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Early Vertebrate Evolution

New cranial material of *Discosauriscus pulcherrimus* (Seymouriamorpha, Discosauriscidae) from the Lower Permian of the Boskovice Basin (Czech Republic)

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ABSTRACT: We describe four newly discovered and three-dimensionally preserved specimens of the discosauriscid seymouriamorph *Discosauriscus pulcherrimus* from the Lower Permian lacustrine sediments of the Boskovice Basin (Czech Republic). Their excellent preservation revealed new cranial features that allowed us to present a new skull reconstruction of middle-sized specimens of this tetrapod. The new features include: (1) the sculpturing of the anterior wedge-like process of the parasphenoid consisting of irregular ridges, grooves, low elevations and pits; and (2) the presence of a pair of semicircular crests on the posterodorsal surface of the parasphenoidal plate. We discuss the intraspecific variability of several characters, such as the type of dermal cranial ornamentation, and the morphology of the sensory grooves, nasolacrimal canal, dentition on the pterygoids and parasphenoid. The lengths of the skulls of four new specimens range from about 18 to 31 mm and represent larval ontogenetic stages.

KEY WORDS: individual variability, morphology, ontogeny, skull reconstruction.

Tetrapods belonging to the family Discosauriscidae (Symouriamorpha) are known from lacustrine sediments of the Lower Permian of Europe (Czech Republic, Poland, France, Germany) (e.g., Špinar 1952; Werneburg 1985; Klembara & Meszároš 1992; Werneburg & Kiersnowski 1996; Steyer *et al*. 2012) and Asia (Tajikistan) (Klembara & Ruta 2005a, b). The specimens of *Discosauriscus* from the Boskovice Basin (Czech Republic) are three-dimensionally preserved, permitting detailed studies of their anatomy (Klembara & Meszároš 1992; Klembara 1997; Klembara & Bartík 2000).

Discosauriscus austriacus is known from several hundred specimens from the Czech Republic (Boskovice Basin) and several tens of specimens from France (Bourbon l'Archanbault Basin; Steyer *et al*. 2012). *Discosauriscus pulcherrimus* is known from Poland (Intrasudetic Basin; Werneburg & Kiersnowski 1996), the Czech Republic (Intrasudetic and Boskovice Basins) and Germany (Döhlen Basin, Saale Basin, Saar-Nahe Basin; Werneburg 1985, 1988, 1989; Boy 2007), and probably also from France (Autun, Sarre-Lorraine/Palatinat and Bourbon l'Archanbault Basins; Heyler 1969; Werneburg 1989), although the specimens from the French localities require some revision. Despite the fact that the finds of *D. pulcherrimus* from these countries are relatively common (tenths of specimens), they are poorly preserved and many of them are dorsoventrally compressed. There are only five specimens of *D. pulcherrimus* known from the Boskovice Basin, which are more-or-less three-dimensionally preserved (Klembara 1995, 1997; Klembara & Bartík 2000).

Recently, four new specimens of *Discosauriscus pulcherrimus* were found in the Boskovice Basin. Two of them (MHK (Museum of Eastern Bohemia, Hradec Králové, Czech Republic) 61803 and MHK 61804) represent the best, three-dimensionally preserved specimens of this species known to date. The aims of this paper are as follows: (1) to re-describe the cranial structures of *D. pulcherrimus*, which were either previously unknown or poorly known; (2) to compare these structures with those of *D. austriacus* in order to find any possible further differences between these two species; and (3) to present a novel reconstruction of the skull based upon information from specimens representing middle-sized individuals.

1. Material and methods

Four new three-dimensionally preserved specimens of *Discosauriscus pulcherrimus* are described here. Skull length (SL) is the total length of the lengths of the postparietal, parietal, frontal and nasal bones, measured in the median plane: MHK 61803, SL = 31 mm (Fig. 1a, b); MHK 61804, SL = 31 mm (Fig. 1c, d); MHK 70572, SL = 23 mm (Fig. 2a, b); SNM (Slovak National Museum, Bratislava, Slovak Republic) Z 15619, SL = ~18 mm (Fig. 2c). The newly described specimens attained a SL of 31 mm and are thought to belong to larval stages, based upon the following combination of features: simple dentine infolding; absence of crests along the tooth surface; distinct radiating sculpture on the skull roof bones; unossified

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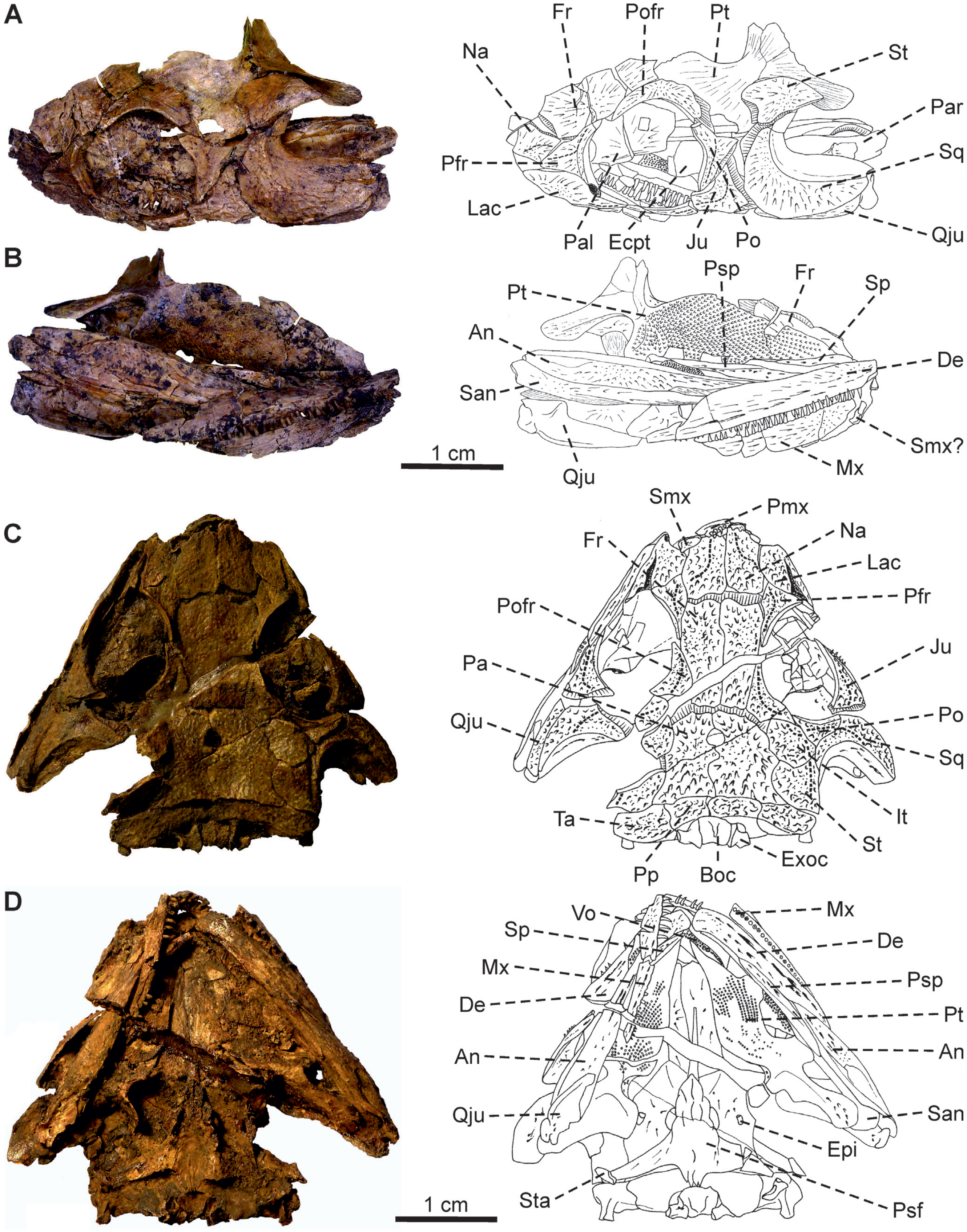

