbital part of the skull roof. Ventrolaterally it meets a triangular, nearly vertical, quadratojugal.

The sensory grooves are not very distinct and in some parts are completely covered by sculpture. The supraorbital sensory groove runs along the suture between the nasal and lacrimal (ZPAL Ab III 1173), or on the lacrimal (ZPAL Ab III 471/25), with the infraorbital groove forming a Z-shaped flexure on the same bone.

Palate. The premaxilla (Text-fig. 3C) forms the anterior border of the single, oval anterior palatal vacuity. Medially, it bears a

posteriorly directed rugose process. The choanae are slightly elongated. The vomer, palatine and maxilla all contribute to the choanal rim, but the premaxilla is excluded. Each vomer (Text-fig. 3C) sends a long, tapering posteromedial process along the inner border of the interpterygoid vacuity. Vomerine tusks are situated at the anterolateral corner of each bone, at the junction of the vomer, premaxilla and maxilla. The circumvomerine tooth arcade consists of a transverse row of medially curved teeth. The interchoanal tooth row runs in a gentle curve along the posterior border of the anterior palatal vacuity, while the parachoanal row continues onto the palatine. Shagreen denticles cover a large area of the vomer and some parts of palatine and pterygoid.

The maxilla is one of the main tooth-bearing elements. Anteriorly it bears a flat medial projection that forms the entire lateral choanal border. A broad conspicuous furrow extending along the suture with the ectopterygoid and palatine corresponds to the tooth row of the dentary.

The palatine (Text-fig. 3C) forms the posterior border of the choana. Its dentition consists of a lateral row of about 12 similar-sized teeth, a pair of large anterior tusks and the posterior part of the row of tiny parachoanal teeth. In some specimens the palatines and vomers have both tusks preserved. The palatine forms a lamina, clearly visible in specimen ZPAL AB III 471/16, that extends transversally and is directed posterodorsally. It widens into a suture with the lacrimal; the suture with the pterygoid is very short. The ectopterygoid (Text-fig. 3C) is long and narrow but does not reach the margin of the subtemporal window. The ectopterygoid–jugal suture is visible in ZPAL Ab III 471/20.

The quadrate and palatal rami of the pterygoid meet at an angle of 90–95 degrees, as seen in disarticulated specimens ZPAL AB III 471/8, 471/19, 471/45, 471/49, and 115 degrees in specimen ZPAL AB III 1173 (Text-fig. 3E–H).

The median parasphenoid (Text-fig. 3C) is subdivided into a basal plate and a keeled cultriform process. The former is an elongated trapezoidal plate sutured laterally with the pterygoid and posteriorly with the exoccipital. The cultriform process is thickened along the suture with the vomer, its palatal exposure extending to a point in front of the choanae.

The occiput. The skull roof is flat in occipital view (Text-fig. 4), but the medial part of the ventral margin is strongly concave. The tabular contributes to the massive parotic process, with the ventral process of the postparietal making up part of the columna verticalis. Together, the columna verticalis and parotic process form a triangular structure. Between them, the posttemporal fenestra is very low and wide. The process lamellosus of the exoccipital is strongly developed, and the oval occipital condyles lie at a level above that of the quadrate condyles. The lamina ascendens of the pterygoid forms an oblique ridge. The quadrate extends well dorsally and contacts the pterygoid, the occipital flange of the squamosal and the quadratojugal. The latter contributes to the margins of a small foramen paraquadatum and the lateral part of the quadrate condyle. In this view, the quadratojugal contour is vertical and protrudes ventrally to a point below and behind the quadrate condyles.

The mandible. The right ramus of the mandible ZPAL Ab III 680 (Text-fig. 5E–G) is well preserved, although slightly

compressed and lacking some posterior fragments. Almost all sutures are visible. In ZPAL Ab III 1173 the whole mandible is perfectly preserved but cannot be seen in dorsal view.

The dentary is the largest bone and the only tooth-bearing element. It forms the dorsal surface, contributes to the labial and lingual surfaces anteriorly, and extends back to the midpoint of the angular. It also forms a sharp wedge on the labial surface between the angular and surangular. In lingual view, only a small field of the symphyseal region is visible, equipped with one or two large tusks and small rows of inner dentary, parasymphysial teeth lying posterior to the tusk.

