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Revision of the Triassic European turtles *Proterochersis* and *Murrhardtia* (Reptilia, Testudinata, Proterochersidae), with the description of new taxa from Poland and Germany

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A recently discovered Norian outcrop in Poreba, Poland, has yielded numerous well-preserved turtle remains. These, together with historical materials from Germany, enabled the identification of two new proterochersid taxa: ***Proterochersis porebensis* sp. nov.** from Poland and ***Keuperotesta limendorsa* gen. et sp. nov.** from Germany. Moreover, two problematic taxa, *Proterochersis intermedia* Fraas, 1913; and *Murrhardtia staeschei* Karl & Tichy, 2000; are shown to be conspecific with *Proterochersis robusta* Fraas, 1913. New diagnoses for the family Proterochersidae Nopcsa, 1923 and all included taxa are provided. Proterochersids are of great importance to turtle phylogeny because of their age (they comprise the oldest fully shelled turtle species known to date) and their still-debated phylogenetic position (classically they are considered the basalmost Pleurodira, but in some analyses they are placed on the stem of Testudinata). Newly discovered plesiomorphic aspects of the anatomy of these three species included in the phylogenetic analysis demonstrate that they are not only the oldest, but are also the most basal fully shelled turtles. The unique features of their shell (e.g. the first thoracic rib unreduced and costal-bearing, and the osseous contact between the carapace and sacral vertebra) are of special significance for future research of the earliest stages of turtle shell evolution. This is the first contribution focused solely on the new, phylogenetically informative, and important characters of this group since the initial description of *P. robusta* more than 100 years ago.

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ADDITIONAL KEYWORDS: Löwenstein Formation – Norian – origin of turtles – Stubensandstein – Upper Triassic – vertebrate phylogeny – Zbaszynek Beds.

INTRODUCTION

The origin and early evolution of turtles (Testudinata) remain unclear, despite constant, intensive research and increasing palaeontological data. The position of turtles on the phylogenetic tree used to change a lot during the 19th and 20th centuries (for a short, historical review of hypothesized turtle relationships, see Młynarski, 1956), and even today three main hypotheses, supported by different data sets, are being discussed (for a brief but comprehensive review of the modern research on turtle origins, see Joyce, 2015).

The early evolution and diversifications of turtles (beginning from the Middle Triassic) are slightly better understood. *Pappochelys rosinae* Schoch & Sues, 2015; from the Ladinian of Germany, is unambiguously the oldest and most basal stem turtle known to date. *Odontochelys semitestacea* Li *et al.*, 2008 from the Carnian of China, is the oldest amniote with a turtle-like plastron. During the Norian the turtle lineage spread worldwide, as shown by fossils from Germany (e.g. Baur, 1887; Fraas, 1913; Karl & Tichy, 2000), Thailand (de Broin *et al.*, 1982; de Broin, 1984), Argentina (Rougier, de la Fuente & Arcucci, 1995; Sterli, de la Fuente & Rougier, 2007), Greenland (Jenkins *et al.*, 1994), and Poland (Sulej, Niedźwiedzki & Bronowicz, 2012). For a long time the German *Proganochelys quenstedti* Baur, 1887 was recognized as the most basal fully shelled turtle. An older turtle found in strata lying directly below those yielding

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Proganochelys quenstedti, *Proterochersis robusta* Fraas, 1913; also from Germany, was initially described as the earliest pleurodire for its sutured pelvis, therefore implying a more derived position on the phylogenetic tree; however, all more recent studies interpret *Proterochersis robusta* as a stem turtle (Rougier *et al.*, 1995; Joyce, 2007; Sterli, 2010; Anquetin, 2012; Joyce, Schoch & Lyson, 2013), but it remains fairly poorly known. The initial description (Fraas, 1913) of *Proterochersis robusta* was based on two fragmentary specimens (Fig. 1), mostly consisting of internal moulds of the shell. Fraas (1913) described two species, *Proterochersis robusta* and *Proterochersis intermedia*, based solely on differences in inferred shell geometry and plastron thickness. Although several new specimens assigned to that genus have been collected since then, only one was adequately described (Joyce *et al.*, 2013). Another taxon from Germany is *Murrhardtia staeschei* Karl & Tichy, 2000. As a result of disputable character recognition (Danilov, 2005; Gaffney, Tong & Meylan, 2006; see Fig. 1C, D), both *M. staeschei* and *Proterochersis intermedia* are virtually missing from the literature, and the name *Proterochersis robusta* is used instead for all relevant material.

A new turtle-yielding locality from the Norian of Poland has been described by Sulej *et al.* (2012). The turtle presented therein was not named and was referred to cf. *Proterochersis* based on overall shell structure. Since then numerous new specimens have been found at that site and prepared, including girdles and limb bones (Figs 2–6). The purpose of this paper is to review the previously described specimens of *Proterochersis* and *Murrhardtia* from Germany and the Triassic turtles from Poland, to describe several new Polish specimens, and to assess their systematic identities.

INSTITUTIONAL ABBREVIATIONS

CSMM, Carl-Schweizer-Museum, Murrhardt, Germany; IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences, Beijing, China; PULR, Universidad Nacional de La Rioja, Argentina; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; ZPAL, Roman Kozłowski Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland.

GEOLOGICAL SETTING

All Late Triassic turtles from Germany originate from the Löwenstein Formation (locally called Stubensandstein), from overlying red claystones of the Trossingen Formation (formerly Knollenmergel), both localized in Baden-Württemberg, or from the keuper strata of Halberstadt (potentially of different age, possibly representing the Trossingen Formation, see Deutsche Stratigraphische Kommission, 2005), localized in Saxony-Anhalt, and all considered to be Norian (Gaffney, 1990; Deutsche Stratigraphische Kommission, 2005; Joyce *et al.*, 2013; Schoch & Seegis, 2014). The Löwenstein Formation, lying at the border of Keuper Basin, is approximately 100–140 m thick and has a down-dip size of 200 km. It has the characteristics of semi-arid or subhumid terminal alluvial plains (Hornung & Aigner, 1999). It is composed of interdigitated layers of yellowish, reddish, and white sandstone, and playa-like claystones, which are interpreted as a record of cyclical episodes of rising and lowering water level, lasting approximately 6 Myr (for detailed characteristics of the Löwenstein Formation, see Aigner *et al.*, 1996; Hornung & Aigner, 1999, 2002a, b; Deutsche Stratigraphische Kommission, 2005). All German *Proterochersis* and *Murrhardtia* material known to date was collected from the lower Löwenstein Formation (Lower Stubensandstein). All *Proganochelys quenstedti* material was found in younger sediments of the Trossingen Formation (possibly contemporaneous with the upper Löwenstein Formation elsewhere or altogether younger than the Löwenstein Formation), middle Löwenstein Formation, and from around Halberstadt (Gaffney, 1990; Deutsche Stratigraphische Kommission, 2005), so these taxa did not coexist in the same place or at the same time. The exact correlations between these strata and other European formations are unfortunately unclear. It is universally accepted, however, that the middle and upper Löwenstein Formation are middle to late Norian in age, whereas the lower Löwenstein Formation is estimated to be mid-Norian (e.g. Deutsche Stratigraphische Kommission, 2005; Franz, 2008), and possibly at least partially early Norian (e.g. Hornung & Aigner, 1999; Heunisch & Nitsch, 2011; Lucas *et al.*, 2012).

The Polish Triassic turtle material originates from the town of Poreba (Silesian Voivodeship, southern Poland), from sediments classified as the Zbaszynek Beds (Sulej *et al.*, 2012; Niedźwiedzki *et al.*, 2014) and palynologically dated to middle or late Norian, subzone IVb of the *Corollina meyeriana* zone (Niedźwiedzki *et al.*, 2014). These fluvial strata consist of interdigitated layers of conglomerates, mudstones, and sandstones, all of which are at least in part rich in vertebrate (turtles, fishes, amphibians, aetosaurs, and dinosauriforms) and plant remains. The appearance of conglomerates and some taphonomical aspects of the site (bones are isolated, often broken, or heavily worne, and much rarer complete turtle shells are always heavily broken, some

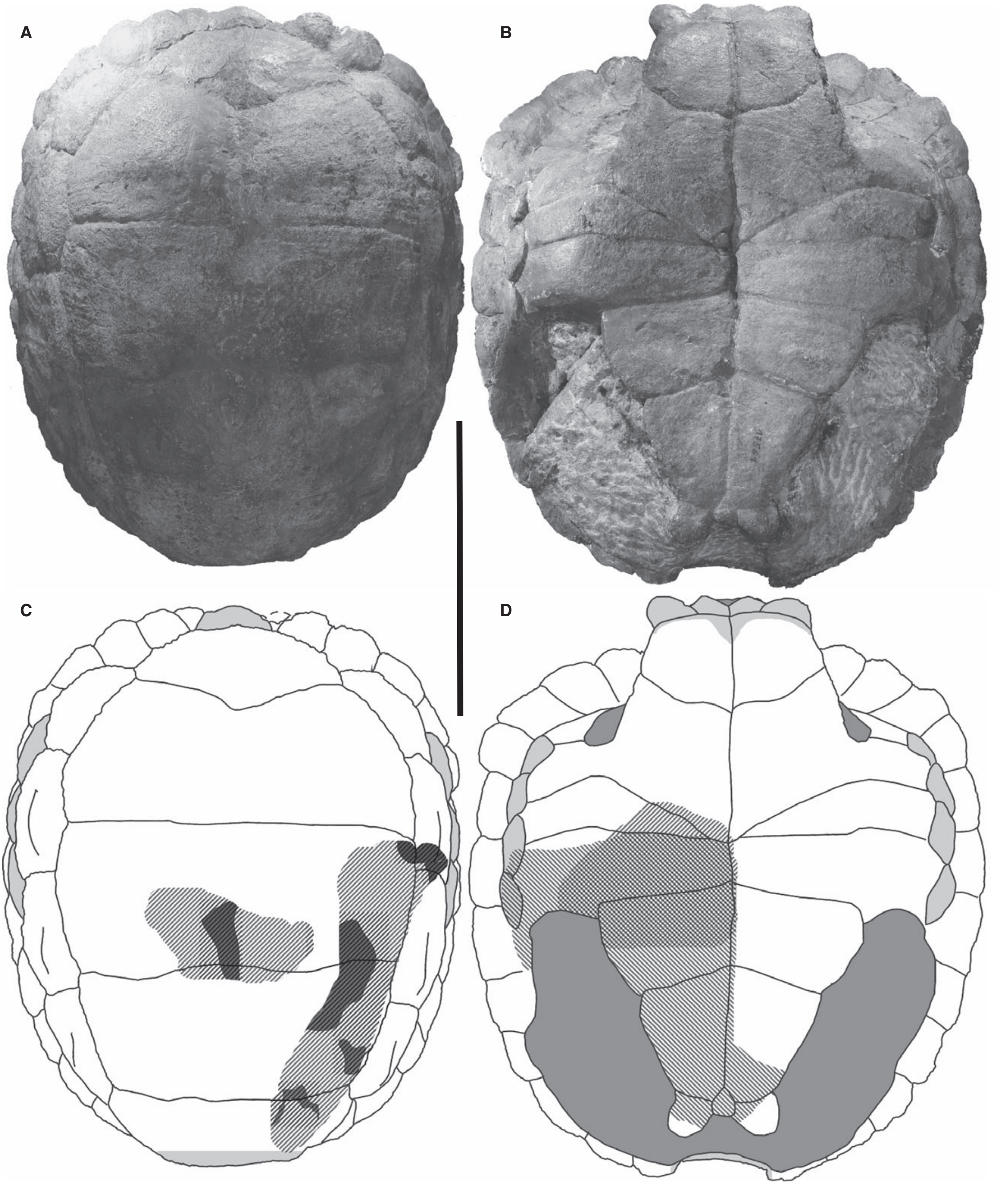

Figure 1. *Proterochersis robusta*, SMNS 17561: A, C, shell in dorsal view; B, D, shell in ventral view. C, D, approximate extent of preserved bone in holotypes of *Proterochersis robusta* (hatched right upwards) and *Proterochersis intermedia* (hatched right downwards, shaded areas show approximate extent of plaster covering the dorsal surface of the specimen), and the characters noted by Karl & Tichy (2000) as diagnostic to *Murrhardtia* (light grey), are shown. Dark grey is matrix. Scale bar: 30 cm.

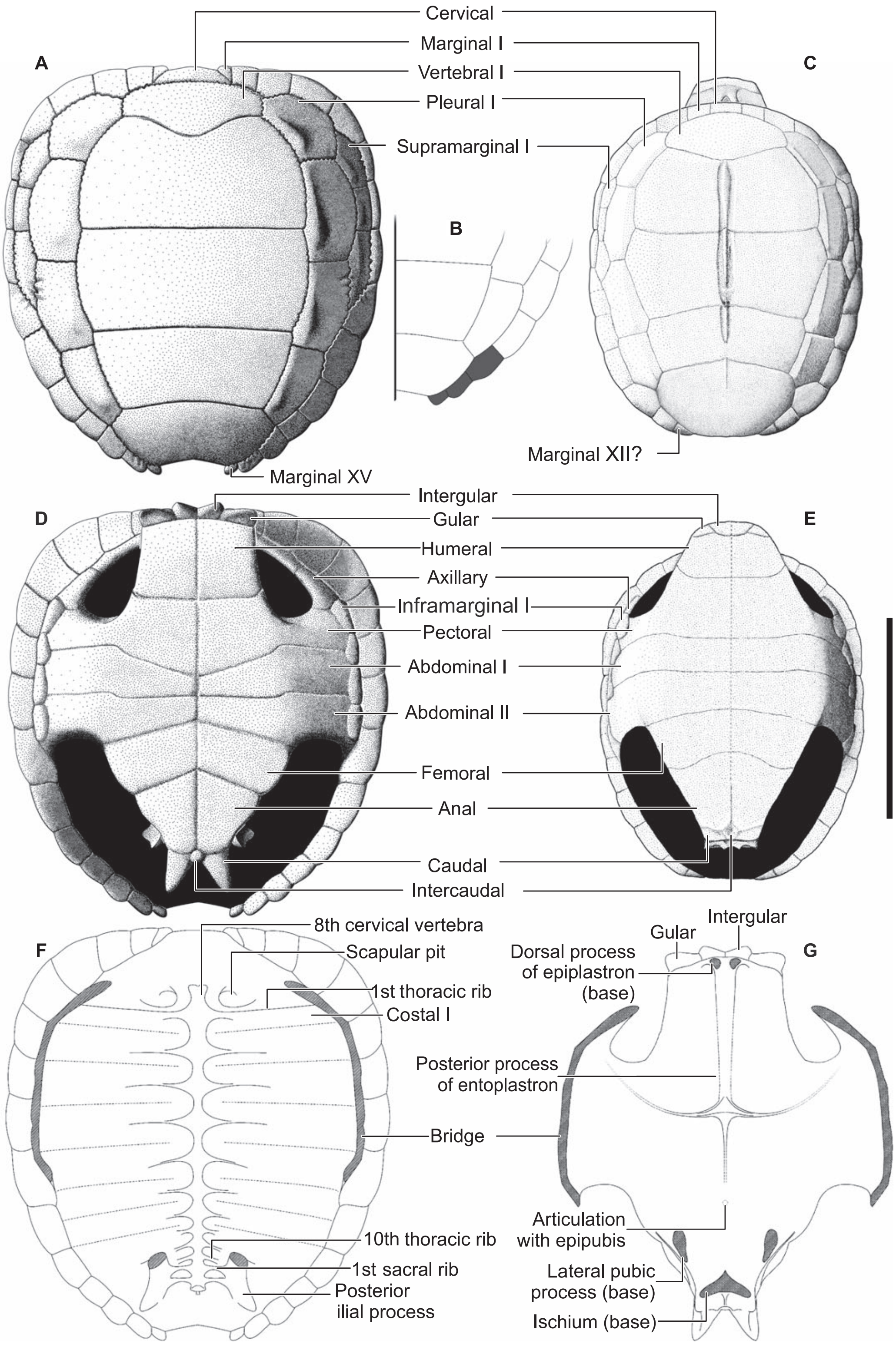

Figure 2. ***Proterochersis porebensis* sp. nov.**, shell reconstruction: A, adult in dorsal view; B, posterior right quarter of the carapace in variant with 14 marginals (ZPAL V.39/49); C, juvenile in dorsal view; D, adult in ventral view; E, juvenile in ventral view; F, visceral view of the carapace with pelvis cut at ilial neck; G, visceral view of the plastron with dorsal processes of epiplastra and pelvis cut at base. A, B, D, F, and G based on ZPAL V.39/48 and ZPAL V.39.49; C and E modified from Sulej *et al.* (2012), based on ZPAL V.39/34. Scale bar: 20 cm.

fragments are partially eroded, and possibly redeposited) demonstrate that the energy in the system was temporarily high, but the layers of much finer sediments, frequently containing very small, fragile yet very well preserved bones, suggest that the energy in the system might have greatly varied with time. These sediments may have been carried by a braided river, and changes in the energy of the system could be attributed to changes in the network layout or to episodes of flooding. For more detailed characteristics of the Poreba site, see Niedźwiedzki *et al.* (2014). These strata may be of the same age as the lower Löwenstein Formation in Germany, but it is also possible that they are significantly younger. An early Norian age is not consistent with the megaspores present in the Zbaszynek Beds, which suggest a middle–late Norian to early Rhaetian age (Marcinkiewicz & Orłowska-Zwolińska, 1985; Franz, 2008; Marcinkiewicz, Fijałkowska-Mader & Pieńkowski, 2014). Therefore, any possible temporal overlap with the lower Löwenstein Formation is uncertain, and the turtles from Poreba may in fact be temporally closer to German *Proganochelys quenstedti* than to *Proterochersis robusta*.

