Juvenile sea turtles *Glarichelys* from the Oligocene of Czechia and Poland provide new insights into early ontogeny and distribution of the genus

TOMASZ SZCZYGIELSKI, MILAN CHROUST, MAŁGORZATA CZAJA, RAFAŁ PIECHOWSKI, GEORGIOS L. GEORGALIS, IWONA KANIA-KŁOSOK, and PIOTR WĘGIEREK



Szczygielski, T., Chroust, M., Czaja, M., Piechowski, R., Georgalis, G.L., Kania-Kłosok, I., and Węgierek, P. 2026. Juvenile sea turtles *Glarichelys* from the Oligocene of Czechia and Poland provide new insights into early ontogeny and distribution of the genus. *Acta Palaeontologica Polonica* 71 (4): 743–779.

Glarichelys knorri (Chelonioidea) is one of the most famous fossil sea turtles; however, our knowledge about its taxonomy, geography, or stratigraphy is poor. Here, we revised the Swiss holotype material from the Canton of Glarus, together with the Polish and Czech referred material from the Menilite Formation: Winnica (Poland), Hermanowa (Poland), and Litenčice (Czechia), all dated to the Oligocene. All of the described material exhibits juvenile characters, except for the presence of well-ossified autopodia, which makes the diagnosis of the taxon even more puzzling. Thanks to the exceptional preservation of the Polish specimens, remnants of soft tissues, such as imprints of paddles, shell scutes, and digestive tract are described. After our review, the representatives of the genus *Glarichelys* are restricted to the Oligocene of Switzerland, Czechia, and Poland, with a single valid species.

Key words: Testudines, Chelonioidea, Pan-Cheloniidae, turtle, juvenile, ontogeny, Menilite shales, Oligocene, Europe.

Tomasz Szczygielski [t.szczygielski@twarda.pan.pl; ORCID: https://orcid.org/0000-0001-5108-8493] and Rafał Piechowski [rdpiechowski@gmail.com; ORCID: https://orcid.org/0000-0003-2779-6929], Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, 00-818 Warsaw, Poland.

Milan Chroust [chroust@gli.cas.cz; ORCID: https://orcid.org/0000-0003-3301-5578], Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, 00-818 Warsaw, Poland; Institute of Geology, Czech Academy of Sciences, Rozvojová 269, 16500, Prague, Czechia.

Małgorzata Czaja [malgorzata.a.czaja@gmail.com; ORCID: https://orcid.org/0009-0002-1634-4230], Faculty of Biology and Environmental Science, Cardinal Stefan Wyszyński University, Wóycickiego 1/3, 01-938 Warsaw, Poland.

Georgios L. Georgalis [georgalis@isez.pan.krakow.pl; ORCID: https://orcid.org/0000-0001-7759-6146], Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland.

Iwona Kania-Kłosok [ikania@ur.edu.pl; ORCID: https://orcid.org/0000-0002-2325-4308], Faculty of Biology, Nature Protection and Sustainable Development, University of Rzeszów, Zelwerowicza 4, 35-601 Rzeszów, Poland.

Piotr Węgierek [piotr.wegierek@us.edu.pl; ORCID: https://orcid.org/0000-0001-9960-0433], Institute of Biology, Biotechnology and Environmental Protection, Faculty of Natural Sciences, University of Silesia, Bankowa 9, 40-007 Katowice, Poland.

Received 24 April 2026, accepted 24 July 2026, published online 27 November 2026.

Copyright © 2026 T. Szczygielski et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License (for details please see http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Glarichelys knorri (Gray, 1831) is among the historically oldest mentioned fossil turtles, with the history of publications reaching the mid-18th century and far preceding the formal establishment of the species. The first report of a fossil turtle from the Oligocene of Matt, Glarus Canton, Switzerland (now catalogued under the number PIMUZ A/III 596; Fig. 1) was reported by Knorr (1755), accompanied by rather poor and uninformative drawings of unprepared slab and counterslab, with bones obscured by a layer of sediment. The specimen was mentioned soon after by Gessner (1756). Andreae (1776) provided somewhat more informative figures and further description. Gmelin (1778) reprinted Andreae's (1776) figures and referred the specimen to *Amphibiolithus*

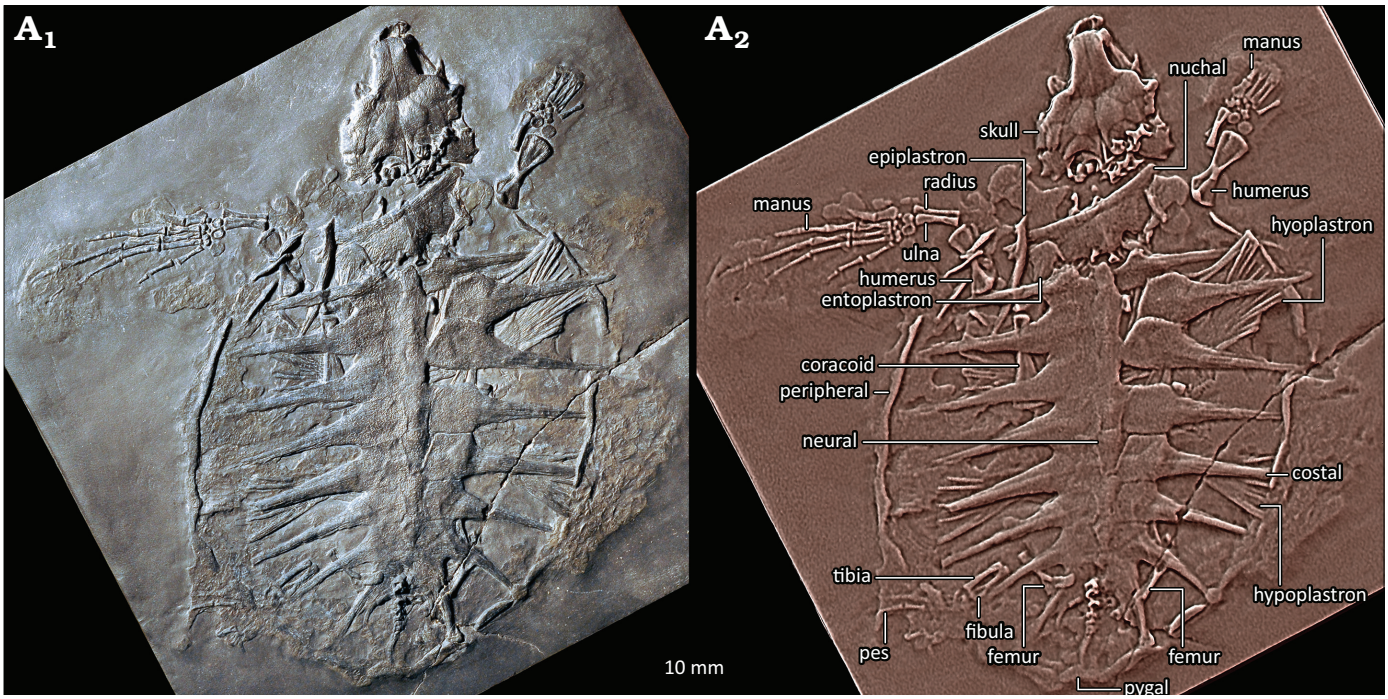


Fig. 1. Sea turtle *Glarichelys knorri* (Gray, 1831), PIMUZ A/III 596 (holotype) from Glarus, Switzerland, Rupelian. Almost complete skeleton: A_1, specimen exposed in dorsal view (photograph courtesy of Torsten Scheyer, © Paläontologisches Institut, Universität Zürich); A_2, 3D model presented with the Radiance Scaling (Lit Sphere) shader enabled.

testudinis, a taxon of fossils (separate from animal taxonomy) first established by Linnaeus (1735), and subsequently repeated this referral in the 13th edition of "Systema naturae" (1793). Cuvier (1809, 1812, 1824) published a redrawing of one of Andreae's (1776) figures and was the first to explicitly identify the specimen as a marine turtle (Cuvier 1809, 1810a, b, 1812, 1824, 1836b). Note, however, that despite Cuvier's claim that the fossil was interpreted as a pond turtle by Andreae (1776), this is not apparent in Andreae's text: he first mentioned it in a note regarding another specimen from "the limestone of Berling", which he referred to "Testudine aquarum dulcium" (freshwater turtle), but treated them separately and did not state that both turtles represented the same form (Andreae 1776: 5). The official establishment by Gray (1831) of the new species *Chelonia knorri*, referred at the time to the wastebasket genus *Chelonia*, took place over 75 years after the discovery. Even though Gray (1831) lacked any description, illustrations, or definition of characters, he still listed some indications to earlier documentation of the specimen and therefore the name *Chelonia knorri* became available according to ICZN (1999). Soon after, an objective younger synonym, *Chelonia glaricensis* Keferstein, 1834, was proposed with no reference to Gray's (1831) work. A reprint of Cuvier's (1809, 1812, 1824, 1836a) figure with a short description but with no taxonomic identification was also published by Buckland (1836a, b). Meyer (1838) examined the original fossil, redescribed it in much more detail. Later, Meyer (1856) provided another set of figures, albeit still prior to preparation. The second specimen (slab NWSGL-EF-100789 and counterslab NWSGL-EF-100790) from the same area (first mentioned by Steinmüller 1802) was briefly described as *Chelonia ovata* Heer, 1865, based on a more pronounced posterior elongation of the carapace (Fig. 2), a conclusion accepted later by Maack (1869). Wettstein (1886) provided a photograph of another specimen (articulated costals and neurals exposed in visceral view) referred to *Chelonia ovata*. Peyer (1950: pl. 14) was the first to include a photograph of the prepared Matt specimen, labelled simply as "Glarner Schildkröte", and Stüssi (1950) attempted to retrodeform it using mathematical equations. A more complete description of the Glarus slate turtles by Zangerl (1958), with a much better documentation (the Matt specimen PIMUZ A/III 596 as the holotype, NWSGL-EF-100789 + NWSGL-EF-100790, and three more: PIMUZ A/III 85, PIMUZ A/III 594 [Fig. 3] and PIMUZ A/III 593 [Fig. 4]) explicitly synonymized the species *Chelonia ovata* with *Chelonia knorri*, and erected the new genus, *Glarichelys* Zangerl, 1958. This synonymy was followed by Kuhn (1964). A summary of the early history of the holotype and NWSGL-EF-100789 + NWSGL-EF-100790, as well as photographs of casts of both slabs of the holotype in the unprepared state, accompanied by reproductions of early drawings, were later published by Leu (1998). Furrer (1998) presented additional photographs of three of the specimens described by Zangerl (1958).

The second half of the 20th and beginning of the 21st century brought a number of finds from various localities being referred to the genus *Glarichelys* and several taxa being synonymized with that genus or its species. A specimen from the Eocene Mo Clay Formation of the Island of Fur, Denmark, was referred to *Glarichelys* sp. by Nielsen (1959), who noted that its first neural is proportionally larger than in *G. knorri*. Madsen (2008) provided new photographs of that

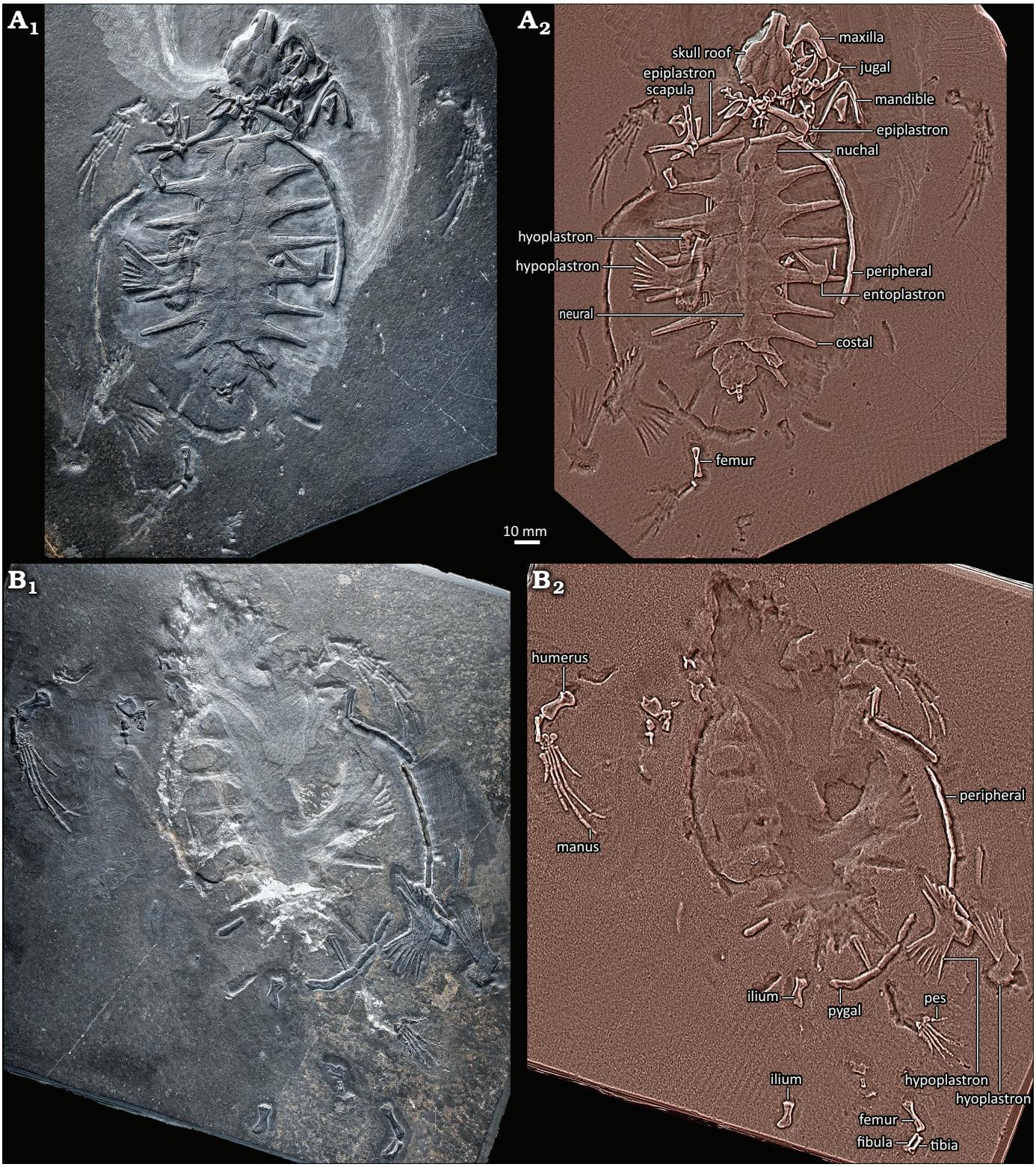


Fig. 2. Sea turtle *Glarichelys knorri* (Gray, 1831) (holotype of *Chelonia ovata* Heer, 1865) from Glarus, Switzerland, Rupelian. **A**. NWSGL-EF-100789, slab presenting most of the skeleton in dorsal view. **B**. NWSGL-EF-100790, counterslab with a partial imprint of the dorsal surface of the skeleton and some bones exposed in ventral view. A_1, B_1, photographs, A_2, B_2, 3D models presented with the Radiance Scaling (Lit Sphere) shader enabled. Photographs courtesy of Heinz Furrer (© Canton Glarus).

specimen and expressed doubts about its generic identity, whereas Karl and Madsen (2012) reassessed it as a juvenile of *Puppigerus* sp. Two individuals attributed to *Glarichelys knorri* were found in the Rupelian (lower of the two formal divisions of the Oligocene) Menilite shales of Winnica (near Jasło), Poland—one of them subsequently lost and the other

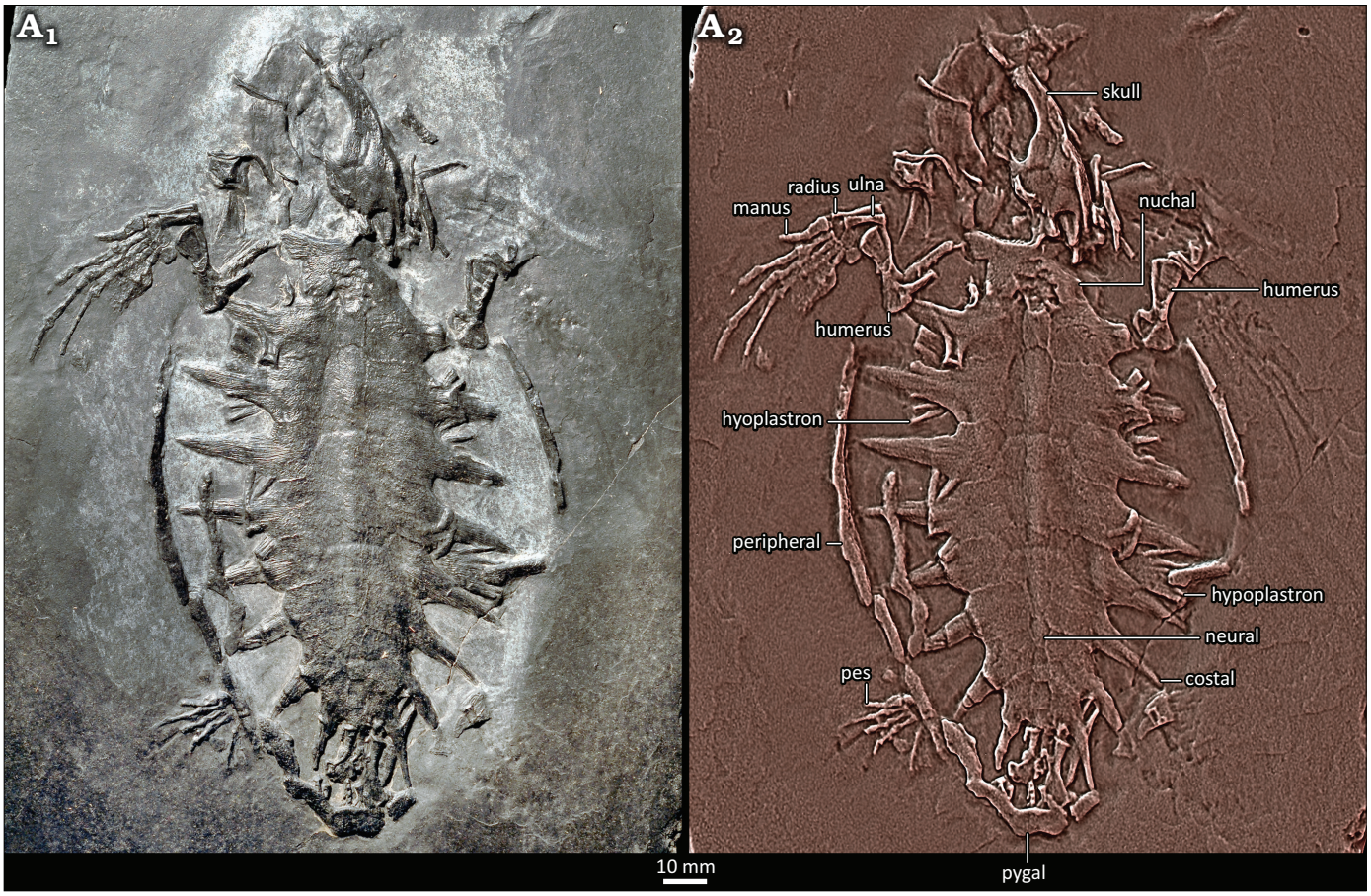


Fig. 3. Sea turtle *Glarichelys knorri* (Gray, 1831), PIMUZ A/III 594 from Glarus, Switzerland, Rupelian. Subcomplete, mostly articulated skeleton: A_1, specimen exposed in dorsal view (photograph courtesy of Torsten Scheyer, © Paläontologisches Institut, Universität Zürich); A_2, 3D model presented with the Radiance Scaling (Lit Sphere) shader enabled.

one (first announced by Kadyi 1958) published by Młynarski (1959). Later, Młynarski (1984) revised the identification of the Winnica turtle to *Glarichelys* cf. *knorri*, citing the small sample and the juvenile ontogenetic stage of the individual. However, Gregorová and Młynarski (1992) once again referred to the Polish material as *Glarichelys knorri* and reported a new specimen, MZM Ge 27364, from the Rupelian Litenčice locality of Moravia (Czechia). Subsequently, Přikryl et al. (2016) reported but did not figure a specimen of ?*Glarichelys* sp. from the Rupelian Hermanowa locality of Poland. The presence of *Glarichelys knorri* in Germany was inferred by Darga et al. (1999), based on an isolated scapula and coracoid (two specimens but presumably belonging to a single individual; however, later listed as coming from two different horizons by Karl 2002a) from the Chattian (upper Oligocene) of Hochberg (Galon-Graben) described as cf. *Glarichelys knorri*. Micklich and Hildebrandt (2010) presented a new small specimen from the Rupelian of Unterfeld (Germany) which they tentatively referred to cf. *Glarichelys* sp. Alexander and Frey (2010) and Maxwell et al. (2016) reported several specimens of juvenile and adult turtles from the Rupelian of Rauenberg (Germany) resembling either *Glarichelys knorri* or "*Chelonia*" *gwinneri* Wegner, 1911, at least one of them with fossilized contents of the digestive tract, but they also noted their unique combination of morphological characters, so they did not identify them at the generic level and considered a possibility of interspecific hybridization.

