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Upper Albian chelonioid turtles from Poland^{\star}

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ABSTRACT

Remains of chelonioid turtles assigned to Protostegidae are recorded from the upper Albian (Lower Cretaceous) sands at Annopol, Poland. These are the first remains of Cretaceous marine turtles from Poland. A semi-articulated partial carapace with an associated postorbital bone is referred to as Protostegidae gen. et sp. indet. A. Scute sulci are visible on each preserved costal and neural plate of this specimen, which suggests hypertrophy and multiplication of vertebral scutes, a unique feature among chelonioids. An isolated humerus from the same level as the carapace is referred to as Protostegidae gen. et sp. indet. B. The massive lateral process of this humerus extends significantly onto the ventral surface of the bone, like in some humeri of primitive protostegids from the European Cretaceous, including the Albian "Lytoloma cantabrigiense" from England and Turonian "Rhinochelys (?) cf. carusiana" from Germany.

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1. Introduction

Members of the Chelonioidea (sea turtles *sensu stricto*; see Hirayama, 1997) are well adapted to marine life through modification of their limbs into paddles allowing them to perform "underwater flight" (Zangerl, 1953b; Walker, 1973; Hirayama, 1992, 1994). Conventionally, Chelonioidea have been subdivided into three major clades: the Cheloniidae, Protostegidae, and Dermochelyidae, although there are differences in the nomenclature and position of some particular taxa (compare cladograms in Hirayama, 1994, 1997, 1998; Hooks, 1998; Lehman and Tomlinson, 2004; Kear and Lee, 2006; Bardet et al., 2013; Lapparent de Broin et al., 2014).

The oldest member of the Chelonioidea known to date is the protostegid *Santanachelys gaffneyi* Hirayama, 1998 from the uppermost Aptian/Albian of Brazil (Hirayama, 1998). Morphological variation amongst isolated humeri and skulls indicates that at least five distinct sea turtle clades were present during the Albian (Hirayama, 1997; Kear and Lee, 2006). This means that the basic radiation of the Chelonioidea must have taken place even earlier, possibly prior to the Aptian (Hirayama, 1997). About 80% of chelonioid material from the early phase (Albian–Turonian) in chelonioid radiation is assignable to the Protostegidae (Hirayama, 1997). However, this phase is comparatively poorly known when

http://dx.doi.org/10.1016/j.geobios.2015.07.002 0016-6995/© 2015 Elsevier Masson SAS. All rights reserved. compared to better preserved and more numerous collections of Late Cretaceous chelonioids, such as from the Santonian– Campanian of the US Western Interior (Wieland, 1896; Zangerl, 1953a, b) and the Maastrichtian type area in the southeast Netherlands and northeast Belgium (Mulder et al., 1998; Mulder, 2003).

In the present paper, we describe new early protostegid material from the upper Albian of Annopol, east-central Poland. This material comprises a partial, semi-articulated carapace associated with the postorbital bone and an isolated, wellpreserved humerus. Both specimens have been collected underground, in an abandoned phosphate mine at Annopol. This is the first report of Cretaceous marine turtles from Poland. Until now. merely a juvenile individual of the cheloniid Glarichelys knorri (Gray, 1831) was known from the Oligocene Menilitic shales at Winnica near Jasło, in the Polish Carpathians (Młynarski, 1959). The material studied herein also adds to our knowledge of the predominantly marine vertebrate faunas at Annopol. These Albian-Turonian assemblages comprise sharks (Marcinowski and Radwański, 1983), chimaeroid fish (Radwański, 1968; Popov and Machalski, 2014), ichthyosaurs and plesiosaurs (Marcinowski and Radwański, 1983; Bardet et al., 2015), as well as pterosaurs (Machalski and Martill, 2013).

2. Paleontological background

In Europe, the fossil record of the early chelonioids refers mainly to isolated skeletal elements and partial skeletons described from England, France, Germany and the Czech Republic.

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These include skulls and isolated mandibles (Owen, 1851; Moret, 1935; Collins, 1970), limb bones, mostly humeri (Geinitz, 1875; Lydekker, 1889a, b; Diedrich, 1999; Diedrich and Hirayama, 2003; Hirayama, 1992, 1994), and carapaces (Mantell, 1841; Owen, 1851; Reuss, 1855; Laube, 1896; Kear et al., 2014). Only rarely are carapace fragments encountered in association with limb bones (Bardet et al., 1996).

Taxonomically, a key position amongst European early chelonioids is occupied by skulls of the genus *Rhinochelys* Seeley, 1869, from the Cambridge Greensand of southeast England (Collins, 1970), a fossil Konzentrat-Lagerstätte (*sensu* Seilacher, 1970) formed in a nearshore setting during the early Cenomanian transgression by reworking and concentration of the late Albian phosphates and fossils (Hart, 1973; Unwin, 2001). Postcranial elements, found dissociated from skulls, cannot be firmly assigned to taxa based on such skulls. This concerns mainly the more or less complete carapaces described from offshore chalks (Mantell, 1841; Owen, 1851; Karl et al., 2012) and Plänerkalk-type limestones (Reuss, 1855; Laube, 1896; Kear et al., 2014).