MATERIAL AND METHODS

Referred specimens

Twenty specimens referred to *Proterochersis robusta*, *Proterochersis intermedia*, or *Murrhardtia staeschei* currently exist in collections (SMNS 11396, 12777, 15479, 16442, 16603, 16668, 17561, 17755, 17755a, 17756, 17757, 17930, 18440, 19103, 50917, 50918, 51441, 56606, 81917; CSMM uncat.), and 239 catalogued turtle specimens are available from Poreba (ZPAL 1–28, 34, 48–72, 155–300, 331–366, 367–369). With the exception of one specimen (SMNS 50918, which was unavailable at the time), all the existing German and Polish *Proterochersis* and *Murrhardtia* material was studied in detail by the first author. Herein we only list the specimens referred to in the text, previously mentioned in the literature, or as an example displaying the characters used in the taxonomic and phylogenetic analysis, but the taxonomic conclusions are based on the whole collection, taking into account the possible intraspecific diversity or sexual dimorphism as inferred from the paradigm.

SMNS 11396

The holotype of *Proterochersis intermedia* Fraas, 1913. Found in Stuttgart-Rohracker, Germany. A fragmentary specimen, consisting of a natural internal mould of the posterior part of the carapace (with impressions of dorsal ribs IV–X and with corresponding rib heads and vertebrae embedded in rock matrix), some bone fragments of the carapace (a quite large part of the right side), a median fragment including contact spots with fifth, sixth, and right fourth ribs, as well as the neural spines of the vertebrae visible on the visceral surface (and some rather uninformative fragments), and a fragment of the right side of the plastron (parts of the first and second abdominal, and femoral), along with an impression of the visceral surface of that element (Fig. 1C, D). The mould of the carapace is reconstructed from two rock fragments, and a large part of it (probably even half) is actually painted plaster. The dorsal surface of the reconstruction seems to be modelled upon the visceral surface of the bony remains, but the large carapace fragment, which was used for that, is itself partially restored with plaster. Therefore, the overall shape of the reconstruction may not be very accurate, and even the visceral surface of the reconstructed carapace does not closely fit the corresponding dorsal surface of the mould reconstruction. The carapace fragments are weathered and the extensive use of plaster (at places hard to discern from bone, and probably in some places covering parts of bone) makes any surface characters difficult to interpret. No unambiguous sulci or sutures are identifiable. The thickness of the carapace is relatively uniform. The plastron element is in a much better state of preservation, with the surface pattern and sutures between the two first mesoplastra, and between the second mesoplastron and hypoplastron, visible. This specimen was never illustrated. Herein we refer it to *Proterochersis robusta*.

SMNS 12777

The holotype of *Proterochersis robusta* Fraas, 1913. Found in Rudersberg, Germany. This is a natural mould of the inside of the shell, with some bone fragments preserved (Fig. 1C, D). Most of the visceral shell surface is represented, excluding the posteriormost part of the carapace (with caudal notch), anteriormost part of the plastron, and the posterior end of the right caudal scute. Most of the posterior right quarter of the plastron is preserved, including the right second abdominal, femoral, anal scute areas, and bases of the caudal processes, as well as the intercaudal scute area, and damaged fragments of the left anal and caudal scute areas. The right bridge is partially preserved, and the damaged fourth inframarginal and a fragment of the ninth marginal scute area can be seen. There are few impressions of sulci between marginals on the surface of the mould in the anterior left and posterior left sections. Other than that, there is no trace of marginals, so their number and shape cannot be determined. The right side of the mould was prepared, thus the acetabu-

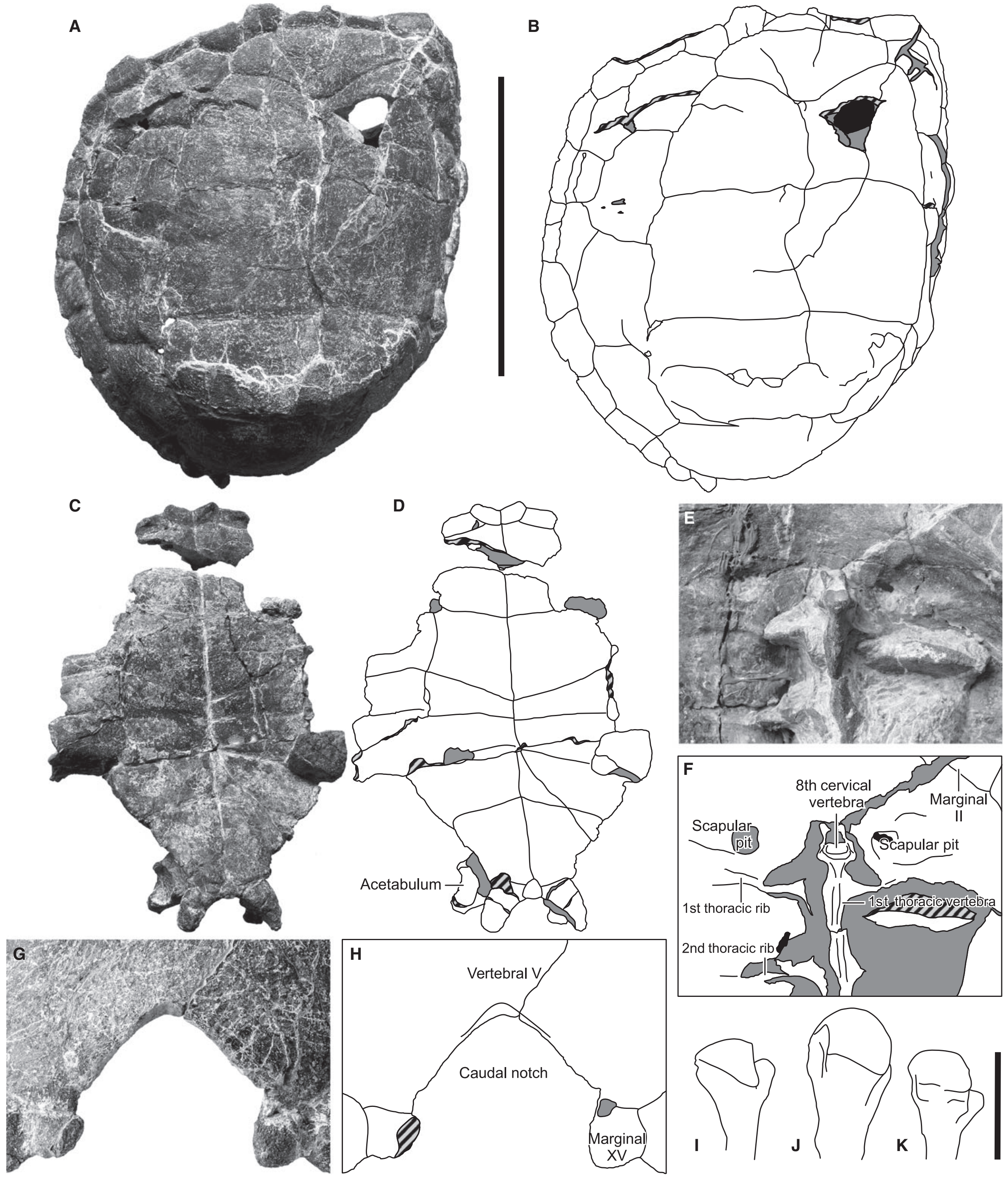

Figure 3. ***Proterochersis porebensis*** **sp. nov.**: A, B, carapace of holotype (ZPAL V.39/48) in dorsal view; C, D, plastron of holotype (ZPAL V.39/48) in ventral view; E, F, anterior part of carapace and vertebral column of ZPAL V.39/72 in ventral view, with the fused last cervical vertebra (note the first thoracic rib parallel with the second, and forming a costal); G, H, caudal notch of the holotype (ZPAL V.39/48) in posterior view; I–K, comparison of the proximal heads of right femur of ***Proterochersis porebensis*** **sp. nov.** (I, ZPAL V.39/48), *Proganochelys quenstedti* (J, SMNS 16980), and *Palaeochersis talampayensis* (K, PULR 68, left-mirrored for easier comparison, based on Sterli *et al.*, 2007) in dorsal view. Scale bars: A–D, 30 cm; I–K, 5 cm; E–H, not drawn to scale.

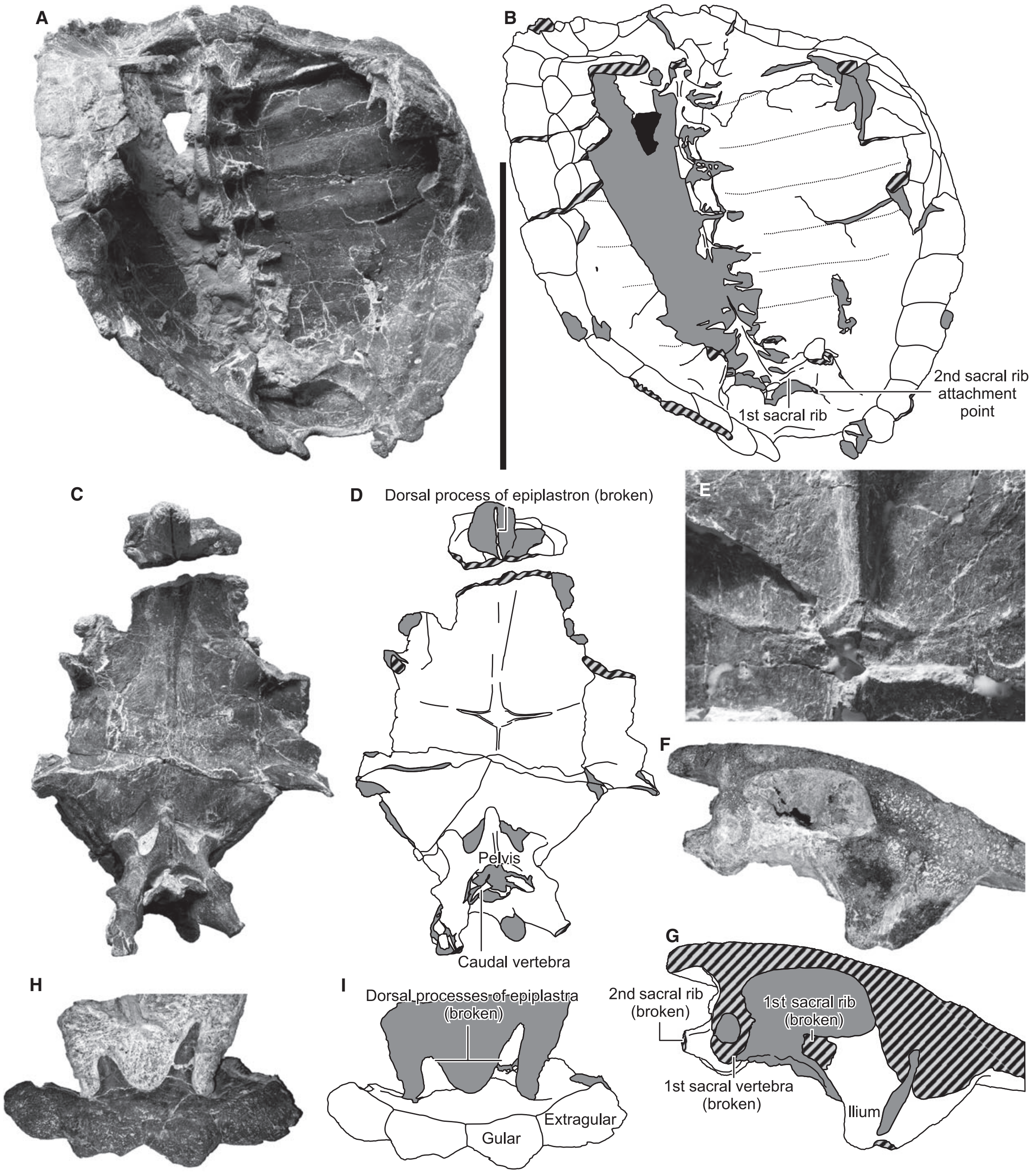

Figure 4. ***Proterochersis porebensis*** **sp. nov.**: A, B, carapace of holotype (ZPAL V.39/48) in ventral view; E, F, plastron of holotype (ZPAL V.39/48) in visceral view, with pelvis attached and caudal vertebra lying at its top; E, caudal end of the posterior process of entoplastron with lateral branches visible; F, G, ZPAL V.39/370 in anterior view, showing a cross section through the carapace and the first sacral vertebra with a visible osseous contact between these elements; H, I, cranial margin of plastron in anterior view. Scale bar: A–D, 30 cm; E–I, not drawn to scale.

lum, ilium, part of the ischium, and lateral pubic process are exposed. Both right sacral ribs, ninth and tenth thoracic rib, and corresponding vertebrae are also visible in ventral view. There are bone fragments remaining on the surface of the mould, where the ischium contacted the carapace and where the

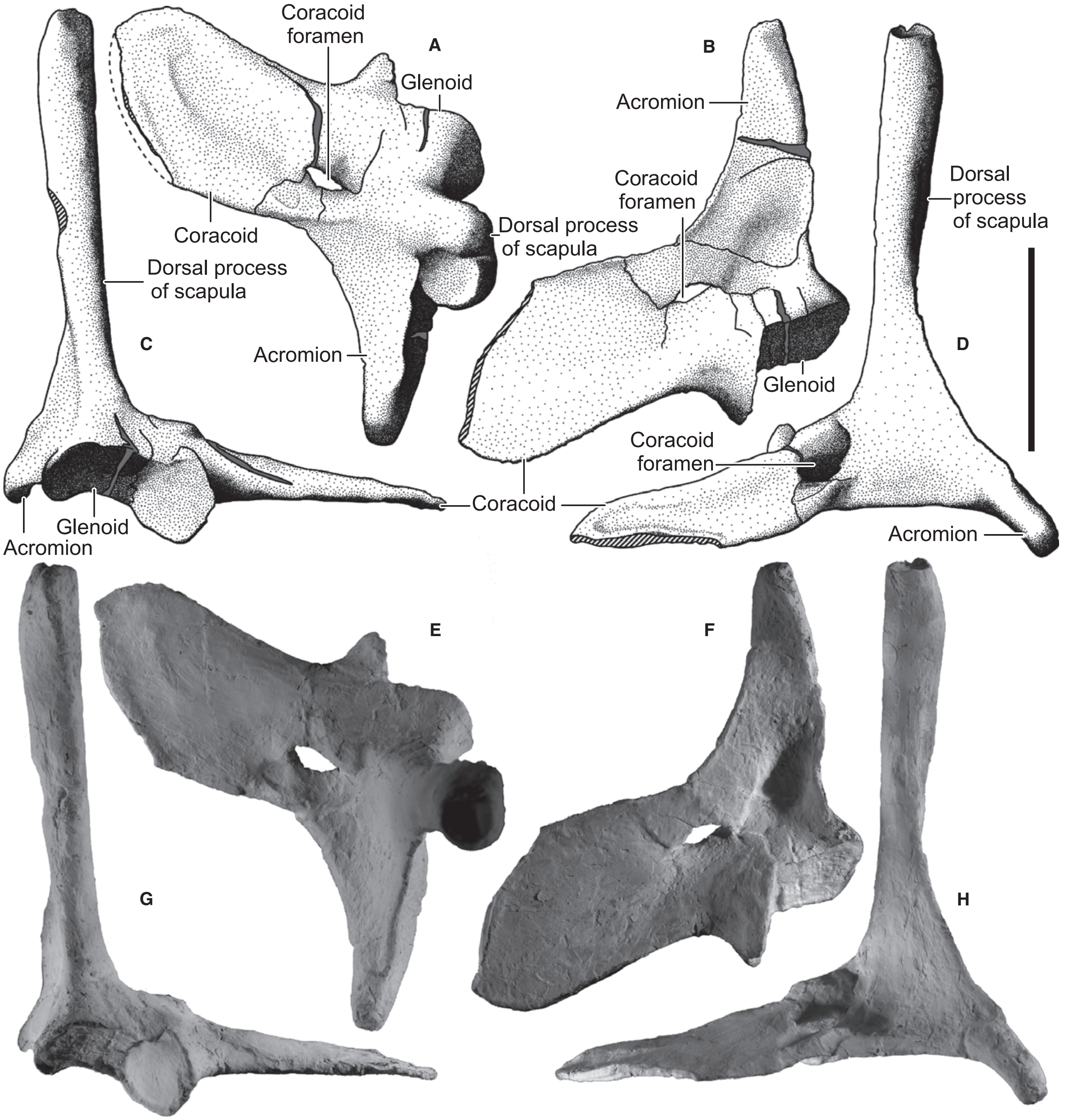

Figure 5. *Proterochersis porebensis* sp. nov., holotype (ZPAL V.39/48), left scapulocoracoid: A, E, dorsal view; B, F, ventral view; C, G, lateral view; D, H, posteromedial view. Scale bar: 5 cm.

left lateral pubic process contacted the plastron. Only sutures between costals are identifiable, but the structures on the visceral surface of the plastron that are associated with sutures are imprinted in the mould. This specimen was illustrated in Stromer (1912), Fraas (1913), and (in part) in Młynarski (1976). We agree with its identity as *Proterochersis robusta*.