The question of a further expansion of the taxonomic contents of *Glarichelys* was mostly related to the generic identity of the largely complete skeleton of a similar but larger form from Rupelton near Flörsheim (Germany), SMF-R 263, described initially (Wegner 1911) as *Chelone gwinneri* and soon after (Wegner 1914) emended to *Chelonia gwinneri* (the holotype also figured by Drevermann 1914). Although Zangerl (1958) acknowledged the fact that the known individuals of *Glarichelys knorri* were immature, discussed the possibility that "*Chelonia*" *gwinneri* may be an adult stage of the same species and contested its referral to the genus *Chelonia*, he noted several differences in the skull (paired parietal scale and broader interorbital bridge, which he deemed insignificant), shell (possibly ontogenetic), and forelimbs (elongation of the distal phalange of the first digit and four phalanges in the fourth digit, considered much more substantial) of that species. Młynarski (1959) noted some resemblances between the Winnica turtle and "*Chelonia*" *gwinneri* and agreed with the doubtful generic identity of the later species, but he ultimately refuted a close relationship between

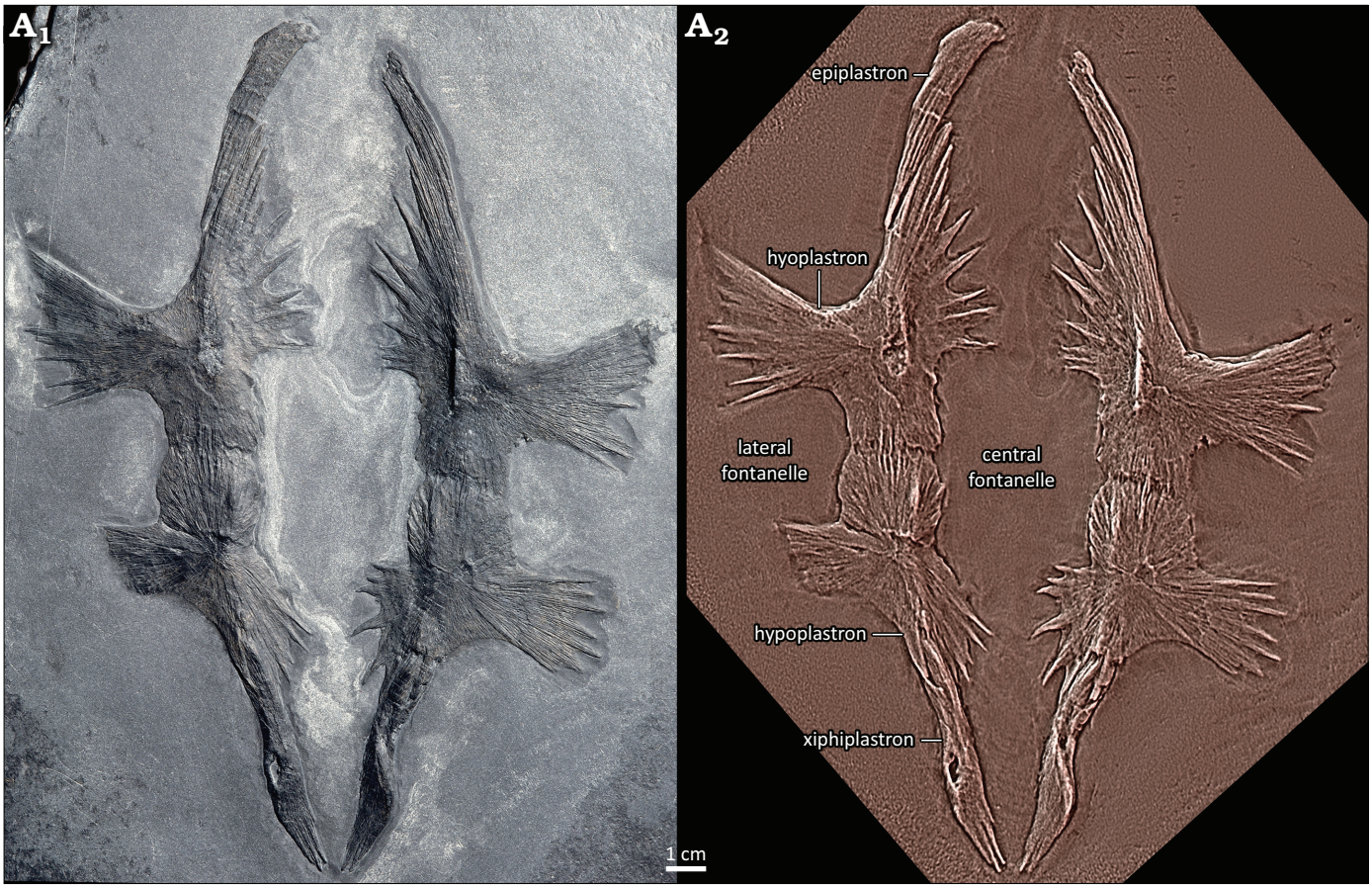


Fig. 4. Sea turtle *Glarichelys knorri* (Gray, 1831), PIMUZ A/III 593 from Glarus, Switzerland, Rupelian. Isolated plastron of a large individual missing anterior part of the left epiplastron and the entoplastron exposed in ventral view: A_1, photograph courtesy of Heinz Furrer (© Canton Glarus); A_2, 3D model presented with the Radiance Scaling (Lit Sphere) shader enabled.

the two (and, by extension, with *G. knorri*). Kuhn (1964) reiterated Zangerl's (1958) and Młynarski's (1959) systematic assessment. However, later Młynarski (1976) suggested that "*Chelonia*" *gwinneri* could be identical to *G. knorri* but did not explicitly synonymize them. Kuhn (1971) listed "*Chelonia*" *gwinneri* as possibly belonging either to the genus *Glarichelys* or a new genus. Aslanova et al. (1979) were the first to formally and explicitly recombine "*Chelonia*" *gwinneri* as *Glarichelys gwinneri*, ignoring Zangerl's (1958) reservations, and referred to that species finds from Chelkar-Tenis (Tchelkar-Teniz) of Kazakhstan (Chkhikvadze 1969, 1983), Oligocene of Piatra Neamţ of Romania (described two years earlier as *Chelonia oligocena* Ciobanu, 1977; unjustly considered a nomen nudum by Vremir 2004), as well as new specimens from the Oligocene outcrops of Ashchitaypak (Kazakhstan) and Perekishkul (Azerbaijan; introduced as *Islamichelys azerbajdzanica* in the unpublished thesis of Aslanova (1969), which is apparently a nomen nudum, as it was eventually aptly deemed so by Chkhikvadze 1977). Gregorová and Młynarski (1992), seemingly independently from Aslanova et al. (1979), considered Ciobanu's (1977) specimen to likely represent the same species. Karl and Tichy (1999) and Karl (2002b) synonymized "*Chelonia*" *gwinneri*, the Oligocene "*Chelyopsis*" *holsaticus* Dames, 1894, and "*Chelyopsis*" *halleri* Karl, 1989 (see also Müller 1983; Karl 1995) from Germany, "*Chelyopsis littoreus*" Van Beneden in Smets, 1886, from the Oligocene of Belgium, as well as the Eocene "*Chelyopsis*" *raabei* Karl & Schleich in Schleich et al., 1994 from Germany with *Glarichelys knorri* providing no morphological explanation and ignoring Zangerl's (1958) arguments against it. Note that *Chelyopsis littoreus* (the type species for the genus, described in more detail by Smets 1887) is a non-valid taxon, revealed already by Smets (1888) to be a chimaera of *Psephophorus rupeliensis* Van Beneden, 1883, and "*Chelone*" *vanbenedenii* Smets, 1886 (see Weems and Sanders 2014), thus we consider the genus to be a nomen dubium. This extended synonymy of *Glarichelys knorri* was not accepted by Averianov (2002), who repeated Aslanova's et al. (1979) referral and listed the material from Kazakhstan and Azerbaijan as *Glarichelys gwinneri* but with some reservations regarding the material from Tchelkar-Tenis. Lapparent de Broin (2001) referred "*Chelonia*" *gwinneri*, as well as the material from Romania ("*Chelonia*" *oligocena* Ciobanu, 1977) and Kazakhstan (Chkhikvadze 1969, 1983; Aslanova et al. 1979), to the genus *Glarichelys*, but did not specify their specific identity. The attribution of the species "*Chelonia*" *gwinneri* to the genus *Glarichelys* was also accepted by Kordikova (2000).

Vremir (2004) considered Romanian material to represent *Glarichelys* sp., possibly *Glarichelys knorri*, rejecting Aslanova's et al. (1979), Karl and Tichy's (1999), and Karl's (2002b) synonymy of that species with "*Chelonia*" *gwinneri*. Danilov (2005) mentioned the genus *Glarichelys* but considered it restricted to Switzerland only. Karl (2007) reiterated the earlier proposed synonymy between *Glarichelys knorri*, "*Chelyopsis*" *halleri*, and "*Chelonia*" *gwinneri*, dismissing all the differences as variability, and referred new material from the Oligocene of Germany. Alexander and Frey (2010) treated "*Chelonia*" *gwinneri* and "*Chelyopsis*" spp. as separate from *Glarichelys knorri* but at the same time considered the material described by Aslanova et al. (1979) and Karl (2002b) to represent the latter species. Weems and Sanders (2014) and Zvonok et al. (2015) accepted the synonymy of *Glarichelys knorri* and "*Chelonia*" *gwinneri* proposed by Karl and Tichy (1999) and Karl (2002b), however, Lapparent de Broin et al. (2014) rebutted it, noting lack of convincing arguments that would support it. Likewise, Maxwell et al. (2016) dismissed the synonymy between those two species but (probably mistakenly) listed Aslanova's et al. (1979) specimens within the hypodigm of *Glarichelys knorri* rather than "*Chelonia*" *gwinneri*. Danilov et al. (2017) refuted Aslanova's et al. (1979) referral of the material from Azerbaijan and Kazakhstan to the genus *Glarichelys* (instead listing them as Cheloniidae indet.) and considered the genus *Chelyopsis* to be valid and distinct. Finally, Lapparent de Broin et al. (2018) accepted the congenericity of the species *Glarichelys knorri* and "*Chelonia*" *gwinneri* but considered them distinct and in their comparisons only acknowledged specimens of *Glarichelys knorri* from Glarus tackled by Zangerl (1958) and the specimen SMF-R 263 (holotype) of "*Chelonia*" *gwinneri* from Flörsheim (Wegner 1911, 1914).

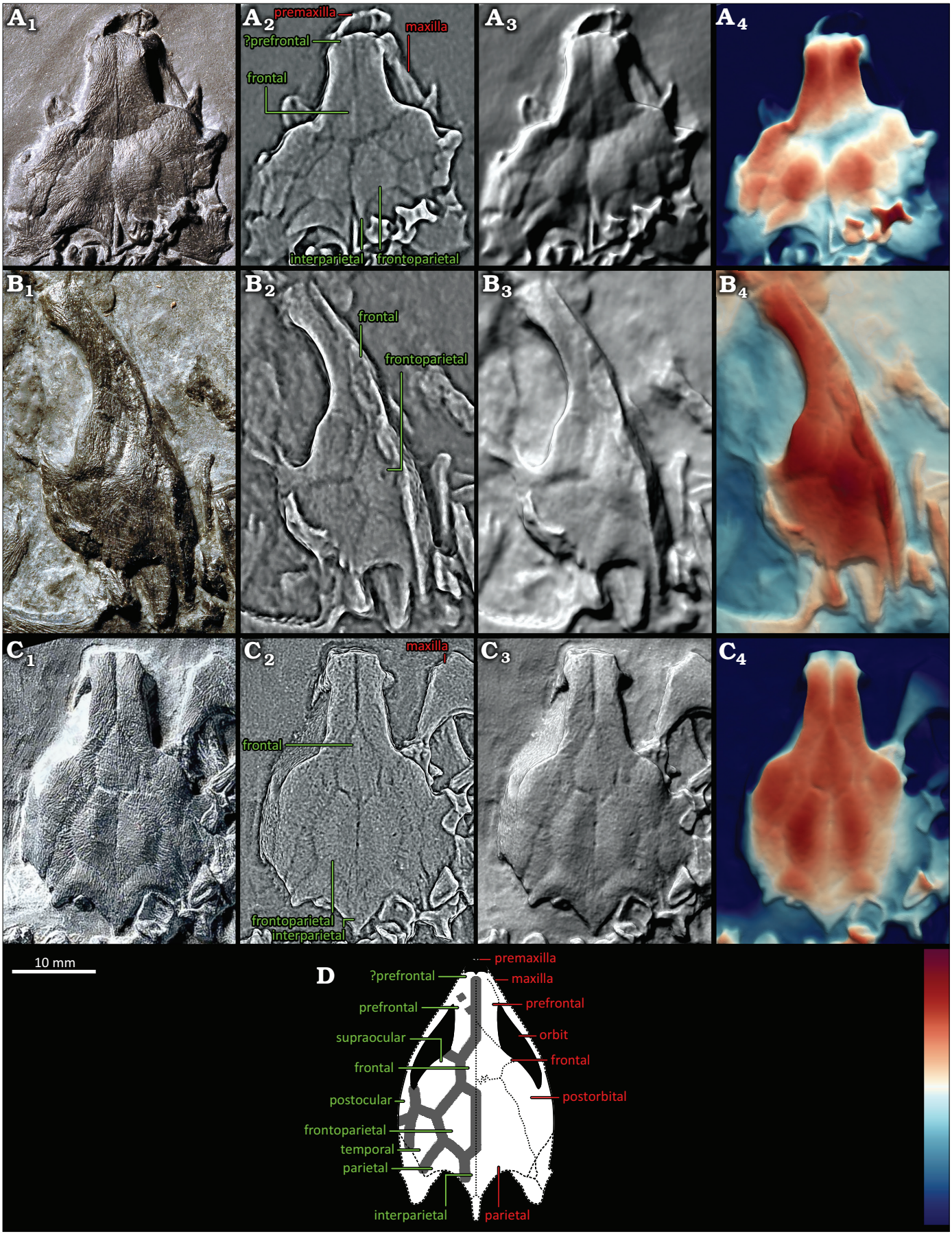
The aim of this work is to revise the specimens from Poland and Czechia historically attributed to the genus *Glarichelys*, document their morphology, and validate their taxonomic identification.

Institutional abbreviations.—CSIP, UK Cetacean Strandings Investigation Programme, London, UK; DK, Danekræ, Danish national treasure registration (formally maintained by the NHMD), Copenhagen, Denmark; FAUHS, Florida Atlantic University High School Owls Imaging Lab and Collection, Boca Raton, USA; FUM, Fur Museum, Fur, Denmark; ISEA, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland; KHG, Kunsthaus Glarus, Glarus, Switzerland; KU, University of Kansas Biodiversity Institute, Lawrence, USA; MB, Museum für Naturkunde, Berlin, Germany; MIM, Mineral Museum, Beirut, Lebanon; MNSPN, Museum of Natural Sciences of Piatra Neamț, Romania; MSNUP, Museo di storia naturale dell'Università di Pisa, Calci, Italy; MRJ, Kadyi Regional Museum, Jasło, Poland; MZM, Moravské Zemské Muzeum, Brno, Czechia; NHMD, Natural History Museum of Denmark, Copenhagen, Denmark; NHMUK, Natural History Museum, London, UK; NKM, Südostbayerisches Naturkunde- und Mammut-Museum Siegsdorf, Germany; NML, Naturkundemuseum Leipzig, Germany; NWSGL, Naturwissenschaftliche Sammlungen Glarus, Switzerland; PIMUZ, Paläontologisches Institut, Universität Zürich, Switzerland; SMF, Naturmuseum Senckenberg, Frankfurt am Main, Germany; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany; UF, Florida Museum of Natural History, University of Florida, Gainesville, USA; UR, University of Rzeszów, Poland; WAM, Western Australian Museum, Perth, Australia; YPM, Yale Peabody Museum, New Haven, USA.