Beyond Europe, the best-preserved and phylogenetically most important chelonioid material stems from plattenkalks of Konservat-Lagerstätte type (Seilacher, 1970) in eastern Brazil (Aptian/ Albian; Hirayama, 1998) and Lebanon (Cenomanian; Tong et al., 2006). Specimens from other facies originate from the Albian of Australia (Owen, 1882; Kear, 2003, 2006; Kear and Lee, 2006) and the upper Cenomanian-Turonian of USA and Japan (Zangerl, 1953a, b; Zangerl and Sloan, 1960; Hirayama, 1997, Hirayama and Chitoku, 1996; Hooks, 1998). Coeval material from the former USSR (summarized by Averianov, 2002) generally is poorly preserved and does not contribute much to our general knowledge of the chelonioid radiation. In contrast to extant members of the families Cheloniidae and Dermochelidae, the Cretaceous sea turtles were essentially endemic, with the possible exception of a few protostegids (Hirayama, 1997; Hirayama and Tong, 2003; Bardet et al., 2014).

3. Geological and taphonomical settings

The present chelonioid material originates from a condensed, phosphate-rich mid-Cretaceous (uppermost lower Albian to lower Turonian) succession as exposed near Annopol, east-central Poland (Fig. 1(A, B)), along the limbs of a small anticline (Samsonowicz, 1925; Marcinowski and Radwański, 1983; Walaszczyk, 1987; Machalski and Kennedy, 2013). Both specimens are from unit 3 (Fig. 1(A, C)) as exposed in the abandoned phosphorite mine Jan 1.

Unit 3 is the most fossiliferous interval of the Annopol succession (Popov and Machalski, 2014). Apart from remains of invertebrates, mostly phosphatized sponges and calcite-shelled bivalves, unit 3 yields remains of diverse marine vertebrates: bony fish, sharks, chimaeroid fish, marine turtles, ichthyosaurs, and plesiosaurs. Rare remains of pterosaurs are also present. Unit 3 is *ca*. 50 cm thick, dark greenish in color, and is composed of quartz sand with abundant glauconite, passing gradually upward into a quartz-glauconitic marl (Fig. 1(A)). A distinct horizon replete with dark brown phosphatic clasts and fossils occurs in the upper part of this unit.

Unit 3 was deposited during a late late Albian transgressive pulse, in a shallow-marine, highly productive and phosphogenic environment (Walaszczyk, 1987). The unit contains ammonites preserved as attachment scars on oyster shells (Machalski and Kennedy, 2013). These fossils are indicative of the upper upper Albian *Mortoniceras perinflatum* Zone (Machalski and Kennedy, 2013). Therefore, unit 3 corresponds to the Vraconnian of French authors (Amédro, 2002).

Both specimens available have been recovered from the lowermost, phosphate-poor part of unit 3 which directly overlies a layer of phosphatic nodules forming the top of the underlying unit 2 (Fig. 1(A)). Unit 3 and the phosphatic bed at the top of unit 2 were collectively referred to as "the Phosphorite Bed" by previous authors (e.g., Marcinowski and Radwański, 1983).

In terms of taphonomy, remains of marine reptiles from the Annopol succession illustrate three preservational states (Bardet et al., 2015):

(1) isolated skeletal elements;

- (2) disarticulated partial skeletons;
- (3) articulated partial skeletons.

Specimen ZPAL V.38/155, here listed as Protostegidae gen. et sp. indet. A, is intermediate between categories 2 and 3, being found in a semi-articulated state of preservation. It is a fragmentary carapace (fragmentary costal and neural plates, plus vertebral centra) associated with a single skull bone (a postorbital). All these elements were found together, very close to their presumed anatomical arrangement, albeit displaced to some degree (Figs. 1(C), 2). Particular elements were oriented with their ventral surfaces upwards (Fig. 2). The long axis of the animal was more or less perpendicular to the outcrop face with its anteriormost preserved parts visible. The postorbital was clearly dislocated, having been found near the posteriormost preserved pair of costals. As it matches the rest of the material in size and preservation, we believe it belongs to the same individual as the carapace. This individual underwent partial disintegration on the sea floor (within days: compare Meyer, 1991; Brand et al., 2003). and was finally buried in "belly-up" position. Specimen ZPAL V.38/ 903, here referred to as Protostegidae gen. et sp. indet. B, is an isolated left humerus which belongs to the first category. Preservation is flawless, without any signs of wear or redeposition.