SMNS 16442

A specimen referred to *Murrhardtia staeschei* by Karl & Tichy (2000). Found in Murrhardt, Germany. It consists of a damaged anterior part of the carapace (with nuchal bone, first few neurals, parts of first few costals, and possibly a few peripherals), a damaged part of the carapace margin, with a fragment of the anterior part of the bridge, an anterior

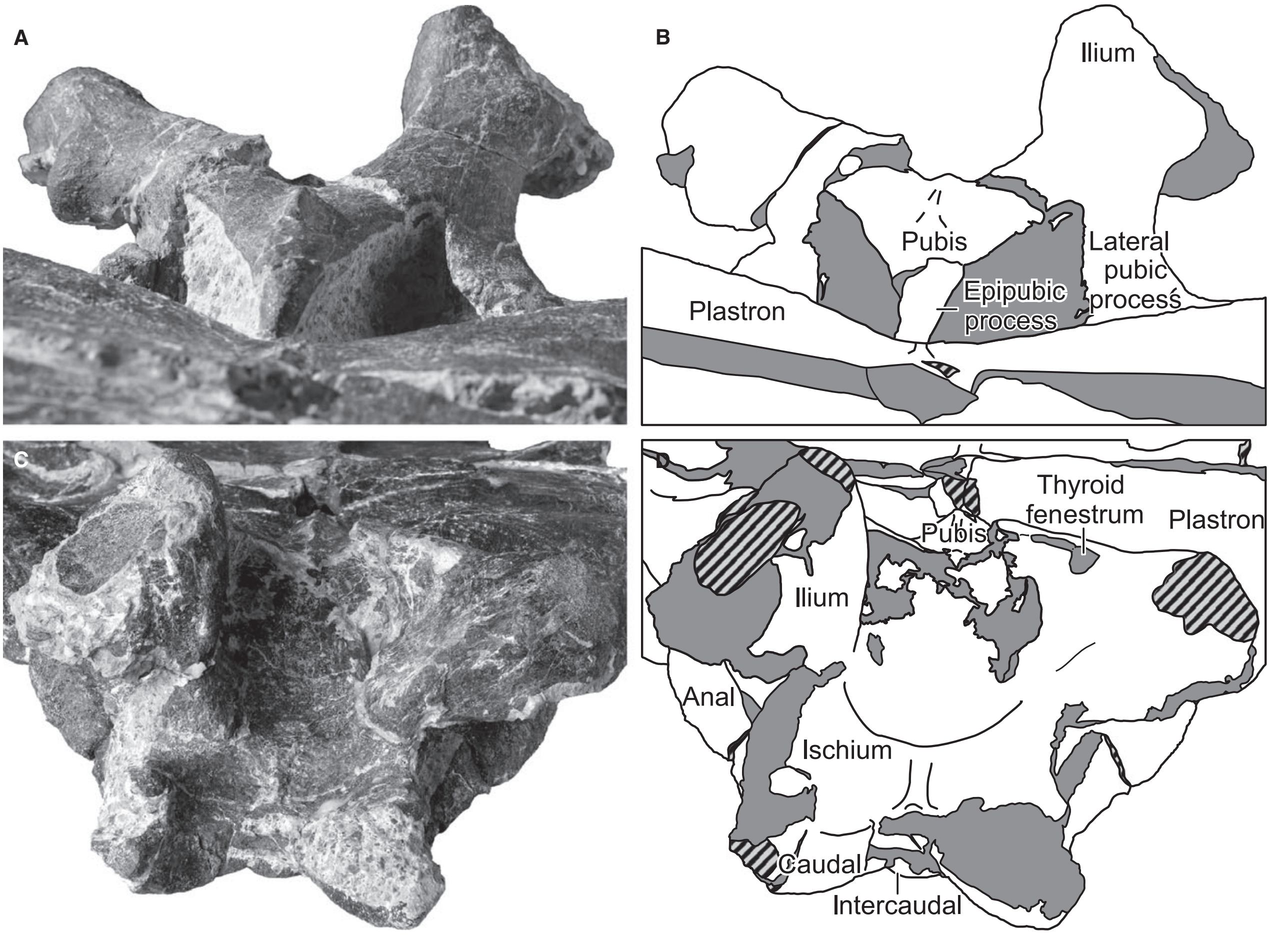

Figure 6. ***Proterochersis porebensis* sp. nov.**, ZPAL V.39/49, pelvis: A, B, in anterior view; C, D, in posterior view.

lobe of the plastron (humeral scute area and entoplastron, with epiplastra seemingly missing), a rock impression of the latter, a posterior lobe of the plastron (area of femorals and anals with a base of the right caudal process), and some difficult to interpret fragments and impressions in the plaster (one of them probably of a marginal sulci). This specimen was illustrated (in part) in de Broin (1984). We identify it as *Proterochersis robusta*.

SMNS 16603

A specimen referred to *Proterochersis* sp. by de Broin (1984). Found near Lorch, Germany. A small specimen, mostly a natural mould of the inside of the shell. There are two fragments of the plastron preserved: part of the right axillary buttress and an anterior part of the plastron. In the latter, right extragular and gular (note that we follow the scute nomenclature proposed by Hutchison & Bramble, 1981; but for discussion see Gaffney, 1990: 138), fragment of the left gular, medial parts of humeral scute areas, and about a half of the posterior process of entoplastron are present. The dorsal processes of epiplastra are broken off, but their impressions are visible on the mould and probably their dorsal ends are embedded inside. A small fragment of the first left costal and a posterior right part of the carapace, with a fragment of the fourth vertebral scute area, whole right side of the fifth vertebral, and fragments of the third and fourth pleural scute areas are preserved. This specimen was illustrated (in part) in de Broin (1984). We identify it as *Proterochersis robusta*.

SMNS 17561

A specimen referred to *Murrhardtia staeschei* by Karl & Tichy (2000). Found in Murrhardt, Germany, in 1934. The best-preserved specimen, virtually complete (Fig. 1). The areas of the left extragular, the last pair of inframarginals, right parts of the third and fourth vertebral, posterior part of the second right pleural, right pleurals III and IV, parts of the right supramarginals, right marginals II–V and ?X–?XII, left third marginal, and posterior part of the right bridge seem to be at least partially restored. Unfortunately, some parts of the shell are expansively covered with plaster, probably because of small superficial damage, effectively obscuring the bone, and the extent of such repairs is sometimes difficult to evaluate. Unfortunately, no sutures are visible. This specimen was illustrated in Gaffney (1986) and Karl & Tichy (2000), and the line drawing of the shell of *Proterochersis robusta* that was first presented in Gaffney (1990), and has frequently been used since, is based mainly on that specimen. We concur with Gaffney (1986, 1990) in his identification of this specimen as *Proterochersis robusta*.

SMNS 17757

A specimen referred to *Proterochersis robusta* by Joyce *et al.* (2013). Found near Rudersberg, Germany. It consists of a natural mould of the visceral surface of costals, with bone tissue remaining in some sections (fragments of the areas of the cervical scute and vertebrals I–V, left marginals I–IV, and fragments of right marginals ?XI–?XII, most of the first and fragment of the second left pleural, whole fourth right pleural, fragment of the first left supramarginal), and most of the plastron (excluding the anteriormost and posteriormost parts, and the bridge region; however, on the right side at least one inframarginal is preserved; Figs 9, 10I, L, M). The specimen was recently prepared, exposing parts of the seventh and eighth cervical vertebrae, the last pair of cervical ribs, two first thoracic vertebrae, with part of the first pair of thoracic ribs, two scapulocoracoids, most of the pelvis, both sacral vertebrae, with both pairs of sacral ribs, and two first (and the right rib of the third) caudal vertebrae (Joyce *et al.*, 2013). This specimen is asymmetrical as a result of compaction, with its left side flatter than the right side. Although some cracks are visible on the surface of the bone, it is difficult to say whether any of them is reflecting the actual layout of sutures, and the poor condition of some parts of the bone make it difficult to interpret whether the exhibited surface is natural or damaged. This specimen was illustrated (in part) in Joyce, 2013. Here we interpret it as a new taxon, *Keuperotesta limendorsa* gen. et sp. nov.

CSMM uncat

The holotype of *Murrhardtia staeschei* Karl & Tichy, 2000. Found in Mettelberg Quarry, near Murrhardt, Germany. This specimen is quite complete, and most of the plastron as well as a large part of the carapace are preserved. The plastron lacks only a part of the right side of the anterior lobe, with areas of right extragular and most of the right gular, most of the right bridge (only the axillary buttress is present), most of the left extragular, and a part of the left bridge (the inframarginals are not preserved, with the exception of a fragment of the second left inframarginal scute area). Caudals and intercaudal scute area are present, but their ventral surface is weathered. The carapace is more damaged. All five vertebral scutes are present, but only the fourth vertebral area is preserved intact. The areas of vertebrals I and V lack small fragments, more than a half of the area of vertebral III is preserved, and less than a third of the second vertebral area is present. There are parts of the areas of the cervical scute and the second, third, and possibly first left marginals preserved, but their outer rim is broken. Two last right marginal areas are present. There is no bone on the flanks of this specimen, so no pleurals (with the exception of a small fragment of the last pleural), supramarginals, and marginals can be observed in that region. No sutures are visible. This specimen was illustrated in Wild (1987) and Karl & Tichy (2000). We identify it as *Proterochersis robusta*.

ZPAL V.39/34

A specimen referred to cf. *Proterochersis* by Sulej *et al.* (2012). Found in Poreba, Poland. It is a nearly complete and mostly well-preserved shell (Fig. 2C, E). Some parts are nonetheless severely damaged as a result of breakage, compaction, and errors made during *in situ* retrieval from the large block of conglomerate in which the fossil was embedded. The left side of the specimen was prepared, exposing a broken, but otherwise complete pelvis. No sutures are identifiable. This specimen was illustrated in Sulej *et al.* (2012). Here we assign it to *Proterochersis porebensis* sp. nov.

ZPAL V.39/48

Previously undescribed and never illustrated specimen. Found in Poreba, Poland. A complete shell with only a small fragment of the second vertebral scute area, most of the right dorsal process of epiplastron, and some small elements from the bridge area, with the second pair of the sacral ribs missing (Figs 3A–D, G, H, I, 4A–D, H, I). The shell was prepared from the outside and from the inside, revealing the pelvis, the somewhat broken and misplaced but complete row of the thoracic vertebrae, both sacral vertebrae, left scapulocoracoid, and right, slightly damaged femur. Unfortunately, the shell is slightly distorted and broken, which obscures its geometry. The state of preservation is good, but the bone surface is marked with numerous small cracks and fissures. Therefore it is difficult to trace any sutures. It appears, however, that there are some definite sutures visible between the costals and in the posterior part of the plastron. Here we assign it to *Proterochersis porebensis* sp. nov.

ZPAL V.39/49

Previously undescribed and never illustrated specimen. Found in Poreba, Poland. Another nearly complete, yet vertically cracked shell. It lacks some small fragments of the carapace, but unsymmetrically, so every element of the shell is represented entirely at least once. Almost the whole thoracic vertebral column (most likely vertebrals I–VII and X) is preserved, but most of it is broken off from the carapace and moved from the original position. Dorsal processes of epiplastra are broken, with only the bases preserved. This shell was also prepared from the outside and from the inside, and the state of preservation is identical as in ZPAL V.39/48. Here we assign it to *Proterochersis porebensis* sp. nov.

ZPAL V.39/72

Previously undescribed and never illustrated specimen. Found in Poreba, Poland. A mostly complete carapace with parts of the fourth and fifth vertebral scute areas missing. On the ventral surface the last cervical and the first, the second and the anterior part of the third thoracic vertebra, as well as the left ilium, are preserved. The carapace was associated with one proximal caudal vertebra.

ZPAL V.39/370

Previously undescribed and never illustrated specimen. Found in Poreba, Poland. A part of the posterior left section of a carapace with most of the dorsal part of the left ilium, the posterior part of the first and the complete second sacral vertebra, short fragment of the first sacral rib and complete second sacral rib preserved. The first sacral vertebra is broken and the contact between its neural process and the carapace is clearly visible.

PHYLOGENETIC ANALYSIS

A phylogenetic analysis was performed using TNT 1.1 (Goloboff, Farris & Nixon, 2008). The matrix created by Gaffney *et al.* (2007) was used, with updates by Joyce *et al.* (2013; for the full character list and matrix, see Appendix S1). *Proterochersis porebensis* sp. nov. and *Keuperotesta limendorsa* gen. et sp. nov. were added, and characters for *Proterochersis robusta* were updated based on personal observations of German and Polish specimens.

Modifications were introduced to characters 83 (coracoid columnar: 0, no, flat rectangular; 1, yes, at least at the base; 2, no, flat bee wing-shaped), 87 (first thoracic rib: 0, extends, nearly to peripherals but does not form a costal; 1, extends less than halfway across costal; 2, well developed, forms a costal plate), 99 (dorsal process on epiplastron: 0, large, reaches carapace; 1, smaller than length of epiplastron; 2, absent; 3, larger than length of epiplastron, does not reach the carapace), 103 (mesoplastra: 0, two pairs present; 1, one pair present; 2, absent; 3, one pair present, but without contact at the midline), and 108 (abdominal scutes relative to midline: 0, one pair present, meets on midline; 1, one pair present, withdrawn from midline; 2, two pairs present, meet on midline). Ten new characters were introduced, covering caudal notch (112: 0, absent; 1, large, inverted, U–shaped; 2, large, inverted, V–shaped; 3, small, with sinuous edge), thoracic rib number (113: 0, more than ten; 1, nine pairs; 2, ten pairs), number of costals (114: 0, eight pairs; 1, ten pairs; 2, nine pairs), fusion of ribs into carapace (115: 0, ribs not fused; 1, ribs fused), presence of peripheral bones (116: 0, absent; 1, present), presence of marginal teeth (117: 0, present; 1, absent), angle between coracoid and acromion (118: 0, ≤130°; 1, >130°), shape of the articular surface of femoral head in dorsal view (119: 0, ancestral amniotic condition, articular surface of femoral head poorly differentiated dorsally; 1, articular surface triangular in dorsal view; 2, articular surface rectangular or oval in dorsal view), and contact of the neural spines of sacral vertebrae with carapace (120: 0, ossified; 1, chondral, ligamentous, or none).

