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A surface scan of the "Tübingen Steinkern", holotype of *Proganochelys quenstedtii* (Testudinata), with some historical remarks.

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Abstract

Turtles are one of the most impressive vertebrates. Much of the body is either hidden in a shell or can be withdrawn into it. Turtles impress with their individual longevity and their often peaceful disposition. Also, with their resilience, they have survived all extinction events since their emergence in the Late Triassic. Today's diversity of shapes is impressive and ranges from the large and high domed Galapagos turtles to the hamster-sized flat pancake turtles. The holotype of one of the oldest fossil turtles, *Proganochelys quenstedtii*, is housed in the paleontological collection in Tübingen/Germany. Since its first mention in 1873 , *P. quenstedtii* has represented the 'prototype' of the turtle and has had an eventful scientific history. It was found in Neuenhaus (Häfner-Neuhausen in Schönbuch forest), Baden-Württemberg, Germany, and stems from Löwenstein-Formation (Weißer Keupersandstein), Late Triassic. The current catalogue number is GPIT-PV-30000. The specimen is listed in the historical inventory "Tübinger Petrefaktenverzeichnis 1841 bis 1896, [folio 326v.]", as "[catalogue number: PV]16549, Schildkröte Weiser Keupersandstein Hafnerhausen" [turtle from White Keuper Sandstone]. Another, more recent synonym is "GPIT/RE/9396". The same specimen was presented as uncatalogued by Gaffney (1990). Here we provide a surface scan of the steinkern for easier access of this famous specimen to the scientific community.

Keywords: Friedrich August Quenstedt, history of science, holotype, steinkern, surface scan

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Inv nr.	Description
GPIT-PV-30000	Surface model of the steinkern of the shell.

Table 1. Model of *Proganochelys quenstedtii* (collection: GPIT, Tübingen, Germany)

INTRODUCTION

The fossil enters the collection

The forest official Friedrich August von Tscherning (1854–1892, Fig. 1A) from Bebenhausen near Tübingen has shown the curator of the palaeontological collection, Friedrich August von Quenstedt (1809–1889, Fig. 1B), a fossil 57 cm long, 55.6 cm wide, 25.4 cm high, and weighting 82 kg (Fig. 1F-I, 2, 3B, D-F; see also table 1). Quenstedt's son wrote in the unpublished memoirs on his father: "One fine day, Herr Oberforstrat Tscherning came to visit my father in Bebenhausen: »Professor, I've found something strange! In the woods near Walddorf on a small road there is a block of Keuper Stubensandstein as a curb, which has a strange shape. It resembles a human thorax, but is much larger. If you could take a look!«"[1] According to Quenstedt (1889a), in a Schönbuch quarry, the specimen had been "put aside to the cathedral building blocks of the White Keupersandstein from Häfner-Neuhausen"[2] years earlier, "but it was not escaped from my dear friend's connoisseur glance that it might show signs of some vertebrate, which, to my astonishment, turned out to be a turtle when cleaned properly."[3] The exact site of the discovery could no longer be reconstructed, but the "workers still working there"[4] testified that there was a dark-colored mass on the specimen that could have represented a bone substance: "In the next few days, cabman Schmid, Tscherning, and my father drove on the spot. My father looked at the block: Well, what is that, Tscherning, you made a remarkable find. This is the steinkern of a large turtle from the Keuper that was otherwise only found

[1] Archive of the University of Tübingen, UAT signature 236/59: Ernst Quenstedt: Erinnerungen von Ernst Quenstedt an seinen Vater Friedrich August Quenstedt, typoscript from 1935, p. 21–22: section on ‚Keuperschildkröte': „Eines schönen Tages kam Herr Oberforstrat Tscherning in Bebenhausen meinen Vater besuchen: »Herr Professor, ich habe was Merkwürdiges gefunden! Im Walde bei Walddorf an einer kleinen Straße liegt ein Block Keuperstubensandstein als Randstein, der eine merkwürdige Form hat. Er gleicht einem menschlichen Thorax, ist aber viel größer. Wenn sie den mal ansehen könnten!«; all translations in this article by the authors.

[2] Quenstedt (1889a), p. 9: „in den Dombausteinen des weissen Keupersandsteins von Häfner-Neuhausen."