Geological setting

The Hermanowa outcrop (GPS latitude 49.934266; longitude 22.019500) is located in the SE Poland, ca. 8 km south of Rzeszów, Podkarpackie Voivodeship. It is located in the ichthyofaunistic zone IMP2 with the presence of the index species *Trachinus minutus* (Jonet, 1958), distributed in all parts of the profile (Kotlarczyk et al. 2006; Přikryl et al. 2016). The age of the site is determined to be Rupelian (Oligocene), NP 23 calcareous nanoplankton Zone (Kotlarczyk et al. 2006). Fossils of fish skeletons occur throughout the profile, but some of the layers are definitely richer in remains. These layers include the "R" layers, H28, H31, H3, H5, H8, H10/H9, H13, H21, H22 (Alfred Uchman, personal communication 2007; Přikryl et al. 2016). However, the layers richest in fish skeleton fossils are H3 and H5. In the lower part of the H5, early developmental stages of some taxa, mainly *Glossanodon musceli* (Paucă, 1929), are the most common. The specimens of *Glarichelys knorri* UR/1055 and UR/1056 were found in the layer H4 of the profile. The profile is very abundant in fossilized *Glossanodon musceli*,

Fig. 5. Details of the skulls of *Glarichelys knorri* (Gray, 1831), from Glarus, Oligocene. **A**. PIMUZ A/III 596 (holotype), closeup of the skull in dorsal view: →
A_1, photograph; A_2, 3D model presented with the Radiance Scaling (Grey Descriptor) shader enabled and increased contrast to visualize the sutures and scale borders; A_3, 3D model lit at a low angle to enhance geometry of the skull roof; A_4, the same with elevation map. Note the presence of subtly marked triangular fields in the anteromesial part of the snout, and a pentagonal or hexagonal field wedging between the frontoparietal scute areas, interpreted here, respectively, as prefrontal and interparietal scale areas. **B**. PIMUZ A/III 594, closeup of the skull roof in dorsolateral left view: B_1, photograph; B_2, 3D model presented with the Radiance Scaling (Grey Descriptor) shader enabled and increased contrast to visualize the sutures and scale borders; B_3, 3D model lit at a low angle to enhance geometry of the skull roof; B_4, the same with elevation map. **C**. NWSGL-EF-100789, closeup of the skull in dorsal view: C_1, photograph; C_2, 3D model presented with the Radiance Scaling (Grey Descriptor) shader enabled and increased contrast to visualize the sutures and scale borders; C_3, 3D model lit at a low angle to enhance geometry of the skull roof; C_4, the same with elevation map. **D**. Reconstruction of the skull showing scales on the left and bones on the right (modified from Zangerl 1958, not to scale). Green lettering, scales; red lettering, bones. A, B, photograph courtesy of Torsten Scheyer (© Paläontologisches Institut, Universität Zürich); C, photograph courtesy of Heinz Furrer (© Canton Glarus).


A1
A2
premaxilla
?prefrontal
maxilla
frontal
interparietal
frontoparietal
A3
A4
B1
B2
frontal
frontoparietal
B3
B4
C1
C2
maxilla
frontal
frontoparietal
interparietal
C3
C4
10 mm
D
premaxilla
?prefrontal
maxilla
prefrontal
prefrontal
supraocular
orbit
frontal
frontal
postocular
postorbital
frontoparietal
temporal
parietal
interparietal
parietal

Sardinella cf. *S. sardinites* (Heckel, 1850), not so numerously represented are species such as *Keasius parvus* (Leriche, 1908), *Physogaleus latus* (Storms, 1894), and other representatives: *Holosteus* sp., *Eophycis jamnensis* Jerzmańska, 1968, *Palaeogadus* sp., Hemiramphidae gen. et sp. indet., Syngnathidae gen. et sp. indet., *Hipposyngnathus neriticus* Jerzmańska, 1968, Centriscidae gen. et sp. indet., *Priacanthus longispinus* Lednew, 1914, *Repropca sabbai* Paucă, 1929, Carangidae gen. et sp. indet., *Oliganodon budensis* (Heckel, 1856), Ammodytidae gen. et sp. indet., *Capros rhenanus* (Weiler, 1920), *Capros* cf. *C. caprosoides* (Cosmovici, 1887), Scombridae gen. et sp. indet., *Anenchelum* sp., *Propercarina problematica* Přikryl et al., 2014, and Pleuronectiformes gen. et sp. indet. (Přikryl et al. 2011, 2014, 2016). In addition, fossilized crabs are found at this site, whereas amniotes (birds, turtles) are rare. The assemblage is dominated by neritic fishes, with a highly diverse range of acanthopterygians. The original bathyal conditions of this site have not been assessed, and typical taxa of meso- and bathypelagic fishes are absent from this outcrop (Přikryl et al. 2016).

The Winnica fossil site is located in the SE Poland, Podkarpackie Voivodeship, ca. 10 km east of Jasło, in the outcrop of Jasiołka stream near the farm Winnica (Kadyi 1958; Młynarski 1959). The material is represented by siliceous brown-grey or beige marlstone (claystone) belonging to the Menilite Formation within the Silesian Unit of the Polish Outer Carpathian Basin and dated to the Rupelian. More particularly, the locality corresponds to the NP 23 calcareous nanoplankton Zone and ichthyofaunal zone IPM2 (Kotlarczyk et al. 2006; Bochenski et al. 2018; Bienkowska-Wasiluk et al. 2025). Besides the turtle found, the locality is famous for plant remains, fish specimens such as *Oliganodon budensis*, *Repropca sabbai*, and *Palaeogadus simionescui* Danil'chenko, 1950, and birds *Eurotrochilus noniewiczi* Bochenski and Bochenski, 2008 and *Winnicavis gorskii* Bochenski et al., 2018 (Kadyi 1958; Kotlarczyk et al. 2006; Bochenski and Bochenski 2008; Bochenski et al. 2018).

The Litenčice site is located in SE Czechia, south Moravia, 42 km east of Brno (Gregorová 2011). Geologically, these sediments belong to the Ždánice Unit (Carpathian flysch), specifically to the Menilite Formation. The Menilite Formation is formally divided into four members: the Subchert Member, the Chert Member, the Dynów Member, and the Šitbořice Member (Krhovský et al. 2001; Jirman et al. 2018). The fossiliferous horizon with fossil turtle remains (MZM Ge 27364) belongs to the Dynów marls, especially rich in fossil fish assemblages (Gregorová and Młynarski 1992; Gregorová 2011; Přikryl 2013). Stratigraphically, the Dynów marls correspond to the NP 23 calcareous nanoplankton Zone (Rupelian). The sediment consists of brown-grey or beige marlstone with siliciferous admixture. The turtle specimen was found in the horizon together with mesopelagic species, which is explained as a carcass drop from the epipelagic level to the deeper water or a simple allochthonous transport (Gregorová and Młynarski 1992).

Material and methods

Specimens ISEA FR/WNC-1 (former ISEA RF/10/74), MRJ 70.1P.-P, MZM Ge 27364, NWSGL-EF-100789 (part of holotype of *Chelonia ovata*), NWSGL-EF-100790 (part of holotype of *Chelonia ovata*), PIMUZ A III/85, PIMUZ A III/594, PIMUZ A III/596 (holotype of *Glarichelys knorri*), UR/1055, UR/1056, and MB.R.5596 (cast of PIMUZ A/III 596 [holotype of *Glarichelys knorri*]) were studied firsthand, photographed, and digitized by the authors (Figs. 1–9A, B, 10–15, 16A–F, SOM: fig. S1 (Supplementary Online material available at http://app.pan.pl/SOM/app71-Szczygielski_etal_SOM.pdf). The holotype (SMF-R 263) of "*Chelonia*" *gwinneri* was preliminarily examined, but the way the specimen is currently mounted and exhibited hampers a more scrupulous study and documentation. For comparative purposes, 3D models of segmented skulls of adult *Caretta caretta* (Linnaeus, 1758) NHMUK 1938.1.9.1 (ark:/87602/m4/372894), juvenile *Caretta caretta* KU-H269218 (ark:/87602/m4/516014), *Chelonia mydas* (Linnaeus, 1758) FAUHS 10.02.2023_001 (ark:/87602/m4/618079) and UF Herp 51413 (ark:/87602/m4/615952), *Eretmochelys imbricata* (Linnaeus, 1766) FAUHS 10.03.2023_001 (ark:/87602/m4/618101), *Lepidochelys kempii* (Garman, 1880) CSIP M009-08 (ark:/87602/m4/377063), *Lepidochelys olivacea* (Eschscholtz, 1829) SMNS 11070 (ark:/87602/m4/M42685), and *Natator depressus* (Garman, 1880) WAM Rept 112123 (ark:/87602/m4/374743), as well as a full body scan and a segmented forelimb of a juvenile *Chelonia mydas* YPM Herr 004058 (ark:/87602/m4/M72562, ark:/87602/m4/602425) and a full body scans of the juvenile *Caretta caretta* KU-H269218 (ark:/87602/m4/M75042) and *Lepidochelys olivacea* KU-H319112 (ark:/87602/m4/M75050) were downloaded from MorphoSource (https://www.morphosource.org). A surface scan of a skeleton of an adult *Caretta caretta* MSNUP B 32 by SimoneFarina77 was accessed through Wikimedia Commons (https://commons.wikimedia.org/wiki/File:Caretta_caretta_3d_scan_Natural_History_Museum_University_of_Pisa_B_32.stl).

As mentioned above, according to Młynarski (1959), ISEA FR/WNC-1 and MRJ 70.1P.-P (the slab and counterslab of the same individual; Fig. 6) were found 30 m above the foot of the Jasiołka riverbank near Winnica, 10 km east of Jasło in grayish-brown Menilite shales intercalating the Krosno sandstone beds. The specimens were found by Stanisław Kadyi (Kadyi 1958), a local oculist and naturalist, although there is disagreement regarding the exact date of the find. Czernicki (1981) stated that they were collected in 1954, but according to Młynarski (1959) they were obtained "about 10 years ago" (that is, 1948–1949, depending on whether the submission or publication date of that paper is considered). Młynarski (1959) noted that yet another specimen of roughly the same size and with a better preserved skull was found alongside them, but that one was unfortunately lost before it could be examined. Although Młynarski (1959) called both slabs the negative and positive, they are better characterized as molds (negatives) of the

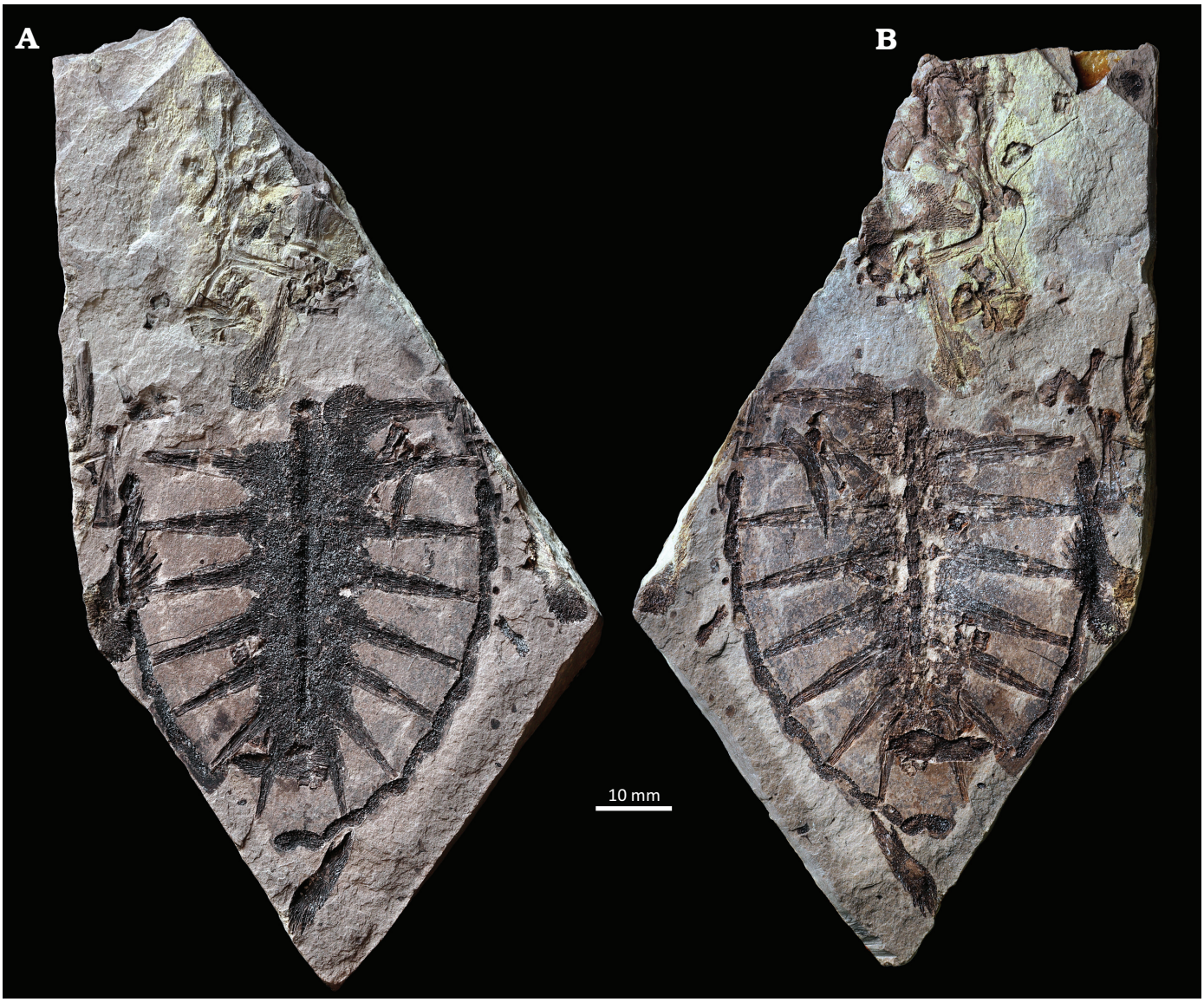


Fig. 6. Sea turtle *Glarichelys knorri* (Gray, 1831), from Winnica near Jasło, Poland, Rupelian. Specimen in two counterslabs: ISEA FR/WNC-1 (**A**) individual in dorsal aspect and MRJ 70.1P.-P (**B**) individual in ventral aspect.

dorsal (ISEA FR/WNC-1, not figured in the original paper) and ventral (MRJ 70.1P.-P) surfaces of the semiarticulated carapace, associated disarticulated cranial, shell, and appendicular elements, and with some bone residues. The bones of the plastron are dislocated, and the nuchal is turned around and upside down. The specimen is strongly compressed but some three-dimensional information can be inferred, especially when the specimens are virtually inverted to create digital positives. Additionally, the periphery of the carapace on both slabs reveals a pattern of lighter lines interpreted by Młynarski (1959) as scute sulci. We agree with that interpretation. The locality of Winnica is otherwise known from abundant fish fossils (Jerzmańska 1968) and rare remains of birds (Bochenski et al. 2018).

UR/1055 and UR/1056 (Fig. 7) originate from the Hermanowa locality (Poland). The discovery of turtle remains in the locality was mentioned for the first time by Přikryl et al. (2016) as ?*Glarichelys* sp. UR/1055 is a larger slab and covers the whole posterior half of the body (fourth costal pair and seventh peripheral pair onwards, including the pygal, partial hyoplastra, xiphiplastra, distal parts of two longest digits of the manus, pelvis, complete left hindlimb and mostly complete right hindlimb, and vertebral column nearly reaching the end of the tail). UR/1056 is a smaller fragment of rock and corresponds to the posterior left part of the shell (costals IV–VIII and associated elements), starting very slightly more anteriorly than the other slab and thus capturing a small fragment of the posterolateral part of the hypoplastron. Both specimens were found independently and at least UR/1056 comes from the H2 layer of the Hermanowa locality (Tomáš Přikryl, personal communication 2024). According to the specimen label, UR/1056 was apparently later reencountered in 2015 in a box with undetermined specimens from the locality and for a time

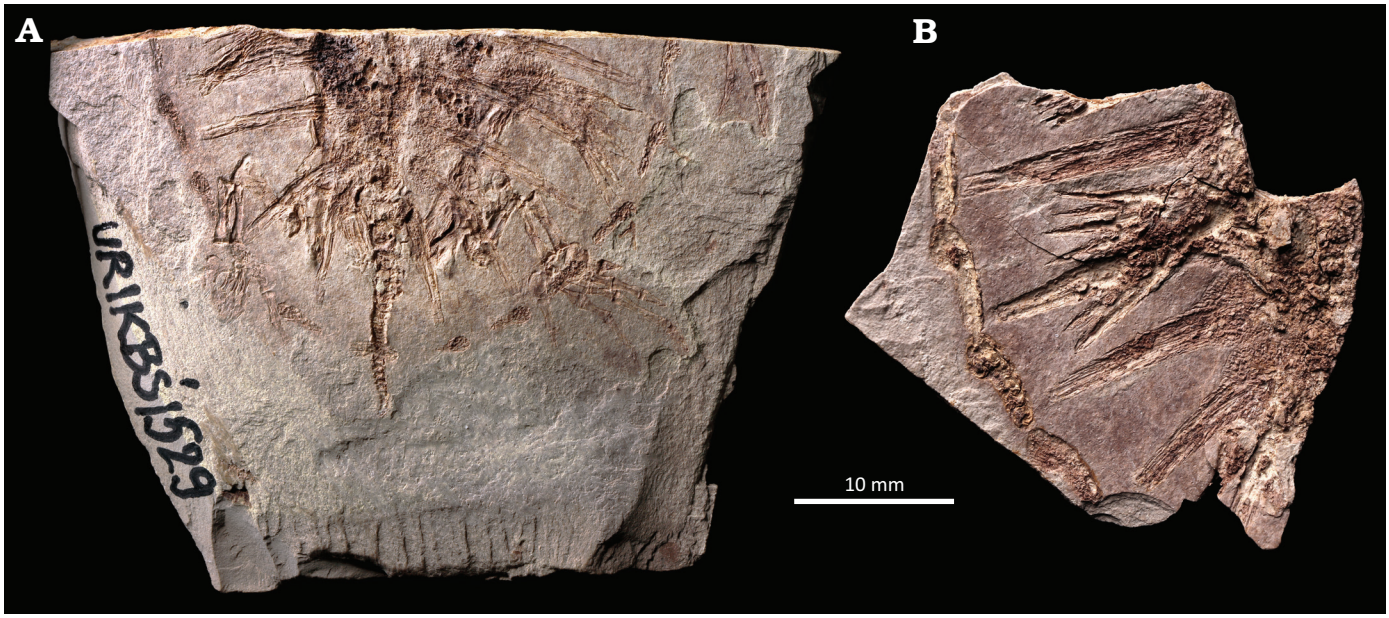


Fig. 7. Sea turtle *Glarichelys knorri* (Gray, 1831), from Hermanowa, Poland, Rupelian. **A**. UR/1055, dorsal aspect of the posterior part of the body. **B**. UR/1056, ventral aspect of the posterior right part of the shell.

interpreted as a possible counterslab for UR/1055. However, the preserved individuals differ slightly in size (UR/1055 being smaller than UR/1056), shape of the lateral hypoplastral process, degree of ossification of peripherals (more advanced in UR/1056), and position of the femur. As in the case of the Winnica specimen, both slabs are mostly molds of the skeleton containing some bone residue, with UR/1055 representing its dorsal aspect and UR/1056 capturing the ventral aspect. The specimens preserve a beige-colored halo around the shells and limbs, representing the outline of soft tissues. Additionally, the UR/1055 exhibits lumpy, linear structures (concave in the negative mold, so originally convex) between the carapace and the plastron which we interpret as remnants of its digestive tract.

Due to incompleteness or disarticulation, the exact size of the studied individuals is uncertain. The impression of the disarticulated nuchal of ISEA FR/WNC-1 and MRJ 70.1P.-P is either incomplete (ISEA FR/WNC-1) or partially obscured by the skull (MRJ 70.1P.-P), and the flattening might have influenced linear dimensions of the shell to a presumably minor extent, but either way, the carapace (straight carapace length) of this individual was about 7 cm long, within a several millimeter error margin (about 70% the size of the holotype of *Glarichelys knorri*). We estimate UR/1056 to be roughly the same size. UR/1055 is estimated to measure about 4 cm of carapace length.