Each taxon, excluding *Proterochersis* spp., *Keuperotesta limendorsa* gen. et sp. nov., and *Proganochelys quenstedti*, which were personally studied by the first author, was scored based on the literature: *Australochelys* (Gaffney & Kitching, 1994, 1995); *Dracochelys* (Gaffney & Ye, 1992; Brinkman, 2001); *Kayentachelys* (Gaffney *et al.*, 1987; Sterli & Joyce, 2007; Gaffney & Jenkins, 2010); *Meiolania* (Gaffney, 1983, 1985, 1996); *Odontochelys semitestacea* (Li *et al.*, 2008; Lyson *et al.*, 2014); *Ordosemys* (Brinkman & Wu, 1999; Tong, Ji & Ji, 2004); *Palaeochersis* (Rougier *et al.*, 1995; Sterli *et al.*, 2007); *Solnhofia* (Gaffney, 1975a; Joyce, 2000); *Xinjiangchelys* (Kaznyshkin, Nalbandyan & Nesov, 1990; Peng & Brinkman, 1993; Matzke *et al.*, 2004; Brinkman *et al.*, 2013); *Platychelys* (Wagner, 1853; Bräm, 1965; Cadena & Joyce, 2015); *Ninjemys* (Gaffney, 1992); Pleurodira (Gaffney *et al.*, 2006, 2011); *Kallokibotion* (Nopcsa, 1923b; Gaffney & Meylan, 1992); *Otwayemys* (Gaffney *et al.*, 1998); *Judithemys* (Parham & Hutchison, 2003); *Chubutemys* (Gaffney *et al.*, 2007; Sterli, de la Fuente & Umazano, 2013a); *Sinemys* (Brinkman, 1993; Tong & Brinkman, 2013); *Niolamia* (Sterli & de la Fuente, 2011); *Mongolochelys* (Khosatzky, 1997; Suzuki & Chinzorig, 2010); Pleurosternidae (Hay, 1908; Evans & Kemp, 1975; Gaffney, 1979; Milner, 2004); Baenidae (Gaffney & Hiatt, 1971; Gaffney, 1972, 1982; Archibald & Hutchison, 1979; Brinkman & Nicholls, 1993; Brinkman, 2003; Lyson & Joyce, 2009, 2010; Lyson *et al.*, 2011); Plesiochelyidae (Bräm, 1965; Gaffney, 1975b, 1976; Lapparent de Broin, 1996; Anquetin, Deschamps & Claude, 2014; Pérez-García, 2014). *Hangaiemys* (Sukhanov & Narmandakh, 1974); Chelydridae (Whetstone, 1978; Hutchison, 2004); Chelonioidea (Zangerl, 1953, 1958); Testudinoidea (Joyce & Bell, 2004; Danilov, Claude & Sukhanov, 2012); Trionychoidea (Meylan, 1987; Meylan & Gaffney, 1989; Tong, Li & Ouyang, 2014). Additionally, we also referred to Młynarski (1969, 1976), Sukhanov (2000), and Danilov (2005). The suprageneric taxa were scored with the most common (and most likely plesiomorphic) character states. Scorings for some taxa were corrected (see Appendix S1).

A traditional search was performed (default settings with 100 000 replications, and with 1000 trees saved per replication) and a majority rule (50%) consensus cladogram was created. Jacknife frequency difference values and bootstrap frequency difference values were calculated for 10 000 replicates.

REASSESMENT OF CONTROVERSIAL TAXA

PROTEROCHERSIS INTERMEDIA

Both *Proterochersis robusta* and *Proterochersis intermedia* were named in the same paper by Fraas (1913) on the basis of turtle material from the same strata (Norian, Löwenstein Formation) and region (area around Stuttgart) of Germany. According to Fraas (1913), *Proterochersis intermedia* differs from *Proterochersis robusta* in shell curvature and plastron thickness. Such discrimination is problematic for two reasons. Firstly, Fraas (1913) had only two specimens at his disposal, thus having no insight into ontogenetic and intraspecific variability. Secondly, the holotype of *Proterochersis intermedia* is fragmentary, possibly compacted, and its overall shape most likely changed during restoration (see description of SMNS 11396 in Material and methods). Additionally, our studies on turtle material from the lower Löwenstein Formation demonstrate that the height and curvature of the shells may vary, possibly ontogenetically, taphonomically, or diagenetically, not only between several otherwise morphologically identical specimens, but also between two sides of the same specimen (SMNS 17757). The putative fontanelles between rib endings of *Proterochersis intermedia* were considered by Fraas to be juvenile characteristics and specific at the same time, whereas we consider them to be artefacts of preservation. The rib tips, which seem to protrude from the distal ends of the first two preserved costal plates (thus bordering 'fontanelles') are in fact painted plaster, as shown by the fracture in one of them. No actual bone material indicates their existence. Even if any real bone fragments are embedded in this part, the interpretation of their nature is impossible, but most likely they originated from breakage or weathering. Although the internal mould might have been informative in that case, the condition cannot be inferred from it because the corresponding part is also entirely reconstructed. The only comparable diagnostic part, the fragment of plastron, is structurally identical, with the exception of thickness. Changes in thickness of plastron may be attributed to intraspecific diversity, age of the specimens, or sexual dimorphism. Bearing this in mind, the validity of *Proterochersis intermedia* is doubtful. Therefore, there is no basis to distinguish between *Proterochersis robusta* and *Proterochersis intermedia*, and the latter should be synonymized with the former.

MURRHARDTIA STAESCHEI

Murrhardtia staeschei, described in 2000 by Karl & Tichy, is another ambiguous taxon. Karl & Tichy (2000: 66) summarized all of the similarities and differences between the seven Triassic and Jurassic turtle taxa (including *Proterochersis* and *Murhardtia*) by listing 17 statements (characters) in a table. Eight of the nine characters proposed by the authors as diagnosing *Murrhardtia staeschei* from *Proterochersis robusta* are actually absent in the type *Proterochersis robusta* (and *Proterochersis intermedia*, herein treated as synonymous) material (Fig. 1), so the comparison is not meaningful. As correctly noted by Gaffney *et al.* (2006), most of these characters seem to be taken from the illustration created by Fraas (1913). In that drawing Fraas (purely hypothetically) reconstructed the parts that were absent in the fossil material available to him (i.e. the anterior lobe of the plastron and the carapacial rim) as a generalized turtle, and did not indicate which areas of his reconstruction are actually based on fossils. Even though in the text it was clearly stated which fragments were missing, and the holotypes of both *Proterochersis robusta* and *Proterochersis intermedia* are in the SMNS collection, which was studied by Karl & Tichy, the autors appear to have treated Fraas' reconstruction as the only base for comparisons. The characters used by Karl & Tichy (2000: 66) are listed as follows.

A pair of mesoplastra present (character 3)

In the third column of their table, Karl & Tichy (2000) stated that *Murrhardtia* is diagnosed by a pair of mesoplastra (unlike *Proterochersis*), but in the eighth column ('two pairs of mesoplastra present') both *Proterochersis* and *Murrhardtia* are listed as having two pairs of mesoplastra. In fact, it is impossible to infer the number of the mesoplastra in any of the three specimens referred to in that paper, and although Karl & Tichy indicate that they analysed more material from SMNS, they fail to refer to it using catalogue numbers.

Complete separation of epiplastra by entoplastron (character 4)
Karl and Tichy stated that epiplastra in *Murrhardtia* are completely separated by entoplastron, and that in *Proterochersis* they are not separated. Fraas illustrated the epiplastra of *Proterochersis* contacting each other in front of the entoplastron (a common condition in modern turtles), but this part is missing from the original fossil material.

Distinct caudal notch present (character 5)
A distinct caudal notch was reported to be present in *Murrhardtia* and absent in *Proterochersis* by Karl and Tichy. That part is missing in the original material for *Proterochersis*.

Inframarginals present (character 9)
Karl and Tichy stated that inframarginals are present in *Murrhardtia* and absent in *Proterochersis*. It is the only character that can actually be compared in *Proterochersis* and *Murrhardtia* material. Unfortunately, it is wrongly interpreted – in the holotype of *Proterochersis robusta* the outline of the last inframarginal is visible, albeit with surface damage (Fig. 10G, J).

Infraplastrals present (character 10)
Karl and Tichy stated that infraplastrals are present in *Murrhardtia* but absent in *Proterochersis*. In fact they refer to abdominals, as they incorrectly interpret the gulars (not present in the original material; note that Karl & Tichy does not follow the scute terminology proposed by Hutchison & Bramble, 1981; so their intergulars and gulars are gulars and extragulars of Hutchison & Bramble, 1981; respectively) portrayed by Fraas (1913) as humerals. Nonetheless, type specimens of *Proterochersis robusta* and *Proterochersis intermedia* have abdominals as discussed for *Murrhardtia* material.

Gulars separated by two intergulars (character 11)
Karl and Tichy state that gulars (extragulars *sensu* Hutchison & Bramble, 1981) of *Murrhardtia* are separated by paired intergulars (gulars *sensu* Hutchison & Bramble, 1981), and that this is not the case in *Proterochersis*. Once again this character is not applicable to *Proterochersis* because of the absence of that part in the fossil material, and is only based on the hypothetical reconstruction by Fraas.

Nuchalzack may be formed (character 12)
The nuchalzack is stated as present in *Murrhardtia* and absent in *Proterochersis*. An enigmatic character, not appropriately explained in the text. Illustrated as a triangular process on the cervical scute, it is actually absent in any of the shells. A similar structure is visible in the CSMM specimen of *Murrhardtia*, but the anterior margin of its cervical scute is clearly broken off, so the protruding prickle is just a rough edge of the break (but this specimen is rather unique in having its cervical scute bowed dorsally). Karl & Tichy pinpoint SMNS 16442 as having the strongest 'nuchalzack', but its cervical scute is virtually the same as that of SMNS 17561, which is supposed to be weakly expressed. Nonetheless, this character is not applicable to *Proterochersis*.

Only one unpaired gular present (character 14)
Karl and Tichy state that only one unpaired gular is present in *Proterochersis*, whereas two are present in *Murrhardtia*. As already mentioned, characters concerning that part are not applicable to *Proterochersis*.

Nuchal bone no wider than peripherals (character 15)
Nuchal bone being no wider than peripherals was stated as present in *Proterochersis*, and a wider nuchal was suggested for *Murrhardtia*. There is no trace of nuchal or peripheral sutures on the *Proterochersis robusta* or the *Proterochersis intermedia* holotypes, and therefore this character is not applicable. Unlike the other characters this was not taken from the illustration made by Fraas, and no source is given.

In sum, none of the characters used by Karl and Tichy to discriminate between *Proterochersis* and *Murrhardtia* is valid, and therefore we agree with the conclusion of Gaffney *et al.* (2006) that *Murrhardtia staeschei* should be considered a younger synonym of *Proterochersis robusta*.

SYSTEMATIC PALAEONTOLOGY

ORDER TESTUDINATA KLEIN, 1760
FAMILY PROTEROCHERSIDAE NOPCSA, 1923A
TYPE GENUS *PROTEROCHERSIS* FRAAS, 1913

Occurrence and distribution. Norian of Germany and Poland.
Diagnosis. Five vertebrals wider than long, the first semicircular anteriorly, with rounded posterior process invading the medial anterior area of the second vertebral; supramarginals and inframarginals present; dorsal process of epiplastra large, not

contacting the carapace; pelvis sutured to carapace and plastron; posterior process of ilium flattened dorsoventrally, fully attached to carapace; epipubic process long. More advanced than *Odontochelys semitestacea* in having fully developed carapace with carapacial rim elements (peripherals, nuchal bone) and well-developed costals contacting each other suturally. Less advanced than *Proganochelys quenstedti* in having two pairs of mesoplastra contacting at the midline, two pairs of abdominal scutes contacting at the midline and, a bee wing-shaped coracoid.
Included genera. *Proterochersis* Fraas, 1913; *Keuperotesta* gen. nov.

PROTEROCHERSIS FRAAS, 1913

Proterochersys Fraas (nomen nudum): Zittel, 1911: 247.
Proterochersis Fraas, 1913: 13, figs 1–6.
Proterochersis Fraas, 1913: Wild, 1987: 33, fig. 22.
Murrhardtia Karl & Tichy, 2000: 57.
Murrhardtia Karl & Tichy, 2005: Danilov, 2005: 350.
Murrhardtia Karl & Tichy, 2000: Karl, 2012: 13, fig. 4.

Occurrence and distribution: Norian of Germany and Poland.

Diagnosis: Three pairs of supramarginals present; caudal notch present; paired extragular scutes divided by paired gulars; paired caudal scutes and the anal scute present in the posterior part of the plastron; sacral vertebra fused or sutured to carapace. Less advanced than *Proganochelys quenstedti* in having the first pair of ribs forming fully developed costals. Differing from *Keuperotesta* in: dorsal surface of the carapace almost even; the last cervical vertebra co-ossified to the carapace and thoracic vertebrae; anterior margin of the carapace, at most, moderately serrated; marginal series starting anterolaterally in relation to the cervical scute, contacting it widely; first vertebral scute contacting the first pleural anteromedially, rather than posteromedially.
Type species. *Proterochersis robusta* Fraas, 1913.
Included species. *Proterochersis porebensis* sp. nov.

PROTEROCHERSIS ROBUSTA FRAAS, 1913
(FIGS 1, 10A–H, J, K, N)

Proterochersys nov. spec. Fraas (nomen nudum): Stromer, 1912: 119, fig. 116.
Proterochersis robusta Fraas, 1913: 26, fig. 7.
Proterochersis intermedia Fraas, 1913: 27, fig. 8.
Proterochersis intermedia Fraas, 1913: Młynarski, 1969, 1976: 49.
Proterochersis intermedia Fraas, 1913: Młynarski, 1976: 23, fig. 22.5.
Proterochersis sp. Fraas, 1913: de Broin, 1984: 88, pl. 1, figs 4, 5.
Proterochersis robustum Fraas, 1913: Gaffney, 1986: 184 (lapsus calami).
Proterochersis robusta Fraas, 1913: Wild, 1987: 33, fig. 21.
Proterochersis robustum Fraas, 1913: Gaffney, Meylan & Wyss, 1991: 3164 (lapsus calami).
Murrhardtia staeschei Karl & Tichy, 2000: 57, figs 1, 2A, pl. 1–5, app. 1 fig. 3.
Murrhardtia staeschei Karl & Tichy, 2000: Karl, 2012: 13, fig. 3.

Occurrence and distribution: Lower Löwenstein Formation (?lower or middle Norian) around Stuttgart, Baden-Württemberg, Germany.

Diagnosis: Differs from *Proterochersis porebensis* sp. nov. in caudal notch semicircular, anterior margin of the carapace slightly serrated or undulated, shell high.

Holotype: SMNS 12777.

Carapace
Proterochersis robusta was a middle-sized and high-domed turtle. Its carapace was covered by a wide but short cervical scute, five vertebrals, four pairs of pleurals, three pairs of supramarginals, and 14 pairs of marginals. The first vertebral is semi-oval, wider than long, and mediocaudally forms a rounded projection, invading the area of the second vertebral. Vertebrals III and IV are wide, roughly trapezoid, and have straight posterior and anterior margins. The fifth vertebral forms the posterior edge of the carapace, and posteromedially has a semicircular embayment (caudal or pygal notch). Three supramarginals lie in a row between pleurals II–IV) and marginals V–IX. The pleurals and supramarginals are slightly domed, but the remaining scutes are rather flat. Most of the sulci are sinuous and slight radial ridges can be seen on the scutes, similarly as in *Proganochelys quenstedti*. Some specimens have additional characteristics to the carapace (medial grooves or ridges, growth lines, wavy surface), but the individual variations and scute pathologies will be discussed in future papers.