Figure 1 (A–D) *Discosauriscus pulcherrimus*, photographs of skulls and their drawings. (A, B) MHK 61803 in dorsal (A) and ventral (B) views. (C, D) MHK 61804 in dorsal (C) and ventral (D) views. Abbreviations: An = angular; Boc = basioccipital; De = dentary; Ecpt = ectopterygoid; Epi = epipterygoid; Exoc = exoccipital; Fr = frontal; It = intertemporal; Ju = jugal; Lac = lacrimal; Mx = maxilla; Na = nasal; Pa = parietal; Pal = palatine; Psf = parasphenoid; Pfr = prefrontal; Pmx = premaxilla; Po = postorbital; Pofr = postfrontal; Pp = postparietal; Par = prearticular; Psp = postsplenial; Pt = pterygoid; Qju = quadratojugal; San = surangular; Smx = septomaxilla; Sp = splenial; Sq = squamosal; St = supratemporal; Sta = stapes; Ta = tabular; Vo = vomer.

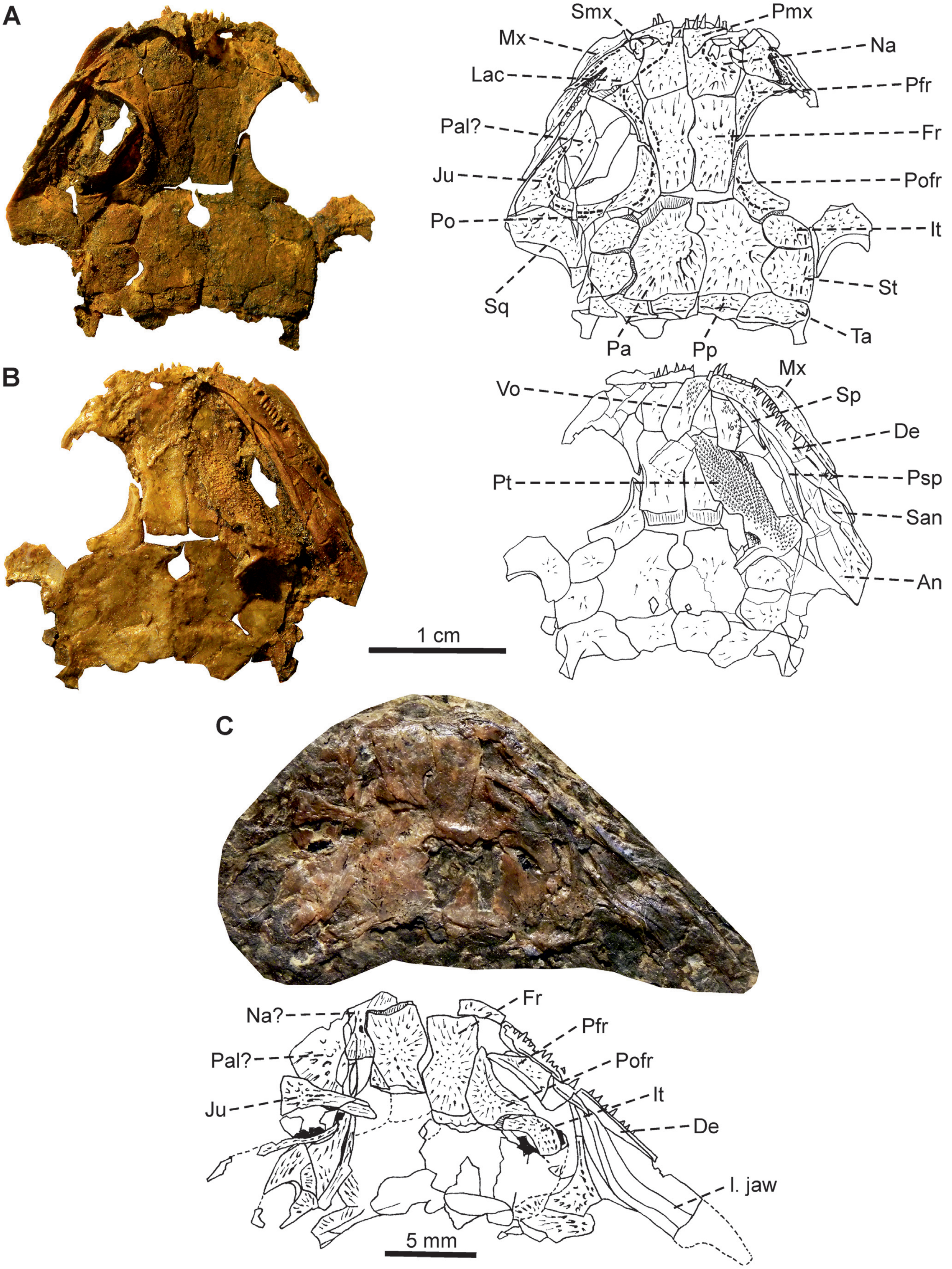

Figure 2 (A–C) *Discosauriscus pulcherrimus*, photographs of skulls and their drawings. (A, B) MHK 70572 in dorsal (A) and ventral (B) views. (C) SNM Z 15619 in dorsal view. Abbreviations: An = angular; De = dentary; Fr = frontal; It = intertemporal; Ju = jugal; l. jaw = lower jaw; Lac = lacrimal; Mx = maxilla; Na = nasal; Pa = parietal; Pal = palatine; Pfr = prefrontal; Pmx = premaxilla; Po = postorbital; Pofr = postfrontal; Pp = postparietal; Psp = postsplenial; Pt = pterygoid; San = surangular; Smx = septomaxilla; Sp = splenial; Sq = squamosal; St = supratemporal; Ta = tabular; Vo = vomer.

quadrate and articular; and poorly ossified neural endocranium and postcranium (*cf.* Klembara 2009).