[3] Quenstedt (1989b): „beiseite gelegt worden [. . .], aber erst dem Kennerblick meines werten Freundes entging es nicht, dass darin Anzeichen von irgend einem Wirbeltier steckten, das sich dann zu meinem Erstaunen beim gehörigen Reinigen zu einer Schildkröte entpuppte."

[4] Universitätsarchiv Tübingen (UAT), signature 236/59: „jetzt daselbst noch thätigen Arbeiter"

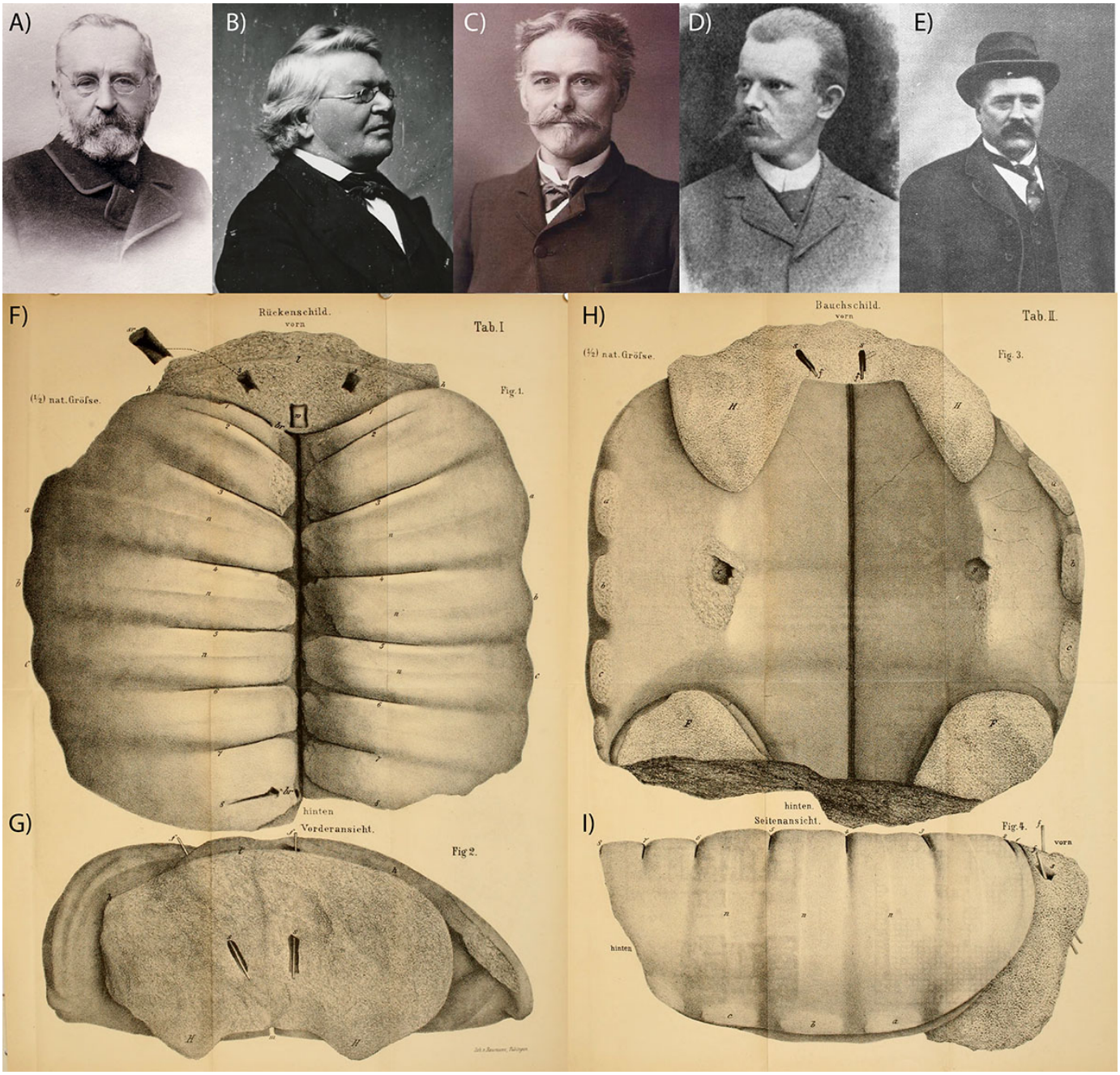

Figure 1. Early history of the Tübingen steinkern. A) Friedrich August von Tscherning, around 1900 (credit: Denksteine im Naturpark Schönbuch), **B)** Friedrich August von Quenstedt, around 1870 (credit: Universität Tübingen), **C)** Edward Drinker Cope, around 1890 (credit: Universitätsarchiv Tübingen), **D)** Georg Baur (credit: archive of Paläontologische Sammlung Tübingen), **E)** Eberhard Fraas (credit: Walther 1922), **F-G)** Plate I of Quenstedt (1889b) with (F) dorsal and (G) anterior view of the steinkern, **H-I)** Plate II of Quenstedt (1889b) with (H) ventral and (I) right lateral view of the steinkern. Anterior is top in F and H, and right in I. Numbers in F and I indicate rib impressions.

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in the Upper Jurassic. 'A new find! Jäger's[5] *Mastodonsaurus*, the *Zanklodon*, and now the turtle. Three important finds from Swabia."[6] In fact, the fossil is 'only' a steinkern (stone core), a fossil preservation that is otherwise found mainly in invertebrates with exoskeletons. In this type of fossilization, the empty shells of ammonites, brachiopods, bivalves, or snails are filled with sediment. It hardens as the animals' outer layers fall off. The surface of the remaining steinkern often shows imprints from the inner wall of the former housing. Steinkerne of vertebrates, such as brain casts (e.g., Edinger 1929) or body inclusions such as those of the Tübingen turtle, are also rarely found. Quenstedt (1889b) first identified the openings for the legs and neck, through which the outlines of the plastron (ventral part of the shell) became clear. Looking up, he recognized the imprints of the eighth (i.e., the most posterior) cervical vertebra (cf. Fig 2G) and eight rib impressions. In a side view, incisions left by the ribs can be seen. Quenstedt (1889b) also found traces of some bone sutures and identified hollows in which the 'shoulder blades'[7] must have sat.

First descriptions