Plastron
The plastron was covered by ten sets of scutes, nine of which are paired: extragulars, gulars, humerals, pectorals, two sets of abdominals (infraplastralia of

Karl & Tichy, 2000), femorals (erroneously called abdominalia by Karl & Tichy, 2000), anals (erroneously called femoralia by Karl & Tichy, 2000), and caudals (erroneously called analia by Karl & Tichy, 2000). The unpaired element, the intercaudal (interanale of Karl & Tichy, 2000), is pentagonal, positioned between the caudals, and slightly protrudes, with its anterior tip between the anals. With the exception of the caudals (and the first abdominal set of SMNS 17561, which appears to be an abnormality of that particular specimen), each of the paired elements contacts its counterpart at the midline. Additionally, there are four pairs of small inframarginals and a pair of axillary scutes (visible on SMNS 17561). The entoplastron lies between the epiplastra, and it projects a long posterior process along the visceral surface of the plastron. Each epiplastron forms a dorsal process. Their exact shape and length are unknown, but unlike in *Palaeochersis talampayensis* Sterli *et al.*, 2007 and *Proganochelys quenstedti*, they did not contact the carapace. The central part of the plastron is concave, similarly as in males of some modern turtles (Leuteritz & Gantz, 2013). There are two pairs of mesoplastra. The bridge region is built by the hyoplastra and mesoplastra, and the visceral surface of each of these elements is slightly convex, such that the corresponding sutures lie in shallow depressions. This allows for the identification of these bones even if the sutures themselves are not visible.

***PROTEROCHERSIS POREBENSIS* SP. NOV.**
(FIGS 2, 3A–I, 4–8, 11B)

cf. *Proterochersis* Fraas, 1913: Sulej *et al.*, 2012: 1034, fig. 4.
cf. *Proterochersis robusta* Fraas, 1913: Niedźwiedzki *et al.*, 2014: 1123.

Occurrence and distribution: Zbaszynek Beds (subzone IVb of the *Corollina meyeriana* zone, middle–upper Norian) in Poreba, Silesian Voivodeship, Poland.

Etymology: From Poreba, the place of discovery.

Diagnosis: Articular surface of femoral head triangular in dorsal view. Differing from *Proterochersis robusta* in caudal notch triangular, anterior margin of the carapace nearly straight, anterior edge of the third marginal only slightly rounded, and lower shell. Differing from *Keuperotesta limendorsa* gen. et sp. nov. in acromion and coracoid forming an angle of ~120°.

Holotype: ZPAL V.39/48.

Paratypes: ZPAL V.39/34, ZPAL V.39/49, ZPAL V.39/72, ZPAL V.39/370.

There are two shell morphotypes known to date from Poreba (Fig. 2). One of them, represented by ZPAL V.39/34, was preliminarily described and reconstructed by Sulej *et al.* (2012). Despite its overall similarity to *Proterochersis robusta*, and because of its somewhat different morphology (especially when it comes to peripheral elements of the carapace and plastron), the exact taxonomical status of this specimen was left undecided. The second morphotype, represented by previously undescribed specimens (among others ZPAL V.39/48, the holotype of *Proterochersis porebensis* sp. nov., ZPAL V.39/49, and ZPAL V.39/72, all described herein), is much more similar to *Proterochersis robusta*.

Carapace and vertebrae

The composition of the shell is almost identical to that of *Proterochersis robusta* (SMNS 17561 and others). There are five vertebrals, four pairs of pleurals, and three pairs of supramarginals; the marginal count is 14 for ZPAL V.39/49 (the same as in SMNS 17561) and 15 for ZPAL V.39/48 (Fig. 2A, B). The anterior marginals have nearly straight outer borders (with the exception of the third one, which is gently rounded), so the anterior rim of the carapace is smooth, in contrast with the slightly serrated condition found in *Proterochersis robusta*. Sulci are usually sinuous and radial ridges are present. There is some variability between ZPAL V.39/48 and ZPAL V.39/49 (as well as the other specimens from Poland and Germany) in the shape and position of some scutes, but this will be discussed in future papers.

The last cervical vertebra is fused with (or sutured to) the first thoracic vertebra, and with the carapace (Fig. 3E, F). There are ten pairs of thoracic ribs, with each apparently forming ten fully developed costals (Figs 2F, 4A, B). The first pair of ribs is different from the others because it forms a distinct ridge on the visceral side of the costal (similar to that of *Proganochelys quenstedti*, but less pronounced; its prominence differs between specimens), but (unlike *Proganochelys quenstedti*) it is roughly parallel with the second pair, and there is what appears to be a clear suture between the corresponding costals. The intercostal sutures, similarly as in *Proganochelys quenstedti*, form long, shallow, and narrow grooves; Gaffney (1990) interpreted them instead as being vascular or nerve imprints, because of their lack of interdigitation. Numerous isolated, disarticulated costals found in Poreba indicate, however, that the intercostal sutures in most cases are indeed straight and longitudinal, and not interdigitated. On some costals there is a second groove, lying along the

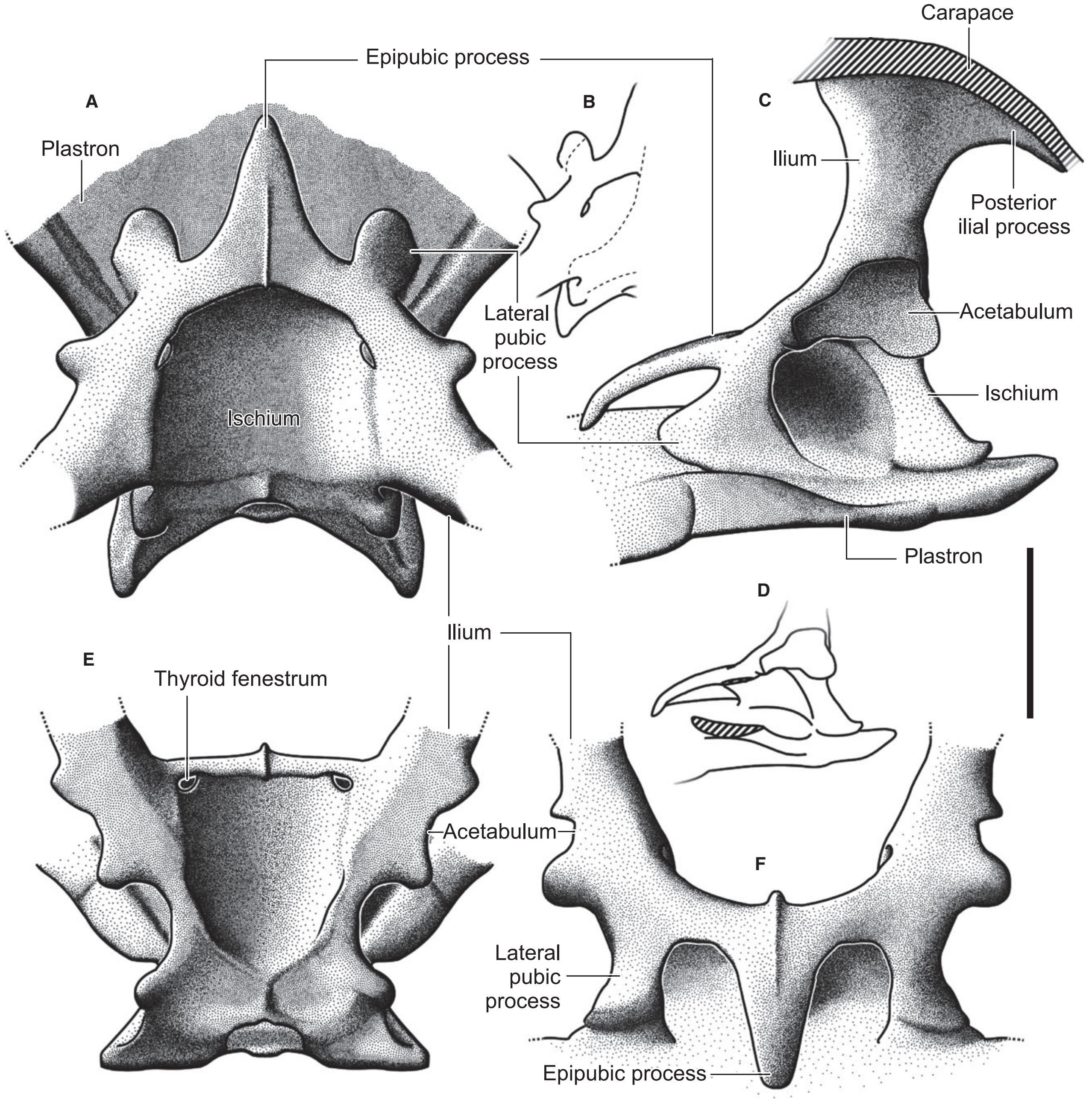

Figure 7. ***Proterochersis porebensis*** **sp. nov.**, reconstruction of pelvis, based on ZPAL V.39/48 (holotype) and ZPAL V.39/49: A, dorsal view; B, outline of the contact between the pelvis and plastron (dotted) in dorsal view; C, lateral left view; D, lateral left view with lateral pubic process removed, showing the ventral pubic process contacting the plastron; E, dorsoposterior view; F, anterior view. Dorsal part of ilium and carapace removed for clarity in all except (C). Scale bar: 10 cm.

suture, possibly where the nerves or vessels were. In any case, even if the grooves seen on the articulated carapaces are not sutures themselves, both of these structures are close to each other and, as concluded by Gaffney (1990), the grooves are at least a good approximation of the sutural positions. The distal tip of the first thoracic rib is visible, yet it is not entirely free, but articulates the carapace with its anterior surface, and is probably sutured. The sutures between bones forming the posterior part of the carapace are not visible, but each of the three last ribs independently reaches the carapace and they do not

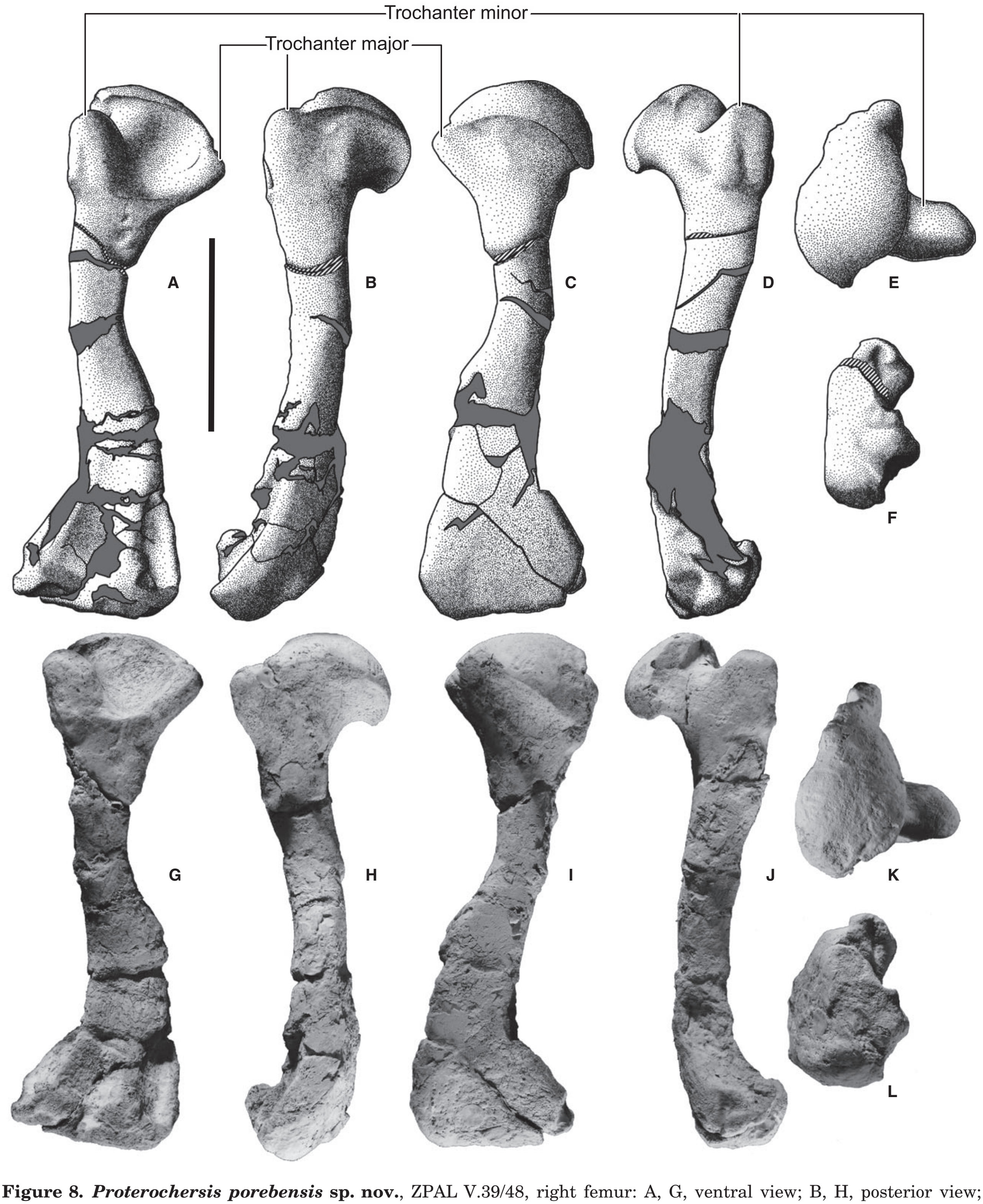

Figure 8. ***Proterochersis porebensis* sp. nov.**, ZPAL V.39/48, right femur: A, G, ventral view; B, H, posterior view; C, I, dorsal view; D, J, anterior view; E, K, proximal view; F, L, distal view. Post-mortem breakage of the specimen and relative relocation of bone fragments resulted in torsion, increasing the angle at which the proximal head is set in relation to the shaft. Scale bar: 5 cm.

meet with each other, so, similarly as in other Late Triassic turtles, each one of them probably forms its own costal as well.

Plastron

The plastron composition does not differ from that of *Proterochersis robusta*, with two pairs of abdominal scutes and an additional three scutes at the caudal end (Figs 2D, E, 3C, D). The dorsal processes of epiplastra (Fig. 4C, D, H, I) are relatively large (the preserved broken process of ZPAL V.39/48 is at least 6 cm long), very thin dorsally (dorsal end of the preserved part has a circumference of 2 mm and is circular in cross section), and lacks a sutural contact with the carapace. No sutures or any signs of discreteness are visible at the base of the processes in any of the specimens, which favours their interpretation as parts of the epiplastra (Gaffney, 1990; Lyson *et al.*, 2013b) and not the cleithra (Jaekel, 1918; Joyce, Jenkins & Rowe, 2006). The posterior process of the entoplastron is large, reaching as far as the middle portion of the bridge (Figs 2G, 4C, D). Its point of contact with the mesoplastra is peculiar, as it splits into two lateral projections (forming a bow, with ends turning anteriorly and nearly reaching the level of the inframarginals, most likely along the suture) and one posterior projection, disappearing halfway towards the point of contact with the epipubic process. In the middle part of this split and along the bases of the lateral arms there is a slight depression with rough surface (Fig. 4E). This structure is visible as an imprint in *Proterochersis robusta* (SMNS 12777 and SMNS 16603) too, but is absent in *Proganochelys quenstedti* (the posterior process of entoplastron ends blindly instead), possibly because only one pair of mesoplastra is present in that taxon. The hypoplastron–mesoplastron suture in *Proganochelys quenstedti* is most probably bowed also, however, as seen in SMNS 17203.

Scapulocoracoid

The scapular process (Fig. 5) is rod-like, almost straight, and set at around 100° to the acromion. In its dorsal part it is tear-shaped in cross section, with a rounded ridge turned lateroposteriorly, and gradually changes to oval in the middle part. At approximately one-third of its height a ridge spans from the scapular process to the acromion. The acromion is relatively long and triangular at its base, projecting three distinct ridges: one towards the scapular process, one towards the glenoid, and one linking it with the medial edge of the coracoid. The glenoid is N–shaped. The coracoid is bee wing-shaped (with the lateral edge straight or slightly concave, the posterior tip rounded, and the medial edge markedly convex), plate-like, thicker near the glenoid, and forms an angle with the acromion of around 120°. Its dorsal surface is wavy, unlike any other Triassic turtle, possibly being imprinted by some soft tissues. A small part of its posteromedial rim is broken, but a comparison with SMNS 17757 and IVPP V15653 as well as the waves on the dorsal surface of the coracoid itself (seemingly parallel with the edge) show that less than 0.5 cm is missing. The coracoid foramen is oval. The dorsal end of the dorsal process of scapula bears a circular pit similar to that in *Proganochelys quenstedti* specimen SMNS 16980. We agree with the statement of Gaffney (1990) that *in vivo* it might have been filled with cartilage, possibly indicating a subadult age of the specimen.