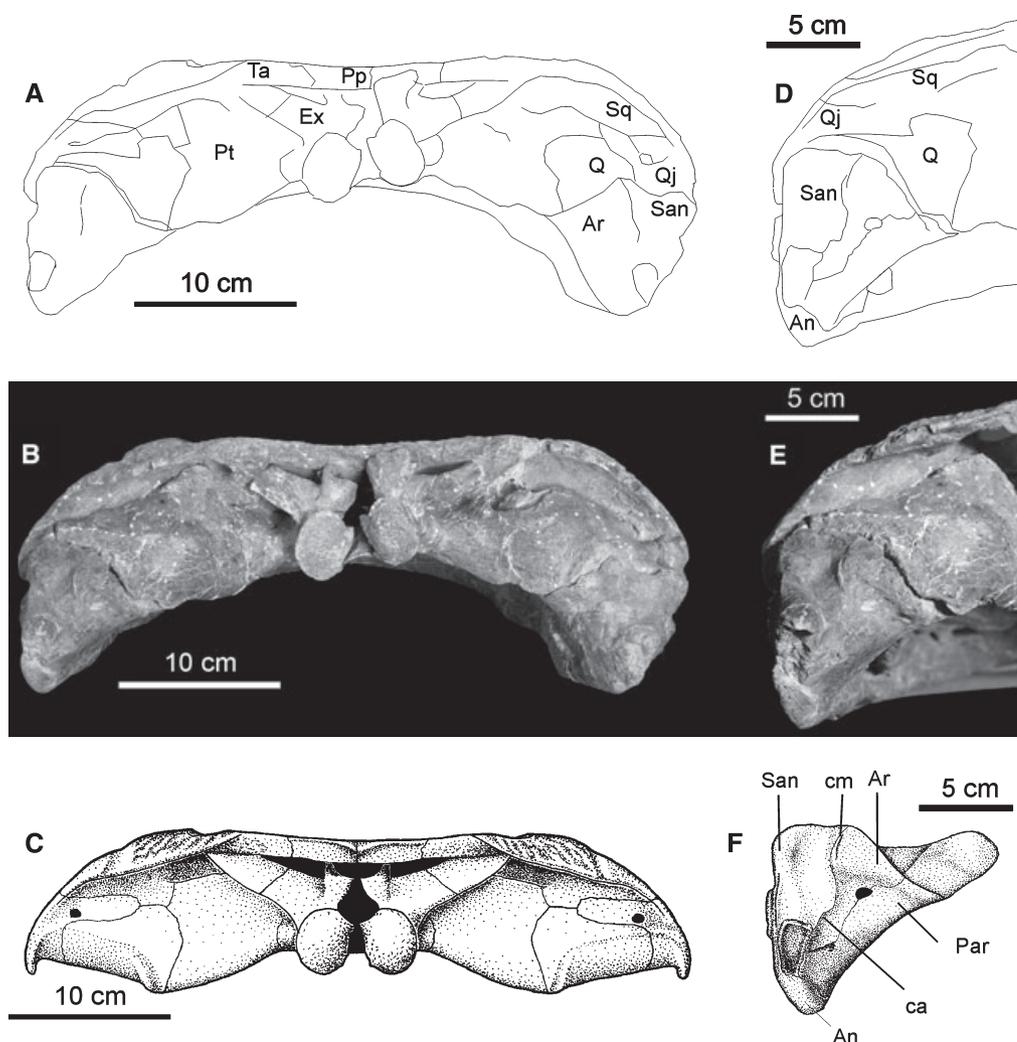
The splenial and postsplenial form the anteroventral surface of the mandible, and are roughly equal in length. A deep lingual horizontal fissure separates the dentary and splenial in the symphyseal region, while the postsplenial has sutures with the prearticular, angular, coronoid and intercoronoid. It terminates posteriorly below the posterior Meckelian foramen. A very small, oval anterior Meckelian foramen is situated in the anterior part of the postsplenial, while the posterior Meckelian foramen is long and posteriorly expanded. Its anteroventral rim is provided by the postsplenial, with the prearticular contributing the posterior and dorsal borders, and the angular completing it posteroventrally.

The angular is bound by the surangular, dentary and postsplenial in labial view, and by the prearticular and postsplenial lingually, embracing the posterior Meckelian foramen. Posteriorly, the angular reaches the end of the mandible. A conspicuous lingual notch lies between the angular, surangular and the posterior end of the prearticular, at the termination of the postglenoid area.

The surangular occupies most of the posterodorsal part of the labial surface, including the postglenoid region, where it is bordered lingually by the articular (Text-figs 4F, 5D). On the dorsal surface, the surangular extends medially up to the crista medialis and the posterior part of the crista articularis. The crista medialis forms the border of the articular. In the labial border of the adductor fossa, the surangular is thickened along its flattened upper margin to form the torus arcuatus. The most prominent sensory groove (Bystrow and Efremov 1940) on the surangular is the oral one.

The coronoid series extends from the symphyseal region to the anterior edge of adductor fossa. The precoronoid is shorter. The prearticular provides the lingual margins of both the adductor fossa and the glenoid fossa. At the anteromedial angle of the latter, the prearticular forms a strong hamate process, which is twisted about 90 degrees around its vertical axis. The articular is enclosed labially by the surangular and lingually by the prearticular, with part of the articular suture running across the foramen chordae tympani. The glenoid fossa is concave dorsolingually and lies on the same level as the tooth series. Together, the articular and surangular contribute to a postglenoid ridge, which is nearly equal in height to the hamate process.

Postcranial skeleton. The interclavicle has the rhomboidal shape typical for capitosaur (Schoch and Milner 2000), with the anterior process usually elongated (Text-figs 6H, 8E–F). The bone is rather thin even near the ossification centre. The ornament is



TEXT-FIG. 4. *Cyclotosaurus intermedius*. The skull and associated mandible, holotype ZPAL Ab III 1173, in occipital view (A–B, D–E), and reconstructions (C, F), based on ZPAL Ab III 1173, 471/113 and 472/28. A, explanatory drawing of the skull and mandible. B, the skull and mandible. D, explanatory drawing of the mandible. E, an enlargement of the mandible. For abbreviations, see Appendix.