Even at the old age of almost 80 years, shortly before his death, Quenstedt (1889b) was forced to quickly describe this steinkern, which had "been unprocessed in the Tübingen collection for so many years"[8] (Fig. 2F-I). The famous American paleontologist Edward Drinker Cope (1840–1897, Fig. 1C) first reported on the find in 1873 based on an oral note from a person who had studied in Tübingen:[9] "The order [Testudinata] makes its appearance in the Triassic period, for I am assured by Dr. F. Endlich of Reading, Pennsylvania, that the species obtained by Professor Quenstedt in Würtemburg [sic] belong undoubtedly to the Testudinata. With their special structure we are not yet fully acquainted."[10] In 1887, paleontologist Georg Baur (1859–1898, Fig. 1D) presented a first characterization of the Tübingen specimen in a longer footnote to a text about other fossils of unclear origin.[11] He coined the generic name *Proganochelys*, literally: the precursor turtle, and in recognition of the Tübingen researcher the species name '*quenstedtii*'.

[5]Jaeger (1828), see also: Plieninger (1846).

[6]UAT signature 236/59: „In den nächsten Tagen fuhren mit dem Kutscher Schmid, Tscherning und mein Vater zur Stelle. Mein Vater beguckte sich den Block: »Ja, was ist das, Tscherning, da haben sie einen merkwürdigen Fund gemacht. Das ist der Steinkern einer großen Schildkröte im Keuper die sonst erst im oberen Jura zu finden waren.« Ein neuer Fund! Jägers *Mastodonsaurus*, der *Zanklodon* und jetzt die Schildkröte. 3 wichtige Funde aus Schwaben."

[7]It actually contained the epiplastral processes of the plastron, structures that were reduced in later turtles and which likely correspond to our collarbones (clavicle).

[8]Fraas (1899), p. 402: „manches Jahr [...] unbearbeitet in der Tübinger Sammlung lag"

[9]Ibid.

[10]Cope (1873), see also Cope (1883).

[11]Baur (1887): comments on the steinkern on p. 17–18; The origin of the ichthyosaurs was and is, like that of the turtles, relatively unclear - hence the note about our turtle appears in this article on ichthyosaurs.

METHODS

The 3D surface of the steinkern was generated using an Artec Eva hand scanner and associated software Artec Studio 14. The 3D surface model is provided in .ply format, and can therefore be opened with a wide range of freeware.

DISCUSSION

Fight for reputation and priority?