Sacrum and pelvic girdle

There are two sacral vertebra and two pairs of sacral ribs. Unlike in other turtles, the neural spines of the sacral vertebrae are sutured or fused to the visceral surface of the carapace (Fig. 4F, G). This osseous contact is visible in lateral view in ZPAL V.39/49, and in cross section in ZPAL V.39/370. The first sacral rib is strong, triangular in cross section (with flat dorsal surface, apex turned ventrally, and posterior surface slightly concave), and the second pair is weaker and compressed dorsoventrally. At the level of their contact with the ischium a thin medial lamella of bone is present, linking both articular sites and projecting caudally beyond the second sacral rib. Above the lamella there is a noticeable depression (the structure is more pronounced in ZPAL V.39/49 than in ZPAL V.39/48). The pelvis (Figs 6, 7) is fused with the carapace (via ilia) and plastron (in three spots, with lateral pubic processes and with ischium, and possibly also involving posterior part of pubis). Its overall shape is similar to that in *Palaeochersis talampayensis* (as illustrated by Sterli *et al.*, 2007) and *Proganochelys quenstedti* (as illustrated by Gaffney, 1990). Anteriorly it projects a long, triangular epipubic process, which in ZPAL V.39/49 turns downwards at about two-thirds of its length, and contacts a pit on the visceral surface of the plastron. In ZPAL V.39/48 the epipubic process is shorter and does not reach the plastron. There are paired small, ovoid thyroid foramina located laterally just in front of the anterior flange of triangular acetabulum, similar to those in *Odontochelys semitestacea* (as shown by Li *et al.*, 2008). No sutures are visible, but it appears that the ischia have grown together at the midline, and anteriorly they contact the posterior part of the pubis, forming a rounded depression of the posteromedial part of the pelvis, similarly as in *Proganochelys quenstedti* and probably as in *Palaeochersis talampayensis*, but deeper. The ilium is broadened at the point of contact with the carapace, and it is L–shaped in cross section at that point, where it projects two processes – laterally and posteriorly (or slightly lateroposteriorly). The posterior process of ilium is similar to that in *Odontochelys semitestacea* (Li *et al.*, 2008), *Palaeochersis talampayensis* (Sterli *et al.*, 2007), and *Proganochelys quenstedti*; however, its caudal tip is not free, but instead it contacts the ventral surface of the carapace in its entirety. An identical composition seems to be present in *Proterochersis robusta*.

Femur

The femur (Fig. 8) is very similar to that of *Proganochelys quenstedti* and *Palaeochersis talampayensis*, but in its slenderness is more similar to the femur of *Odontochelys semitestacea*. It is 12.5 cm long, broken, and distorted in a few places along the shaft (causing an unnatural angle between its ends), and its distal end is slightly damaged (probably as an effect of the post-mortem transport of the specimen before burial). The trochanter minor is finger-like, roughly hexagonal in cross section, seems to be less angled than in *Palaeochersis talampayensis*, and its tip is rounded and slightly slanted ventrally. At its base there are two small tubercles or condyles turned anteriorly and separated by a very shallow fossa. Posterodorsally the trochanter minor is linked to the femoral head by a strong, rounded ridge, being about two-thirds of its height, almost half its width at its top, and gradually broadening towards its base. The intertrochanteric fossa is similar to that of *Palaeochersis talampayensis*; however, its ventral end is not well rounded, but it is rimmed by a low ridge connecting bases of both trochanters instead. The trochanter major is weaker than the trochanter minor, being only about half its width. It is more angled than in *Proganochelys quenstedti* or *Palaeochersis talampayensis*. It forms a slight protrusion along its anteroventral surface (apparently weaker than in *Palaeochersis talampayensis*), and anterodorsally it projects a strong ridge (as high and almost as broad as itself) towards the femoral head, merging with it fluently. The femoral head is the highest and largest structure on the proximal end of the femur, and although in proximal view it is similar as in other Triassic turtles, in dorsal view the articular surface is triangular, not rectangular (Fig. 3I–K). This is caused by a lack of a distal posterior apex of this surface. A similar condition is present in *Odontochelys semitestacea* (T. Sulej, pers. observ.), but the distribution of this character may have low phylogenetic value, as a similar shape (albeit with less acute anterior apex) seems to be present in Cretaceous *Kallokibotion* (Gaffney & Meylan, 1992), as well as in recent trionychids and emydids (Zug, 1971). The shaft is slender, slightly S–shaped, circular in cross section near the proximal end, and gradually broadening towards the distal end. The distal end is roughly triangular and has three ridges projecting along its ventral surface, terminating in three epicondyles (the anterior and middle ridges are particularly distinct). Even further anteriorly, another small epicondyle is visible. There are some grooves and pits on the articular surface (most notably a distinct pit on the surface contacting tibia), but this area is damaged, so any visible structures may be artificial or distorted.

Caudal notch

Unlike *Proterochersis robusta*, the caudal notch in turtles from Poreba is an inverted V–shape, not an inverted U-shape (Figs 3G, H, 10A–F). The exact geometry of the carapace, however, is difficult to restore because of compaction and breakage. The right side of ZPAL V.39/48 is geometrically similar to that of *Proterochersis robusta* (SMNS 17561), but paradoxically it is more broken than the flatter left side and appears to be compacted laterally, resulting in its more vertical arrangement. A lower carapace profile (closer to that of *Proganochelys quenstedti*) appears to be consistent with other specimens from Poreba, but again an unambiguous determination of the degree of shape distortion is currently impossible.

Second morphotype

After a detailed study of ZPAL V.39/34 it turns out that there are some errors in the reconstruction from Sulej *et al.* (2012; Fig. 2C, E). There are at least 12 marginals (not 11), the pattern of scutes at the posterior end of the specimen is somewhat different, and the anterior end of the plastron is not as featureless as was illustrated. Paired extragulars and gulars are clearly present, although they are flat and do not form the tubercles seen in other specimens. This, however, is congruent with the condition seen in SMNS 16603 (see figs 4A–C of plate I in de Broin, 1984). Both shells are roughly the same size (around 31 cm), and notably smaller than the other specimens (SMNS 17561 is around 35 cm, ZPAL V.39/48 is 43.5 cm, and ZPAL V.39/49 is 48 cm). Thus the differences most likely arise from their young age, and we include this specimen in *Proterochersis porebensis* sp. nov.

***KEUPEROTESTA LIMENDORSA* GEN. ET SP. NOV.**
(FIGS 9, 10I, L, M, 11C)

Proterochersis robusta Fraas, 1913: Joyce *et al.*, 2013: 1, figs 1–3.

Occurrence and distribution: Lower Löwenstein Formation (?lower or middle Norian) of Rudersberg, Baden-Württemberg, Germany.

Etymology: From Keuper, the geological unit where the animal lived, and 'testa', Latin for shell. 'Limen' from the Latin for threshold; 'dorsum' from the Latin for back (referring to the surface of its shell).

Diagnosis: Differing from *Proterochersis* in: acromion and coracoid forming 140° angle; bone distinctly thickened at the level of the posterior ends of vertebral scutes II–IV (even three times thicker than at their anterior parts); anterior marginals spiky; marginal series lacking the element corresponding to the first marginal of *Proterochersis*; contact between the cervical scute and the first marginal dorsally very narrow, with marginal positioned laterally instead of anterolaterally relative to cervical scute; first vertebral scute contacting the first pleural posteromedially rather than anteromedially; the last cervical vertebra not co-ossified with carapace nor with the first thoracic vertebra.

Holotype: SMNS 17757 (the only specimen).

The shell (Figs 9, 10M) and scapulocoracoids (Fig. 11C) of the specimen described recently by Joyce *et al.* (2013) turn out to be somewhat different than those of *Proterochersis robusta*. The shell is fragmentary, but the arrangement of preserved sulci (Fig. 9) is nearly the same as in *Proterochersis* spp. There are some differences nonetheless: the first vertebral reaches farther posterolaterally, resulting in posteromedial rather than anteromedial contact with the first pleural. There is no equivalent of the first marginal of *Proterochersis* spp., instead the cervical scute contacts the first marginal (equivalent of the second marginal of *Proterochersis* spp.) via a narrow lateral lamella (the anterior margin of that region is tapered and does not seem to be broken). The rest of the marginals visible in the specimen occupy the same positions as marginals III–V and XI–XIII of *Proterochersis*. The first two marginals are pointed, in contrast to the slightly sinuous anterior carapace rim in *Proterochersis robusta* (SMNS 17561) and the almost straight carapace rim in specimens of *Proterochersis porebensis* sp. nov. The whole posterior margin of the fifth vertebral is missing, so there is no natural rim of the caudal notch present and therefore its shape, or even presence, cannot be established. There are no unambiguous sutures visible on the shell, but slight depressions on the visceral surface of plastron (corresponding to the sutures seen in *Proterochersis robusta*) indicate that two pairs of mesoplastra were present. In lateral view distinct bulges are visible in the posterior parts of the second, third, and fourth vertebral scute areas, caused by much higher bone thickness there: whereas the carapace thickness in the anterior part of the third vertebral area is 0.5 cm, in the posterior part it reaches 1.5 cm (Fig. 10M). Although some gradual bone thickening is visible in the vertebrals of *Proterochersis robusta* specimen SMNS 17561, the resulting shape is different (more round, in contrast to the almost straight lines of vertebrals with noticeable 'bumps' just before their posterior edges in SMNS 17757), and it appears to affect every vertebral, not just the second–fourth vertebrals. Even though SMNS 17757 is the largest proterochersid specimen from Germany (measuring around 38.5 cm in length), there is evidence that the thickening of the bone underlying the vertebral scutes did not simply occur during ontogeny, because in slightly smaller *Proterochersis robusta* specimens from CSMM and SMNS the dorsal surface is almost uniform (with bone thickening greatest in the previously mentioned SMNS 17561; Fig. 10N), and in even larger specimens of *Proterochersis porebensis* sp. nov. (ZPAL V.39/48 and ZPAL V.39/49) no changes in vertebral thickness are visible at all. The posterior process of the entoplastron in SMNS 17757 is similar to that of *Proterochersis robusta* (SMNS 12777) or *Proterochersis porebensis* sp. nov., but its caudal end has a different shape (it ends abruptly and is only slightly expanded distally, with much weaker lateral projections and posterior projections). Whether this is caused by superficial damage or is an accurate reflection of the morphology as it was *in vivo* it is hard to tell.

Joyce *et al.* (2013) correctly noted that the eighth cervical vertebra is free and not fused to the first thoracic vertebra, nor to the nuchal bone (Fig. 10I, L). This is different than is the case in *Proterochersis porebensis* sp. nov. specimen ZPAL V.39/48, in which the last cervical is fused both with the thoracic vertebral column and with the carapace (Fig. 3E, F). Although ZPAL V.39/49 and SMNS 16442 lack the last cervical vertebra, a broken lamina of bone is present where the vertebra contacted the carapace, indicating that it was fused. *Proterochersis robusta* specimens SMNS 12777 and SMNS 16603 do not have this vertebra preserved, as well, but its impression is visible as an empty cavity not separated from the thoracic vertebrae row, suggesting that it grew together with the first thoracic vertebra and probably contacted the carapace (Fig. 10H, K).

The configuration of the scapulocoracoid is also notably different. The dorsal process of the scapula is at its base turned slightly more towards the glenoid than in *Proterochersis porebensis* sp. nov. specimen ZPAL V.39/48, and the angle between the acromion and the coracoid (Fig. 11) is noticeably larger than in ZPAL V.39/48 (about 150° versus 120°). Such differences might have been caused by

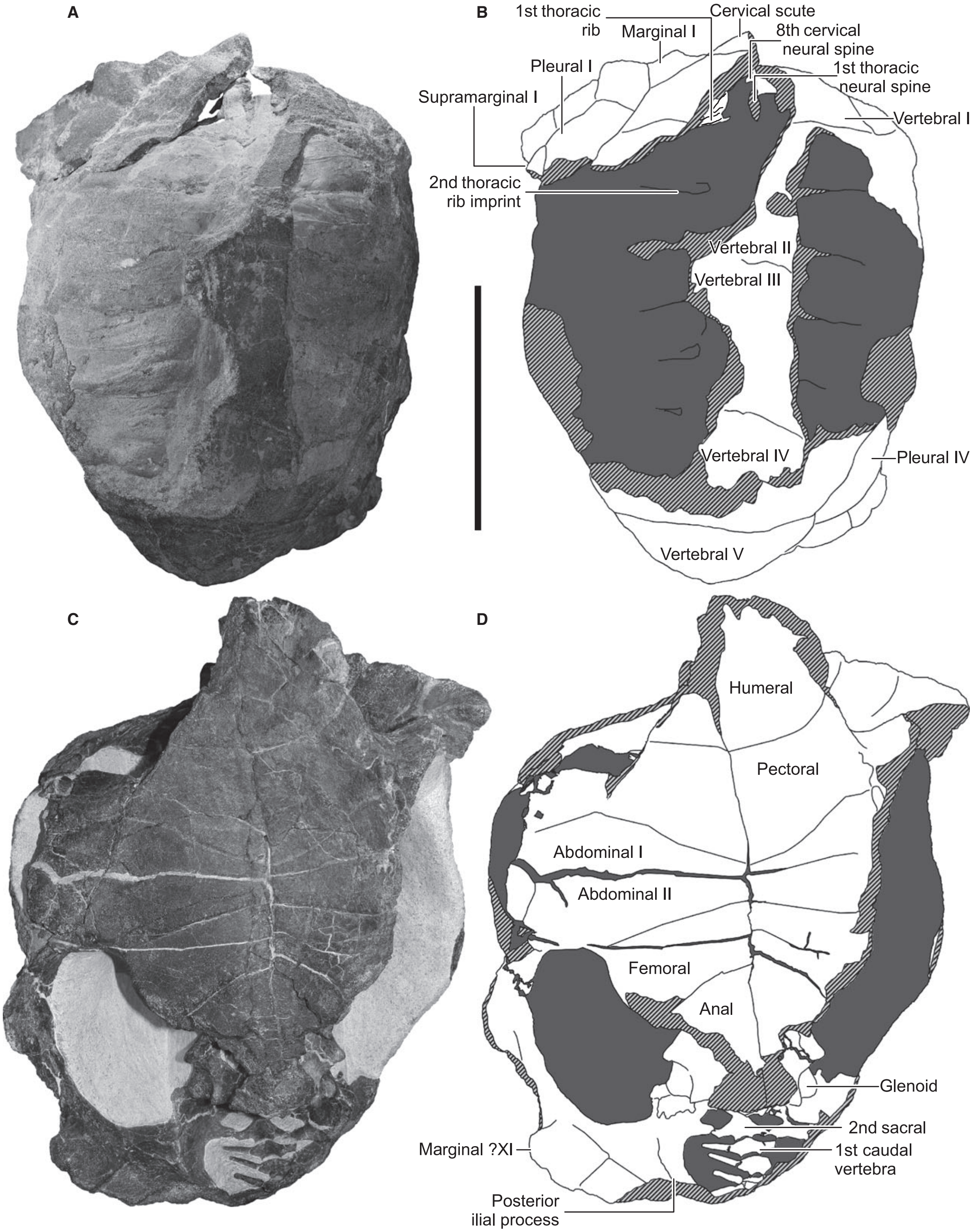

Figure 9. ***Keuperotesta limendorsa* gen. et sp. nov.**, SMNS 17757, shell: A, B, dorsal view; C, D, ventral view. Dark grey is matrix; hatched is damaged or broken bone. Note the unbroken, free dorsal surface of the eight cervical vertebra neural spine. Scale bar: 20 cm.