Both chelonioid specimens studied appear to have been preserved *in situ* and thus are of late late Albian age. The carapace of Protostegidae gen. et sp. indet. A from Annopol, although battered and incomplete, is the first carapace specimen of an European mid-Cretaceous chelonioid to be recorded from shallow-water, sandy facies. All other carapaces of comparable age across Europe stem from offshore chalks and limestones (see above). The depositional setting of the latter strata certainly was more conducive to the preservation of more or less complete carapaces.

4. Systematic palaeontology

Carapace terminology follows Zangerl (1969), while humerus terminology is adopted from Walker (1973). Chelonioid systematics follows Hirayama (1994, 1997), and all higher taxon names are after Joyce et al. (2004).

Institutional Abbreviations: BAF, Technische Universität/ Bergakademie Freiberg, Germany; FMNH, The Field Museum of Natural History, Chicago, USA; MNA, Museum of Northern Arizona, Flagstaff, USA; NHMUK, The Natural History Museum, London, UK; SaK, Senckenberg Natural History Collections, Dresden, Germany; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

TESTUDINES Batsch, 1788 CHELONIOIDEA Baur, 1893 PROTOSTEGIDAE Cope, 1872 Protostegidae gen. et sp. indet. A Figs. 2–5

Material: Fragmentary carapace and a single, postorbital skull bone; all elements collectively labelled ZPAL V.38/155. The skull bone and carapace were collected together, and they are regarded here to belong to the same individual.



Fig. 1. Geological and geographical setting of the chelonioid material studied. A. Mid-Cretaceous succession at Annopol; 1-9, sedimentary units (see Machalski and Kennedy, 2013 for further explanation). B. Sketch-map of the Annopol anticline and its location in Poland; indicated is the entrance to the underground mine Jan 1 which yielded the material described herein. C. Part of the carapace of Protostegidae gen. et sp. indet. A, as visible during its excavation in the lowermost part of unit 3. Scale bars: 50 cm (A), 3 cm (C).



Fig. 2. Sketch showing the position of particular elements of specimen ZPAL V.38/ 155 during excavation of the specimen in the underground mine Jan 1 at Annopol. Abbreviations: c2?-c6?, 2nd? to 6th? costal plates; n3?-n6?, 3rd? to 6th? neural plates; po, postorbital; dashed line marked outcrop surface. Scale bar: 4 cm.

Occurrence: Lower part of unit 3, upper upper Albian. Abandoned phosphorite mine Jan 1 at Annopol, east-central Poland.

Description: The left postorbital bone (Fig. 3) is almost complete, 38 mm in length (measured along the parasagittal axis). The dorsal surface of the bone bears two sulci (marked "s" in Fig. 3(A2, B2)), the first one in the proximal part, and the second one located approximately medially. The first sulcus is shallow, short and extends transversally. The second sulcus is deep, extends transversally and tapers laterally. These sulci are left by supraocular and postocular scutes. The concave incision of one side of the bone is interpreted as the orbital emargination ("oe" in Fig. 3(A2)). The general aspect of the opposite end of the bone precludes its interpretation as part of the border of the temporal fossae. In such a case, it should have contacted the squamosal, but traces of this contact are obscure. A flattened anteroventral surface, which extends onto the lateral wall of the postorbital, had extensive overlap from the jugal ("js" in Fig. 3(A2)). Posterior to it, the quadratojugal surface is not distinct. The anterodorsal part of



Fig. 3. Left postorbital of Protostegidae gen. et sp. indet. A, ZPAL V.38/155, from the upper upper Albian of Annopol, in lateral (**A**), dorsal (**B**) and ventral (**C**) views. Abbreviations: js, jugal suture; oe, orbit emargination; ps, parietal suture; s, sulcus. Scale bar: 1 cm.

the bone is damaged, so that its original length cannot be measured. It should have contacted the prefrontal and overlapped it as is demonstrated by its ridged ventral surface. The medial border is slightly sinuous and bears narrow facets on its ventral surface for the suture of parietal bone ("ps" in Fig. 3(B2)).

The carapace includes four near-complete neurals with neural arches and three vertebral centra (Figs. 2, 4, 5). There are also five incomplete costals in varying states of preservation. The numerical position of these elements within the shell is reconstructed on the basis of their orientation in the host rock and their shape. The sequence of elements in the host rock seems to reflect their original anatomical arrangement. However, there are problems with location of the preserved parts of the specimen within the original carapace. We assume that the latter consisted orginally of eight pairs of neurals and costals, a standard for primitive chelonioids of the mid-Cretaceous age. Two last elements of the carapace (na7 and na8, c7 and c8) seem to be absent in the present specimen. Ribs in these elements should be strongly oriented backwards, which is not seen in the present material. Our preserved set of elements may thus correspond to sets 1 or 2 to 5 or 6 of the standard chelonioid carapace. We arbitrarily selected the option 2-6, marking however all the elements with a querry in Figs. 2, 4.