The fossils were found in a laminated, highly bituminous, greyish-black limestone in the Boskovice Basin in the Czech Republic. The specimens MHK 61803, MHK 61804 and MHK 70572 were chemically prepared using acetic acid solutions (for the method, see Klembara & Meszároš 1992) and completely removed from the rock (Figs 1, 2a, b, 3–5). The skulls are more or less dorsoventrally compressed, but the individual bones are three-dimensionally preserved.

The reconstruction of the skull presented here is based primarily on the middle-sized specimen MHK 61803. Missing bones were reconstructed on the basis of the anatomy of the bones of the similarly sized specimen MHK 61804. To reconstruct the original shape of the skull, an enlarged, paper model was constructed. All the bones of the skull were measured, modelled at 7.5 times natural size and then glued together.

2. Systematic palaeontology

Seymouriamorpha Watson, 1917
Discosauriscidae Romer, 1947
Discosauriscus Kuhn, 1933
Discosauriscus pulcherrimus (Fritsch, 1880)

Specimens and localities. MHK 61803, almost complete skull, Kochov-Horka (near Letovice, approximately 40 km N of Brno). MHK 61804, complete skull and postcranial skeleton, Kochov-Horka. MHK 70572, almost complete skull and incomplete postcranial skeleton, Kochov-v poli (near Letovice, approximately 39.5 km N of Brno). SNM Z 15619 (K 103), almost complete skull and incomplete postcranial skeleton, Kochov-Horka.

3. Description

All three autapomorphic features of *Discosauriscus pulcherrimus* (Klembara 1997) are detected in the new material presented here. These features include: (1) the prefrontal–postfrontal contact lies at the level of the anterior and middle thirds of the frontal length (Figs 1a, c, 2a, c); (2) the pointed lateral process of the postorbital anteriorly overlaps at a short section of the dorsomedial pointed process of the jugal (Figs 1a, c, 4e); and (3) the rows of small pointed denticles on the ventral surface of the palatal ramus of the pterygoid diverge anteromedially and anterolaterally from the midline, running about at the mid-width of the palatal ramus of the pterygoid (Fig. 5a). In the following, only the best-preserved bones and bones displaying new data relative to the previous descriptions are presented.

3.1. Skull

3.1.1. Parietal. The distinctly ornamented dorsal surface of the parietal (Fig. 3a, b) displays narrow grooves and ridges radiating from the ossification centre, which is situated slightly posterolateral to the pineal foramen.

The ventral surface of the bone is mostly smooth, but distinctive narrow grooves occur posteriorly and posterolaterally. A tall, medially convex crest runs anteroposteriorly on the ventral surface. The crest occurs lateral to the pineal foramen and terminates anteriorly in proximity to the anterolateral corner of the parietal. The posterior extremity of the crest turns medially close to the posterior margin of the pineal foramen. A similar crest was described in *Discosauriscus austriacus* and interpreted as a crest/groove marking the junction of the dorsal outline of the neural endocranium; the posterior section of the crest runs posterolaterally (Klembara 1997). Immediately lateral to the crest, and at the level of the pineal foramen, there is a pit interpreted as a place for the anterior extension of the epipterygoid (Klembara 1997). In the parietal studied here, the crest is mediolaterally widened at the level of the parietal foramen and probably also marks the place of the attachment of the dorsal extension of the epipterygoid.

3.1.2. Intertemporal. The intertemporal is a subelliptical bone (Fig. 3c, d). Its dorsal surface bears low ridges and shallow grooves radially diverging from the ossification centre, lying in about the central region of the bone. The anterolateral margin bears a short sensory groove.

The ventral surface is smooth, with the exception of surfaces overlapping the adjacent bones; these surfaces are formed of short radiating grooves and ridges. In the central portion of the bone, small pits are present.

3.1.3. Supratemporal. The supratemporal is a quadrangular bone (Fig. 3e, f). The ossification centre lies in about the mid-length of the bone, close to its lateral margin. Distinct tubercles and intervening grooves lie in the region of the ossification centre. A well-developed sensory groove runs along the lateral margin of the bone.

The ventral surface of the supratemporal (MHK 61803) is smooth except for the surfaces which overlap the ventral laminae of the squamosal, tabular and parietal. Deep grooves and short pits lie in the region of the ossification centre.

3.1.4. Postparietal. The postparietals of MHK 61803 are of rectangular shape and the suture between them is more or less straight (Fig. 4a, b). The dorsal surface of the postparietals bears low ridges and broad grooves radiating from the ossification centre, lying posteriorly, in roughly the mid-width of the postparietal. The occipital flange is triangular in dorsal view and is flexed posteroventrally. Its dorsal surface is slightly roughened. The posterior margin of the ornamented surface bears a distinct and deep postparietal sensory groove.

The anterior half of the ventral surface is smooth and slightly dorsally excavated. In the mid-length of the ventral surface, a high, transverse ridge is present. The ventral wall of the ridge bears three excavations, the middle one being most distinct. Posteriorly to the transverse ridge, the surface of the postparietals is roughened, bearing many ridges and grooves. A similar morphology of the ventral surface of the postparietal is present in that of *Discosauriscus austriacus* (Klembara 1997). The ridge and rugosities represent the places of the attachment of the posteromedial portions of the neural endocranium.

3.1.5. Tabular. The tabular is of quadrangular or triangular shape (Fig. 4c, d). The ornamented surface consists of elevations and depressions of various sizes. A deep and narrow sensory groove runs along the posterior margin of the ornamented surface. A well-developed tabular process extends posteriorly and slightly laterally. Its dorsal surface is smooth. The occipital flange is of quadrangular shape and projects posteroventrally. The dorsal surface of the occipital flange is covered by distinct rugosities.

The ventral surface of the tabular is smooth and its central portion is elevated. The crescent arcuate ridge is high, with a smooth medial wall and roughened lateral wall. The arcuate ridge is posteromedially, bordered by a short ridge turning towards the occipital flange. A small triangular depression is situated on the posterolateral corner of the tabular process. The ventral surface of the occipital flange is smooth, with the exception of its striated posteromedial portion.