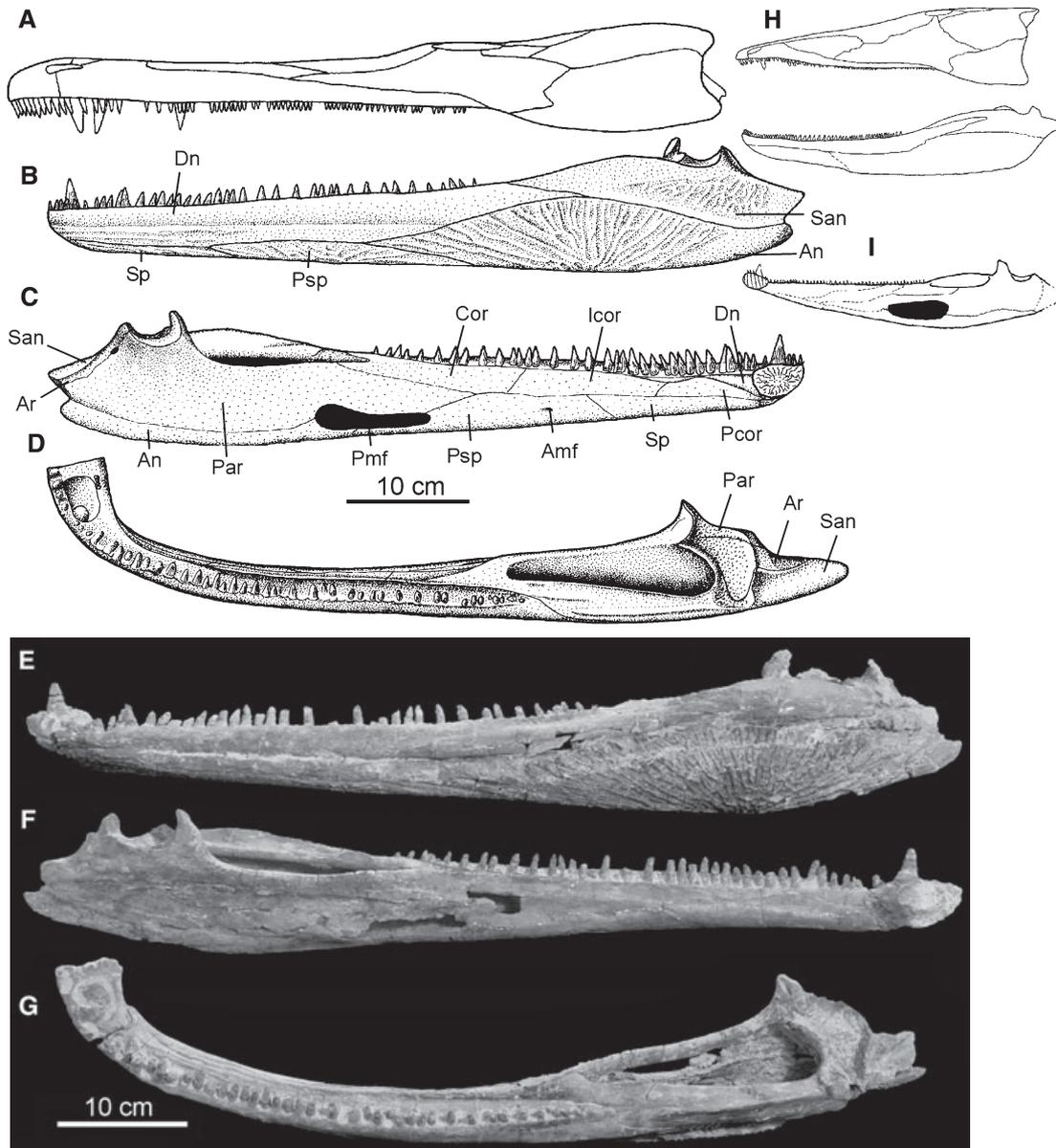
very clear, but the anterolateral borders bear strips of unornamented surface for articulation with the clavicles.

The clavicle (Text-fig. 6F–G) has a slender basal plate that is elongated in the sagittal plane. The angle between it and the slim dorsal process is about 90 degrees in posterior view and 45 degrees in lateral view. The lamina of the dorsal process is thin and rather low with a separate rib and an almost vertical anterior margin. The prescapular cavity (Damiani 2001a) is weak.

The cleithrum (Text-fig. 6C–E) has a slender well-ossified dorsal head. In anterior view, the bone is flattened laterally and slightly concave medially. Near the head, the cleithrum develops vertical, posteriorly directed lamellae on its lateral and medial faces. The medial face of the cleithrum also bears grooves along the anterior and posterior borders. The anterior groove probably abutted the dorsal process of the clavicle, while the posterior one probably abutted the scapula. Both are roughened with numerous parallel ridges and bosses.

The scapulocoracoid (Text-fig. 7) consists of the vertical scapula and the smaller coracoid, enclosing a concave posterior margin. No suture is visible between them. The scapula is strongly flattened, with a rounded dorsal end. The anterodorsal corner of the blade bears a rugose articulation for the cleithrum, but the ventral continuation of this area is broken off. The glenoid surface is markedly widened and directed posteroventrally. It consists of two rectangular areas. The medial area is ventrally oblique and perforated by a large supracoracoid foramen with a pronounced anteroventral rim. It leads to a vertical canal close to the upper margin of the glenoid. Lateral to the glenoid, the coracoid forms a thin convex lamina that is separated from the scapula by a deep fissure.