The neurals are approximately rectangular, up to 44 mm in length and up to 15 mm in width. They are unkeeled (Fig. 4(A1, A2)), similar to those of *Desmatochelys lowi* Williston, 1894 (see Zangerl and Sloan, 1960: figs. 8, 13). The external surface is rough and finely corrugated at the margins, reflecting sutures with other carapace elements. The anterior part of each neural plate is considerably swollen upwards (Fig. 4(A1, B1)). The interneural sutures seem to be positioned almost in line with the intercostal sutures.

The largest preserved costal fragment, a left c6? (Fig. 4), measures 74 mm in length and 45 mm in basal width. The c6? pair of costals is the most complete. Their shape suggests the former

existence of large costoperipheral fontanelles within the carapace. The ribs beneath the costal plates are flat, with only slightly protruding heads (Fig. 4(C1, C2)). The dorsal surfaces of costal plates bear fine ridges, radiating from the middle of the proximal end of each costal, and becoming parallel and transverse in their more distal parts. The same pattern, albeit much more delicate, is visible on the ventral surfaces of costals.

The three preserved mid-dorsal vertebral centra (3rd?, 4th? and -6th? of thorax) are isolated (Figs. 2 and 4) but they can easily be attributed to the corresponding neurals (3rd?-6th?) due to the matching shapes and unique sutures between them. The centra are ventrally rounded, constricted medially, with elongated dorsalventral foramina in their anterior and posterior surfaces ("ncf?" in Fig. 5), probably remaining after notochordal canal. The centra are up to 38 mm in length. All preserved neural and costal plates, with the exception of a small fragment of c2, reveal transverse sulci ("s" in Fig. 4(A2, B2)) which mark the original position of the margins of the epidermal scutes. No sulci which can be regarded as contacts between the vertebral and pleural scutes are preserved. Taking into account a standardized Chelonioid shell, such markings would have been visible at least in the preserved parts of costalia c6 and c3. This pattern suggests an atypical development of the epidermal shell cover, which is interpreted here as being predominated by multiplicated and hypertrophied (wide, laterally expanded) vertebral scutes, as reconstructed in Fig. 6. Nine vertebral scutes are here inferred to have been present, in contrast to the more typical number of five in the majority of turtles, including chelonioids (Zangerl, 1969; Młynarski, 1976; Hirayama, 1997, 1998: Cherepanov, 2006).

Remarks: The postorbital in ZPAL V.38/155 is similar in shape to that in skulls of the genus Rhinochelys from the Late Albian Cambridge Greensand (Lydekker, 1889a; Collins, 1970) and from the Vraconnian of the La Fauge Valley near Grenoble, France (Moret, 1935). One of the English specimens, referred to as R. cantabrigiensis Lydekker, 1889a, has two sulci of a course similar to those seen in Protostegidae gen. et sp. indet. A (Collins, 1970: pl. 68, fig. 16). The largest known skull of Rhinochelys from the Cambridge Greensand, referred to as *R. pulchriceps* (Owen, 1851), is 64 mm in length. The approximate length of the postorbital in that particular skull is 30 mm (measured from Collins, 1970: pl. 68, fig. 5). In view of the fact that the length of the (incomplete) postorbital of Protostegidae gen. et sp. indet. A is 38 mm, the estimated length of the complete skull would have been around 90 mm. This suggests that the carapace length in Protostegidae gen. et sp. indet. A ranged between 350 and 450 mm, provided that the ratio head/ carapace was similar to that in other mid-Cretaceous chelonioids (ca. 1:4 in Santanachelys, ca. 1:5 in Desmatochelys; see Zangerl and Sloan, 1960 and Hirayama, 1997, respectively).

The presence of narrow, subrectangular neurals and the position of the intercostal and interneural sutures almost in line, indicates that ZPAL V.38/155 is a primitive member of the Protostegidae, as characterized by Hirayama (1997). In the Cheloniidae, the neurals are hexagonal and intercostal sutures alternate with the interneural ones; advanced Protostegidae have strongly reduced costals (Hirayama, 1997).

Protostegidae gen. et sp. indet. A is much smaller, but generally comparable in the shape of neurals and costals to *Desmatochelys lowi* from the upper Cenomanian–lower Turonian strata of the United States (Nebraska, South Dakota, and Kansas) and Japan (Hokkaido) (Williston, 1894; Zangerl and Sloan, 1960; Hirayama, 1997; Elliott et al., 1997; Hooks, 1998). Both forms share the absence of keels on neurals, a rather rare feature in early protostegids. From *Cimochelys benstedi* (Mantell, 1841) of the British Chalk [= *Emys benstedi* Mantell, 1841: pls. 11, 12; *Chelone* (*Cimochelys) benstedi* of Owen, 1841: pls. 41–43; *Cimochelys benstedi* (Mantell, 1841) of Milner, 1987: pl. 59, fig. 1], the present



Fig. 4. Carapace of Protostegidae gen. et sp. indet. A, ZPAL V.38/155, from the upper upper Albian of Annopol. A. Dorsal view. B. Left side of 4th? neural. C. Ventral view. Abbreviations: c2?-c6?, 2nd? to 6th? costal plates; ce3?-ce6?, 3rd? to 6th? vertebral centra; n3?-n6?, 3rd? to 6th? neural plates; na3?-na6?, 3rd? to 6th? neural arches; r3?-r6?, 3rd? to 6th? costal ribs; s, sulcus. Scale bar: 4 cm.