3.1.6. Postorbital. The postorbital is a triangular bone with a high anterior wall forming the posterior margin of the orbit (Figs 1a, c, 2a, 4e). The pointed posterior process of

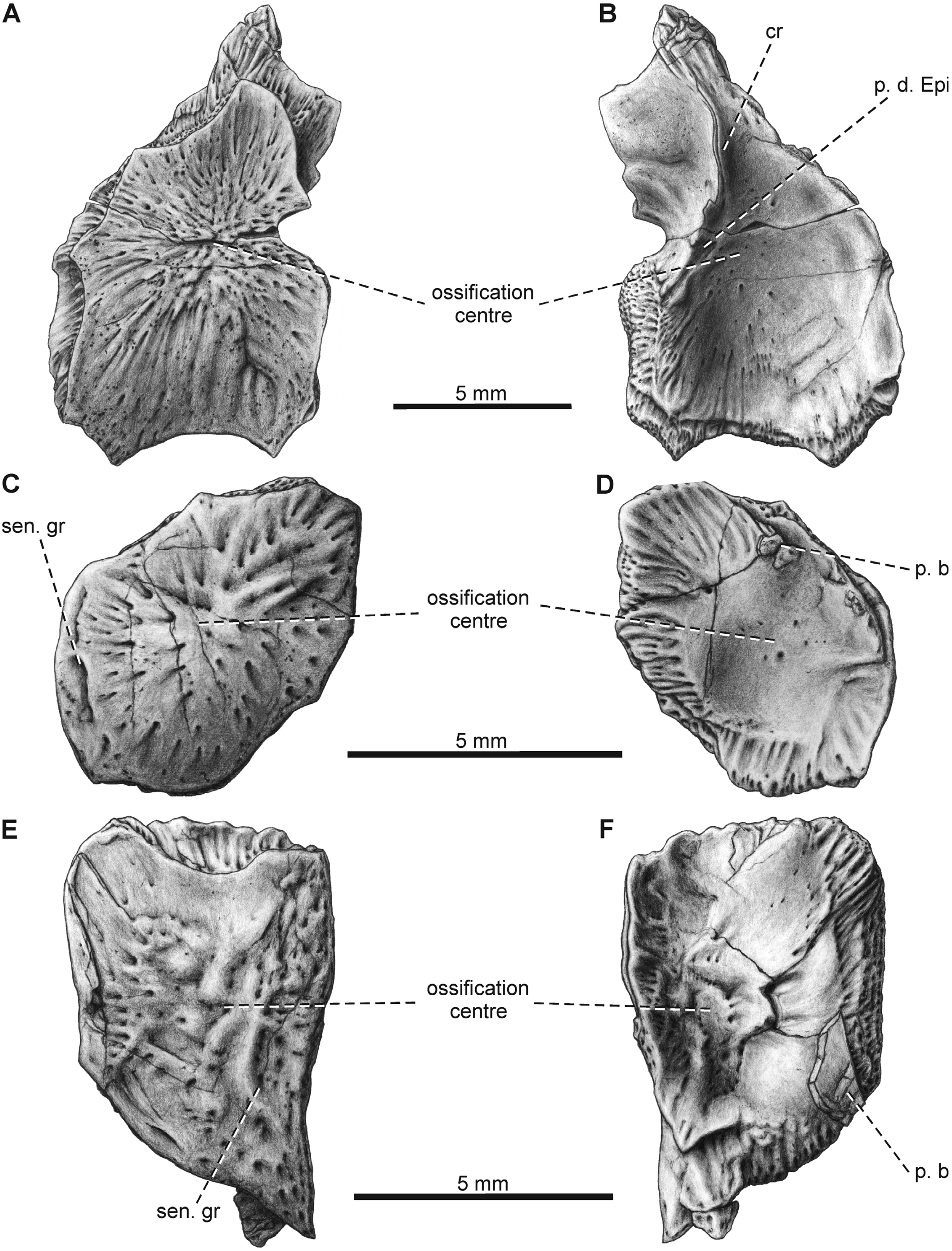

Figure 3 *Discosauriscus pulcherrimus*, MHK 61803. (A, B) Left parietal in dorsal (A) and ventral (B) views. (C, D) Left intertemporal in dorsal (C) and ventral (D) views. (E, F) Right supratemporal in dorsal (E) and ventral (F) views. Abbreviations: cr = crest; p. b = piece of bone; p. d. Epi = pit for dorsal extension of epipterygoid; sen. gr = sensory groove.