MB.R.5596, NWSGL-EF-100789, NWSGL-EF-100790, PIMUZ A III/85, PIMUZ A III/594, and PIMUZ A III/596 (holotype of *Glarichelys knorri*) were digitized using a Shining 3D EinScan Pro 2X 3D scanner fixed on a tripod with EinScan Pro 2X Color Pack (texture scans) and EXScan Pro 3.2.0.2–4.0.1.0 software. The models were meshed using the Watertight Model and High Detail presets. ISEA FR/WNC-1, MRJ 70.1P.-P, closeup of the skull of NWSGL-EF-100789, UR/1055, and UR/1056 were digitized using photogrammetry with Agisoft Metashape Professional 2.1.2–2.2.1 (photographs aligned on the High setting, mesh produced from depth maps on the Ultra High setting), and the resulting models were automatically scaled based on printed scale-markers. Additionally, UR/1055 and UR/1056 were CT scanned using an XRadia MicroXCT-200 (ZEISS) system housed at the Laboratory of Microtomography, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland. The first scan included both specimens and consisted of 1601 6 second-long exposures amounting to a total scan time of 4 hours at 70 kV, 6 W, and 84 µA, with a LE#2 filter, resulting in a 42.31 micron voxel. The second scan, focused on the abdominal region of UR/1055, consisted of 1601 exposures of duration varying between 2 to 5.38 s, depending on the angle; total scan time 3 hours at 80 kV, 8 W, and 100 µA, with a LE#2 filter, resulting in a 21.44-micron voxel. The CT data revealed no clear detail (e.g., bone remains) below the surface of the slab but it allowed visualization of the soft tissue outline (Fig. 12A$_4$) and a high-resolution 3D surface reconstruction of the abdominal region (Fig. 14A$_6$) of UR/1055. The soft tissue outline was visualized using TXM3DViewer in VRT (Volume Rendering Technique) mode. The 3D surface was reconstructed based on the generated TIF image series using Slicer 5.2.1 (Fedorov et al. 2012; Kikinis et al. 2014). In order to facilitate interpretation of the morphology and enhance the visibility of surface details, the original negative geometry was inverted in MeshLab 2022.02 (Cignoni et al. 2008) by trimming the bottom of the 3D models and using the Invert Faces Orientation filter, and snapshots of 3D models were captured in orthographic view and with the Radiance Scaling (Lambertian or Lit Sphere) shader enabled (Vergne et al. 2010). Elevation maps of selected regions were generated in ParaView 5.13.0 (Ahrens et al. 2005; Utkarsh 2015).

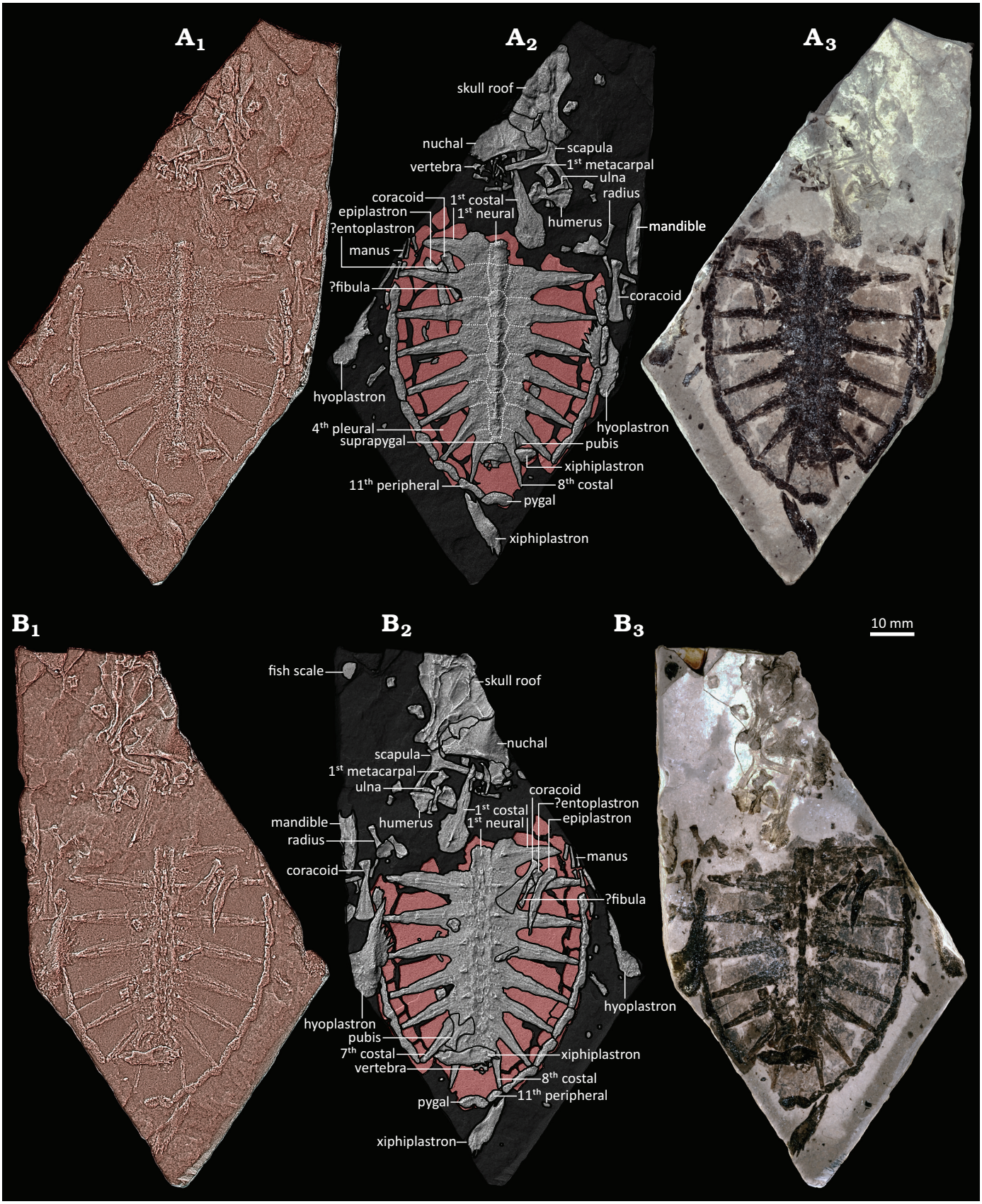


Fig. 8. General morphology of juvenile specimens of the sea turtle *Glarichelys knorri* (Gray, 1831), from Winnica near Jasło, Poland, Rupelian. **A**. ISEA FR/WNC-1. **B**. MRJ 70.1P.-P. B_1, digital positive; B_2, digital positive with outlined bone borders, background rock matrix darkened, and presumed scute areas indicated in red; B_3, 3D model with shading disabled, presenting coloration.

Finally, mosaic images composed of high-resolution Scanning Electron Microscopy photographs of the surface of UR/1055 (non-coated and under low vacuum) were captured using a Thermo Fisher Quattro S Environmental SEM housed at the Institute of Paleobiology, Polish Academy of Sciences. For the acquisition and stitching of images, the MAPS3 software was employed. The software allows the creation of large, composite images. Imaging was done simultaneously employing both the Secondary (SE) and Backscatter Electron (BSE) detectors. A Directional Backscatter electron (DBS) detector was used to enhance topography features of samples. Imaging was performed with the accelerating voltage of 20 kV. The H_2O vapour was used to maintain an elevated pressure of 50 Pa in the chamber during measurements in the Low Vacuum mode. Although the effect of charging in the samples was significantly reduced, some artefacts were present. To equalize such, e.g., the uneven exposition at the top and bottom of frame rows, resulting in banding of the composite picture, rows of rectangles with a semi-transparent black to fully transparent gradient were manually overlain onto the image in CorelDRAW 2021.5 (v. 23.5.0.506).

3D scans of all specimens, photogrammetric image series, and CT slices obtained for the purposes of this contribution are available in MorphoSource project 000852189 (https://www.morphosource.org/projects/000852189). The occurrence data and additional media are included in the Turtle Evolution Database (TED) at https://ted.paleo.pan.pl/ (Chroust and Szczygielski 2025).

Directional and anatomical nomenclature follows Zangerl (1969) for the shell and Hermanson et al. (2024) for the humerus.

Systematic palaeontology

Testudines Batsch, 1788 (sensu International Turtle Nomenclature Committee et al. 2020a)

Cryptodira Cope, 1868 (sensu International Turtle Nomenclature Committee et al. 2020b)

Pan-Chelonioidea Joyce et al., 2004 (sensu Joyce et al. 2021a)

Genus *Glarichelys* Zangerl, 1958

Type species: *Chelonia knorri* Gray, 1831.

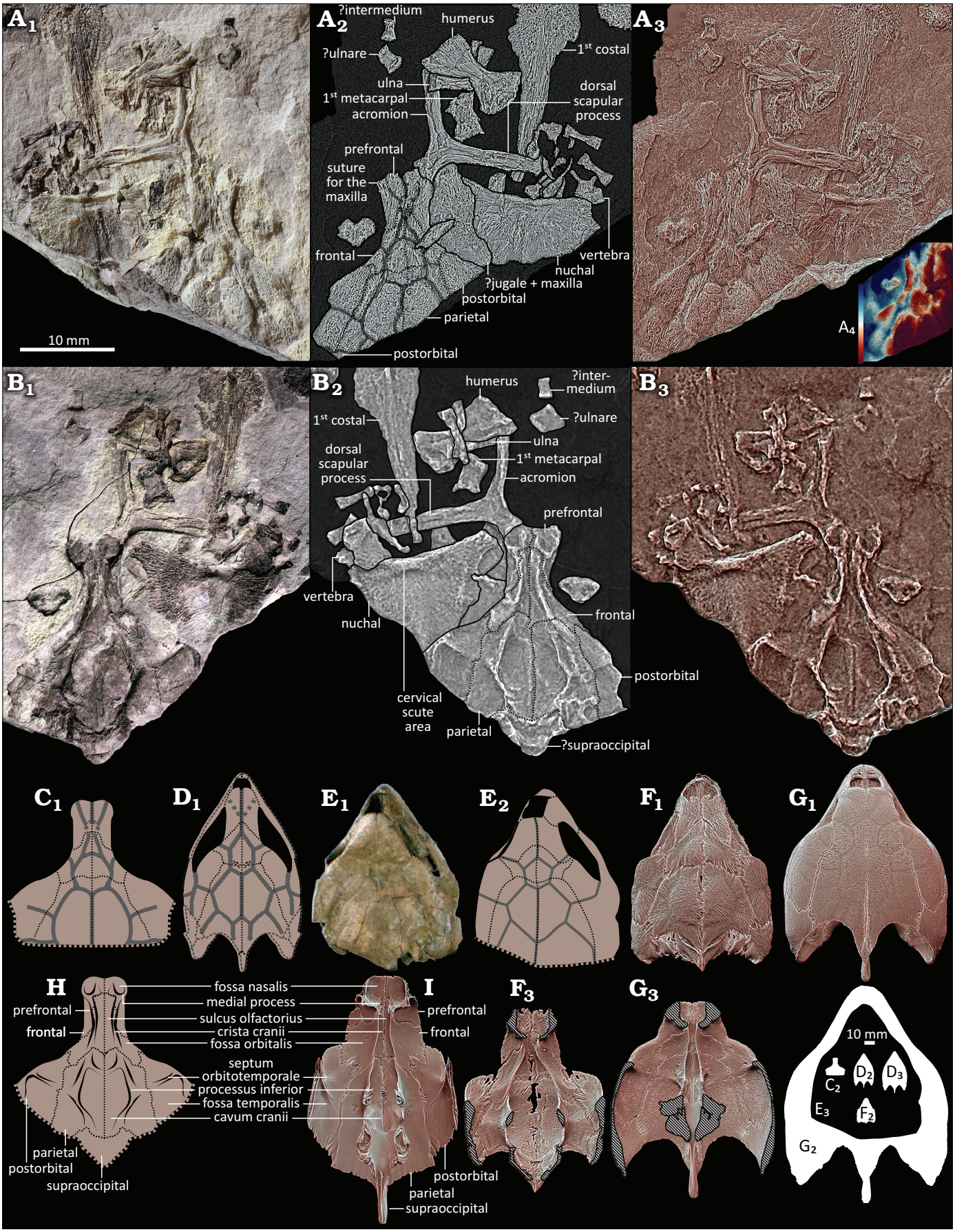
Type locality: Matt, Canton Glarus, Switzerland.

Diagnosis.—As for the monotypic type species.

Glarichelys knorri (Gray, 1831)

1755 Schildkröte; Knorr 1755: 27–28, pl. 34.
1756 Testudinis petrificatae; Gessner 1756: 5.
1776 Schildkröte; Andreae 1776: 53, 330, pl. 16.
1778 *Amphibiolithus testudinis*; Gmelin 1778: 463, pl. 6: 81–82.
1793 *Amphibiolithus testudinis*; Gmelin 1793: 388.
1802 Schildkröte; Steinmüller 1802: 207.
1809 tortue de mer; Cuvier 1809: 240–241, pl. 18: 4.
1810 *Chelone*; Cuvier 1810a: 79.
1810 *Chelone*; Cuvier 1810b: 8.
1812 tortue de mer; Cuvier 1812: part V: chapter VI: 12–13, pl. 2: 4.
1822 Schildkröte; Krüger 1822: 370.
1823 *Chelonia*; Krüger 1823: 700–701.
1824 tortue de mer; Cuvier 1824: 243–244, pl. 14: 4.
1827 Meeres-Schildkröte; Leonhard 1827: 10.
1831 *Chelonia Knorri* sp. nov.; Gray 1831: 54.
1834 *Chelonia glaricensis* sp. nov.; Keferstein 1834: 253.
1835 *Chelonia Knorri* Gray, 1831; Fitzinger 1835: 128.
1836 tortue de mer; Cuvier 1836a: pl. 242: 4.
1836 tortue de mer; Cuvier 1836b: 484–486.
1836 marine turtle; Buckland 1836a: 256–257.
1836 turtle; Buckland 1836b: 36, pl. 25: 4.
1838 *Chelonia Knorrii* Gray, 1831; Meyer 1838: 414.
1839 *Chelonia Knorrii* Gray, 1831; Meyer 1839: 684.
1846 *Chelonia Knorrii* Gray, 1831; Fitzinger 1846: 380.
1856 *Chelonia Knorrii* Gray, 1831; Meyer 1856: 84–90, pl. 16.
1856 *Chelonia Knorri* Gray, 1831; Pictet and Humbert 1856: 2–3.
1856 *Chelonia Knorrii* Gray, 1831; Giebel 1856: 71.
1865 *Chelonia ovata* sp. nov.; Heer 1865: 234–235, fig. 141.
1865 *Chelonia Knorri* Gray, 1831; Heer 1865: 235–236.
1869 *Chelonia Knorri* Gray, 1831; Maack 1869: 244, 276.
1869 *Chelonia ovata* Heer, 1865; Maack 1869: 244, 276–277.
1886 *Chelonia ovata* Heer, 1865; Wettstein 1886: 93, pl. 8: 7.
1886 *Chelonia Knorri* Gray, 1831; Wettstein 1886: 93.
1950 Meeresschildkröte; Peyer 1950: pl. 14.
1950 *Chelonia knorri* Gray, 1831; Stüssi 1950: 524–525, figs. 5, 12.

Fig. 9. Morphology of the cranium and associated disarticulated elements of juvenile specimens of the sea turtle *Glarichelys knorri* (Gray, 1831), from Winnica near Jasło, Poland, Rupelian (A–C) and comparisons with crania of other cheloniid specimens (D–I). **A**. ISEA FR/WNC-1, dorsal aspect of the skull roof intermixed with postcranial elements: A_1, photograph of the specimen lit from the bottom right corner to simulate convexity of the concave natural mold; A_2, digital positive with outlined bone borders and background rock matrix darkened; A_3, the same, complete view; A_4, elevation map of the digital positive of the dorsal (external) surface of the skull roof to visualize cranial scales. **B**. MRJ 70.1P.-P, ventral aspect of the skull roof intermixed with postcranial elements: B_1, photograph of the specimen lit from the bottom right corner to simulate convexity of the concave natural mold; B_2, digital positive with outlined bone borders and background rock matrix darkened; B_3, the same, complete view. **C**. Schematic reconstruction of the external (dorsal) surface of the skull roof: C_1, scale and bone borders; C_2, scaled outline. **D**. Reconstruction of *G. knorri* skull in dorsal view (modified from Zangerl 1958): D_1, scale and bone borders; D_2, scaled outline based on the size of the holotype specimen; D_3, scaled outline based on the size of the *Chelonia* "*ovata*" specimen. **E**. "*Chelonia*" *gwinneri* Wegner, 1911, from Flörsheim, Germany, Rupelian, SMF-R 263 (holotype), skull in dorsal/dorsolateral view: E_1, photograph (courtesy of Krister Smith and Sven Tränkner, Senckenberg Gesellschaft für Naturforschung); E_2, scale and bone borders (based on Wegner 1911, 1914; Drevermann 1914); E_3, scaled outline. **F**, **G**. *Caretta caretta* (Linnaeus, 1758). **F**. KU-H269218, skull of juvenile specimen from Leticia, Colombia, Recent: F_1, 3D model, dorsal view; F_2, scaled outline; F_3, 3D model of the skull roof in ventral view. **G**. NHMUK 1938.1.9.1, skull of adult specimen from Tmannar, Sri Lanka, Recent: G_1, 3D model, dorsal view; G_2, scaled outline; G_3, 3D model of the skull roof in ventral view. **H**. *Glarichelys knorri*, schematic reconstruction of the internal (ventral) surface of the skull roof based on MRJ 70.1P.-P. **I**. *Chelonia mydas* (Linnaeus, 1758), from Montserrat, Caribbean, Recent, UF Herp 51413, 3D model of the skull roof in ventral view. A_4, C_1, D_1, E_1, F_1, F_3, H, and I not to scale. Striped areas indicate cross-sections through bones. →


A1
A2
?intermedium
humerus
?ulnare
1st costal
ulna
1st metacarpal
acromion
dorsal scapular process
prefrontal
suture for the maxilla
frontal
vertebra
nuchal
?jugale + maxilla
postorbital
parietal
postorbital
A3
A4
10 mm
B1
B2
humerus
?inter-medium
1st costal
?ulnare
ulna
dorsal scapular process
1st metacarpal
acromion
prefrontal
vertebra
nuchal
frontal
postorbital
cervical scute area
parietal
?supraoccipital
B3
C1
D1
E1
E2
F1
G1
H
fossa nasalis
prefrontal
medial process
sulcus olfactorius
frontal
crista cranii
fossa orbitalis
septum orbitotemporale
processus inferior
fossa temporalis
cavum cranii
parietal
postorbital
supraoccipital
I
prefrontal
frontal
postorbital
parietal
supraoccipital
F3
G3
10 mm
C2
D2
D3
E3
F2
G2