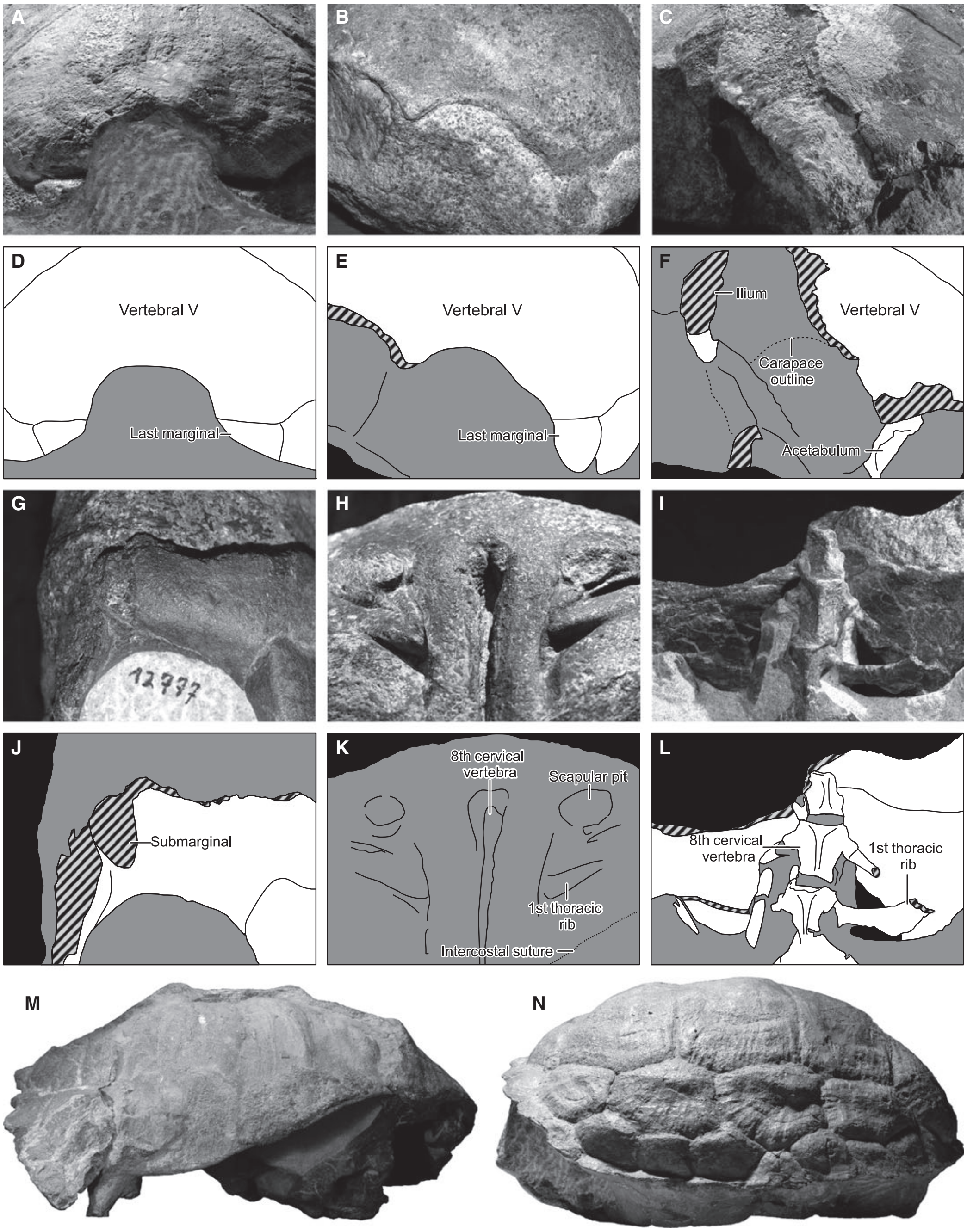

Figure 10. A–F, caudal notch of *Proterochersis robusta* in posterior view, SMNS 17561 (A and D), unnumbered CSMM (B and E), and SMNS 16603 (C and F, note that despite the lack of the central part of the last vertebral, the outline of the caudal notch is visible thanks to coarser, differently coloured sediment); G, J, posterior part of the right bridge of the holotype of *Proterochersis robusta* (SMNS 12777) in ventral view, revealing an outline of the damaged last inframarginal; H, K, anterior part of the holotype of *Proterochersis robusta* (SMNS 12777) in dorsal view, with an empty cavity left by the last cervical vertebra (note that it was not displaced, and nor can any discontinuities with the thoracic vertebral column be seen, indicating fusion as described in ***Proterochersis porebensis* sp. nov.**); I, L, anterior part of carapace and vertebral column of the holotype of ***Keuperotesta limendorsa* gen. et sp. nov.** (SMNS 17757) in ventral view, with the two last cervical vertebra free and relocated; M, the holotype of ***Keuperotesta limendorsa* gen. et sp. nov.** (SMNS 17757) in lateral left view (note the distinct broadened posterior parts of vertebrals II–IV and nearly straight profile of the first vertebral); N, *Proterochersis robusta* (SMNS 17561) in lateral left view (note the rounded profile and smooth changes of the vertebral elevation). Dark grey is matrix; hatched is damaged or broken bone. Not drawn to scale.

compaction, but this would distort fragile ridges of the acromion, and these are straight and seem to be undisturbed in both specimens, hence the organization of the pectoral girdle was probably the same *in vivo* as in fossils, and is not disfigured by diagenetic processes. A similarly large coracoid–acromion angle is present only in *Proganochelys quenstedti*, and other turtles seem to have about 120° or less. This condition is unfortunately unknown for *Odontochelys semitestacea*.

Other features of the vertebral column and the pelvic girdle were adequately described by Joyce *et al.* (2013), and are essentially the same as in *Proterochersis* spp., but some corrections are needed. The thyroid foramina were rather smaller and more regular (more similar to their shape in *Proterochersis porebensis* sp. nov.) in life than was illustrated in Joyce *et al.* (2013), and their ridges are damaged in the specimen described. The sutures that led Joyce *et al.* (2013) to believe that the ilia contacted the carapace via the descending process are ambiguous. This purpoted descending process forms, in its dorsoposterior part, a caudally oriented process (even more clearly visible in some of the *Proterochersis* specimens), which is very similar to the posterior ilial process of *Odontochelys semitestacea*, *Proganochelys quenstedti*, and *Palaeochersis talampayensis* (but fully grown to the shell), and its relationship with the sacral ribs is identical. Therefore that part is best interpreted as the true point of contact between the pelvis and carapace. The extent of preparation does not allow for a clear view of the articulation shape, but the lateral process of the ilium similar to this of *Proterochersis* spp. is not visible.

The shape of the dorsal and anterior surface of the carapace, as well as the configuration of the scapulocoracoid and the last cervical vertebra indicate that this specimen is notably different from both *Proterochersis* species. Because of that, its assignment to a new genus, *Keuperotesta*, and a new species, *Keuperotesta limendorsa*, is proposed.

NEW TAXA AND INTRASPECIFIC VARIABILITY AND DEFORMATIONS

The relative morphological similarity of the species of *Proterochersis* and *Keuperotesta* recognized here raises the question of whether these three taxa should indeed be considered as separate, or if instead they represent one varied species. The problem arises because of a lack of skull material and the largely unknown layout of sutures of the postcranium, both of which are the main basis for the species recognition in Testudinata. Even worse, the German proterochersid material is quite fragmentary. Fortunately, a number of specimens allow for some insights into morphological variability and the consistency of some characters. Our assumption is that characters that are simply variable should occur in various combinations within the population, and there should be a set of intermediate forms observable. On the other hand, sexually dimorphic characters should appear in the adult or subadult specimens in either of two possible variations. In addition, both of the possible sexual variants and similar (or even larger, because of the much greater number of specimens) degrees of intraspecific variety should be present in the German and Polish populations alike. The second problem is the possible deformation of bones, which is common among Triassic fossils.

The distinctiveness between *Proterochersis robusta* and *Proterochersis porebensis* sp. nov. is the most problematic in this aspect. Nonetheless, the characters provided in the diagnoses appear to be consistent in all specimens with these areas preserved. The caudal notch in both Polish specimens with this part preserved well enough for interpretation (ZPAL V.39/48 and V.39/48) is triangular, whereas in all five German specimens (SMNS 16603, 17561, 17755a, and 56606, and the CSMM specimen) it is semicircular, with slight variation, but never close to the condition of Polish specimens. The anterior margin of the carapace is well preserved in five specimens from Poland (ZPAL V.39/34, V.39/48, V.39/49, V.39/57, and V.39/72), four of which are adults or subadults, and all of them exhibit nearly no serration in that region, and no variation in that aspect is visible. This is different than is the case in SMNS 17561, even though this specimen is smaller (and thus probably younger) than all Polish specimens, excepting ZPAL V.39/48. The only other German specimen with anterior marginals, SMNS 17930, shows morphology more similar to Polish turtles, but it is even smaller than SMNS 17561 and the anterior rim of the carapace seems to be damaged, possibly obscuring the serration. The relative height of the carapace is the most dubious of these characters because of breakage and the possible compaction of the shells. Nonetheless, no specimen from Poland unequivocally suggests that the shell of *Proterochersis porebensis* was proportionally as tall, as the shell of *Proterochersis robusta*. Given the number of specimens and assuming a 1 : 1 ratio of females to males it is improbable that these small, but notable differences should be attributed to sexual dimorphism or intraspecific variability. It is unlikely that the Polish and German material is represented by just one sex each, and if these characters were based on intraspecific variability a set of intermediate states should also be observable, at least. This is not the case for disputed characters. The variable layout of some sulci, shape of caudal scutes, and

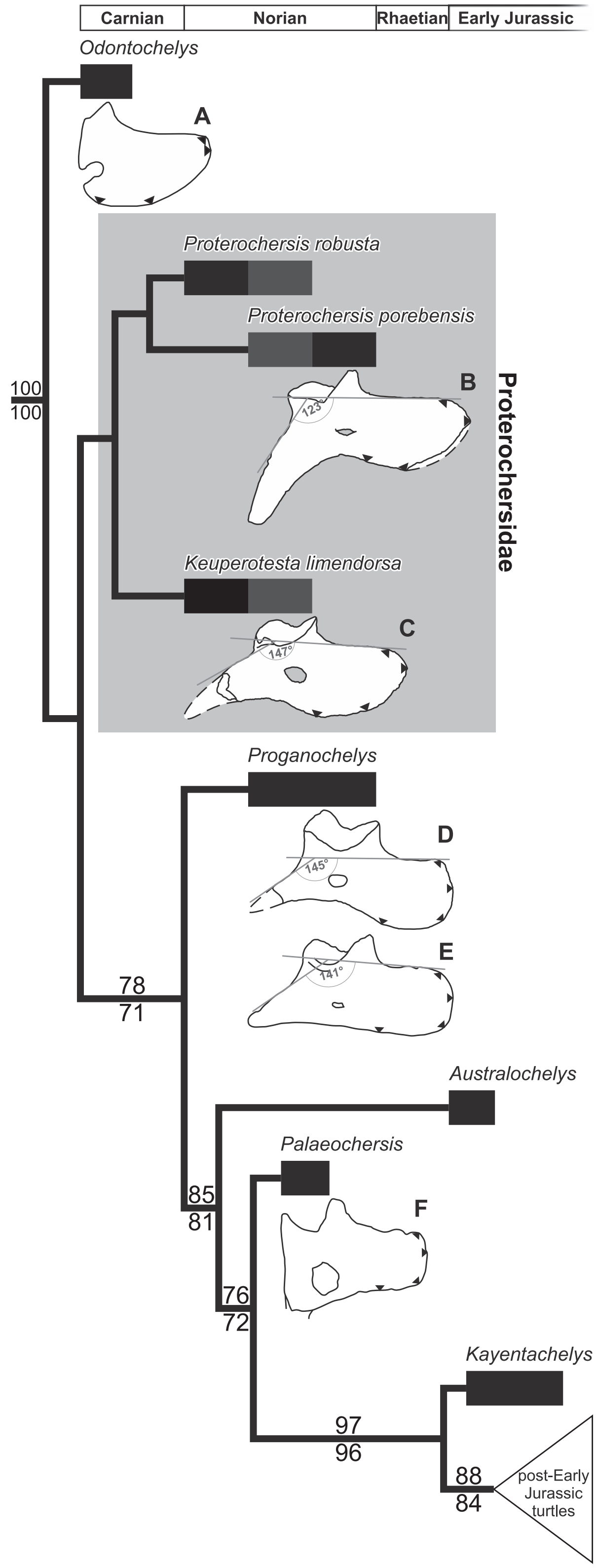

Figure 11. Majority rule (50%) consensus cladogram of the relationships of Proterochersidae with other Late Triassic and Early Jurassic turtles, with stratigraphic ranges and ventral outline of left scapulocoracoids (not drawn to scale) of the Triassic taxa presented. Jacknife frequency difference values are given above and bootstrap frequency difference values are given below the branches (both 10 000 replicates). The maximum temporal ranges of Proterochersidae are shown in black, with maximum possible overlap of the German and Polish taxa shown in dark grey (see text for discussion). The approximate angles between the coracoid and the acromion were measured as the angle between the extrapolated tangential to the lateral rim of the coracoid and to the most anterolateral part of the acromion, in order to avoid errors arising from the incompleteness and curvature of the acromion. A, *Odontochelys semitestacea*, coracoid of IVPP V 15653 (based on Li *et al.*, 2008); B, ***Proterochersis porebensis* sp. nov.**, ZPAL V.39/48; C, ***Keuperotesta limendorsa* gen. et sp. nov.**, SMNS 17757 (right-mirrored for easier comparison); D, *Proganochelys quenstedti*, SMNS 16980 (subadult); E, *Proganochelys quenstedti*, SMNS 51600 (mould of original; adult); F, *Palaeochersis talampayensis*, PULR 68 (right-mirrored for easier comparison, based on Sterli *et al.*, 2007). The angle for (F) is not given because there was no possibility of examination the specimen in person, but appears to be relatively low.

number of posterior peripherals are visible in German and Polish collections independently of the diagnostic characters, and indicate that these specimens are indeed a random sample from the population. The presence of the same states of these characters in specimens of varied size indicates that they do not simply represent ontogenetic stages either. Based on the consistency of the differential characters we conclude that two populations of *Proterochersis*, one from Poland and one from Germany, should be considered two separate, but closely related species. In particular, the shape of the caudal notch appears to be a clear distinction. Although their times of occurrence might have overlapped (if they both lived during the middle Norian), because of the problems with the time correlation of the oldest Löwenstein Formation unit with the other European Late Triassic sediments, and with existing evidence supporting the view of the Zbaszynek Beds being younger than the lower Löwenstein Formation (see discussion above in Geological setting), the time criterion cannot be used to support their synonymy. Future discoveries, especially of cranial material, may provide further support or negate this hypothesis.

The matter of *Keuperotesta limendorsa* gen. et. sp. nov. is less complicated. The shape of the scapulocoracoid, although potentially prone to deformation, appears to be well preserved in both *Keuperotesta limendorsa* gen et sp. nov. and *Proterochersis porebensis* sp. nov. The acromion projects in three directions thin lamellae of bone, one of which is attached relatively high to the dorsal scapular process. Any pressure affecting the anteroposterior direction of the acromion would cause visible torsion or bending of this lamella. This is not the case. Additionally, both of the scapulocoracoids of *Keuperotesta limendorsa* gen. et sp. nov. are more or less symmetrical, supporting the assumption that their shape is natural. The undisturbed direction of the acromion relative to the base of the dorsal scapular process in *Proterochersis porebensis* sp. nov. is supported by an isolated fragment of scapula (ZPAL V.39/162). The different shape of the scapulocoracoid is difficult to explain by intraspecific variation or by sexual dimorphism, because it is a major anatomical difference, most likely affecting the animal's locomotion. The difference in the attachment of the last cervical vertebra in *Keuperotesta limendorsa* gen. et sp. nov. and *Proterochersis* spp. is also important and unexplainable by these factors, given that such a character was never reported as sexually dimorphic or variable in any other Triassic turtle (or, according to our knowledge, in any turtle at all). Analogously, this can also be said for the posterior thickening of the vertebral scute areas (this is also different to the pyramiding occurring in modern turtles, as it affects only the posteriormost part of the vertebral scutes, and not the central parts). Potentially, the morphology of the anterior part of the carapace may be subject to variation or dimorphism (especially when we consider the presence or absence of the first marginal in *Proganochelys quenstedti*, as shown by Gaffney, 1990), but remains unique to SMNS 17757, and does not appear in any other specimen from Poland or Germany. We conclude that *Keuperotesta* is distinct enough to be erected as a new genus in the family Proterochersidae.

PHYLOGENETIC ANALYSIS

The analysis performed resulted in 45 equally parsimonious trees, of 263 steps each (consistency index, CI 0.563; retention index, RI 0.739). Each of these trees agrees upon the position of a monophyletic clade *Keuperotesta limendorsa* gen. et sp. nov. + (*Proterochersis porebensis* sp. nov. + *Proterochersis robusta*), which is here referred to as Proterochersidae Nopcsa, 1923a (supported by pelvis sutured to shell), as more derived than *Odontochelys semitestacea*, and as sister clade to other turtles, including *Proganochelys quenstedti*, and on the position of Pleurodira as sister to *Platychelys*.