Fig. 5. Vertebrae of Protostegidae gen. et sp. indet. A, ZPAL V.38/155, from the upper upper Albian of Annopol. **A.** 3rd? thoracic centrum in ventral (A1), dorsal (A2), right side (A3), anterior (A4), and posterior (A5) views. **B.** 4th? thoracic centrum in ventral (B1), dorsal (B2), right side (B3), anterior (B4), and posterior (B5) views. **C.** 6th? thoracic centrum in ventral (C1), dorsal (C2), right side (C3), anterior (C4), and posterior (C5) views. ncf?: probable foramen for notochordal canal. Scale bar: 1 cm.

specimen differs by its much larger size and also in having unkeeled neural plates.

The most important feature which seems to distinguish Protostegidae gen. et sp. indet. A not only from all other known protostegids, but also from all other known chelonioids, is the unusual development of epidermal scutes with laterally hypertrophied and multiplicated (nine instead of five) vertebral scutes. This arrangement is inferred from the pattern of intervertebral sulci clearly visible on all preserved neural and costal plates which are large enough to preserve such imprints (see above).

PROTOSTEGIDAE gen. et sp. indet. B

Fig. 7(A–C)

Material: A single, well-preserved left humerus (ZPAL V.38/ 903).

Occurrence: lower part of unit 3, upper upper Albian. Abandoned phosphorite mine Jan 1 at Annopol, east-central Poland, *ca*. 300 meters north of the carapace of Protostegidae gen. et sp. indet. A (ZPAL V.38/155) described above.

Description: ZPAL V.38/903 is 90 mm in length, and relatively slender, with the shaft (corpus humeri) constricted at mid-length to form a prominent waist (13 mm in the narrowest part). A large proximal region is provided with a pronounced medial process (processus medialis), large head (caput humeri) and prominent

Fig. 6. Schematic interpretative restoration of the carapace of Protostegidae gen. et sp. indet. A, based on specimen ZPAL V.38/155 from the upper upper Albian of Annopol. Solid lines: carapace; shaded areas: preserved fragments of carapace (with sulci marked in thick dashed lines); thin dashed lines: boundaries between vertebral shields of epidermal shell (see text for further explanation). Scale bar: 5 cm.

lateral process (processus lateralis). The head is well separated from the adjoining processes. The shaft is nearly straight in antero-posterior view. The distal region of the humerus is relatively flat and widened. All articular surfaces of the humerus are nearly smooth, indicating the former presence of overlying avascular cartilage (Snover and Rhodin, 2007).

Head is strongly convex, oval in outline, the longer axis extending dorsoventrally. Its articular surface extends onto both dorsal and ventral surfaces of the bone, but more so dorsally. The neck of the caput humeri is placed under an angle of 138° to the shaft axis (i.e., the α angle of Zangerl, 1953b), which means that the head is less strongly inclined dorsally than ventrally. The angle between the shaft axis and the plane of humerus movement (the β angle of Zangerl, 1953b) is 68°.

Medial process is massive, prolonged and situated posteriorly of the caput humeri. It strongly protrudes over the articular surface of the head. This process is the insertion point of the mm. coracobrachialis magnus and subscapularis in sea turtles (Walker, 1973; Wyneken, 2001), and its prominent length reflects the requirements of these muscles which are responsible for flipper retraction.

Lateral process is strongly developed, subtriangular in dorsal and medial aspects. The apex of the triangle is situated close to the humerus mid-length and strongly protruding anteriad. The attachment surface of the lateral process is roughly tetragonal in anterior view; it extends significantly into the ventral surface of the humerus. The apex of the lateral process bears two facets, facing anteriad and anteroventrad, respectively. A ridge surrounds the facets and extends from the anterior side of the head to the ventralmost edge of the process (Fig. 7(B)). The lateral process

Fig. 7. Humeri of Protostegidae gen. et sp. indet. **A–C**. Left humerus of Protostegidae gen. et sp. indet. B, ZPAL V.38/903 from the upper upper Albian of Annopol, in ventral (A), anterior (B), and dorsal (C) views. **D–F**. Right humerus of *L. cantabrigiense* (Lydekker, 1889a), (NHMUK) PV OR 35175, of late Albian age, from the lowermost Cenomanian Cambridge Greensand, Cambridge, southeast England, in ventral (D), anterior (E), and dorsal (F) views. Abbreviations: ca, capitellum; cb, m. coracobrachialis brevis insertion scar; ch, caput humeri; p, m. pectoralis insertion scar; ef, ectepicondylar foramen; fcr?, probably insertion for m. flexor carpi radialis; lp, lateral process; lt, m. latissimus dorsi and m. teres major insertion scar; mp, medial process; r, ridge of lateral process; re, radial epicondyle; tr, trochlea; ue, ulnar epicondyle. D1 and E1 reversed for easier comparison. Scale bar: 1 cm.