The humerus (Text-fig. 6A–B) resembles that of most basal temnospondyls. It is short with broad proximal and distal heads. The proximal head has a very weakly defined deltopectoral ridge. The distal head is rounded, with a thin entepicondyle, a more



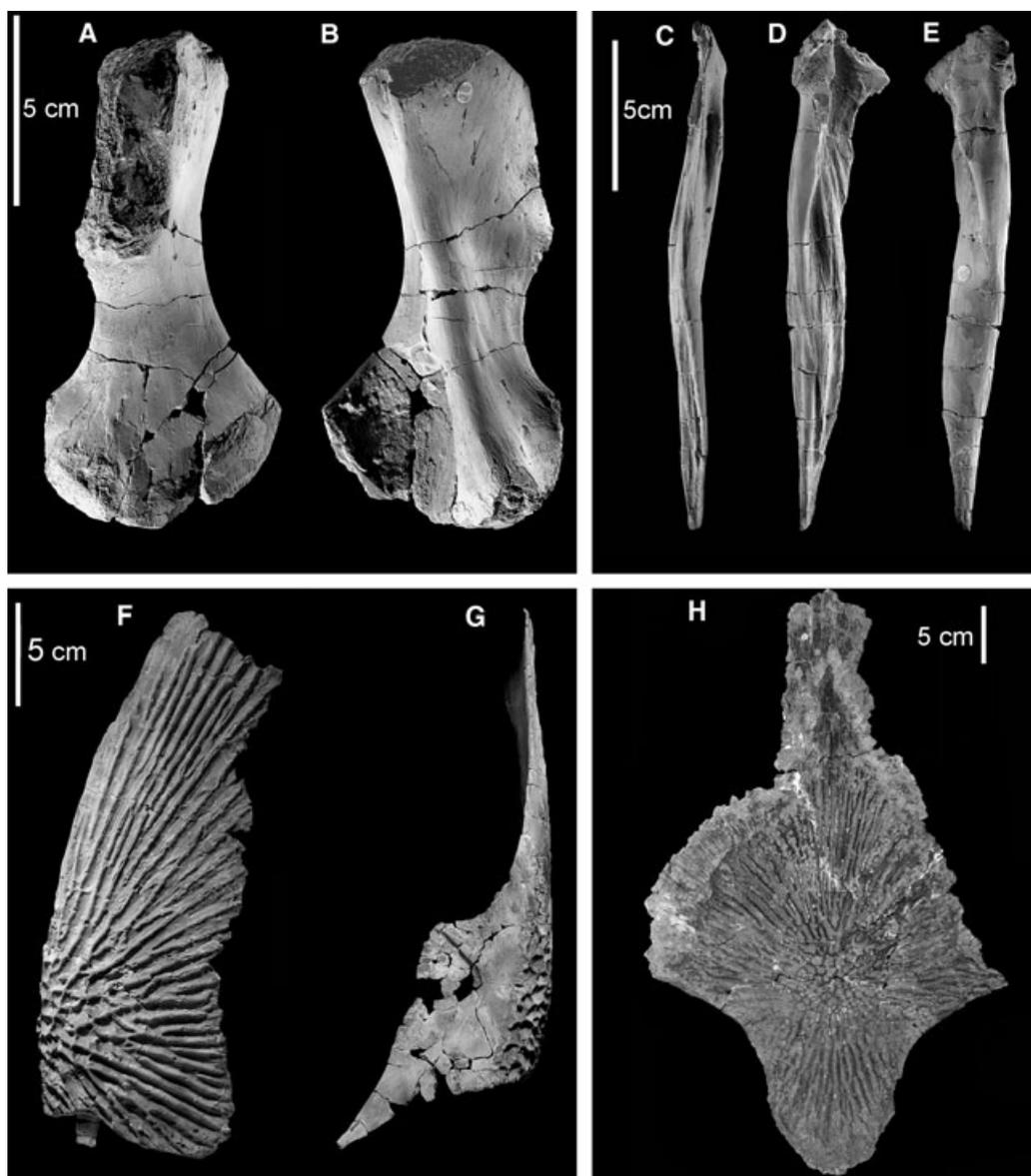
TEXT-FIG. 5. Reconstructions of the skull and left mandible of *Cyclotosaurus intermedius* (A–D) and *Paracyclotosaurus davidi* (H; from Watson 1958). The drawings of *C. intermedius* are based on ZPAL Ab III 1173 and Ab III 680. E–G, the left mandible ZPAL Ab III 680. I, the mandible of *Cyclotosaurus mordax* (from Schoch and Milner 2000, fig. 90). A, H, lateral view. B, E, labial view. C, F, I, lingual view. D, G, dorsal view. H and I not drawn to scale. For abbreviations, see Appendix.

pronounced ectepicondyle, and a weakly differentiated supinator process. The humeral shaft is twisted so that the long axes of the heads lie at about 70 degrees.

DISCUSSION ON RELATIONSHIPS

Among the remains from Krasiejów attributed to *Cyclotosaurus intermedius*, the skull is taxonomically most informative. The new material shows all the characters

considered diagnostic of *Cyclotosaurus*: otic notch closed by a sutural contact of the tabular and squamosal behind it; frontals connected to the roof of the sphenethmoid via a broad descending processes, which meet the wide braincase; anterior palate with foreshortened vomers; and a tabular horn with an elongated and slightly expanded terminal part directed posterolaterally (Maryńska and Shishkin 1996; Schoch and Milner 2000). It can thus be safely classified in the genus.