1958 *Glarichelys knorri* (Gray, 1831) gen. nov.; Zangerl 1958: 1–54, figs. 1–16, 19, 26, pls. 1–7, 9–15.
1958 Cheloniidae; Kadyi 1958: 23, 26.
1959 *Glarichelys knorri* (Gray, 1831); Młynarski 1959: 177–189, 191–192, figs. 1, 2, pl. 1, 2.
1959 *Glarichelys knorri* (Gray, 1831); Nielsen 1959: 98, 110–112.
1964 *Glarichelys knorri* (Gray, 1831); Kuhn 1964: 167.
1964 *Glarichelys knorri* (Gray, 1831); Sukhanov 1964: 420, 424, fig. 430.
1968 *Glarichelys knorri* (Gray, 1831); Jerzmańska 1968: 386.
1969 *Glarichelys knorri* (Gray, 1831); Młynarski 1969: 100–101; fig. 60.
1974 *Glarichelys knorri* (Gray, 1831); Moody 1974: 179.
1976 *Glarichelys knorri* (Gray, 1831); Młynarski 1976: 46, fig. 46.2–46.6.
1979 *Glarichelys knorri* (Gray, 1831); Aslanova et al. 1979: 18, 21.
1980 *Glarichelys knorri* (Gray, 1831); Zangerl 1980: 586, 591, figs 8, 9.
1980 *Glarichelys knorri* (Gray, 1831); Chkhikvadze 1983: 35–36.
1981 *Glarichelys knorri* (Gray, 1831); Czernicki 1981: 598.
1992 *Glarichelys knorri* (Gray, 1831) [partim]; Gregorová and Młynarski 1992: 63, 65, 68.
1998 Schildkröte; Leu 1998: 53–66, figs 58–66.
1998 zeeschildpad; Machalski 1998: 85.
1998 *Glarichelys knorri* (Gray, 1831); Furrer 1998: 95–96, figs. 110–114, 126; table 1.
1999 *Glarichelys knorri* (Gray, 1831); Darga et al. 1999: 108.
1999 *Glarichelys knorri* (Gray, 1831) [partim]; Karl and Tichy 1999: 74.
2001 *Glarichelys knorri* (Gray, 1831); Lapparent de Broin 2001: 184.
2002 *Glarichelys knorri* (Gray, 1831) [partim]; Karl 2002a: 171, 177, 191, map 2.
2002 *Glarichelys knorri* (Gray, 1831) [partim]; Karl 2002b: 71, fig. 3.
2004 *Glarichelys knorri* (Gray, 1831); Vremir 2004: 149.
2006 *Glarichelys knorri* (Gray, 1831); Tong et al. 2006: 132, 134, fig. 9G.
2007 *Glarichelys knorri* (Gray, 1831) [partim]; Karl 2007: 29, 38, 40, figs. 8.1–8.4, 9.1, 10.10, pl. 4: 2.
2008 sea turtle; Bochenski and Bochenski 2008: 211.
2010 *Glarichelys knorri* (Gray, 1831); Alexander and Frey 2010: 90, 92–94.
2012 *Glarichelys knorri* (Gray, 1831); Karl and Madsen 2012: 198, 200, 203, fig. 3.3.
2014 *Glarichelys knorri* (Gray, 1831); Lapparent de Broin et al. 2014: 128.
2014 *Glarichelys knorri* (Gray, 1831) [partim]; Weems and Sanders 2014: 90, 91, 92, 95.
2015 *Glarichelys knorri* (Gray, 1831); Kapuścińska and Machalski 2015: 385.
2015 *Glarichelys knorri* (Gray, 1831) [partim]; Zvonok et al. 2015: fig. 9l.
2016 *Glarichelys knorri* (Gray, 1831); Gard and Fordyce 2017: 138.
2016 *Glarichelys knorri* (Gray, 1831) [partim]; Maxwell et al. 2016: 251, 253.
2016 ?*Glarichelys* sp.; Přikryl et al. 2016: 439.
2017 *Glarichelys knorri* (Gray, 1831); Danilov et al. 2017: 189.
2018 *Glarichelys knorri* (Gray, 1831); Lapparent de Broin et al. 2018: 257, 260, 262–265, fig. 11g, table 2.
2020 cheloniid; Bajdek and Bienkowska-Wasiluk 2020: 4.
2025 *Glarichelys* aff. *knorri* (Gray, 1831) [partim]; Choust and Szczygielski 2025: 2, 4.

Holotype: PIMUZ A/III 596, mostly complete skeleton (Figs. 1A, 2A).

Type locality: Matt, Canton Glarus, Switzerland.

Type horizon: Slate Formation (Engi Glarner-Scheifer Formation), North-Helvetic Flysch Group; Rupelian, Oligocene.

Diagnosis.—Emended from Zangerl (1958): Pan-chelonioids of probably meager size. Skull with moderately elongated snout and a very narrow interorbital bridge; secondary palate of small extent; mandibular symphysis relatively short; scales visible on the skull roof, arranged similarly to those in "*Chelonia*" *gwinneri*, but with an additional pair of triangular frontal scales in the posterior part of the snout and an additional mesially positioned third parietal (or interparietal) scale invading the area of the frontoparietal scales. Carapace probably with intercostal fontanelles throughout life; plastron with relatively large central and lateral fontanelles; bridge index of the plastron ±70. Shoulder girdle plesiomorphic; scapular processes approximately equal in length; coracoid not elongated. Radius and ulna probably superimposed, but without contact rugosity (at least in the juvenile stage); paddle and pes significantly longer than in extant cheloniids.

Material.—Holotype and PIMUZ A/III 85 (slab and counterslab with an isolated forelimb from Attinghausen, Canton Uri, Switzerland, Rupelian), PIMUZ A/III 593 (isolated plastron from Engi, Canton Glarus, Switzerland, Slate Formation, Rupelian), PIMUZ A/III 594 (Figs. 1B, 2C; mostly complete skeleton from Matt-Engi area, Canton Glarus, Switzeraland; Slate Formation, Rupelian), NWSGL-EF-100789 and NWSGL-EF-100790 housed at the KHG (slab and counterslab with the holotype skeleton of *Chelonia ovata* Heer, 1865, from Engi, Canton Glarus, Switzerland; Slate Formation, Rupelian; cast numbered PIMUZ A/III 1034), ISEA FR/WNC-1 and MRJ 70.1P.-P (Fig. 6A, B; two slabs presenting impressions of the ventral and dorsal aspect of a single semiarticulated skeleton with some bone residue from Winnica near Jasło, Jasiołka riverbank, Poland; the Menilite shales intercalating the Krosno sandstone beds, presumed Rupelian), UR/1055 (Fig. 7A; an impression of the dorsal surface of the posterior part of an articulated and largely complete individual from the Hermanowa locality, Poland; Rupelian), UR/1056 (Fig. 7B; an impression of the ventral surface of a shell with bone residue from the Hermanowa locality, Poland; Rupelian), and likely the specimen figured by Wettstein (1886: pl. 8: 7) from the private collection of Rathsherr Blumer, from Engi, Canton Glarus, Switzerland; Slate Formation, Rupelian. Additionally, a number of specimens from various sites was historically referred to *Glaricherys knorri*, although either based on dubious or specifically uninformative characters (see Introduction and Discussion), therefore we consider their alpha taxonomy indeterminate.

Description.—Zangerl's (1958) documentation of the Swiss specimens is adequate, even though his photographs of NWSGL-EF-100789, 100790, and PIMUZ A/III 596 (holotype) show galvanoplastic copies rather than original specimens. For that reason, we mainly focus our descriptions on the Polish juvenile specimens, which are either new (UR/1055 and UR/1056) or have been previously underdocumented (ISEA FR/WNC-1, MRJ 70-1P.-P).

Skull: Impressions of the skull roof are preserved in ISEA FR/WNC-1 (dorsal surface, Figs. 6A, 8A, 9A) and MRJ

70.1P.-P (ventral surface, Figs. 6B, 8B, 9B). Because the specimens preserve the negative image, the morphology is much easier to interpret based on digital positives (Figs. 8, 9A, B). Thus, for simplicity, we will refer to the bones as if they were present, but keep in mind that only molds with minor residues of bone are preserved in the actual specimens.

In both specimens represented are the prefrontal, frontal, postorbital, and parietal bones. The prefrontals and frontals are damaged, whereas the left postorbital is incomplete laterally (and, possibly, posteriorly, where the slabs end), and the parietals are incomplete posteriorly. The dorsal surface of the right postorbital is partially obscured in ISEA FR/WNC-1 by another bone (possibly squamosal) but its ventral surface is well exposed in MRJ 70.1P.-P. In the latter specimen, the posterior edge of the preserved skull roof preserves a wide, V-shaped area which is either a collapsed anterior part of the supraoccipital (as suggested by the lack of visible midline suture and lamellar characteristics of the sutural surface), or an attachment site for that bone. Sutures between bones are variably distinct. The sagittal, circumparietal, and fronto-postorbital sutures are relatively clear, whereas the fronto-prefrontal sutures are somewhat ambiguous, but their position seems to be consistent with that of other cheloniids. As currently exposed in MRJ 70.1P.-P, only the top part of the ascending processes of the skull roof bones are detectable and accessible for photogrammetry; it is unknown whether these are broken or if they continue as preserved bone deeper into the rock matrix. The skull roof preserves virtually no doming, either transversely or along the anteroposterior axis.

The prefrontals are longer than wide, with expanded, rounded anterior ends. Laterally, they formed the anterodorsal edges of the large orbits. As in larger *Glarichelys knorri*, the interorbital bridge is very narrow, its minimum width being about 60% of the prefrontal length. Viscerally, each prefrontal bears a Y-shaped layout of ridges: a laterally concave crista cranii, separating the fossa orbitalis from the sulcus olfactorius and an anteriorly concave medial process, delineating the fossa nasalis posteriorly and continuing anteromedially and anterolaterally into the descending process (Fig. 9B, H). The fossa nasalis takes the form of a peanut-shaped, shorter than transversely wide, concavity. In the digital positive, close to the midline, its roof bears two parallel, anteriorly directed ridges. This morphology may be exaggerated by the mesially preserved bone residue (Fig. $9B_1$), although much more subtle ridges are also present in the corresponding area in *Chelonia mydas* (Fig. 9I). The nasal cavity is proportionally much shorter than in extant cheloniids, and this trait seems to exhibit only minor ontogenetic variability, as suggested by the comparison between the juvenile (KU-H269218, Fig. $9F_3$) and adult (NHMUK 1938.1.9.1, Fig. $9G_3$) *Caretta caretta*.

The frontals are slightly longer than wide and each forms an anteromedially directed suture with the prefrontal anteriorly, anterolaterally convex dorsal edge of the orbit laterally, a sublongitudinal suture with the postorbital posterolaterally, and a roughly transverse (slightly anteromedially inclined) suture with the parietal. The fronto-prefrontal suture is not entirely clear, but the contribution of the frontals to the orbit seems to be proportionally larger than in the known larger specimens of *Glarichelys knorri* and, even more so, "*Chelonia*" *gwinneri*. Ventrally, the frontals project nearly parallel cristae cranii with only minor posterior divergence.

The preserved portion of the postorbitals (more complete on the right than on the left side) is roughly triangular, widening posteriorly. Ventrally, they bear a distinct, predominantly transverse (gently sloping posteromedially) septum orbitotemporale, separating the fossa orbitalis from the fossa temporalis, and the topmost part of the ascending process.

The preserved parts of the parietals are trapezoid, wider posteriorly than anteriorly, and form nearly transverse (gently anteromedially inclined) sutures with the parietals and posterolaterally diverging sutures with the postorbitals. Their ventral surface of each parietal bears the topmost part of the processus inferior, which anteriorly connects to the posterior terminus of the crista cranii, laterally projects the medial portion of the septum orbitotemporale, and extends posteromedially towards the contact with the supraoccipital. The border between the sulcus olfactorius and the cavum cranii is indicated by a low, anteriorly concave ridge, located anteriorly relative to the septum orbitotemporale. A similar ridge, albeit at the level of the septum orbitotemporale, is present in *Eretmochelys imbricata* (FAUHS 10.03.2023_001) and a subtle bulge is present in the same area in the juvenile *Caretta caretta* (KU-H269218, Fig. $9F_3$) but seems to be otherwise either absent or very indistinct in other extant cheloniids. The cavum cranii is clearly laterally expanded relative to the sulcus olfactorius, being approximately 4.6 times as wide in its widest part as the sulcus olfactorius in its narrowest part (note that the measurements may not be entirely accurate due to the missing bone and deformation). This is more than in adult extant cheloniids (between 2.7 times as wide in *Lepidochelys olivacea* SMNS 11070 and 3.9 times as wide in *Chelonia mydas*) but not quite to the extent seen in the juvenile *Caretta caretta* KU-H269218 (5.7 times as wide), especially in the posterior part.

Only a minor part of the supraoccipital is preserved ventrally (MRJ 70.1P.-P, Fig. 9B). Its preservation disallows observation of any significant detail.

ISEA FR/WNC-1 presents impressions of the cranial scales (Fig. 9A), which were distinctly convex (preserved as concavities), and had rounded edges. This morphology is consistent with the scale impression morphology in the juvenile *Caretta caretta* KU-H269218 (Fig. $9F_3$), so it is interpreted here as a juvenile character. In ISEA FR/WNC-1 identifiable are two pairs of prefrontal, probably two unpaired interprefrontal, one unpaired frontal, one pair of supraocular, one pair of frontoparietal, and one pair of temporal scales. Our examination of PIMUZ A/III 594, A/III 596 (holotype), and MB.R.5596 (cast of the holotype), and comparison with Polish specimen reveal indistinct, anterolaterally directed sulci in the anterior part of the snout which

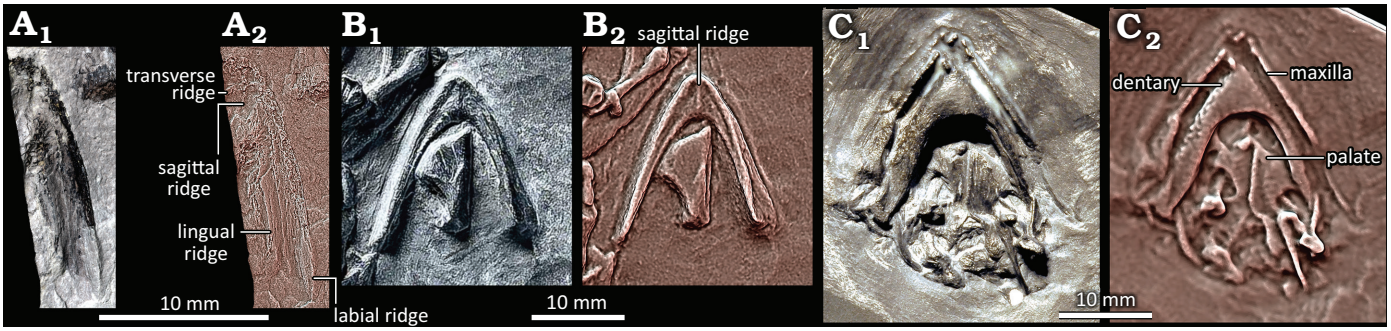


Fig. 10. Comparison of madibulae of *Glarichelys knorri* (Gray, 1831), from Winnica near Jasło, Poland (A) and Glarus, Switzerland (B, C), Rupelian. **A**. ISEA FR/WNC-1, juvenile specimen, closeup of the mandible in ?dorsal view. **B**. NWSGL-EF-100789 (holotype of *Chelonia ovata* Heer, 1865), closeup of the mandible in dorsal view. **C**. PIMUZ A/III 596 (holotype), closeup of the mandible in ventral view exposed on the backside of the slab. A_1–C_1, photographs; A_2–C_2, 3D models.

we interpret as a likely evidence of a previously unnoticed anterior pair of prefrontal scales even in larger individuals (Fig. 5). Their inconspicuousness makes their earlier omission or misinterpretation as deformations understandable, even though they are faintly visible in Zangerl's (1958) photographs and their form does not differ substantially from other cranial sulci in that species. The second pair of the prefrontal scutes was narrow and much longer laterally than medially. This pair seems to have no medial contact in ISEA FR/WNC-1 due to the presence of the interprefrontal, frontal, and frontoparietal scales. Posteriorly, it wedged between the frontal and the supraocular scales but did not separate them completely. The second pair of interprefrontals have had a medial contact in larger *Glarichelys knorri* (Fig. 5; Zangerl 1958). There is no evidence of two pairs of these scales in "*Chelonia*" *gwinneri*—instead, a single pair of medially contacting prefrontals covered most of the interorbital bridge (Wegner 1911, 1914). The outline of the presumed first interprefrontal scale of *Glarichelys knorri* ISEA FR/WNC-1 is indistinct but it seems that it was roughly oval, longer than wide, and button-like (Fig. 9A). It had a short contact with the first pair of prefrontal scales anteriorly, a longer contact with the second prefrontal scale pair laterally, and a very narrow contact with the second interprefrontal scale posteriorly. The area of the presumed second interprefrontal scale of ISEA FR/WNC-1 takes the form of a triangular, narrow anteriorly, less convex than the surrounding scales and smoother surface (Fig. 4A). While it may possibly represent an anterior extension of the frontal scale, it differs quite significantly in the relief and convexity from the main area of the latter (Fig. $4A_4$). If interpreted correctly, it was slightly asymmetrical. As a result, the right second prefrontal scale reached the midline of the skull roof, but it was still separated from its left counterpart by an off-center anterior projection of the second interprefrontal scale. Posteriorly, the presumed second interprefrontal scale contacted the frontal scale via a concave edge. The frontal scale in ISEA FR/WNC-1 was roughly diamond-shaped with rounded corners, slightly longer than wide, closer approaching "*Chelonia*" *gwinneri* rather than larger *Glarichelys knorri* in proportions but proportionally larger than in either of them (Wegner 1911, 1914; Zangerl 1958). It contacted the second interprefrontal scale anteriorly, the second pair of prefrontal scales anterolaterally, the supraocular scales laterally, and the frontoparietal scales posteriorly. The supraocular scale areas are not fully preserved in ISEA FR/WNC-1 due to the damage to the postorbitals and the right postorbital being partially obscured dorsally. The sulcus between the supraocular and the temporal scale, at least in the medial part, was straight and directed anterolaterally. The frontoparietal scale pair of *Glarichelys knorri* ISEA FR/WNC-1 likely had a similar outline as in larger *Glarichelys knorri* and "*Chelonia*" *gwinneri*, with a shallow anteromedial embayment receiving the posterior tip of the frontal scale and the widest part located at the level of the supraoculo-temporal sulcus. However, in ISEA FR/WNC-1 the circumfrontoparietal edges were rounder, possibly due to its juvenile age. The surfaces of the frontoparietal scute areas are distinctly convex and there is a slight asymmetry causing the right frontoparietal scute area to be slightly wider than the left. The temporal scale area is preserved only on the left side of the skull roof, it seems roughly complete, and it is wider than long, with a posterior edge parallel to the anterior (note that the sulcus continues onto the parietal bone, so it is not a suture between the postorbital and squamosal bones, Fig. $9A_4$). It is shorter than the temporal scale of larger *Glarichelys knorri* and "*Chelonia*" *gwinneri*, in which the temporoparietal scale sulcus is directed posterolaterally (Wegner 1911, 1914; Zangerl 1958). This hints at either a farther lateral expansion of the parietal scales or at the presence of another, more posteriorly positioned temporal scale in *Glarichelys knorri* ISEA FR/WNC-1. A small, convex anterior portion of the area of that succeeding scute is preserved, testifying to its presence, but is otherwise uninformative. The part of the skull roof potentially bearing the interparietal scale is not preserved. Lapparent de Broin et al. (2018) noted the presence of mesial third parietal (or interparietal) scale in the Swiss specimens of *Glarichelys knorri*. Although it is also indistinct, a small scale wedging posteriorly between the frontoparietal scales seems to indeed have been present (Fig. 5). This region is, sadly, not represented in ISEA FR/WNC-1.