roughly corresponds to the deltopectoral crest; it served attachment of the muscles responsible for protraction and abduction of the flipper (mm. pectoralis and supracoracoideus on the ventral side, and deltoideus dorsally). There is no distinct area that corresponds to the median concavity (Hirayama, 1997) in the present specimen. The lateral process bears two distinct scars on the ventral side of its base. The proximal one is large, directly distal of the caput humeri and facing proximo-ventrally. This scar is part of the insertion area of m. coracobrachialis brevis, the second of which is situated in the intertubercular fossa. The distal scar serves insertion of m. pectoralis and faces ventro-distally. A shallow concave scar, situated on the dorsal side of the humerus, distal of the caput humeri and at the base of the lateral process, receives the m. latissimus dorsi and m. tres major. This scar is located anteriorly of the humeral axis (Fig. 7(C)).

Shaft is almost straight and with a narrow waist at mid-length, expanding distally into epicondyles. The distal end of the bone is broad and dorsoventrally flattened, up to 29 mm wide. The distal articular end is rather poorly developed. The capitellum is located on the distal surface of the shaft and passes only insignificantly onto the ventral surface of the bone. The trochlea is still less extensive as well, the ulnar epicondyle is less developed than the radial. The ectepicondylar foramen is well developed and fully enclosed by bone. On the posterior edge of the shaft, on its ventral side, fairly close to the ulnar condyle, there is a small tuberosity which probably represents the insertion area for the m. flexor carpi radialis.

Remarks: There is no doubt that ZPAL V.38/903 belongs to chelonioids. The "underwater flight", specific for these turtles (Zangerl, 1953b; Walker, 1973), is reflected in the following features of their humeri: a near-straight shaft, the lateral process located distally of the caput humeri (Hirayama, 1994), and the angle of the caput humeri with respect to the shaft significantly exceeding 90° (angle α of Zangerl, 1953b). All these characters are seen in this humerus.

The length of ZPAL V.38/903 is 90 mm. Humeral length in an Aptian/Albian subadult individual of *Santanachelys gaffnei* is 23 mm, the carapace of which measured 145 mm in length (Hirayama, 1998). By analogy, carapace length of the Annopol protostegid may be estimated to have been 500–600 mm, thus probably slightly larger than Protostegidae gen. et sp. indet. A, with an estimated carapace length of about 450 mm (see above). Smooth articular subchondral surfaces and a distally closed ectepicondylar foramen indicate a fully-grown adult. Articular surfaces in young marine turtles are rough, with large holes illustrating the presence of vascular channels penetrating into the cartilage above (Snover and Rhodin, 2007: fig. 2.3). The ectepicondylar foramen, developed in young stages at the distal

end of a distinct groove, becomes gradually overgrown during ontogeny, and completely closed in adults (Zug et al., 1986: fig. 2).

In the literature, Cretaceous chelonioid humeri similar to ZPAL V.38/903 usually are firmly assigned to the Protostegidae, based on morphological criteria proposed by Hirayama (1992, 1994, 1997). The anteriorly-faced lateral process and median concavity of this process, visible in all protostegids, with the exception of Santanachelys, have been regarded as the most important synapomorphies defining the Protostegidae by this author. However, ZPAL V.38/903 does not match the above definition, because its prominent lateral process extends significantly onto the ventral surface of the humerus, and there is no area on the lateral process that could be recognised confidently as "the median concavity" outlined by Hirayama. In contrast to the Annopol humerus, those of advanced protostegids have the lateral process restricted onto the ventral surface of the humerus, essentially paralleling the humeral axis (Hirayama, 1992: fig. 6J–U). On the other hand, the strong development of the head and its distinct separation from prominent adjoining processes in ZPAL V.38/903 permits exclusion from the toxochelyid grade. Moreover, the absence of the V-shaped crest on the lateral process sets it apart from cheloniids. ZPAL V.38/903 also differs from the very robust humeri of advanced protostegids, such as Protostega Cope, 1871 and Archelon Wieland, 1896, and dermochelyids, such as Dermochelys de Blainville, 1816, in having less distally displaced and differently constructed lateral processes and a less flattened and widened distal region. In summary, ZPAL V.38/903 is best considered as a protostegid humerus, with some reservation because it does not correspond to the humeral definition of this family as given by Hirayama (1992, 1994, 1997). Actually, this definition appears to match only humeri of advanced protostegids (see Wieland, 1900; Hirayama, 1992).