Quenstedt was angry with Baur's (1887) publication of 'his' turtle. His son Werner Quenstedt reported: "The block was brought to the Tübingen collection and my father studied it for a long time. The news spread among the specialists. One day professor Georg Baur, the son of forest professor Baur in Munich, came from Chicago and scientifically acquired the find. Without asking my father, he published the turtle and named it. It wasn't until a year later that my father came to publish the find [...]. He named the animal »*Psammochelys Tscherningi*[12]« (ψάμμος sand and Χέλυς turtle). Georg Baur described the find incorrectly and mixed up the front and back of the turtle."[13]

However, in his publication, Quenstedt (1889b) argued very confidently in relation to Baur's (1887) article and referred only to the scientific flaw: "Dr. G. Baur in New Haven, from whom I, like many other friends of the matter, did not want to withhold the visit, unfortunately, seems to have not noted this most important of all marked characteristics [namely: 'the fusion point of the dorsal and abdominal shield in the area of the middle ribs'], on which the former [sic] secure position in the [phylogenetic] system is based. At this fleeting and not entirely error-free remark, I was therefore a little shocked to find a name *Proganochelys Quenstedtii* for our cause without having been asked about it beforehand [...]."[14]

That Baur (1887) carried out intensive investigations on the steinkern himself is testified by the detailed measurements of the stone core given above - Quenstedt (1889b) gave more coarse measurement data.[15] Was it for Baur about priority when he named the species? Quenstedt was probably not annoyed that someone had published the find - as a researcher he was mainly

[12]The term "*Tscherningi*" was never used by F. A. Quenstedt or elsewhere in the scientific literature and might have been coined as such only in the memories of his son.

[13]UAT 236/59, p. 21: „Der Block wurde in die Tübinger Sammlung gebracht und Vater studierte noch lange an ihm herum. Die Kunde verbreitete sich unter den Fachgenossen. Eines Tages kam Georg Baur aus Chicago, Professor, der Sohn von Forstprofessor Baur in München, und eignete sich den Fund wissenschaftlich an. Ohne meinen Vater zu fragen, veröffentlichte er die Schildkröte und benannte sie. Mein Vater kam erst ein Jahr später zur Veröffentlichung des Fundes [...]. Er benannte das Tier »*Psammochelys Tscherningi*« (ψάμμος Sand und Χέλυς Schildkröte). Georg Baur hat den Fund falsch beschrieben und vorn und hinten an der Schildkröte verwechselt."

[14]Quenstedt (1889b), p. 121: „Herr Dr. G. Baur in New Haven, dem ich die Besichtigung, wie manchem andern Freunde der Sache, doch nicht wohl vorenthalten mochte, scheint dieses wichtigste aller markierten Kennzeichen [nämlich: „die Verwachsungsstelle des Rücken- und Bauchschildes in der Gegend der mittleren Rippen"], auf dem vielleicht die einstige [sic] sichere Stellung im Systeme beruht, leider gar nicht bemerkt zu haben. Bei dieser flüchtigen und nicht ganz fehlerfreien Bemerkung war ich daher etwas betroffen, einen Namen *Proganochelys Quenstedtii* für unsere Sache zu finden, ohne darüber vorher befragt zu sein [...]."

[15]Quenstedt (1889b), p. 120; he measured 57 cm x 55 cm x 26 cm.