Fig. 11. Sea turtle *Glarichelys knorri* (Gray, 1831), juvenile specimens from Winnica near Jasło, Poland, Rupelian, close-ups of disarticulated elements. **A**. ISEA FR/WNC-1. **B**. MRJ 70.1P.-P. Panels A_1 and B_1, A_2 and B_2, A_3 and B_3, and A_5 and B_5 present corresponding elements from both specimens. Red lettering. shell bones; green lettering, appendicular bones. Scale bars 1 mm.

Mandible: A presumed mandible is impressed in ISEA FR/WNC-1 (dorsal aspect) and MRJ 70.1P.-P (ventral aspect) just next to the slab edge (Fig. 10A). Due to its incompleteness and preservation, its interpretation is uncertain. It may represent conjoined dentaries (right and the symphyseal part of the left one) or a single mandibular ramus exposed in the mediolateral aspect. Similarly as in the case of the cranium, the mandible is rotated so its anterior tip is directed towards the posterior end of the carapace. The impression in MRJ 70.1P.-P is poor and largely uninformative, whereas the impression in ISEA FR/WNC-1 it preserves some more detail. Nevertheless, its clarity is somewhat hindered by the presence of bone residue occupying some parts of the impression. If interpreted as conjoined dentaries (Fig. 10A), the height of the labial ridge and the presence of a symphyseal hook are not observable. The lingual ridge is well-defined

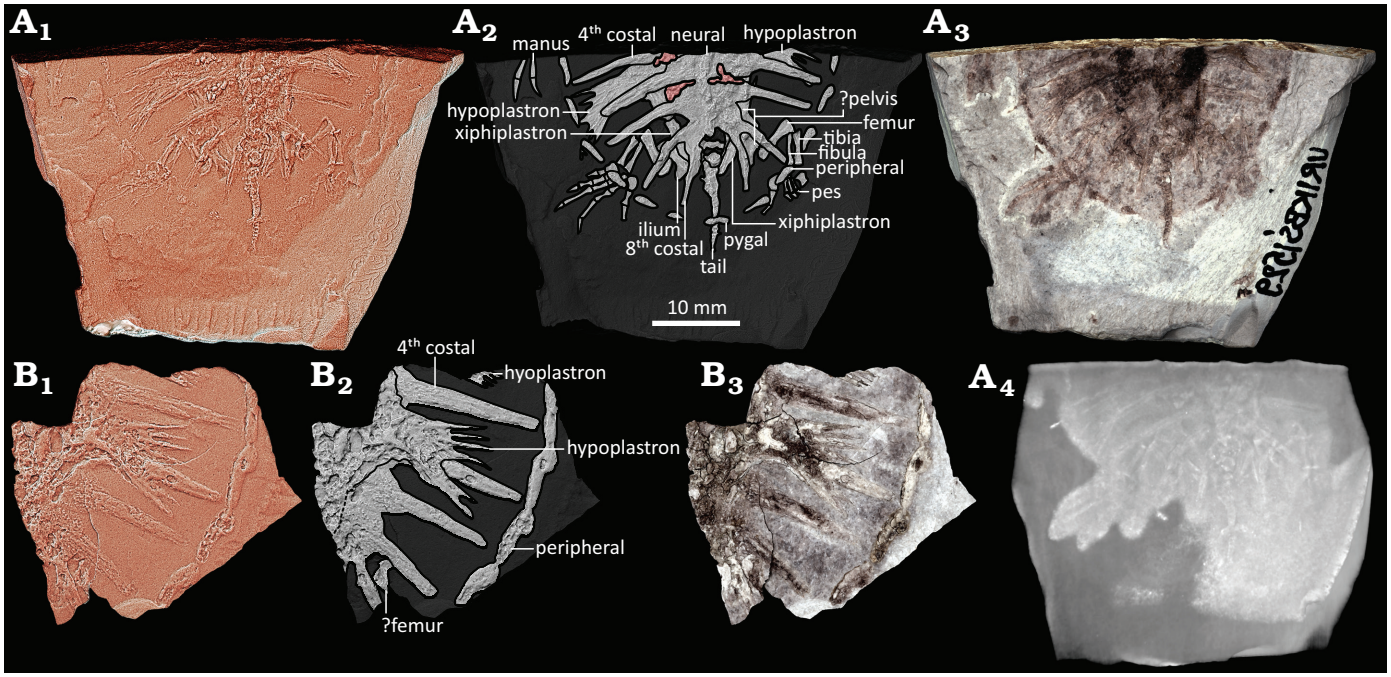


Fig. 12. Sea turtle *Glarichelys knorri* (Gray, 1831), juvenile specimens from Hermanowa, Poland, Rupelian, general morphology. **A**. UR/1055. **B**. UR/1056. A_1, B_1, digital positive; A_2, B_2, digital positive with outlined bone borders, background rock matrix darkened, and presumed digestive tract contents (gastrolites or cololites) indicated in pink; A_3, B_3, 3D model with shading disabled, presenting coloration; A_4, B_4, CT volumetric render with contrast optimized to visualize the outline of soft tissues.

but relatively blunt, it is low posteriorly and gradually increases in height anteriorly. The dorsal surface of the symphysis is gently concave and bears a low sagittal ridge (crista symphysialis) and a bow-shaped transverse accessory ridge. The symphyseal area, as preserved, constitutes just under half of the dentary length. The mandible was apparently relatively narrow, with an acute angle between the rami, seemingly more so than in the known *Glarichelys knorri* specimens (Zangerl 1958). If interpreted as a mandibular ramus impressed in the medial aspect, then little reliable morphological detail can be inferred aside of the ventral outline and impression of the exposed Meckel's groove.

Vertebral column: Several disarticulated vertebrae or bones possibly representing vertebrae are preserved as impressions, sometimes with bone remnants, in ISEA FR/WNC-1 and MRJ 70.1P-P, but their state of preservation and dislocation make them mostly uninformative (Fig. 8). One of those, located in the anterior part of the slabs, has a relatively long neural process and thus may represent one of the posteriormost cervical vertebrae (Figs. 8, $11A_4$), but its orientation in the rock matrix and damage makes identification ambiguous. In MRJ 70.1P.-P, dorsal vertebral centra are not preserved either as bone or impressions, leaving behind only neural bones with the dorsalmost parts of neural arches (Fig. 5B). In both ISEA FR/WNC-1 and MRJ 70.1P.-P, a single sacral or anterior caudal vertebra with a short neural process and massive lateral processes (?sacral ribs) is preserved between the last costals and the dislocated xiphiplastron (Figs. 8, $11A_4$, B_5), which was apparently mistaken by Młynarski (1959) as the posterior part of the suprapygal. At least one of the sacral vertebrae with strong, anteroposteriorly expanded sacral ribs seems to be also exposed in UR/1055 (Figs. 12A, 13).

UR/1055 preserves an impression of a mostly complete tail (Figs. 12A, 13). As preserved, it consists of at least 24 vertebrae and extends far beyond the pygal bone, even though the posteriormost vertebrae seem to be either missing or were not yet ossified. Therefore, the tail is significantly longer than in larger individuals of *Glarichelys knorri* (17 vertebrae, barely reaching the pygal; Figs. 1, 3; Zangerl 1958). The tail of the holotype of "*Chelonia*" *gwinneri* appears to be short, as well, but it was found in a disarticulated state, so its portions may be missing (Wegner 1914). It must be noted that the tail length is sexually dimorphic in cheloniids, with males having longer tails than females, regardless of maturity, even despite some overlap in juveniles (e.g., Deraniyagala 1939; Hendrickson 1958; Pritchard et al. 1983; Wibbels et al. 1987; Wyneken 2001; Godley et al. 2002; Casale et al. 2005; Sönmez et al. 2016).

Carapace: ISEA FR/WNC-1 and MRJ 70.1P.-P preserve a nearly complete and mostly articulated carapace with a disarticulated anterior part and missing only peripherals from the anterior and posterior right side of the shell, together with the suprapygal. The individual is comparatively well-ossified, with most bones maintaining well-developed sutural connections and sutures between the costals, neurals, and most peripherals barely traceable. UR/1055 preserves articulated posterior part of the carapace, apparently without the suprapygals. Even though the individual is poorly ossified, and the peripherals lack sutural connections

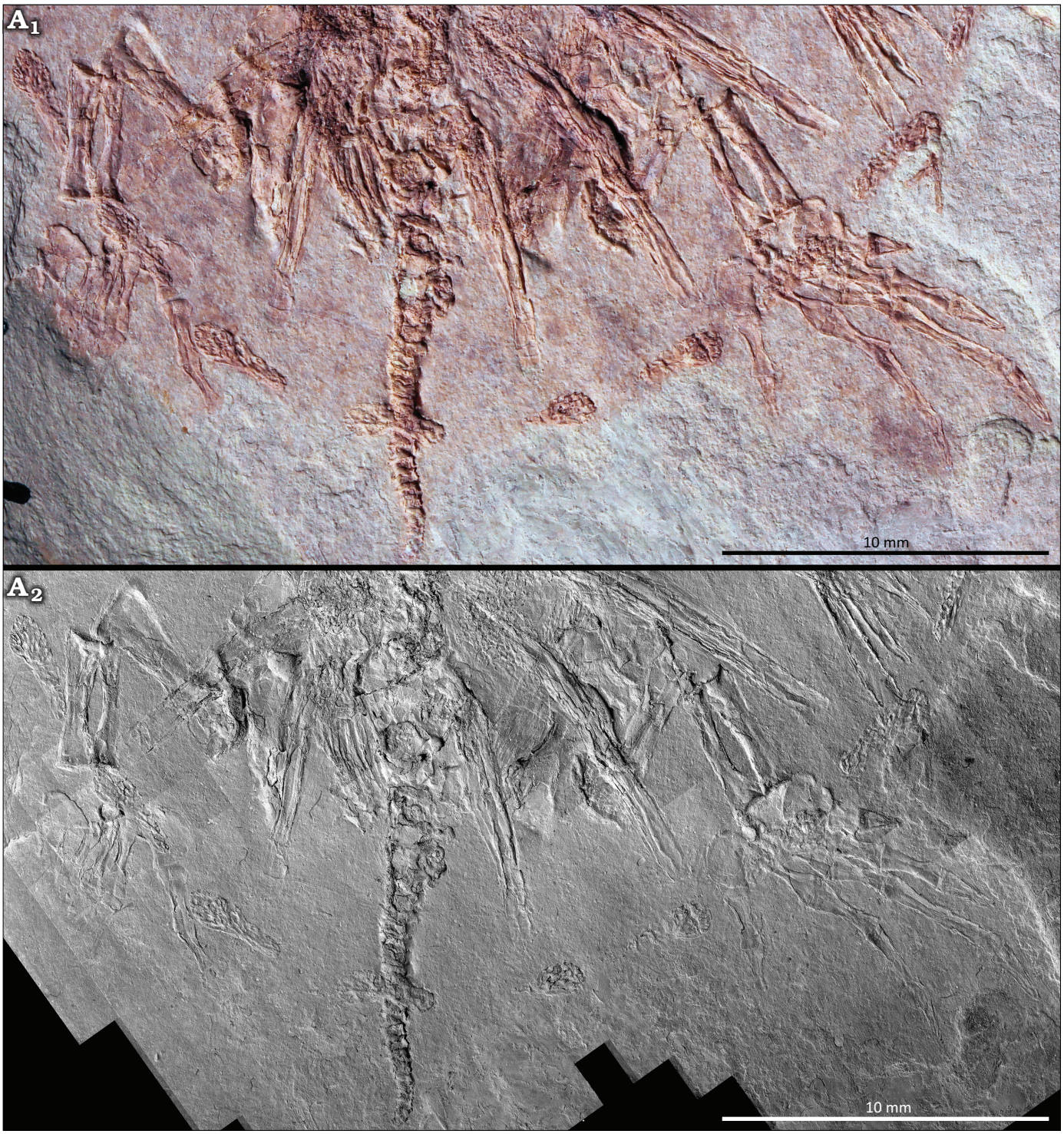


Fig. 13. Sea turtle *Glarichelys knorri* (Gray, 1831), juvenile specimen from Hermanowa, Poland, Rupelian, UR/1055, morphology of the posterior part of the body: A_1, photograph lit from upper left corner to simulate convexity of the concave natural mold; A_2, composite SEM image.

between each other and with the costals and the pygal, they show no dislocation. In combination with articulation of other elements and the remains of the soft tissue outline, this strongly suggests that the cadaver retained structural integrity at the moment of burial. UR/1056 only includes articulated posterior five costals and associated peripherals (presumably 6th–9th) from the left side of the body. Its ossification stage is comparable with ISEA FR/WNC-1 and MRJ 70.1P.-P, which is consistent with their similar size.

The carapace outline of UR/1055 is rounder than the posteriorly elongated ovoid carapace seen in ISEA FR/WNC-1 and MRJ 70.1P.-P. Based on the differences in shell shape in the known larger specimens of *Glarichelys knorri* (holotype PIMUZ A III/596 versus holotype of *Chelonia ovata*

NWSGL-EF-100789 + NWSGL GL-EF-100790 and PIMUZ A III/594; see Zangerl 1958) we consider this simply a form of intraspecific variability rather than an ontogenetically, sexually, or taxonomically driven difference.

In contrast to most other elements, including the disarticulated nuchal, most of the shell molds of ISEA FR/WNC-1 and MRJ 70.1P.-P tend to preserve dark remnants of bone tissue. This may theoretically impact the fidelity of the digital positives, but apparently not by much, especially that the bone layer lining the molds is so thin in most places, that it conforms to the external ornamentation of bones.

The nuchal is represented in ISEA FR/WNC-1 (ventral surface, anterior part; Figs. 8A, 9A) and MRJ 70.1P.-P (dorsal surface, more complete but obscured posteriorly by the skull roof; Figs. 8B, 9B). In both specimens, the left anterolateral process is missing, and the left posterolateral edge coincides with the edge of the slab, making evaluation of its completeness impossible. The preserved surfaces suggest a wider than long outline with laterally directed processes in the anterior part and a wide, posteriorly narrowing main plate mesially, a slightly concave, nearly straight anterior edge, and a sagittally keeled (posteriorly more than anteriorly) external surface, similar to that of larger *Glarichelys knorri* (Fig. 1; Zangerl 1958). However, the nuchal of the Polish juvenile *Glarichelys knorri* seems to be proportionally longer than in the known larger specimens. Its exact length in ISEA FR/WNC-1 and MRJ 70.1P.-P is obscured by damage or other bones, but even as preserved, its width (calculated by doubling the distance from the midline to the lateral tip of the anterolateral process) appears to be less than twice (approx. 1.9 times) the length. In larger *Glarichelys knorri* it varies between approx. 2.1 (PIMUZ A/III 594; Fig. 3) and 2.5 (holotype PIMUZ A/III 596: Fig. 1). In the holotype (SMF-R 263) of "*Chelonia*" *gwinneri* the nuchal is approx. 2.2 times as wide as long, lacks the sagittal keel (possibly ontogenetic), and has a laterally expanded posterior part (Wegner 1911, 1914). Note, however, that the shape and proportions of the nuchal tend to vary intraspecifically in cheloniids (e.g., Zangerl 1958). The visceral surface of the nuchal in *Glarichelys knorri* ISEA FR/WNC-1 (Fig. 9A) bears mesially a low, longitudinal ridge, possibly forming an attachment for the posteriormost (eighth) cervical vertebra or the nuchal ligament. In contrast to larger *Glarichelys knorri* (Figs. 1–3; Zangerl 1958), there is no evidence of postnuchal fontanelles in Polish specimens.

Neural bones are most informative in ISEA FR/WNC-1 (external view; Figs. 6A, 8A) and MRJ 70.1P.-P (visceral view; Figs. 6B, 8B), however, their limits are barely traceable. As correctly noted by Młynarski (1959), there are eight longer than wide neural bones exhibiting no subpartitioning. The first neural is rectangular, the second to fifth and the seventh are coffin-shaped (anterolateral edges shorter than posterolateral), the sixth is nearly equidimensional hexagonal (just slightly longer than wide) and anteroposteriorly symmetrical, and the eight one is nearly rectangular (Figs. 8, $11B_5$). Their external surfaces are gently keeled sagittally; the depth of the keel may be somewhat underrepresented in the digital positive due to the remaining bone tissue. The keeling is a juvenile character but it is also present in all larger specimens of *Glarichelys knorri* (Figs. 1–3; Zangerl 1958). In UR/1055, the shape of the neurals is poorly defined and their trabecular structure suggest a still ongoing ossification (Figs. 7A, 12A, 13, 14). At least some specimens of *Glarichelys knorri* seem to have nine neural bones (e.g., PIMUZ A/III 594: Fig. 3; Zangerl 1958), although recognition of the posteriormost axial elements as neurals or suprapygals based on external morphology, with no information on whether they form attachments with underlying vertebrae or not, is tricky. The only published specimen likely representing that species exposed in visceral view appears to have eight neurals (Wettstein 1886). With the significant variation to the number of shell bones observed in cheloniids, a variable number of eight to nine neurals seems plausible.

Among the Polish juvenile material of *Glarichelys knorri*, the whole sequence of costals is represented by ISEA FR/WNC-1 and MRJ 70.1P.-P (Figs. 6, 8). There are eight pairs of costal bones, most of which are characterized by a mallet-like or club-like shape, with proximal parts spread into costal plates retaining a sutural contact with each other, and distal parts gradually narrowing towards the periphery of the carapace. As in larger *Glarichelys knorri*, the broadened parts extend for about 1/3 of the costal length or less, and are mediolaterally shorter at the intercostal sutures, resulting in large, oblong, roughly V-shaped costoperipheral fontanelles (Figs. 1–3, 6–8, 12–14). The distal, narrower parts of the ribs bear longitudinal striations. In UR/1056 and, particularly, in UR/1055, their edges are more parallel than in ISEA FR/WNC-1 and MRJ 70.1P.-P, resulting in a more splinter-like appearance (Figs. 7, 8, 12, 13). The first costal is directed nearly transversally, with a minor anterolateral divergence, and has a conspicuous anterior projection. The subsequent costals, from the fourth one gradually turn increasingly more posteriorly. The last, eighth costal is directed almost parallel to the sagittal axis and differs from other costals in very minor proximal expansion. The proximal, expanded parts of the costal plates of UR/1055 have a trabecular structure suggesting an early ossification stage, as in the case of neural bones, and are somewhat shorter proximodistally than in other specimens (Figs. 7, 12–14).