The Annopol specimen is similar to some isolated humeri known from the European mid-Cretaceous. Among these, Chelone carusiana Geinitz, 1875 (pl. 46, fig. 1) is based on specimen BAF N.193/4C from the middle/upper Turonian Strehlen Formation (Fig. 8(A); see Wilmsen and Niebuhr, 2014, for an updated stratigraphy, and Niebuhr, 2014, for recommendation on how to quote Geinitz's paper) of Strehlen, Saxony, eastern Germany (= Rhinochelis [sic] (?) carusiana of Diedrich, 1999: fig. 3.1; Protostegidae gen. et sp. indet. of Diedrich and Hirayama, 2003: fig. 4.1). This is a right humerus, much smaller than the Annopol specimen, measuring only 60 mm in length. The lateral process in BAF N.193/4 has no protruding ventral portion, unlike the Annopol specimen. This particular bone is the holotype of Chelone carusiana, but it is best considered as Protostegidae gen. et sp. indet. (Diedrich and Hirayama, 2003). Specimen SaK 10585, from the same locality and horizon (Fig. 8(B); = Rhinochelis [sic] cf. cantabrigiense of Diedrich, 1999: fig. 3.3 [not 3.4 as indicated in caption]; Protostegidae gen. et sp. indet. of Diedrich and Hirayama, 2003: fig. 4.3 [not 4.4]), was also illustrated as Chelone carusiana by Geinitz (1875: pl. 46, fig. 2). This is a right humerus, 60 mm in length, incomplete, with its distal end, and the apex of the lateral process broken off and covered by marcasite encrustations. These features, not noted by earlier workers, preclude any firm conclusions on the affiliation of this specimen, which is best considered as Protostegidae gen. et sp. indet. (Diedrich and Hirayama, 2003).

Next taxon available for comparison with the Annopol specimen is *Lytoloma cantabrigiense* Lydekker, 1889a, based on a series of isolated humeri plus a mandible from the Cambridge Greensand (Albian/Cenomanian) of Cambridge, southeast England (Lydekker, 1889a: fig. 3; *Rhinochelys pulchriceps*? of Hirayama, 1992: fig. 6G–1; cf. *R. pulchriceps* of Hirayama, 1994: fig. 6d; *R. cantabrigiense* of Diedrich, 1999: fig. 3.4 [not 3.3]; Protostegidae

Fig. 8. Humeri of Protostegidae gen. et sp. indet. **A.** Right humerus of *Chelonia carusiana* Geinitz, 1875 (pl. 46, fig. 1), BAF N.193/4C, in ventral view. **B.** Right humerus of *Chelonia carusiana* Geinitz, 1875 (pl. 46, fig. 2), SaK 10585 in dorsal view; both specimens from the upper Turonian of Strehlen, Germany. Scale bar: 1 cm.

gen. et sp. indet in Diedrich and Hirayama, 2003: fig. 4.4 [not 4.3]; *R. pulchriceps* of Danilov, 2005: fig. 74D–F). Specimen (NHMUK) PV OR 35175, the sole individual ever illustrated in the literature, is a right humerus, 94 mm in length. It is reillustrated here, for the first time photographically, in Fig. 7(D-F). This specimen closely matches ZPAL V.38/903 (Fig. 7(A-C)). It has almost the same length and the only significant differences are that its shaft is slender and more constricted, and its proximal portion smaller, with a relatively small head and processes. The distal part of the English specimen is disproportionally larger. However, (NHMUK) PV OR 35175 is in part artificial, a feature not previously noted by Hirayama (1992, 1994). According to Lydekker (1889b: 69), "The middle of the shaft is wanting, and is restored in plaster, so that the contour of this is only approximate". It is therefore possible that the shaft was actually shorter, implying more robust proportions of the humerus. It is also conceivable that the proximal portion came from a smaller individual, and the distal one from a larger. Specimens (NHMUK) PV OR 35175 and ZPAL V.38/903 share the same position and structure of the lateral process, its transgression onto the ventral surface of the humerus, roughly tetragonal outline of the lateral process in anterior view, and also the angle between the head and shaft, which is ca. 138° in both cases. However, there are also some minor differences in morphology. The English specimen bears a small scar for m. coracobrachialis brevis, and a portion of this scar, situated on the ventral part of the lateral process, faces ventrally, whereas in ZPAL V.38/903 it faces proximo-ventrally. There is a ridge in the English specimen, which extends from the anterior side of the caput humeri to the anterior side of the lateral process, surrounding the facets antero-dorsally (Fig. 7(E2)), unlike in the Polish specimen (Fig. 7(B2)). The tuberosity for the m. flexor carpi radialis is not present in (NHMUK) PV OR 35175. Overall, the attribution of the present humerus to the skull-based genus Rhinochelys (see above) is unsubstantiated and L. cantabrigiense is best regarded as Protostegidae gen. et sp. indet. (Diedrich and Hirayama, 2003).