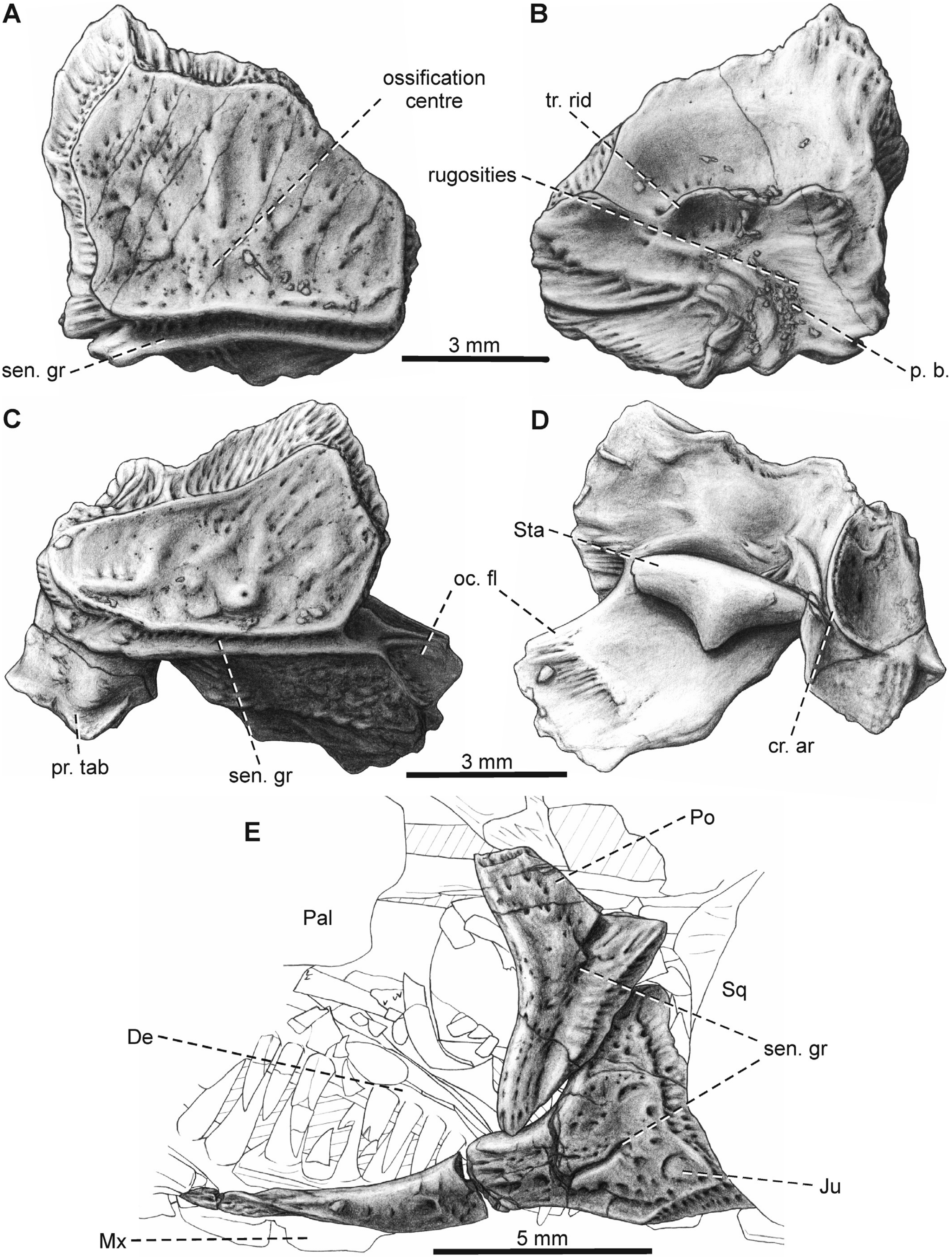

Figure 4 *Discosauriscus pulcherrimus*, MHK 61803. (A, B) Right postparietal in dorsal (A) and ventral (B) views. (C, D) Left tabular in dorsal (C) and ventral (D) views, with attached stapes in (D). (E) Left postorbital and jugal in dorsal view. Abbreviations: cr. ar = arcuate crest; De = dentary; Ju = jugal; Mx = maxilla; oc. fl = occipital flange; p. b. = piece of bone; Pal = palatine; Po = postorbital; pr. tab = tabular process; sen. gr = sensory groove; Sq = squamosal; Sta = stapes; tr. rid = transversal ridge.

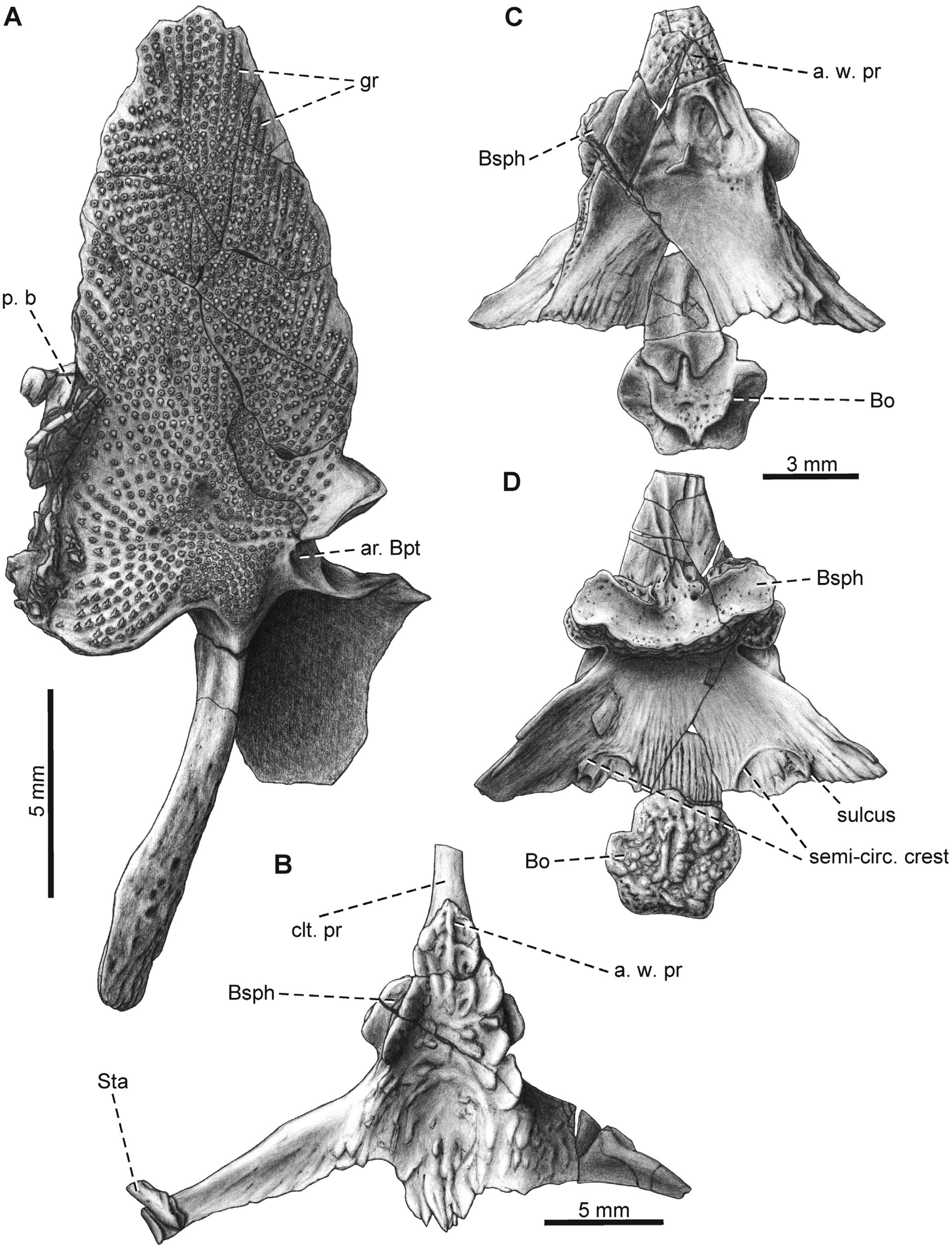

Figure 5 (A–D) *Discosauriscus pulcherrimus*. (A) Right pterygoid of MHK 61803 in ventral view. (B) Parasphenoid of MHK 61804 in ventral view with attached right stapes. (C, D) Parasphenoid of MHK 61803 in ventral (C) and dorsal (D) views. Abbreviations: a. w. pr = anterior wedge-like process of parasphenoid; ar. Bpt = articular surface for basipterygoid process of basisphenoid; Bo = basioccipital; Bsph = basisphenoid; clt. pr = cultriform process of parasphenoid; gr = grooves; p. b = piece of bone; semi-circ. crest = semicircular crest; Sta = stapes.