Peripheral bones are represented in all four specimens from Poland. UR/1055 exhibits an early stage of their ossification, before establishment of interperipheral contacts (Figs. 7A, 12A, 13), whereas ISEA FR/WNC-1, MRJ 70.1P.-P, and UR/1056 have better ossified peripherals in contact with each other (Figs. 6, 7B, 9, 12B). In ISEA FR/WNC-1 and MRJ 70.1P.-P, peripherals 5–11 on the left side of the body and 5–9 on the right side remained in articulation and at least one disarticulated peripheral from an unknown position in the sequence is preserved by the left side of the carapace (Figs. 6, 8, $11A_1$, A_2, A_6). UR/1055 preserves peripherals 6–11 on the left side of the body and 7–11 on

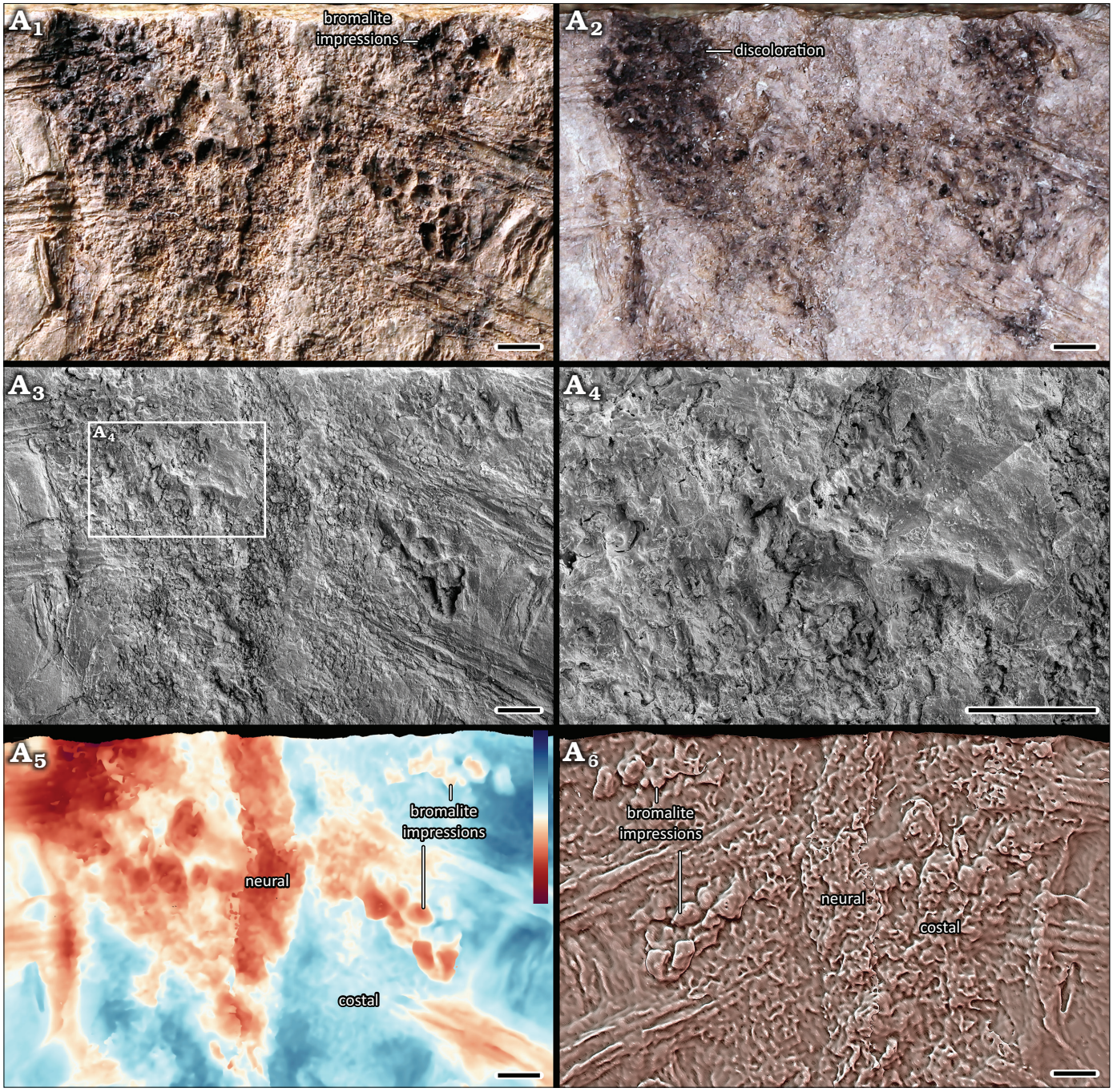


Fig. 14. Sea turtle *Glarichelys knorri* (Gray, 1831), juvenile specimen from Hermanowa, Poland, Rupelian, UR/1055, presumed digestive tract preservation in the abdominal area: A_1, photograph, note nodular concavities between the rib shafts; A_2, photograph lit from the camera's position to reduce shadows and showcase coloration, note dark discoloration; A_3, A_4, composite SEM images; A_5, elevation model of a CT-based 3D model with shading disabled; A_6, digital positive made from a µCT-based 3D model with the Radiance Scaling (Lit Sphere) shader enabled, note the reticular system of bone trabeculae building the neurals and costals, indicative of an early ossification stage. Scale bars 1 mm.

the right side (Figs. 7A, 12A, 13). In UR/1056 only left peripherals 6–9 seem to be preserved (Figs. 7B, 12B). In general, well-preserved peripherals are comma-shaped or kidney-shaped, with convex proximal edges, bulged anterior parts, distinct concavity in the place of the intermarginal sulci, and proximodistally narrower posterior parts. This seems consistent regardless of their degree of ossification (as long as the ossified regions corresponds to two neighboring marginal scutes) and uniform, and differs from the more even edges of the carapaces in larger *Glarichelys knorri* (Figs. 1–3) and "*Chelonia*" *gwinneri*, even if the latter two exhibit some minor edge undulation, especially posteriorly (Figs. 1–3; Wegner 1911, 1914; Zangerl 1958). Moreover, the peripherals are relatively uniform in proximodistal width, showing no widening in the posterior part of the carapace (in contrast to "*Chelonia*" *gwinneri*; Wegner 1911, 1914) and

being uniformly somewhat more massive than in the known larger specimens of *Glarichelys knorri* (Figs. 1–3; Zangerl 1958).

Only a small suprapygal or its fragment is recognizable in ISEA FR/WNC-1 and MRJ 70.1P.-P (Figs. 8, 11A_5, B_5), right in front of a displaced xiphiplastron. It appears to be consistent in shape and relative size with the suprapygal of PIMUZ A/III 594 (Fig. 3; Zangerl 1958). In UR/1055 the suprapygal seems to be either missing, damaged, not yet ossified, or is not recognizable (Figs. 12A, 13).

The pygal is a kidney-shaped (anteriorly convex and posteriorly medially notched), small bone preserved as an impression in ISEA FR/WNC-1, MRJ 70.1P.-P, and UR/1055 (Figs. 6, 7A, 8, 11A_6, 12A, 13). As in larger *Glarichelys knorri*, it is very similar in size and shape to peripheral bones, albeit transversely narrower (Figs. 1–3; Zangerl 1958). It has no discernible structures that would suggest an osseous contact with a suprapygal (Fig. 11A_6).

Plastron: Plastral bones are represented in all four specimens from Poland. In ISEA FR/WNC-1 and MRJ 70.1P.-P, they are disarticulated and scattered and consist of one epiplastron, probable entoplastron, anteromedial parts of hyoplastra, and both xiphiplastra (Figs. 6, 8, 11A_2, A_5, A_6, B_2, B_5). Except of the hyoplastra, which are exposed in dorsal view in ISEA FR/WNC-1 and in ventral view in MRJ 70.1P.-P and remain to be displaced posterolaterally relative to their original positions, the sides of the plastral bones cannot be determined. UR/1055 preserves an impression of the dorsal aspect of both hypoplastra (the left one more complete than the right one) and both xiphiplastra, which show minor dislocation but are obscured by the carapace and other bones (Figs. 7A, 12A, 13). UR/1056 preserves an impression of the ventral surface of a posterolateral part of the left hyoplastron, most of the left hypoplastron, and presumably a minor anterolateral portion of the left xiphiplastron, which appear to remain in their anatomical position but are filled with a mass of fragmented bone, which partially obscures the anatomy (Figs. 7B, 12B). Because of the incompleteness, Zangerl's (1958) bridge index (the shortest distance between the axillary and inguinal notch divided by the breadth of half of the plastron and multiplied by 100) is unknown.

The epiplastron in ISEA FR/WNC-1 and MRJ 70.1P.-P is an elongate, narrow, gently bowed, flattened bone with a squared-off anteromedial end and pointed posterior tip (Figs. 8, 11A_2, B_2). The anterior part shows a punctuated rough surface, whereas in the posterior part longitudinal striation is dominant. It is proportionally shorter than in larger individuals of *Glarichelys knorri* (Figs. 1, 4; Zangerl 1958) but more gracile than in "*Chelonia*" *gwinneri* (see Wegner 1914).

The presumed entoplastron is preserved in ISEA FR/WNC-1 and MRJ 70.1P.-P, stuck between the epiplastron, coracoid, second left costal, and presumed fibula (Figs. 8, 11A_2, B_2). It is diamond-shaped with an abbreviated anterior tip. Its widest part is about thrice the width of the narrowest, posteriormost part. The posterior process is not preserved. The presumed dorsal surface is partially obscured by sediment but a spindle-shaped facet in the anterlolateral left part may represent a contact surface with the epiplastron (Fig. 11A_2).

The hyoplastron has a presumably anteromedially directed, plate-like anterior process, projecting several fingerlike processes (about five visible in ISEA FR/WNC-1 and MRJ 70.1P.-P, although damage cannot be ruled out; Figs. 6, 8), a short, rounded posterior process, and a presumably longer lateral process (visible only in part in UR/1056; Figs. 7B, 12B).

The morphology of the hypoplastron is unclear except of the lateral process which is anteroposteriorly narrow close to the base and widens laterally, ending in about seven radiating processes (six visible in UR/1056 but one likely broken off or obscured due to the overlap with a rib). The anterior process is not clearly visible in any specimen but, based on the anteroposterior length of the lateral plastral fontanelle in UR/1056, it was probably comparable in size to the posterior process of the hyoplastron. The posterior process in only partially visible in UR/1055 and it appears to be somewhat longer than the anterior one (Fig. 8A). There is no evidence on whether it had a smooth medial margin, similarly to larger *Glarichelys knorri*, or if it projected radial processes medially, as in "*Chelonia*" *gwinneri* and extant cheloniids (Wegner 1914; Zangerl 1958).

Impressions of both xiphiplastra are preserved in ISEA FR/WNC-1 (Figs. 6A, 8A, 11A_5, A_6), MRJ 70.1P.-P (Figs. 6B, 8B, 11B_5), and UR/1055 (dorsal surfaces but obscured by other bones; Figs. 7A, 12A, 13), whereas UR/1056 may preserve only a small, anterolateral, poorly preserved and uninformative part of the right xiphiplastron (Figs. 7B, 12B). The xiphiplastron is an elongated, longer than wide, flat, peanut-shaped bone, with a sinuous (concave anteriorly and convex posteriorly) lateral edge, slightly expanded posterior part, and short processes radiating from the anterior and posteromedial ends. At least in ISEA FR/WNC-1 and MRJ 70.1P.-P, in which they can be fully observed, the xiphiplastra are proportionally shorter and less gracile than in *Glarichelys knorri* PIMUZ A/III 593 (Fig. 4; Zangerl 1958: pl. 15; note that Zangerl's reconstruction of the plastron in that species was prepared before PIMUZ A/III 593 was examined by him [see addendum, p. 53], and the xiphiplastra are poorly visible or completely obscured in the remaining specimens) and "*Chelonia*" *gwinneri* (as drawn by Wegner 1914).

The radial projections of the lateral processes of the hyo- and hypoplastron converge laterally and brace a mediolaterally elongate, shorter than wide lateral plastral fontanelle. A central fontanelle was certainly present, but its shape and size are not clearly indicated in any of the specimens.

Scutes: Epidermal scute sulci on the bones are mostly unclear, except of the cervical scute (MRJ 70.1P.-P, Fig. 9B) and intermarginal sulci located at peripheral concavities. Ambiguous, transverse grooves are detectable in the digital positive crossing the third neural bone just posterior to its midlength and the fifth neural bone in the posterior part (Fig. 8A), and thus may represent intervertebral sulci, but

their identification is tenuous. Likewise, shallow and uncertain, oblique (antero- or posterolateral) grooves may represent pleurovertebral sulci but they are not distinct enough to be certain if they are not a result of superficial damage. However, intercostal and circumperipheral areas of ISEA FR/WNC-1 and MRJ 70.1P.-P display relatively sharply defined fields of brown discoloration fragmented by a network of linear areas of non-discolored rock matrix (Figs. 3, 5). These fields were interpreted by Młynarski (1959) as carapacial scute traces, and we agree with this interpretation. Although the edges of these traces and distances between them are somewhat uneven, likely because of post-mortem deterioration and possibly partial detachment, their layout is consistent between both slabs, agrees with the typical turtle pholidosis pattern, and corresponds well with the peripheral shape. UR/1055 and UR/1056 present, within the boundaries of their bodies, similar discoloration of the rock matrix as ISEA FR/WNC-1 and MRJ 70.1P.-P. However, in UR/1055 no linear patterns corresponding to non-cornified areas between scutes are identifiable and the discoloration extends onto the limbs (Figs. 7A, 12A, 13A), so it appears to represent an outline of soft tissues rather than scutes in particular. In UR/1056 some faint lighter lines are present, which may represent circummarginal and circumpleural borders and which seem to be aligned in a pattern similar as in ISEA FR/WNC-1 and MRJ 70.1P.-P, but they are too unclear and ambiguous to be informative (Figs. 7B, 12B). In summary, there seem to have been a single cervical, five vertebrals, four pairs of pleurals, and presumably twelve pairs of marginals (eleven readable in ISEA FR/WNC-1 due to the damage to the anterior part of the carapace but showing space for at least one more).

The cervical scute (Fig. 9B) was short, wider than long and distinctly elevated in the middle part of the nuchal, but laterally increased in length but decreased in depth. Its posterior edge, at least in the middle part, was gently concave.

Only a very small part of the presumed fourth vertebral is visible as discoloration on the left side of ISEA FR/WNC-1 and a larger part of the presumed fifth vertebral is present posteriorly, not distinguished from the last pair of marginals. In combination with very large costoperipheral fontanelles and possible intervertebral sulci localized on the third and fifth neural, this implies that the vertebrals were not particularly wide, possibly of a comparable length and width. The intervertebral sulci were apparently decidedly narrower, especially between the two last vertebrals (based on the visible angles of their lateral borders; the sulcus almost certainly crossed the eighth neural). This agrees with the morphology of vertebrals observed in larger *Glarichelys knorri* and "*Chelonia*" *gwinneri* (Figs. 1, 2A, 3; Wegner 1911, 1914; Zangerl 1958). The fifth vertebral has an obscured anterior part and indistinct posterior edge but it was apparently hexagonal, with the posterior part wider than the anterior and maximum width around the level of 2/3 of its length.

The pleurals were separated from each other and from the last vertebral by posterolaterally directed furrows partially overlapping with the second, fourth, sixth, and eighth costal. The first pleural was apparently subtriangular, with a convex anterolateral edge, whereas the remaining pleurals were presumably pentagonal. The fourth pleural was much smaller than the rest.

The marginals were anteroposteriorly longer than proximodistally wide. Their borders coincided with incisions/concavities of the peripheral rim, so the anterior, bulged part of each peripheral supported the posterior part of one marginal, and the narrower, posterior part of the peripheral underlined the anterior part of the subsequent marginal. There is no imbrication or exaggerated serration produced by the marginals. We were unable to confirm the anterior edges of the last pair of marginals marked by Młynarski (1959: pl. 2), there is an indistinct darker pattern in the area indicated in MRJ 70.1P.-P and the position of the furrow illustrated by Młynarski (1959) appears correct, but this area is ambiguous in the fossils (Figs. 6, 8, 11A_5, A_6) possibly due to slight dislocation of the scutes post-mortem resulting in their partial overlap.

Forelimb: ISEA FR/WNC-1 and MRJ 70.1P.-P preserve impressions of one disarticulated scapula (side undetermined due to crushing, but probably right), both coracoids, one humerus (right), presumed ulna and radius, and partial left manus (Figs. 6, 8, 9A, B, 11A_1–A_4, B_1–B_4). UR/1055 preserves impressions of distal parts of the longest two digits of the left manus (Figs. 7A, 12A).

The scapula is a Y-shaped element, which in digital positives shows clear evidence of crushing, resulting in longitudinal cracking and collapse of the surface (Fig. 9A, B). Its glenoid is positioned on a distinct neck, which shows only a minor constriction, plausibly caused by deformation. The length of the glenoid neck and acromion combined is approximately the same (94%) as the height of the dorsal scapular process. The base of the acromion is set at an angle of about 110° relative to the dorsal scapular process, but it is gently bowed so its distal end slightly converges towards the dorsal process. The glenoid neck is set at an angle of about 120° relative to the dorsal scapular process and about 130° relative to the base of the acromion.

The coracoid (Fig. 11A_1, A_2, B_1, B_2) is only about 10% longer than the dorsal scapular process. There is a distinct constriction at about two-sevenths of its length, from which point the bone consistently expands proximally and distally. The proximal expansion at the glenoid area is only slightly narrower than the distal expansion.

The impression of the right humerus (Figs. 9A, B, 11A_3, B_3) is hourglass-shaped, with comparably widened proximal and distal expansions separated by a midshaft constriction located just proximal to its midlength, and has a generally plesiomorphic testudinate morphology (compare with, e.g., Hermanson et al. 2024). It is somewhat shorter than the dorsal scapular process, being about 81% of its length. ISEA FR/WNC-1 exposes the capitular surface, whereas MRJ 70.1P.-P preserves the impression of the intertubercular surface partially obscured by other bones. The proximal ex-

pansion has a lenticular outline. The humeral head is ovoid, wider than long, and preserved in ISEA FR/WNC-1 as a fragment of detached mineralized cartilage (Fig. 11A$_3$). The lateral and medial processes are located at about the same level, distal to the humeral head. The medial process extends further ulnarily, whereas the lateral process diverges intertubercularily. The proximal edge is gently convex and there are no notches between the humeral head and the lateral and medial processes. Its rugosity suggests that it was covered by a continuous cartilaginous cap, some of which seems to be still present in ISEA FR/WNC-1. As preserved, the intertubercular fossa is shallow and poorly defined, apparently shifted closer to the radial than to the ulnar edge. There is no evidence of the secondary deltopectoral crest (Hermanson et al. 2024). The distal expansion has a triangular outline with a slightly pinched radiodistal corner. It is unclear whether the ectepicondylar canal had a form of a groove or if it was enclosed into a foramen—digital positives of both the capitular and intertubercular surfaces show a groove parallel to the radial edge of the distal expansion, which probably corresponds to the collapsed ectepicondylar canal, but the preservation makes it impossible to verify if it was open or roofed with bone.

The ulna (Figs. 6, 8, 9A, B, 11A$_3$) is a shorter than the humerus, gently bent bone with slightly expanded proximal and distal ends. It lacks a prominent olecranon process.

The radius (Figs. 6, 8, 9A, B, 11B$_4$) differs from the ulna in being slightly longer, having a less expanded distal end, and in the presence of a triangular facet for the proximal carpals. Their morphology of the radius and ulna is congruent with that in extant cheloniids (Zangerl 1958; Wyneken 2001), particularly juveniles (YPM Herr 004058). The slender bone identified in MRJ 70.1P.-P as a radius by Młynarski (1959) appears to be more consistent with a fibula (see below).