The last specimen to be compared with the humerus from Annopol is that of *Rhinochelis* [*sic*; recte *Rhinochelys*] (?) cf. *carusiana* of Diedrich (1999). This is a left humerus from the middle Cenomanian of Ascheloh near Halle, northwest Germany (Diedrich, Cenomanian Charles, Cenoma

1999: figs. 2.2, 4.1-4; Protostegidae gen. et sp. indet. of Diedrich and Hirayama, 2003: fig. 4.2.). This humerus is smaller (55 mm in length) and more robust than ZPAL V.38/903. However, it is similar to the Annopol humerus in having the well-developed lateral process extend well onto the ventral surface of the humerus with its apex located near mid-length of the humerus, and the scar for mm. latissimus dorsi and tres mayor positioned anteriorly of the axis of the humeral shaft (Diedrich and Hiravama, 2003). There is, however, no ridge around the attachment area in the Ascheloh specimen, whereas it is well visible in the Annopol specimen. The angle between the humerus head and shaft is *ca*. 135°, similar to the Annopol specimen (measured from Diedrich, 1999: fig. 4.3). The open ectepicondylar foramen is indicative of a young, not fully-grown individual (Zug et al., 1986). The younger ontogenetic age of the Ascheloh specimen, best regarded as Protostegidae gen. et sp. indet. (Diedrich and Hirayama, 2003), hampers any further comparison with the Annopol specimen.

5. Discussion

Both specimens described in the present paper do not find close match with any of the mid-Cretaceous chelonioid specimens known to date. This concerns mainly the carapace of Protostegidae gen. et sp. indet. A. In view of the apparently symmetrical arrangement of the sulci in this specimen, we consider it unlikely that this atypical pattern resulted from a pathology. Malformations resulting from environmental perturbations or genetic defects usually are asymmetrical and irregular (Zangerl and Johnson, 1957: Zangerl, 1969: Pritchard, 2008). Symmetrical lateral hypertrophisation and multiplication of vertebral scutes occurs in the Plio-Pleistocene tortoise genus Sakya Bogachev, 1960, which has up to ten laterally elongated (wide) vertebral scutes (Cherepanov, 2006: fig. 5D). This feature is held to be of taxonomic value, being characteristic of the genus (Chkhikvadze, 1968; Młynarski, 1976). In full analogy, the convergent secondary polimerization (Cherepanov, 2006) of the horny shell of the Annopol individual would potentially form a basis for erection of a new chelonioid genus and species, but we consider this decision as premature, being not able to entirely exclude that it is an individual anomaly. Certainly, other, better preserved and more complete finds in the Annopol site are needed to clarify the taxonomic and phylogenetetic position of Protostegidae gen. et sp. indet. A.

As far as the humerus assigned to Protostegidae gen. et sp. indet. B is concerned, we noted above that some specimens from the European Cretaceous seem to be closely related in size and morphology. It is conceivable that all these humeri represent a distinct, separate grade in humeral chelonioid organization, charasteristic of the less advanced protostegids. This hypothesis remains to be further tested, based on studies of better preserved and more diagnostic material. What is certain at the moment is that the group of humeri discussed above does not match the definition of the "protostegid" grade sensu Hirayama (1992), which is probably better restricted to the more advanced and specialized protostegids, including the Albian "Protostega" anglica from England and a plethora of Late Cretaceous protostegids, known mainly from the United States (Wieland, 1900; Hirayama, 1992). As noted above, the humeri of these advanced protostegids have the lateral process restricted to the anterior surface of the shaft and generally paralleling the humeral axis. In view of the absence of associated diagnostic material it is best to leave all these humeri, including ZPAL V.38/903 from Annopol, in open nomenclature as Protostegidae gen. et sp. indet.

The taxonomic relationship between specimens ZPAL V.38/155 and ZPAL V.38/903, herein referred to as Protostegidae gen. et sp. indet. A and B, respectively, remains currently not clear. There are no decisive arguments, either for or against, regarding the conspecifity of these specimens, which is fairly probable, however, in view of their co-occurrence at the same stratigraphic level and similar estimates of body sizes.

6. Conclusions

We report remains of chelonioid turtles, assigned to Protostegidae, from the upper Albian (Lower Cretaceous) sands exposed at Annopol, Poland. These are the first remains of Cretaceous marine turtles from Poland. A semi-articulated partial carapace with associated postorbital bone is referred to as Protostegidae gen. et sp. indet. A. The arrangement of scute sulci visible on each preserved costal and neural plate of this specimen suggests hypertrophy and multiplication of vertebral scutes, a unique feature among chelonioids. An isolated humerus from the same level as the carapace is referred to as Protostegidae gen. et sp. indet. B. The massive lateral process of this humerus extends significantly onto ventral surface of the bone, like in humeri of some primitive protostegids known from the European Cretaceous, and unlike those of advanced, Late Cretaceous Protostegidae. The new material from Annopol suggests that the diversity of early chelonioids was greater than previously thought, but better preserved materials from this site are needed for full clarification of its taxonomic and phylogenetic position.

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