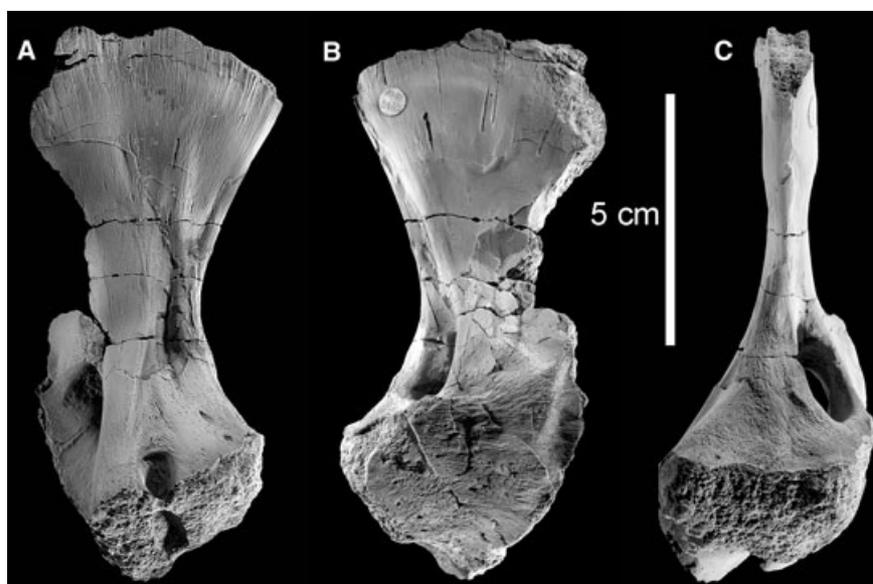
TEXT-FIG. 6. *Cyclotosaurus intermedius*. A–B, the right humerus ZPAL Ab III 887/3. C–E, right cleithrum ZPAL Ab III 471/51. F–G, right clavicle ZPAL Ab III 397. H, interclavicle ZPAL Ab III 887/1. A, F, H, ventral view. B, dorsal view. C, posterior view. D, medial view. E, lateral view. G, dorsolateral view.

The new skull, ZPAL Ab III 1173, has two characters that are absent from all other known cyclotosaurids. The quadrate condyles project behind the posterior margin of the skull roof and shagreen denticles occur on the palatine. The projecting quadrate condyles seem to be related to the obtuse angle formed by the palatal and quadrate rami of the pterygoid. All other cyclotosaurs, except *C. ebrachensis*, have an acute angle between these rami. In the Polish material, the highest value of that angle (115 degrees) is found in the holotype. The pterygoids from the upper horizon are similar in size to those of the holotype (Text-fig. 3E–H) and show the more usual angle for

Cyclotosaurus (95 degrees). The pterygoid angle is thus unlikely to be of taxonomic importance.

The occurrence of the shagreen denticles is unusual in capitosaurids and difficult to explain in either functional or phylogenetic terms.

The skull of *C. intermedius* is similar to skulls of *C. robustus* from the Schilfsandstein of Baden-Württemberg (Fraas 1889) and *C. mordax* from the Stubensandstein (Fraas 1913). *C. robustus*, *C. intermedius* and *C. mordax* have a straight lateral margin to the skull and oval choanae, in contrast to the concave lateral skull margin in *C. posthumus* (Stubensandstein of Baden-Württemberg) and shorter



TEXT-FIG. 7. *Cyclotosaurus intermedius*, right scapulocoracoid ZPAL Ab III 887/2. A, medial view. B, lateral view. C, posterior view.

round choanae (Fraas 1913). *C. robustus*, *C. intermedius* and *C. mordax* also differ from the other Stubensandstein species, *C. hemprichi*, in having a much wider skull with a broader snout. *C. robustus* and *C. intermedius* are considerably larger than *C. ebrachensis* from the older Blasen-sandstein of Franconia, but this species is smaller than all other species of *Cyclotosaurus*. This may be why almost all skull indices differ between the Krasiejów cyclotosaur and *C. ebrachensis* (Table 1). Schoch and Milner (2000) suggested that *C. ebrachensis* is a junior synonym of *C. mordax*, but the differences in indices from other species (Table 1) seem sufficient to keep it as a distinct species. The new species has a much wider skull with a posterior border that is more deeply concave than in *C. ebrachensis*, the anterior palatal vacuity is reniform rather than oval, and the postotic bar of the tabular is narrower.

Although *C. intermedius* is similar to *C. robustus* and *C. mordax*, there are some differences. In *C. intermedius* the interchoanal tooth row bends gently posteriorly, while it is straight in *C. robustus*, and the para- and interchoanal teeth are broadly separated but they form a single arcade in *C. robustus*. There are no data on ontogenetic variation in the pattern of para- and interchoanal teeth in stereospondyls. *C. robustus* also has wider skull (see B/L,

Table 1) than *C. intermedius*, with a more concave posterior border to the skull roof (K/C). The skull of *C. mordax* (Schoch and Milner 2000, fig. 104) is narrower with a less concave posterior border (Text-fig. 9). The shape of the posterior skull margin was previously examined by Welles and Cosgriff (1965), but they did not discern any phylogenetic trend. In *Eocyclotosaurus wellesi* Schoch, 2000b (a capitosauroid from the Middle Triassic of Arizona), Schoch noted that the shape of the posterior margin changed with ontogeny. In a small specimen (skull length 170 mm), the concavity is moderate, but in both medium-sized (275 mm) and large (510 mm) specimens, the concavity is deeper. Warren and Hutchinson (1988) also described changes in skull roof proportions during post-metamorphic growth in capitosaurids. Recently metamorphosed individuals have a slight concavity, but it deepens in juveniles and then remains similar in immature and adult forms. It seems that the differences in size between *C. intermedius* and *C. mordax* are not significant because the smaller skull of *C. mordax* is not juvenile.