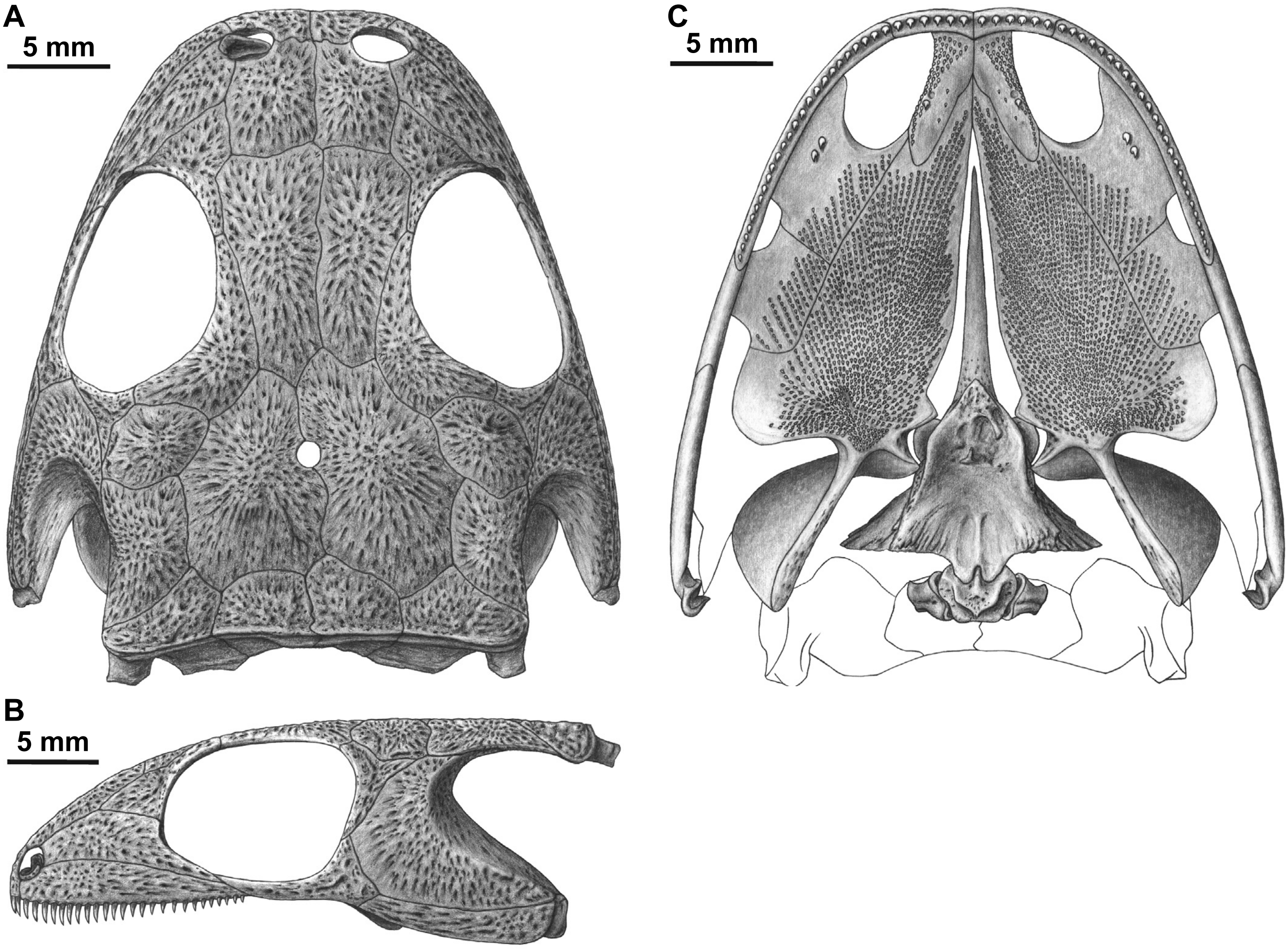

Figure 6 Reconstruction of *Discosauriscus pulcherrimus* skull based on the specimens MHK 61803 and MHK 61804. (A) Dorsal. (B) Lateral. (C) Ventral views.

the postorbital fits between the intertemporal and squamosal. The posterior tip of the postorbital does not contact the supratemporal in any of the studied specimens. The medial ramus of the postorbital has an anteroposteriorly coursing suture with the postfrontal. The lateral process of the postorbital is pointed and more or less anteriorly overlaps the pointed dorsomedial process of the jugal. The dorsal ornamented surface of the postorbital bears a distinct sensory groove.

3.1.7. Jugal. The jugal is a triangular bone with a long anterior process forming the ventral wall of the orbit (Figs 1a, c, 2a, c, 4e). The anterior section of the anterior process of the jugal overlaps the posterior end of the maxilla dorsally. The dorsal and posteroventral corners of the jugal are pointed. The jugal has the posterior and posteroventral underlying lamellae, which are overlapped by the squamosal and quadratojugal respectively. The external surface of the jugal is distinctly ornamented and bears a sensory groove; its most distinctly developed section runs along the posteroventral margin of the orbit (Fig. 4e).

3.1.8. Pterygoid. The pterygoid is very well preserved in the specimen MHK 61803 (Fig. 5a). Its palatal ramus shows a typical arrangement of the denticles representing the autapomorphic feature for *Discosauriscus pulcherrimus*: the rows of small denticles diverge anteromedially and anterolaterally from the mid-width of the palatal ramus of the pterygoid. The ventral surface of the palatal ramus of the pterygoids of MHK 61803 and MHK 70572 is covered with densely arranged rows of small, pointed and posteriorly curved denticles. The distances between the teeth rows on the palatal ramus of the pterygoid of MHK 61804 is bigger than those on the palatal ramus of MHK 61803 and MHK 70572. The rows along medial and lateral margins of the palatal ramus are separated by tiny grooves (MHK 61803, MHK 70572, DE (Department of Ecology, Faculty of Natural Sciences, Comenius University in Bratislava) KO (Kochov-les) 180) (Fig. 5a), as is the case in the juveniles of *Seymouria sanjuanensis* (Klembara *et al.* 2006, 2007). The rows of small denticles on the palatal ramus continue on the palatine and ectopterygoid (well visible in MHK 61803; Fig. 6c).

3.1.9. Parasphenoid. Two new structures not observed so far are visible on the parasphenoid of the specimen MHK 61804 (Fig. 5b). The first feature is the presence of the sculpturing on the ventral surface of the anterior wedge-like process of the parasphenoid. This is also very well developed in MHK 61803 (Fig. 5c, d). The most distinct sculpturing is on the anterior-most section of the anterior wedge-like process and consists of irregular ridges, low elevations, grooves and pits. More posteriorly, the ridges are short, low and are more or less anteroposteriorly oriented. From here, the ridges continue to the ventromedial portions of the posterolateral processes of the parasphenoid (Fig. 5b). Such sculpturing of the ventral surface of the parasphenoid represents the first record for