Proterochersidae share the following characters with *Odontochelys semitestacea* alone (here considered as turtle plesiomorphies): coracoid bee wing-shaped (character 83), first thoracic rib large and forming costal (character 87), dorsal processes of epiplastra large but not contacting the carapace (character 99), and two pairs of mesoplastra (character 103) and abdominal scutes (character 108) contacting at the midline. *Proganochelys quenstedti* and more recent turtles are derived in having one pair or no pairs of mesoplastra (character 103) and abdominal scutes (character 108). For full list of synapomorphies see Appendix S1. The trees differ mainly in the position of taxa more advanced than *Kayentachelys* gen. nov.

The overall topology of the consensus tree (Fig. 11; for the tree including post-Early Jurassic taxa, see Fig. S1) is similar to the topology found by Gaffney *et al.* (2007), with the exception of the positions of *Proterochersis* spp. (more basal than *Proganochelys quenstedti*), *Mongolochelys* (more basal than *Kallokibotion* + Pleurosternidae + Baenidae, with Pleurosternidae the most basal of these three, instead of *Kallokibotion*), *Xinjiangchelys* (more basal than *Solnhofia* + Plesiochelyidae), and Pleurodira (sister to *Platychelys*) in an unresolved polytomy with *Otwayemys*, *Chubutemys*, Meiolaniidae, and *Sinemys* + more advanced turtles – thus resulting in a much less inclusive crown (even to a larger extent than in the analysis provided by Joyce, 2007; and similar to, e.g. Sterli, 2010; Sterli, Pol & Laurin, 2013b). The position of *Proganochelys quenstedti* between Proterochersidae and *Palaeochersis talampayensis* (each with pelvis sutured to shell) is in accord with their stratigraphic succession, and the unsutured pelvis of *Proganochelys quenstedti* and turtles more recent than *Palaeochersis talampayensis* is best interpreted as having been acquired independently. This topology of the stem also has good to strong support, as shown by bootstrap and jacknife values, with the exception of the exact relative position of *Odontochelys semitestacea*, *Proterochersis* spp., and *Keuperotesta limendorsa* gen. et sp. nov.; however, their placement as more basal than *Proganochelys quenstedti* is relatively well supported (jacknife value of 78 and bootstrap of 71 for clade including *Proganochelys quenstedti* and other turtles, with the exclusion of *Odontochelys semitestacea*, *Proterochersis* spp., and *Keuperotesta limendorsa* gen. et sp. nov.), and the clade including *Kayentachelys* and more advanced taxa, and excluding any of the Triassic taxa + *Australochelys*, has very strong support (jacknife value of 97, bootstrap value of 96). The unstable position of *Proterochersis* spp. and *Keuperotesta limendorsa* gen et sp. nov. is most likely caused by the lack of cranial data for these taxa and an abundance of plesiomorphic postcranial characters, and the instability of taxa more derived than Pleurosternidae + (Baenidae + *Kallokibotion*) is probably caused by the relatively low numbers of taxa sampled and characters (the resolution of extinct cryptodires for a given matrix tends to 'break down in bootstrapping', as admitted by Gaffney *et al.*, 2007: 26). This, however, poses little problem, because the cryptodiran phylogeny is well beyond the scope of this study, the topology of the Middle Jurassic and later taxa has little effect on the interrelationships of the Late Triassic turtles, and the stem (including genera relevant to our interests) is nonetheless relatively well resolved and supported.

DISCUSSION

Proterochersis porebensis sp. nov. comes from strata of similar age or younger than *Proterochersis robusta*; their shell, pelvic girdle, and vertebrae morphology are very similar, and therefore it is relatively safe to assume that both their ecology and their limb anatomy were alike. *Keuperotesta limendorsa* gen. et sp. nov. comes from the same sediments as *Proterochersis robusta*, so these taxa may be considered contemporaneous. *Proterochersis robusta* and *Keuperotesta limendorsa* gen. et sp. nov. are older than the oldest known specimens of *Proganochelys quenstedti* (Gaffney, 1990), which the majority of researchers consider to be the most basal fully shelled turtle. Although it is possible for taxa exhibiting ancestral and derived characters to exist at the same time, it is not possible for ancestral character states to appear later than derived states, as would seem to be the case if *Proganochelys* was less derived than proterochersids. Such discrepancies between the results of phylogenetic analyses and the order of appearance of fossils in the fossil record may be easily explained as an artefact or inadequacy of the record available, but it is possible that this results from inadequate character sampling and polarization. Thanks to the redescription of *Proganochelys quenstedti* published by Gaffney in 1990 this taxon is the most completely known Triassic turtle, and as such it received much attention, and was included in virtually every phylogenetic analysis concerning the origin and early evolution of turtles. Its basal position in these analyses is understandable, because of its unique morphology and plesiomorphic skull characteristics. *Proterochersis robusta*, on the other hand, was poorly known, and was thus rarely included and examined because many researchers (e.g. Gaffney, 1975c, 1990; Gaffney *et al.*, 1991, 2006, 2007; Sterli *et al.*, 2007) settled on the original assumption for the derived position of this taxon as the oldest pleurodire (Fraas, 1913). More recently, however, *Proterochersis robusta* was being positioned more often along the stem of the phylogenetic tree and the homoplasic nature of its pelvis was implied (Rougier *et al.*, 1995; Joyce, 2007; Sterli, 2010; Anquetin, 2012; Joyce *et al.*, 2013; Sterli *et al.*, 2013a). Although we here demonstrate that Joyce *et al.* (2013) in fact analysed another taxon (*Keuperotesta limendorsa* gen et sp. nov.), some of the new aspects of the anatomy that they observed are true for *Proterochersis* spp. as well, as revealed by material from Poland, and newly gathered data display even more plesiomorphic characters.

Mesoplastra

Fraas (1913) was the first to note that *Proterochersis robusta* had two sets of mesoplastra contacting at the midline. The only other stem turtle known to date with the same character is *Odontochelys semitestacea* (Li *et al.*, 2008), and now also *Keuperotesta limendorsa* gen et sp. nov. A double set of mesoplastra is therefore most probably a plesiomorphic character for turtles. *Proganochelys quenstedti* had only one pair of these elements (Gaffney, 1990), similar to other stem turtles (Joyce, 2007). Other similarities shared by *Proterochersis* spp., *Keuperotesta limendorsa* gen et sp. nov., and *Odontochelys semitestacea*, but not by *Proganochelys quenstedti*, include a bee wing-shaped coracoid (Fig. 11). Its shape appears to change gradually with time, beginning as a bee wing in the oldest *Odontochelys semitestacea*, through *Keuperotesta limendorsa* gen. et sp. nov. and *Proterochersis porebensis* sp. nov., to rectangular in *Proganochelys quenstedti* (more visible in adult than in subadult, see Fig. 11D, E) and *Palaeochersis talampayensis*. This change may be explained as relative changes in position and angle of some regions of coracoid. The subsequent merging of the coracoid foramen with the edge resulted in a paddle-like or columnar shape of coracoid, typical to modern turtles.

Caudal notch

The presence of the caudal notch in the carapace of proterochersids may also be speculated to be plesiomorphic rather than derived, when we consider that most reptiles form dermal ossifications along the trunk (and, possibly, continuing along the tail), rather than around it. It appears more intuitive to assume that in turtles the peripherals appeared on the sides of the animal first (possibly receiving tips of the ribs and plastron in the bridge region, thus terminating the dorsolateral outgrowth of the plastral bones, very notable in *Odontochelys semitestacea*), and later spread towards the front and to the rear. They never reached the anteriormost edge of the carapace (occupied by the nuchal bone), and it seems possible that in *Proterochersis* spp. they did not yet reach the posteriormost part (in most turtles occupied by pygal) either. This change of peripheral coverage might have been linked to the caudal and rostral expansion of the carapacial ridge, as proposed by Kuratani, Kuraku & Nagashima (2011; see also Hirasawa *et al.* 2014). It is probable that in *Proterochersis* spp. the row of suprapygals and pygal was also incomplete. These elements are absent in *Odontochelys semitestacea*, and in modern turtles they are (along with peripheral bones) the last elements to ossify (Gilbert *et al.*, 2001; Scheyer, Brüllmann & Sánchez-Villagra, 2008; Werneburg *et al.*, 2009; Lima *et al.*, 2011). This late ontogenesis may possibly reflect their relatively late evolutionary origin. In at least one specimen of *Proterochersis porebensis* sp. nov. the neural spines of sacral vertebrae contact the carapace. Unfortunately, no sutures are visible, so it is impossible to tell which carapace elements actually participate in the contact [last vertebral, suprapygal(s) or pygal], and what is its exact nature (sutural or whether the sacral neural spines itself contribute to the carapace, like the neural spines of thoracic vertebrae creating neural bones). It is also unclear whether such articulation is related to the advanced age of the specimen or if it occurred early in ontogenesis. It is possible that at this point of turtle evolution suprapygals (and perhaps pygal) were still morphogenetically indistinguishable from neurals, being parts of the neural spines of the vertebrae, and that only later did they separate. In *Proganochelys quenstedti* the caudal notch is much shallower than in both species of *Proterochersis*, and there is a paired 17th marginal scute and a supracaudal scute in that area, but the sutures are not visible and there is no possibility of inferring whether any peripherals, suprapygals, or pygal were present there (Gaffney, 1990). It is possible that the supracaudal scute and the last pair of marginals (they are of different shape and are in different rows than the preceding marginal plates) do not overlay peripherals, nor pygals, and that they are of a different nature, or that the pygal and/or suprapygal was already present but proportionally not yet as large, as in more recent turtles. The presence of a deeper caudal notch in *Palaeochersis talampayensis* (Sterli *et al.*, 2007) suggests that the smaller caudal notch in *Proganochelys quenstedti* is an apomorphy of that taxon, possibly related to its lower profile (in dorsal view the extent of the notch in the much higher domed *Proterochersis* spp. is no larger than in *Proganochelys quenstedti*, and it is actually visible only in posterior view, i.e. the difference is mostly vertical; this is not true for *Palaeochersis talampayensis*, but this may be an effect of post-mortem disturbance of the shell geometry by dorsoventral crushing or compression and, as a result, pushing the posterior rim of the carapace even further posteriorly).

Dorsal processes of epiplastra

Generally, *Proganochelys quenstedti* was a large animal, sturdier and heavier than any other Triassic turtle known to date, it is also one of the most heavily armoured. Before the description of *Odontochelys semitestacea* such adaptations might have been interpreted as plesiomorphic for Testudinata, but the more gracile osteology of the Carnian turtle suggests that the sturdy build of *Proganochelys quenstedti* should instead be considered its own apomorphy. The presence of strong dorsal epiplastral processes contacting the carapace may be one of the consequences: although the dorsal processes themselves are interpreted by Gaffney (1990) as remnants of ancestral amniote clavicles, their additional articulation with the carapace and strengthening might have stabilized the shell, and thus serve as a more rigid point of attachment for the limb musculature (which probably was required to support the heavy body). Large dorsal epiplastral processes are present in the slightly smaller *Palaeochersis talampayensis* (Sterli *et al.*, 2007), but are weaker and do not articulate with the carapace in more basal *Proterochersis* spp. and *Keuperotesta limendorsa* gen. et sp. nov. In *Odontochelys semitestacea* they obviously do not contact the carapace, because no suitable point of attachment was available (Li *et al.*, 2008), but they possibly played a similar role, temporarily supporting and strengthening the limb musculature (weakened by changes in rib position), and disappeared when the torso of the animal became fully stiffened and the pectoral girdle received its derived shape.

Thoracic ribs

The presence of a well-developed first thoracic rib in *Proterochersis* spp. fits into the evolutionary scenario of rib reduction in turtles (well-developed first rib in Proterochersidae, still large, but excluded from carapace in *Proganochelys quenstedti*, and subsequently reduced in more advanced turtles), but seems to be incongruent with the nine thoracic ribs in *Odontochelys semitestacea*. Given that basalmost reptiles have numerous thoracic ribs (e.g. Romer, 1956), the evolutionary changes towards modern turtles would be indeed nonsensical and counterintuitive: the rib count would be reduced from many to nine (*Odontochelys semitestacea*), then again increased to ten (Proterochersidae), only to be reduced once more to nine plus one reduced (*Proganochelys quenstedti*), and subsequently to eight plus two reduced (more advanced turtles). The increase is particularly difficult to understand, as it would not result in a rise of trunk mobility: at that point the ribs were grown together, their heads were positioned between the vertebral centra, and they were fused together. A more parsimonious explanation is possible: the dorsal rib count of nine present in *Odontochelys semitestacea* is its own apomorphy, and the common ancestor of *Odontochelys semitestacea* and other turtles had in fact ten dorsal vertebrae and ten pairs of dorsal ribs. This would be easily explained from an evolutionary point of view: *Odontochelys semitestacea* did not have a carapace yet, its ribs were still attached to single vertebral centra, and its trunk, although stiffened by the plastron, was not yet completely immobile. *Odontochelys semitestacea* was most likely an aquatic animal using its limbs for propulsion (Li *et al.*, 2008), therefore the mobility of the vertebral column was not desirable and it might have been reduced by lowering the vertebral (and, in effect, rib) count. Although Reisz & Head (2008) suggested that the general form of *Odontochelys semitestacea* ribs might be derived, their morphology still appears to be plesiomorphic. If this scenario is true, the homology of the rib count of turtles and the nine ribbed *Eunotosaurus africanus* Seeley, 1892; proposed recently by Lyson *et al.* (2010, 2013a, b), would become problematic. The presence of well-developed first thoracic ribs in basalmost turtles indicates that the interpretation of the first thoracic vertebra as the incorporated last cervical with cervical ribs hypertrophied, as proposed by Joyce (2015), is unlikely.

Although the recognition of skull characters is essential for our understanding of the earliest turtle evolution, cranial material is lacking for Proterochersidae. This is unfortunate, but the presence of some postcranial characters unique to *Proterochersis* spp. (and, most likely, *Keuperotesta limendorsa* gen. et sp. nov.), or shared only with *Odontochelys semitestacea* (e.g. osseous contact between sacrum and carapace, well-developed costal on the first thoracic rib, shape of the coracoid, and two pairs of mesoplastra contacting at the midline), demonstrate that this group of turtles is much more basal than previously thought.

CONCLUSION

The re-evaluation of the historical specimens from Germany and new material from Poland allowed for a new interpretation of the earliest turtle evolution and shows that *Proterochersis* spp. and *Keuperotesta limendorsa* gen. et sp. nov. are not only the oldest fully shelled turtles, but are in fact the most basal as well. Although the important skull data for *Proterochersis* spp. or *Keuperotesta limendorsa* gen. et sp. nov. is still missing, some important postcranial characters, such as the presence of two pairs of mesoplastra and abdominal scutes, first thoracic rib bearing costal and participating in carapace, or the contact between the sacral vertebrae and carapace, appear to be ancestral, and some of them link Proterochersidae with *Odontochelys semitestacea*, the oldest and basalmost turtle. The discovery of new plesiomorphic characters in proterochersids is important, because it helps to solve the debate on the time of divergence of the turtle crown, ruling out the Proterochersidae as the basalmost Pleurodira and supporting the hypothesis of their stem position, thus postponing the emergence of the side-necked and hidden-necked turtle lines. This is the first contribution focused on presenting these new characters and not just re-evaluating the old ones (most notably the sutural contact of pelvis with the shell), and the first that shows such a basal position of Proterochersidae with relatively good support. This may lead to some new view on the evolution of the turtle shell, proving that *Proganochelys quenstedti*, for years used as a model of an ancestral turtle, is in fact a derived form, not fitting as well into the evolutionary trends of the whole group as we previously thought. At least some of its peculiar aspects of postcranial morphology, such as only four vertebral scutes and numerous osteoderms on limbs, neck, and tail, are its autapomorphies, a consequence of its advanced specialization towards heavy protection. Further studies, centred around the composition of the shell of *Proterochersis* spp., will probably bring more information about the early composition and evolution of this amazing novelty of Testudinata.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. The majority rule cladogram as in Figure 11 of the main text with the post-Early Jurassic taxa included and the node numbers added.
Appendix S1. Character list, character matrix, and listo of synapomorphies.