Kupferzella wildi Schoch 1997, from Oberer Lettenkeuper (Upper Ladinian) in Kupferzell-Bauerbach (German Basin), may be close to the ancestry of the lineage. It belongs to the Tatrassuchinae (Schoch and Milner 2000;

TABLE 1. Indices of skull measurements in *Cyclotosaurus* species. For explanation of abbreviations, see Appendix.

	L	A/L	B/L	B/K + L	S/L	K/C	T/C	N/C	H/B
<i>C. ebrachensis</i>	345	21	66	61	35	22	41	60	12
<i>C. mordax</i>	415	21	80	73	43	23	24	50	?
<i>C. intermedius</i> sp. nov.	510	22	81	73	46	31	35	60	18
<i>C. robustus</i>	365, 560	18	83–85	75	45	33–41	37	61	11

Damiani 2001a), a subfamily included with *Cyclotosaurus* in the Cyclotosauridae by Maryńska and Shishkin (1996). The orbits of *K. wildi* are situated more medially than those of *C. robustus*, suggesting that the lateral position of the orbits in *C. intermedius* and *C. mordax* is derived. If so, then *C. intermedius* may be evolutionarily closer to *C. mordax*.

C. robustus, *C. intermedius* and *C. mordax* all lived in the German Basin and were close to one another in time. Although only a few specimens of each species are available, and the effect of size on skull shape remains poorly known in temnospondyls, the consistent trend expressed in the three separate skull parameters (width, posterior concavity and orbital position) provides support for the conclusion that the three species were members of a single lineage. The specimens from Krasiejów occur in a horizon that corresponds to the Lehrberg Beds of the German Basin (Dzik 2001), located stratigraphically between the Schilfsandstein and Stubensandstein. *C. intermedius* thus bridges both the temporal and the morphological gap between the two more established taxa.

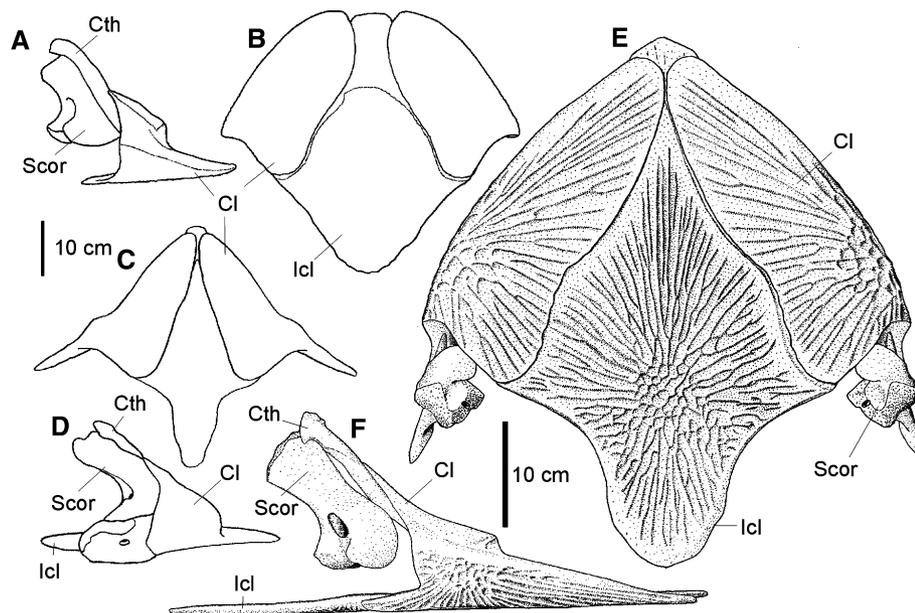
FUNCTIONAL INTERPRETATIONS

Capitosauroida is a large and diverse group of Triassic stereospondyls. Adults were large, semi-aquatic carnivores, crocodile-like in appearance, and have variously been considered as passive, benthic 'death-traps' (Watson 1958,

1962), surface-dwelling hunters (Defauw 1989) or active mid-water predators (Damiani 2001b). The last author stated that the dorsoventrally flattened skull and trunk, well-developed lateral line sensory sulci and streamlined postcranial skeleton all argued for aquatic locomotion, a conclusion supported by the generally small, weak, poorly ossified limbs and features of bone histology. In addition, the very large skull would have hindered effective terrestrial locomotion (Damiani 2001b). One distinctive capitosaurid feature is the presence of deeply incised otic notches, which were gradually closing in some groups as a result of the posterior extension of the squamosal and tabular. The closed otic notch probably surrounded the tympanum (Smithson 1982; Panchen 1985), but the biology of cyclotosaurids and the significance of this trend have not previously been discussed.

Among capitosauroids, an articulated skeleton is known only for *Paracyclotosaurus davidi* Watson, 1958. The postcranial cyclotosaur material from Krasiejów thus offers important information on skeletal parts that are very poorly known in capitosauroids. This is particularly true of the pectoral girdle, which is otherwise known only in a few species: *Eryosuchus garjainovi* Ochev, 1966; *Parotosaurus pronus* Howie, 1970; *Mastodonsaurus giganteus* Jaeger, 1828; *Wellesaurus peabodyi* Welles and Cosgriff, 1965; and *Cyclotosaurus posthumus* (only the interclavicle).