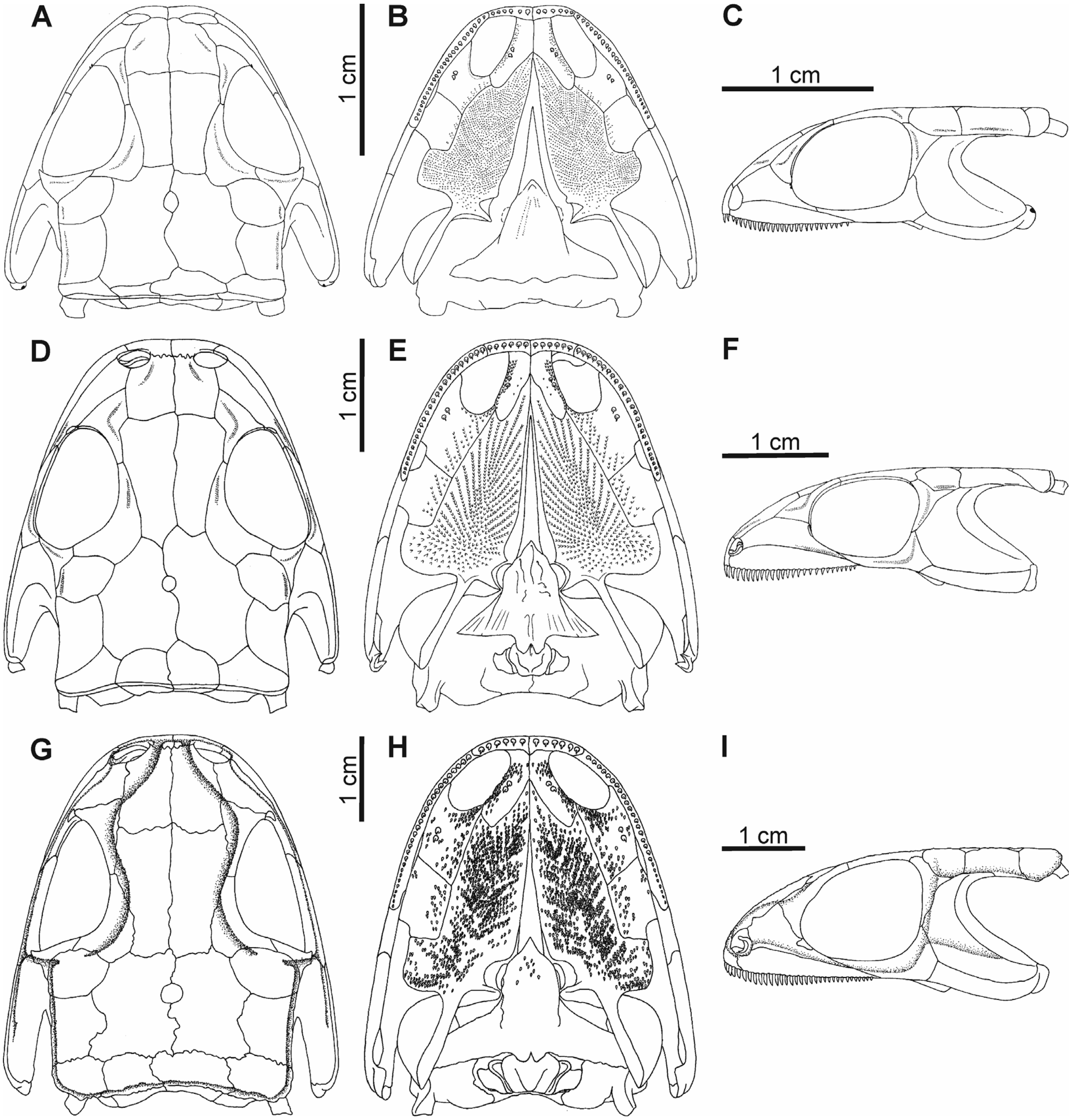

Figure 7 Reconstructed skulls of *Discosauriscus pulcherrimus* of different skull lengths. (A–C) Adapted from Klembara *et al.* (2007). (D–F) Reconstructions of skull on basis of specimens MHK 61803 and MHK 61804. (G–I) Adapted from Klembara (1997). Skulls in dorsal (A, D, G), ventral (B, E, H) and left lateral (C, F, I) views.

Discosauriscus pulcherrimus, although it was already described in *D. austriacus* (Klembara 1997). Such sculpturing is a synapomorphy of the Discosauriscidae.

The second feature is the presence of a pair of semicircular crests on the posterodorsal surface of the MHK 61803 parasphenoid, at the border of the parasphenoidal plate and the root portion of the posterolateral process (Fig. 5d). The posterolateral rim of the crest is elevated and separated from the root portion of the posterolateral process of the parasphenoid by a deep sulcus. The surface surrounded anteriorly by the crest is covered by finely developed anteroposteriorly running elevations and grooves. Topologically, the surfaces lie immediately anterolaterally to the basioccipital, and/or posterolaterally to the unossified portion of the basisphenoid (Fig. 5c, d). The surface anteriorly surrounded by the semicircular crest is probably the place of the attachment of at least the anterior portion of the cartilaginous basal tuber. In the adult specimens of the related *Seymouria baylorensis*, the ossified basal tuber is most likely formed exclusively by the basisphenoid, although the participation of the basioccipital on its formation cannot be excluded (White 1939; see also Watson 1954). Such distinct semicircular crests have, thus far, not been detected in *Discosauriscus austriacus* or *D. pulcherrimus* (Klembara 1997). However, in several specimens of both species, finely developed rugosities composed of short, anterolaterally running crests and grooves are present on the place where the semicircular surfaces are found in MHK 61803. It may be that the development of these impressions on the dorsal surface of the parasphenoid depends on the intensity of the cartilaginous basal tuber–ossified parasphenoid junction.