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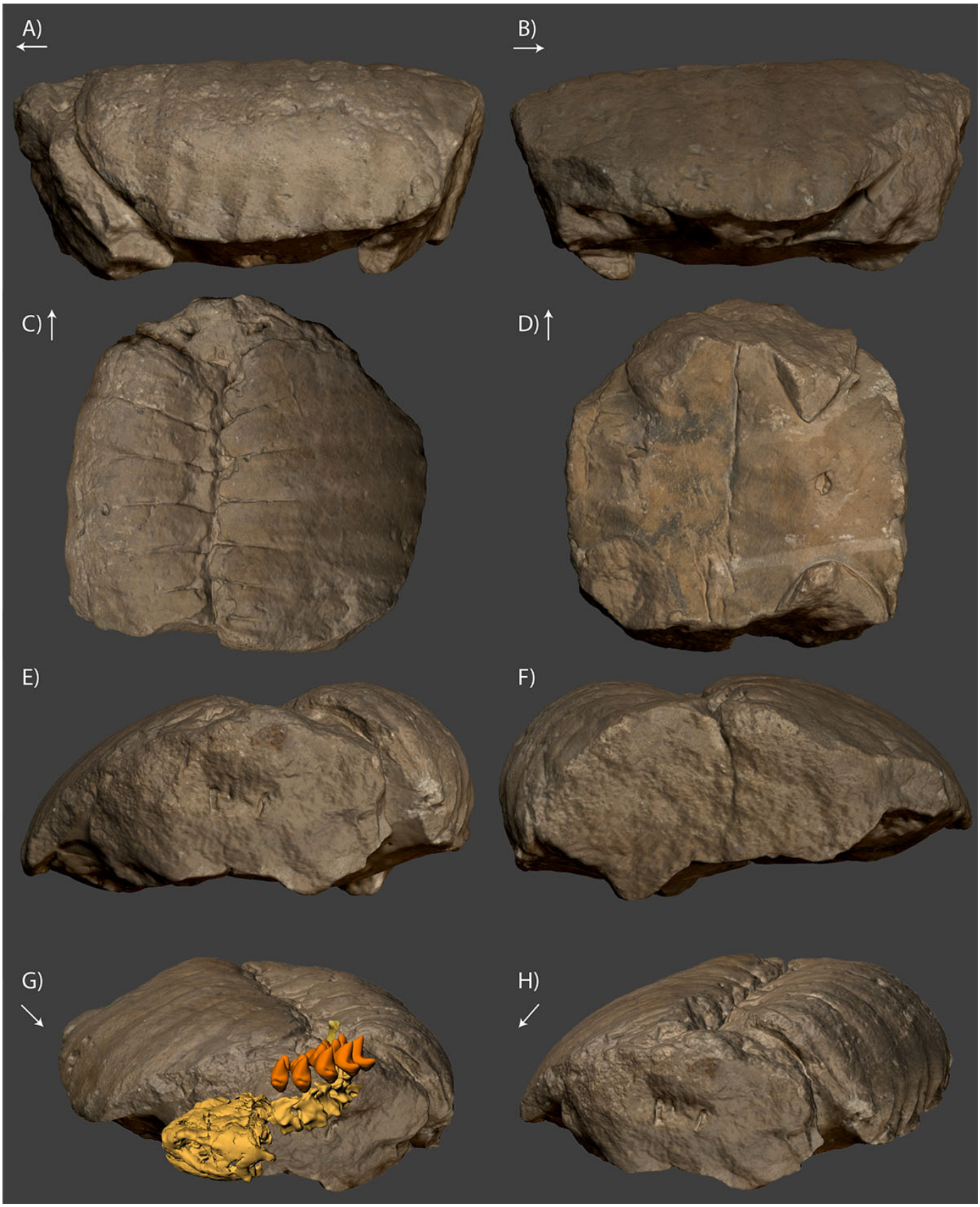

Figure 2. Surface views of the scan of the steinkern of *Proganochelys quenstedtii*. A) left lateral, **B)** right lateral, **C)** dorsal, **D)** ventral, **E)** anterior, **F)** posterior view. Arrows indicate anterior. In G, a 3d model of a retracted neck is added with skull and neck vertebrae (light orange) and dorsal neck osteoderms (dark orange) (modified from Werneburg et al. 2015). The steinkern was scanned with an Artec Surface Scanner. The surface file is available in the online supplement to this article.