In his review of feeding in capitosaurids, Damiani (2001b) proposed that capitosauroids captured prey by rapid

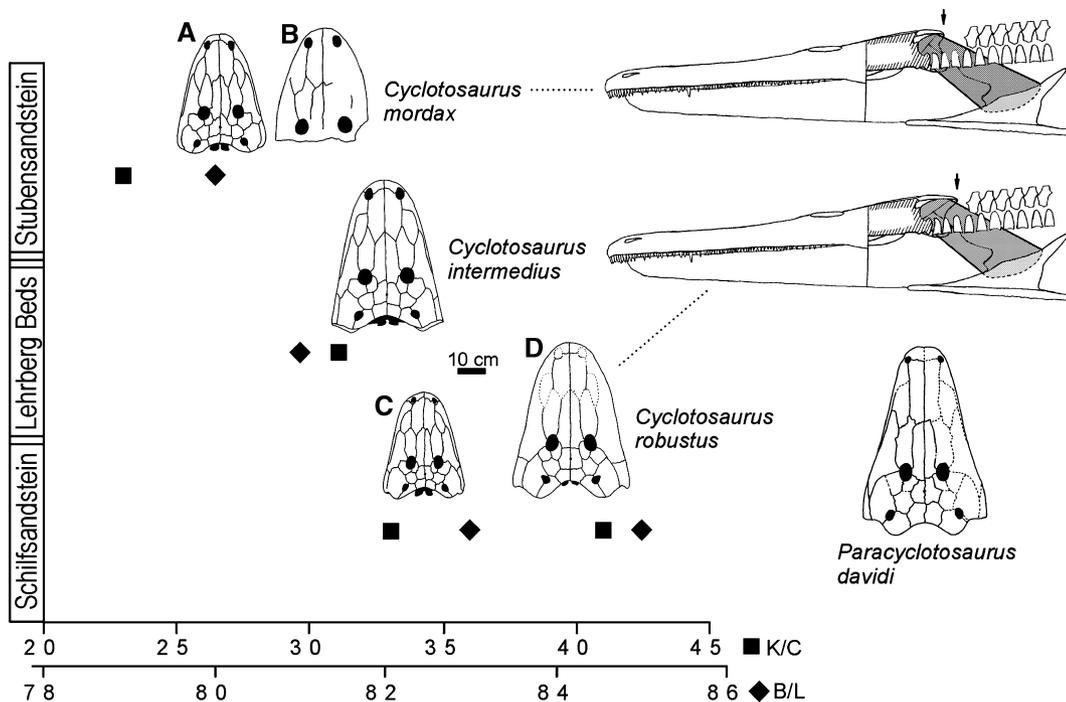


TEXT-FIG. 8. Comparison of shoulder girdles of *Paracyclotosaurus davidi* (A–B) from Watson (1958), *Mastodonsaurus giganteus* (C–D) from Schoch (1999) and *Cyclotosaurus intermedius* (E–F). The drawings are based on ZPAL Ab III 887/1 (interclavicle), ZPAL Ab III 397 (clavicle) and ZPAL Ab III 471/51 (cleithrum). A, D, F, the clavicle and interclavicle in articulation with the cleithrum and scapulo-coracoid in lateral view. B, C, E, the interclavicle and clavicles in articulation in ventral view.

sideways sweeps of the head during active swimming (see also Howie 1970; Chernin 1974; Schoch and Milner 2000). According to Damiani (2001b), the jaws probably remained shut initially so as to reduce drag, and opened only at the last possible moment before striking. Taylor (1987) described such skull movements in modern crocodylians. This model is especially pertinent in the case of *Cheringa megarhina* Damiani, 2001b, which has a very broad, shallow snout, with eyes that were centrally placed and directed backwards as in other capitosauroids. Any elevation of the skull would have blocked the view of prey in front of the animal (Howie 1970). The model proposed by Damiani (2001b) permits the prey to be seen until the point at which it is snapped, but demands strong muscles to raise the skull rapidly. According to Howie (1970), the cleidomastoideus muscles formed the principal skull-raising system in capitosauroids. Each muscle ran between the dorsal process of the clavicle and a pronounced flange on the tabular, offering a possible explanation for the (evolutionary) lateral movement of the tabular horn, which eventually closed the otic notch in cyclotosaurs (Howie 1970). Posterior extension of the tabular may also have increased the strength of the muscle by elongating the lever arm (Text-fig. 9). The result is a deeply concave posterior skull margin like that

in *Cyclotosaurus robustus*. Thus *C. robustus* may have had very strong skull elevators, an important consideration given that it had a very wide snout and thus exerted substantial drag in water (Taylor 1987).

Watson (1958) suggested that *Paracyclotosaurus davidi* was an aquatic animal that waited until prey came near, then quickly opened its enormous mouth and swallowed it, like the living Giant Salamander. In his reconstruction, however, he showed *P. davidi* with an unusually raised skull and suggested it might have occasionally walked on land. The bones of the shoulder girdle are well ossified and much more massive than in those other capitosauroids for which the bones are known (Howie 1970; Schoch 1999) (Text-fig. 8). The clavicle is shorter and wider, and the cleithrum, scapula and interclavicle are thicker. Defauw (1989) interpreted the similar-sized Peltoptachidae as terrestrial on the basis of their well-ossified appendicular skeletons. The girdle of *P. davidi* thus supports the hypothesis that the animal may have been only semi-aquatic (Defauw 1989), waiting in the shallows to catch animals coming to the water (Chernin 1974). Nile crocodiles often capture land mammals in this way (Pooley and Gans 1976). In most capitosauroids, the mandibular articulation lies on the same level as the tooth row (Schoch and Milner 2000, fig. 90). *P. davidi* differs in