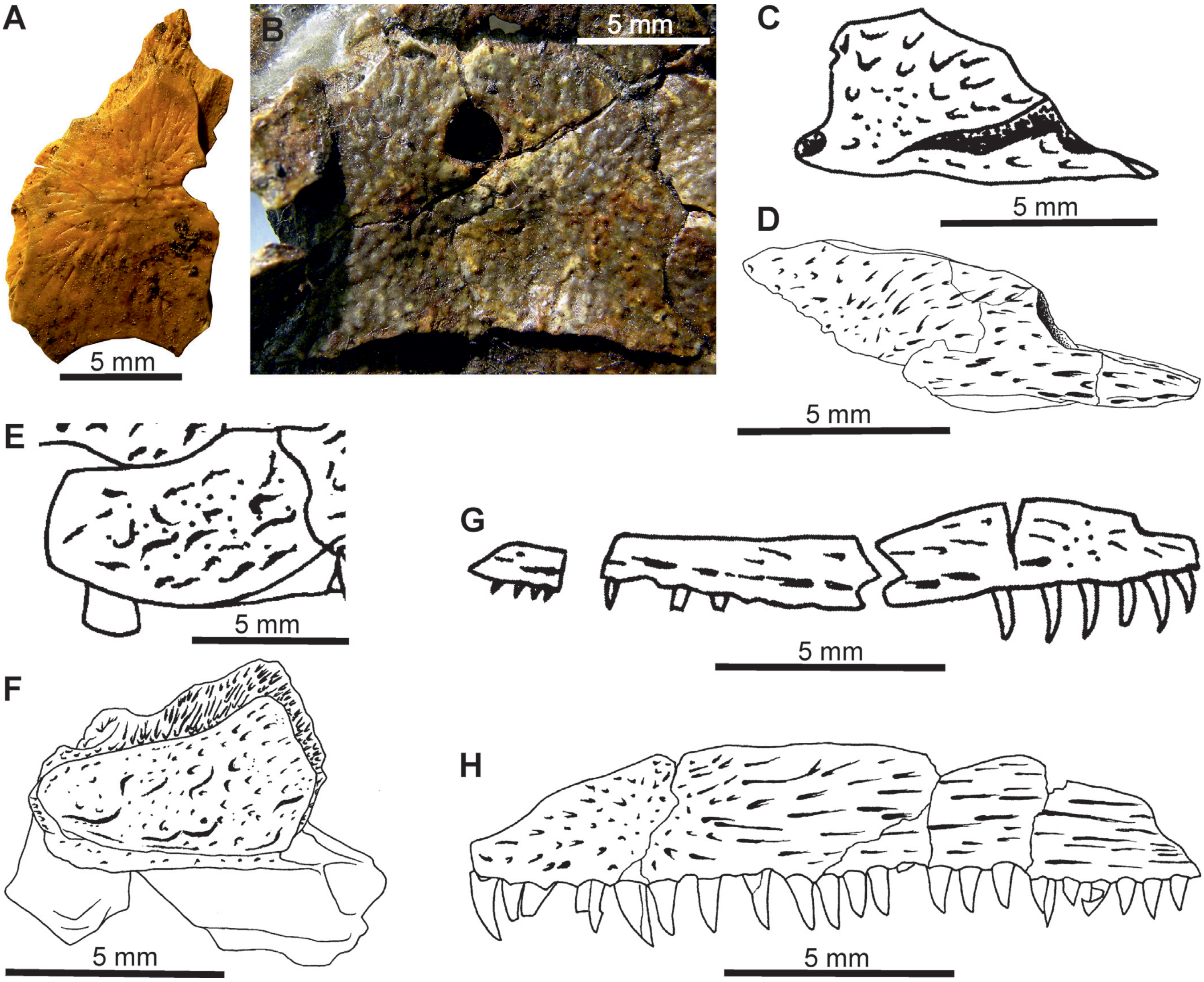

Figure 8 (A–H) *Discosauriscus pulcherrimus*. (A) Parietal of MHK 61803 in dorsal view. (B) Partial skull roof of MHK 61804 in dorsal view. (C) Left lacrimal of MHK 61804 in dorsal view. (D) Left lacrimal of MHK 61803 in dorsal view. (E) Left tabular of MHK 61804 in dorsal view. (F) Left tabular of MHK 61803 in dorsal view. (G) Right maxilla of MHK 61804 in dorsal view. (H) Left maxilla of MHK 61803 in dorsal view.

4. Reconstruction of the skull

The specimens MHK 61803 and MHK 61804 were selected to provide the following reconstruction of the skull (SL = 31 mm; Fig. 6). Both specimens are intermediate in size between the smaller specimen DE KO 180 (SL = ~21 mm) and the bigger specimen SNM Z 15532 (K 16; SL = ~43 mm) illustrated previously (Klembara 1997; Klembara *et al.* 2007, respectively) (Fig. 7). By comparing these three growth stages, the following ontogenetic changes can be proposed (Fig. 7):

1. Prolongation of the preorbital region in the middle-sized and largest specimens.
2. The sutures between individual bones become more complicated, especially in the postorbital region of the skull roof.
3. Posterior prolongation of the jaw joint; in the largest specimen, the jaw joint lies distinctly posteriorly to the supratemporal–tabular suture.
4. A progressive shortening of the distance between the posterior tip of the maxilla and the anterior tip of the quadratojugal.
5. Progressive prolongation of the posterolateral processes of the parasphenoid.
6. Progressive prolongation of the cultriform process of the parasphenoid.
7. Progressive prolongation of the quadrate ramus of the pterygoid.
8. Progressive closure of the interpterygoid vacuities.
9. Bilateral widening of the basioccipital. In the largest specimen, its width equals to that of the parasphenoidal plate measured at the level immediately posteriorly to the basipterygoid processes.

Regarding the size of the orbit, its length and height are shorter in the reconstructed skull (Fig. 7d–f) than it in the smaller (Fig. 7a–c) and larger (Fig. 7g–i) reconstructed specimens. This reflects the individual variability of the size of the individual bones in the specimens of similar size. For example, the skulls of the specimens MHK 61803 and MHK 61804 are of a similar size, but the anterior margins of the frontals lie anterior to the anterior margin of the orbit in MHK 61803 (Fig. 1a; reconstructed skull Fig. 7d, f), whereas the anterior margins of the frontals of MHK 81804 lie slightly posterior to the level of the anterior margin of the orbit. Further, in the middle-sized specimen MHK 61803, the anteroposterior length of the squamosal is much bigger than in the smallest and largest specimens (Fig. 7c, f, i); the same is true for the length of the lacrimal (Fig. 7c, f, i). Such variability in the individual bones of the specimens with similarly sized skulls explains why the length of the orbit is smaller in the reconstructed skull based primarily on the middle-sized specimen MHK 61803 in comparison with those of the largest and smallest skulls. However, the general trend in *Discosauriscus* is that the orbit gradually diminishes during growth (Klembara 1997).

5. Discussion

Although only nine specimens of *Discosauriscus pulcherrimus* from the Boskovice Basin are known, the individual morphological variability of the cranial bones is as high in *D. pulcherrimus* as it is in *D. austriacus* (Klembara 1995, 1997).

The individual variability concerns the type of ornamentation of several bones of the skull roof in similarly sized specimens. For example, the ornamentation of the parietal of MHK 61803 consists of radially running grooves and ridges, and the tubercles and ridges are only very finely developed (Fig. 8a). In contrast, the ornamentation of the parietal of MHK 61804 is composed of pits and distinct tubercles lying in the ossification centre, and short and wide radiating ridges and shallow grooves (Fig. 8b). However, the ornamentation of the skull roof bones of the middle-sized specimen MHK 61803 (Fig. 1a, b) reconstructed here is similar to that of the much smaller specimen KO 180 (Klembara *et al.* 2007, fig. 6). In the largest K 16 specimen, the ornamentation consists of more distinctly developed tubercles present in the region of the ossification centres of the bones (Klembara 1997).

The sensory grooves are distinctly developed on the skull roof of MHK 61804 (Fig. 1c, d). In contrast, the sensory grooves of the similarly sized MHK 61803 are markedly less developed (Fig. 1a, b).

The nasolacrimal canal of the specimen MHK 61804 is dorsally open along the two thirds of its anteroposterior length (Fig. 8c). In the similarly sized MHK 61803, the nasolacrimal canal is dorsally almost enclosed (Fig. 8d). The squamosal and quadratojugal of MHK 61803 are anteroposteriorly slightly longer than those in the similarly sized specimen MHK 61804. Posteriorly they reach the level of the supratemporal–tabular junction.

The tabular of MHK 61804 is of rectangular shape (Fig. 8e), whereas the left tabular of MHK 61803 is of triangular shape (Fig. 8f), similar to that of the seymouriamorph *Ariekanerpeton sigalovi* (Klembara & Ruta 2005a).

In the specimen MHK 61804, the maxilla is dorsoventrally narrower (Fig. 8g) than that of the specimen MHK 61803, where the maxilla is much higher (Fig. 8h); the anteroposterior length of the maxilla is the same in both specimens.

The epipterygoid of the specimen MHK 61803 laying on the dorsomedial surface of the left pterygoid is almost one half longer and better ossified than the left epipterygoid of the similarly sized MHK 61804.

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