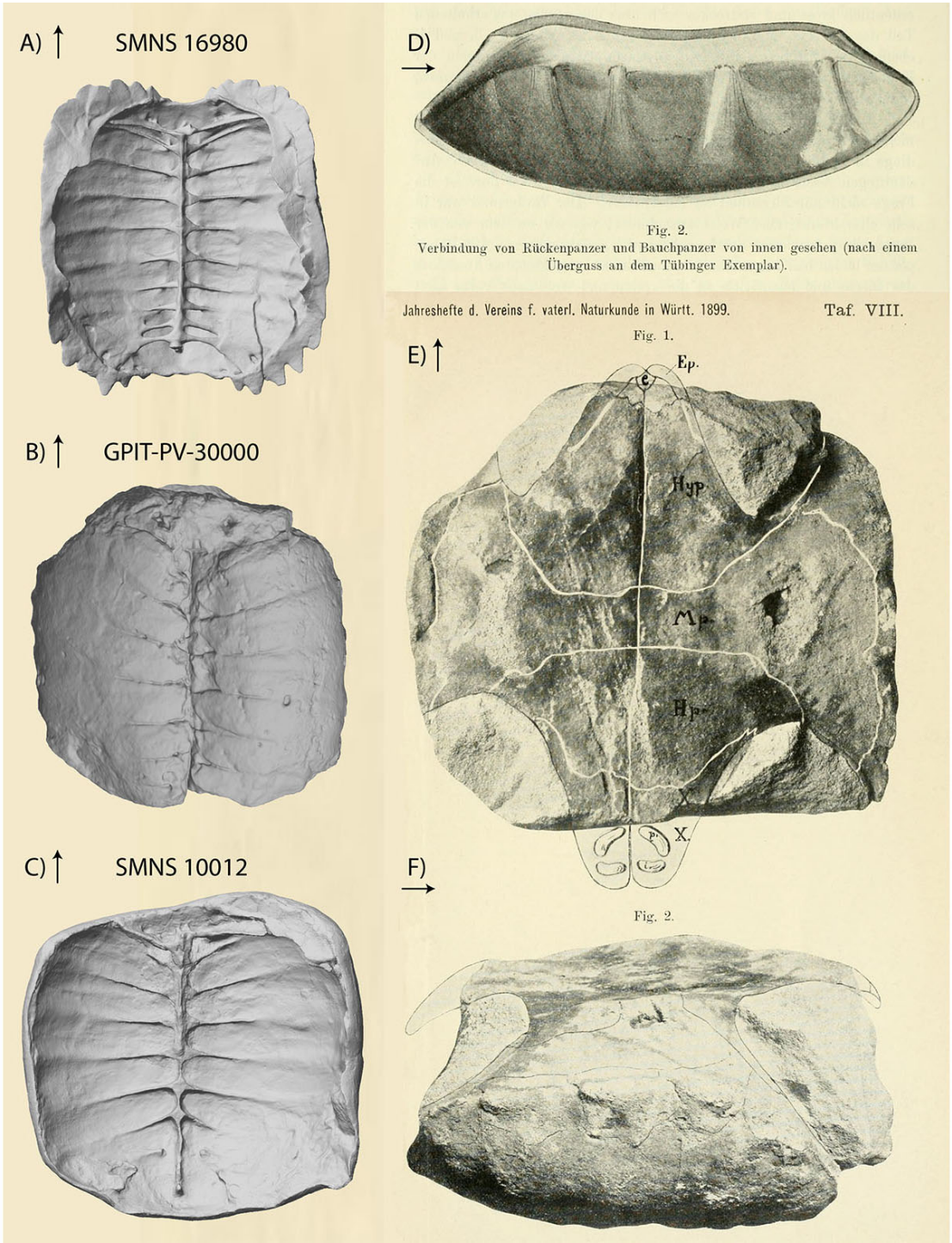

Figure 3. Comparisons of the steinkern. A-C) 3d-models with (B) an inverted view (digital positive from the original negative) of the Tübingen steinkern in comparison with (A, C) inside views of the carapaces stored in Staatliches Museum für Naturkunde Stuttgart (SMNS). A: discovered 1932 in Trossingen, C: discovered 1897 in Aixheim-Neuhaus. **D)** Text figure 2 of Fraas (1899) with the caption: "connection of carapace and plastron from internal view (based on a cast of the Tübingen specimen)". **E-F)** Plate VIII of Fraas (1899) with (E) ventral and (F) left lateral view of the steinkern together with indications of sutures based on a somewhat better-preserved impression of the plastron of SMNS 10012 (partially inaccurate, as evidenced by subsequent specimens). Arrows indicate anterior. Note that the specimen is presented upside down in D and F.

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focused on invertebrate fossils - but he was annoyed that such an important scientific issue, which was very clear to him, was not recognized. Shortly before his death, Quenstedt sat down to the extensive description of the specimen and assigned a new species term for the steinkern: "*Psammochelys keuperina*"; with "*keuperina*" referring to the lithostratigraphic unit of the Keuper in the Late Triassic (about 230-200 million years ago), in which the piece was found. Contrary to Quenstedt's first impression, however, Baur was very conscientious in his work: shortly after his "fleeting" note on *Pr. quenstedtii* (Baur 1887), on June 9th 1888, he submitted a detailed phylogenetic discussion to the journal "Anatomischer Anzeiger". This study, which was still published in the same year (Baur 1888), was a part of an article series on the osteology of all known reptiles. Baur (1888) also discussed the shell connection, which was so important for Quenstedt. So Baur's earlier note was only a pre-emptive of the main publication. Quenstedt apparently knew nothing of this publication when he was writing his own article. Whether he found out about it later - Quenstedt died a year after Baur's extensive publication on December 21, 1889 - is not known.