TEXT-FIG. 9. Lineage of cyclotosaurs with broad parabolic skulls from the German Basin: skulls of *C. robustus*, *C. intermedius* and *C. mordax* in dorsal view. On the right, schematic skulls with clavicles and vertebrae, in lateral view, the left posterior part of the skulls removed to show the right cleidomastoideus muscles (grey); note that the lever arm of this muscle is protracted by elongation of the tabular in *C. robustus* (arrows). On the right, below, *Paracyclotosaurus davidi* from Watson (1958) in dorsal view. A, C, from Schoch and Milner (2000); B, from Fraas (1913); D, modified from Quenstend 1850, after Welles and Cosgriff (1965).

having the glenoid in a much higher position (Text-fig. 5), increasing the lever arm of the mandibular adductor, but decreasing the strength of the bite (Hilderbrand 1974). If *P. davidi* snapped its prey in the air, the muscles raising the skull could be weaker than those of aquatic animals, in which the resistance of the medium is much larger. This might also be the reason why the posterior border of the skull roof was less concave in *P. davidi* than in *C. robustus* (Text-fig. 9).

Paracyclotosaurus davidi and *Cyclotosaurus robustus* probably had very different feeding strategies. *C. intermedius* and *C. mordax* have broad snouts as in *C. robustus*, but the posterior border of the skull roof is less concave. *C. intermedius* has a shoulder girdle and mandible similar to that of other capitosauroids (e.g. *Parotosaurus pronus*; Howie 1970), and less massive than *P. davidi*. It was probably aquatic like *C. robustus*, but may have fed near the surface (Defauw 1989) where it is easier to raise the skull. This hypothesis is supported by the lateral shift of the orbits from *C. robustus* through *C. intermedius* to *C. mordax*. A similar trend has been described for Lydekkerinidae (Schoch and Milner 2000), but without a functional explanation. Metoposaurids, which replaced capitosauroids in the Late Triassic (Schoch and Milner 2000), shared the wide snout but the orbits had shifted to the skull margins, enabling them to see the prey even when the skull was raised (Howie 1970).

CONCLUSIONS

New material of *Cyclotosaurus* from late Carnian deposits in Poland is morphologically and stratigraphically intermediate between congeneric finds in Germany. This is suggestive of a single lineage persisting in the German Basin through the Carnian and Norian, with changes occurring mainly in the shape of the posterior skull margin and the position of the orbits. The deeply concave posterior skull margin in *Cyclotosaurus robustus* is correlated with the elongation of the tabular horn and may reflect an increase in the strength of the cleidomastoideus muscle. This is a skull elevator of particular importance in aquatic animals and suggests that *C. robustus* was more aquatic than *C. intermedius*. The associated postcranial bones of *C. intermedius* also suggest that *Cyclotosaurus* was more aquatic than *Paracyclotosaurus*, the only capitosauroid currently known from an articulated skeleton.

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APPENDIX

Abbreviations used in paper

A, distance between the medialmost points of orbits; Amf, anterior Meckelian foramen; An, angular; Ar, articular; A/L, proportion of the distance between the medialmost points of orbits to midline length of the skull; B, total width of skull; B/K + L, proportion of the total width to sum of midline length of skull and depth of concavity of the posterior skull margin; B/L,

proportion of the total width to midline length of skull; C, distance between the medialmost points of otic notches; ca, crista articularis; Cl, clavicle; cm, crista medialis; Cth, cleithrum; Cor, coronoid; D, postorbital midline length; Dn, dentary; E, distance between the interpterygoid foramen and antorbital foramen; Ex, exoccipital; F, distance between the orbit and nares; Fr, frontal; G, distance between the medialmost points of choane; H, height of the occiput in midline; H/B, proportion of the height of the occiput in midline to distance between the medialmost points of otic notches; I, distance between the orbit and border of the

skull; Icl, interclavicle; Icor, intercoronoid; J, distance between the medialmost points of nares; Jg, jugal; K, depth of concavity of the posterior skull margin; K/C, proportion of the depth of concavity of the posterior skull margin to distance between the medialmost points of otic notches; L, midline length; La, lacrimal; LP, total length; LR, total length of the skull roof; M, distance between the anteriormost points of the nares and the same on the skull; Mx, maxilla; N, distance between orbit and otic notch; NP, distance between the anteriormost point of the interpterygoid foramen and the same on the skull; Na, nasal; N/C, proportion of the distance between orbit and otic notch to distance between the medialmost points of otic notches; O, pre-orbital length; P, distance between orbits and parietal foramen (in midline); Pa, parietal; Par, prearticular; Pcor, precoronoid;

Pf, prefrontal; Pl, palatine; Pmf, posterior Meckelian foramen; Pmx, premaxilla; Po, postorbital; Pp, postparietal; Prf, prefrontal; Ps, parasphenoid; Psp, postsphenial; Pt, pterygoid; Q, quadratum; Qj, quadratojugal; R, distance between the medialmost points of subtemporal fenestra; S, width of the snout (measured at one-fifth length of skull); San, surangular; Scor, scapulocoracoid; Sp, splenial; Sq, squamosal; St, supratemporal; S/L, proportion of the width of the snout to midline length of the skull; T, distance between parietal foramen and otic notches (in midline); Ta, tabular; T/C, proportion of the distance between parietal foramen and otic notches to distance between the medialmost points of otic notches; U, length of otic notch; V, vomer; Y, length of interpterygoid vacuity; Z, width of tabular bar behind closed otic notch.