Comparison with bone material

"In the year [18]87 my father came to Munich and showed [the important paleontologist Karl Alfred von] Zittel [1839–1904] his picture of the animal. He did not know Zittel personally and treated him as if he was talking to Professor Schwager [1837–1891][16]. It was only when my father together with Zittel went over to Groth [1843–1927] [17] to the mineralogical collection that the matter was cleared up. Father had said to Zittel: »Zittel does not want to believe that it is a turtle«. Tableau!"[18] Quenstedt (1889b) commented on his own illustrations (Fig. 1F-H) that "all the figures were not drawn through the mirror"[19], that is, apparently for reasons of limited time, they were only drawn freehand and were not one hundred percent true to scale. It is often proven that Quenstedt himself was not a good draftsman.[20] For that, he had hired university draftsmen. The illustrations in Quenstedt's last scientific work were made by the lithographer Baumann ["lith. v[on] Baumann, Tübingen"], as can be read on the published plates (see Fig. 1F).[21] Also, paleontologist Eberhard Fraas (1862–1915, Fig. 1E) criticized the poor quality of the drawings: "In particular, the illustrations by Quenstedt are not very successful and can often lead to errors".[22] However, he admits that the steinkern itself "gives excellent information about the shape, but unfortunately leaves us in the dark about the composition of the armor in many cases."[23] Fraas' article appeared in the same journal in 1899 as Quenstedt's work ten years earlier, in "Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg" (Fig. 3D-F). In the meantime, Quenstedt had died, Ernst Koken (1860–1919) had become director of the institute (1895–1919) in Tübingen, and in Aixheim-Neuhaus near Trossingen, Baden-Württemberg, Germany, the first unambiguous bones of *Proganochelys quenstedtii* were recovered in 1897 (Staatliches Museum für Naturkunde Stuttgart, Germany, collection number: SMNS 10012; see Fig. 3C) (Gaffney 1990). Fraas (1899) reported on them in his work. With Koken's permission, he examined the Tübingen steinkern again and even made a cast of the scientifically significant side of the shell region, which produced a positive impression of the medial side of the shell (Fig. 3D).[24] With the help of the new bone material (compare to Fig. 3A-C), Fraas finally succeeded in identifying the exact bone boundaries on the steinkern. He also published photographs on which he made drawings for clarification (Fig. 3E-F). But its reconstruction also received some criticism in the period that followed, and Quenstedt's (1889b) interpretations were partially declared valid again.[25] The last detailed description of the steinkern was published by Eugene S. Gaffney (1990) in his famous monograph on the anatomy of *P. quenstedtii*.[26]

[16] Conrad Joseph Johann Schwager, geologist and micropaleontologist

[17] Paul Heinrich Ritter von Groth, cristallographist and mineralogist

[18] UAT 236/59, p. 22: „Im Jahr [18]87 kam Vater nach München und zeigte [dem bedeutenden Paläontologen Karl Alfred von] Zittel [1839–1904] seine Abbildung des Tieres. Er kannte Zittel nicht mehr persönlich und verkehrte mit ihm, als ob er mit Professor Schwager redete. Erst als Vater zu Groth mit Zittel hinüberging in die mineralogische Sammlung, klärte sich die Sache auf. Vater hatte zu Zittel gesagt: »Zittel will es nicht glauben, daß es eine Schildkröte sei«. Tableau!".

[19] [„[s]ämtliche Figuren nicht durch den Spiegel"]

[20] UAT 236/59, p. 19.

[21] University artist Karl Friedrich Baumann (1798–1879), see also: von Engelhardt and Hölder (1977), p. 124.

[22] Fraas (1899), p. 402: „Insbesondere sind die Abbildungen bei Quenstedt nicht sehr gelungen und können vielfach zu Irrtümern führen."

[23] Fraas (1899), p. 402: „über die Formverhältnisse vortrefflichen Aufschluß giebt, aber uns leider bezüglich der Zusammensetzung des Panzers vielfach im Dunkeln lässt."

[24] Ibid.

[25] Ballerstedt (1922).

[26] Gaffney (1990); See also Joyce (2007)

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