ISEA FR/WNC-1 and MRJ 70.1P.-P preserve several irregular or round small bone impressions which may represent carpals (e.g., Fig. 11B$_4$). Out of them two, located close to the association of other forelimb bones, appear consistent with the intermedium and ulnare (Fig. 9A, B). If correct, both bones are slightly expanded proximally and medially, and the intermedium is narrower than the ulnare. Outline of the ulnare differs slightly between the slabs, likely due to its position relative to the bedding plane and possibly some damage but is overall reminiscent of that in *Chelonia mydas* (YPM Herr 004058; Zangerl 1958).

Impressions of several elongated bones that may represent metacarpals or manual phalanges are scattered in ISEA FR/WNC-1 and MRJ 70.1P.-P (Figs. 3, 5, 7A$_4$), but their identification is ambiguous. A probable first metacarpal is located in the association with other forelimb bones and is a relatively massive, elongated and proximally and distally expanded bone (Figs. 6, 8, 11A$_3$, B$_3$). A cluster of manus bone imprints, presumably corresponding to semiarticulated left metacarpals III (proximally incomplete), IV, and V, proximal phalanges III and IV (distally incomplete), and a disarticulated manual ultimate phalange (Figs. 6, 8). A poorly preserved, elongated impression is present more laterally, just at the edges of ISEA FR/WNC-1 and MRJ 70.1P.-P, in a place fitting the proximal phalange II and was interpreted as a part of the manus by Młynarski (1959) but differs in a spongy structure and therefore most likely represents a part of a plastral bone or a disarticulated peripheral. Finally, UR/1055 preserves impressions of the distal parts (ultimate phalanges and the distal parts of the preceding phalanges) of presumably the third and fourth left manual digit. The ultimate phalanges are long, the third one is triangular and nearly straight whereas the fourth one is more distinctly curved. In ISEA FR/WNC-1 and MRJ 70.1P.-P the bones of the manus are separated by small gaps, but it is uncertain whether this is representative of the morphology in vivo, or an effect of partial disarticulation. In UR/1055, despite its smaller size, the bones abut each other at the joints.

Hindlimb: ISEA FR/WNC-1 and MRJ 70.1P.-P preserve the right pubis and a fibula (Figs. 6, 8, 11A$_5$, B$_4$). UR/1055 preserves obscured pelvic elements, a nearly complete left hindlimb missing the ultimate phalange of the fifth digit, and a mostly complete right hindlimb missing the distal part of the pes (Figs. 7A, 12A, 13). UR/1056 preserves a possible badly damaged proximal part of the right femur (Figs. 7B, 12B).

Elements of the pelvic girdle are identifiable in ISEA FR/WNC-1 (Figs. 6A, 8A, 11A$_5$), MRJ 70.1P.-P (Figs. 6B, 8B, 11B$_4$), and UR/1055 (Figs. 7A, 12A, 13). However, in most cases the pelvic bones are obscured by the overlying carapace.

Presumably all three specimens preserve impressions of the pubis, although only MRJ 70.1P.-P offers a good view (right, ventral surface; Figs. 6B, 8B, 11B$_4$). The pubis has a plesiomorphic, triradiate morphology. The medially directed main plate terminates anteromedially in a short process, shorter than the predominantly anteriorly directed and distally widened lateral pubic process. The angle between those two branches is about 80°. The posterolaterally directed process leading to the acetabulum is relatively long. Its acetabular part is slightly expanded. There is no evidence of an elongate epipubic process or a subdivision or complete mesial division of the thyroid fenestra, but it is uncertain if this is representative of adult morphology.

At least one (left) ilium is partly exposed in lateral view in UR/1055 (Figs. 7A, 12A, 13). Its acetabular part is bulky and expanded anteroposteriorly to a similar degree as the dorsal part. The posterior process of the ilium, as preserved, is rounded off and shows little to no dorsal inclination. The same specimen apparently preserves impressions of dislocated other pelvic bones on the right side of the body, but due to the overlying costals they cannot be convincingly identified and interpreted.

The femur (Figs. 7A, 12A, 13) exhibits only subtle sigmoidal curvature and distal expansion. The preservation and overlying costals limit the amount of available information, but at least in UR/1055 the femora appear to be

proportionally stouter and larger than in larger individuals of *Glarichelys knorri* (Figs. 1–3; Zangerl 1958). No useful information on the morphology of the femoral head, trochanters, and the intertrochanteric fossa (if present) can be obtained from the Hermanowa specimens.

The tibia (Figs. 7A, 12A, 13) is a straight, slender, only slightly proximally and distally expanded bone slightly shorter than the femur. Its proximal articular surface is gently concave and well defined by a ridge-like edge. There is no evidence of a pit similar to that present on the tibial shaft in *Eochelone brabantica* Dollo, 1903 and *Oligochelone rupeliensis* Dollo, 1909 (see Zangerl 1980).

The fibula (Figs. 6, 7A, 8, 11A_2, B_2, 12A, 13) is slender, more gracile than the tibia but roughly as long, subtly bowed or sinuous, barely expanded proximally, and more distinctly expanded distally. Laterodistally, it terminates into a short, triangular styloid process.

The tarsals are apparently not yet ossified or not preserved in UR/1055, except for a single rounded element proximal to the third metatarsal and adjacent to the ansulate bone (Figs. 7A, 12A, 13). Its position relative to other bones is bilaterally symmetrical and seems to indicate that it is a distal tarsal rather than the calcaneum.

All five metatarsals are preserved in UR/1055 (Figs. 7A, 12A, 13), but on the left side of the animal they are partially obscured by a peripheral. The first metatarsal is the shortest, followed by the fifth, second, third, and fourth. The first metatarsal is roughly as wide as it is long due to a distinct proximal expansion, giving it a roughly sickle-shaped outline, but with two condyle-like medial convexities located at the proximal and distal end and separated by a notch. The lateral edge is concave; the concavity deepens more abruptly in its proximal than in its distal part. The metatarsals II–IV are elongated, expanded proximally and distally, and constricted at the midshafts. This constriction is the least pronounced in the second metatarsal and the most distinct in the fourth metatarsal. The ansulate bone (Joyce et al. 2013) is slightly longer than wide, crescentic, more symmetrical proximodistally than the first metatarsal. Its lateral edge is uniformly and markedly convex, and the medial edge is uniformly and gently concave. The right pes of UR/1055 shows proximal imbrication of the metatarsals.

The phalangeal formula is 2-3-3-3-?3 (Figs. 7A, 12A, 13). The non-ultimate phalanges are longer than wide and hourglass shaped. In the proximal row, their length increases following the sequence of the digits, with the proximal phalange of the first digit being the shortest, and the proximal phalange of the fifth digit being nearly twice as long. In the second row, the phalange of the third digit is particularly long, followed by the phalanges of the fourth, second, and finally fifth digit. The penultimate phalange of the first digit is hourglass shaped, the penultimate phalanges of the third and (particularly) the fourth digit are of a nearly uniform width along their entire length, and the penultimate phalange of the fifth digit is distinctly narrower distally than proximally. The ultimate phalanges (we refrain here from using the term "ungual" because we are cannot know with certainty whether these digits ended in claws) are straight and triangular with their very distal tips rounded off. The ultimate phalange of the third digit is the longest and the broadest, followed by the ultimate phalanges of the second, fourth (the narrowest), and first digit. The ultimate phalange of the fifth digit is missing in both pedes. Despite its small size, metatarsals and phalanges of UR/1055 of all digits maintain their articular connections and are not separated by gaps.

The limbs of UR/1055 are surrounded by a reddish halo (Figs. 7A, 12A_3, 13), representing the outline of soft tissues. This discoloration of the sediment is correlated with the change of its radio-opacity and thus can be observed in μCT data (Fig. 7A_4). The data reveal that least the third and fourth digit of the manus as well as all the digits of the pes were enclosed in a paddle. The fourth and fifth digits of the pes were separated by notches from the rest of the paddle but still embedded in folds of skin. There is no evidence for the ultimate phalanges extending beyond the outline of the paddle, with the possible exception of the ultimate phalange of the fifth pedal digit, which is missing but could possibly reach the edge of the skin, given the proximity of the distal end of the penultimate phalange. Examination of the specimen under ultraviolet light presents no additional detail.

Digestive tract: The abdominal region in UR/1055 presents linear clusters of nodular concavities, consisting of ovoid, oval, and irregular segments (Figs. 7A, 12A, 14). Because these concavities are exposed exclusively within the shell outline, more precisely in the intercostal areas, and because the specimen is preserved as an impression (negative) of the dorsal surface of the body, we interpret their original form (positive) as convex structures located between the carapace and plastron, that is, within its body cavity (Fig. 14A_6). As revealed by μCT data, the structures do not continue into the slab, which is consistent with their interpretation of imprints as parts of the original individual rather than some form of damage or accumulation of extrinsic more coarse-grained material randomly overlapping with the turtle body impression. Their location and morphology seem, therefore, the most consistent with the digestive tract, particularly intestines of the turtle. The three-dimensional relief is roughly associated with a W-shaped darkening of the sediment and presence of black, charcoal-like residue, which bleed through the overlying costals but do not extend beyond the abdominal cavity (Figs. 7A, 12A_3, 14A_1–A_2). This discoloration is the strongest on the right side of the body. This is the side opposite to stomach, and although some internal displacement of organs due to taphonomic factors is not impossible, we consider this unlikely that this particular part corresponds to the stomach.

Stratigraphic and geographic range.—Rupelian (Oligocene) of Switzerland and Poland.

Glarichelys sp.

1992 *Glarichelys knorri* (Gray, 1831) [partim]; Gregorová and Młynarski 1992: 63–68, fig. 1, photo 1.
2005 *Glarichelys knorri* (Gray, 1831); Gregorová 2006: 90.
2012 turtle; Mayr and Gregorová 2012: 334.
2025 *Glarichelys* aff. *knorri* (Gray, 1831) [partim]; Chroust and Szczygielski 2025: 2.
2025 cf. *Glarichelys* sp.; Chroust and Szczygielski 2025: 4.

Material.—MZM Ge 27364, disarticulated remains (three scapulae, coracoid, pubis, ilium, ischium, several vertebrae, costal, two neurals, at least one peripheral, probably two hyoplastra, hypoplastron, xiphiplastron, autopodial elements, possible dentary, and some undetermined bones) of at least two individuals of juvenile sea turtles mixed with fish remains in a mid-Oligocene menilite slab from Litenčice, Moravia, Czechia (Fig. 15). Most of the elements are preserved as a beige or light brown bone, only slightly darker than the surrounding rock matrix, but some of them are chipped, leaving behind natural molds. Some bones are still mostly embedded in the matrix.

Description.—The presumed dentary is preserved in ventral view, located in the very corner of the slab, and missing much of its left ramus. It seems distorted, with the left side pushed in. The symphyseal portion is moderately long, it has a rounded and medially shallowly grooved but otherwise featureless mental (chin) surface and terminates in a short, rounded off beak. The preserved part suggest that the mandibular rami were set at a more obtuse angle than in *Glarichelys knorri* ISEA FR/WNC-1, more consistent with the morphology observed in larger *Glarichelys knorri* or even "*Chelyopsis*" *raabei* (Schleich et al. 1994).

We agree with Gregorová and Młynarski's (1992) interpretation of two neurals and a single costal. The costal is mostly preserved as an impression missing most of the bone tissue. An elongated apical part of the rib is apparent. One of the neurals is oval (elongated anteroposteriorly), distinctly sagittally keeled, and bears a prominent intervertebral sulcus. Moreover, it seems to be associated with a partially exposed underlying dorsal vertebra. The other neural is hexagonal and bears a slightly less prominent keel. Several more bone elements may represent neurals but their identification is ambiguous. The slab preserves at least one elongated peripheral with a moderately expanded anterior part. We were unable to locate the other peripheral figured by Gregorová and Młynarski (1992: fig. 3B).

At least four elements of the plastron are recognizable: two hyoplastra (right, with a broken off but impressed in the matrix axillary part, and presumed left (partially preserved large plate which may represent the lateral branch), one hypoplastron (right, with broken lateral process), and one xiphiplastron (presumably right). The remnant of the left hypoplastron may be represented by one of two incomplete structures: a plate-like, squared off bone fragment just next to the right hypoplastron, on the edge of the slab, or by a poorly preserved imprint with some bone residue located between the right hypoplastron and the xiphiplastron. Both the hyo- and hypoplastra consist of three branches and differ in their relative size and direction. In the hyoplastron the largest branch is interpreted as the anteromedial process, contributing to the anterior plastral lobe and engaging the entoplastron with an oblique and highly denticulate edge. The lateral (axillary) and posterior (directed towards the hypoplastron) processes are narrower than the anteromedial process and set at a slightly oblique angle to each other. The lateral branch of the right hyoplastron is only partially preserved, partially impressed in the sediment, but is terminal part with radiating processes is missing, so it is not possible to establish its length. If the fragmentary large plate represents the lateral process of the hyoplastron, then this structure is slightly longer than the lateral process of the hypoplastron. The posterior branch is squared off but presumably complete. The largest branch of the hypoplastron is interpreted as the lateral (inguinal) process, it is narrow than the anteromedial process of the hyoplastron and gently bent posterolaterally. The anterior process is squared off and short. The posterior process is nearly as denticulate as the lateral process but much shorter and bears a deep notch for the xiphiplastron. The xiphiplastron is fusiform and elongated, and anteriorly bears a notch for a denticulate process of the hypoplastron. Based on the preserved elements (Fig. 15B), regardless if the lateral (axillary) branch of the hyoplastron is represented or not, the bridge index would exceed 86, possibly approaching 100.

In contrast to Gregorová and Młynarski (1992) we note the presence of three scapulae (Fig. 15A_1–A_4), two of them are of comparable size (one preserved mostly as an impression) and one seems smaller and has broken off dorsal process. All three have glenoids positioned on a distinct necks. The impressed specimen presents the most complete outline and indicates that the acromial and dorsal processes were of subequal length and that the acromion was gently bowed. The coracoid is elongated pentagonal, broadening in a nearly uniform fashion but slightly stronger in the proximal third than more distally. It is missing its proximalmost part. It is, nonetheless, likely that it was originally comparable in length to the scapular processes.

We confirm the presence of a complete albeit crushed pubis, as reported by Gregorová and Młynarski (1992). However, we also notice an associated ischium and a probable ilium. The pubis is distinctly triradiate, presenting an outline very similar to that in *Glarichelys knorri* MRJ 70.1P.-P but with a proportionally slightly larger, more posteriorly expanded main (medial) plate. The ilium is exposed in medial view, it is J-shaped, having a broadened base, constricted neck, and a distinct posteriorly directed process. The posterior apex of the posterior iliac process is obscured by one of the scapulae but at least its proximal part is set at a roughly right angle to the iliac neck. The ischium is significantly smaller than the pubis but also triradiate. It is apparently exposed in dorsal view. Most of its body consists of an expanded, nearly semicircular portion which we interpret as the lateral (acetabular) branch. The posterior ischial

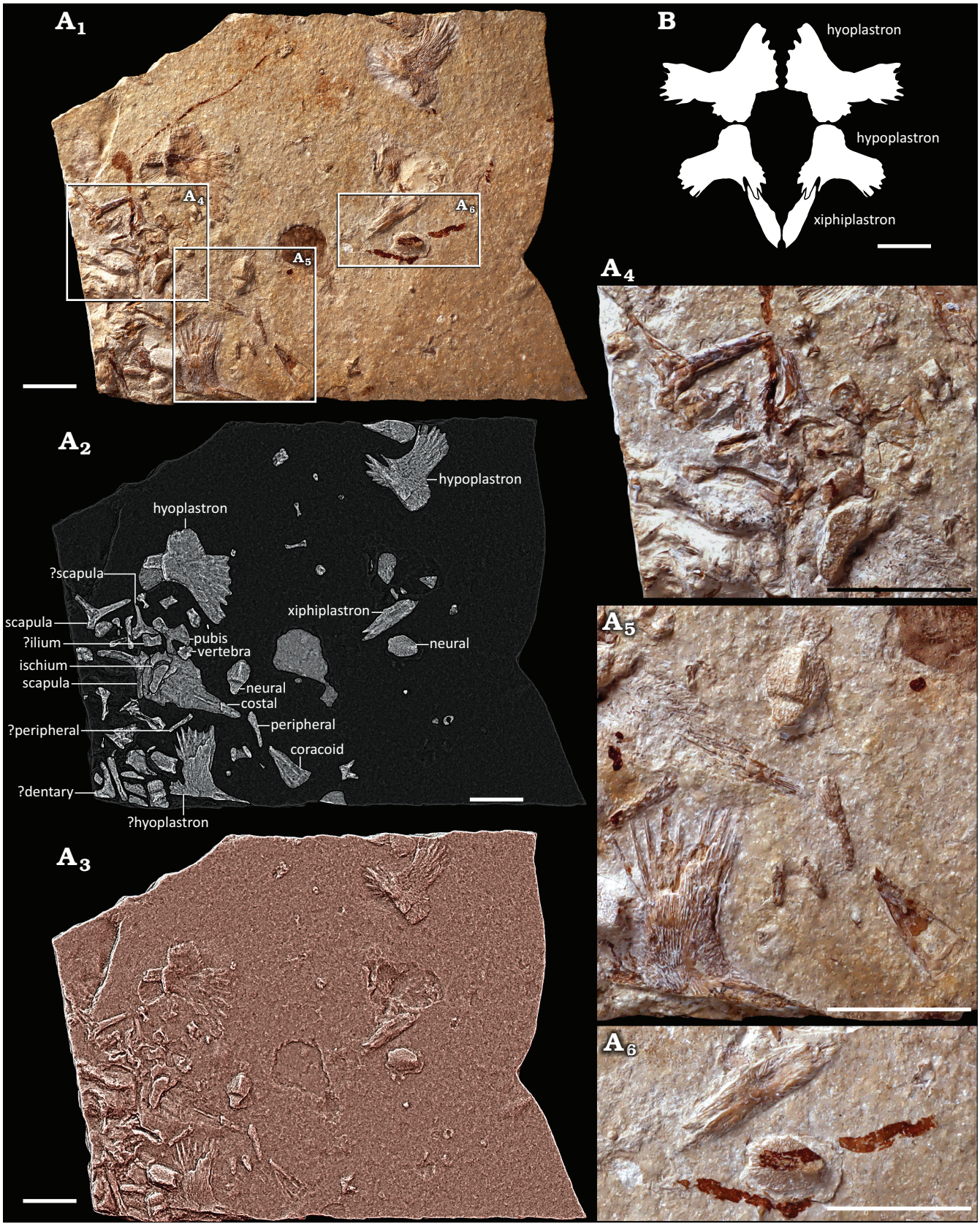


Fig. 15. Sea turtle *Glarichelys* sp. juvenile specimen from Litenčice, Czechia, Rupelian. **A**. MZM Ge 27364, assemblage of scattered bones: A_1, photograph; A_2, 3D model presented with the Radiance Scaling (Lambertian) shader enabled, outlined bone borders, and background rock matrix darkened; A_3, 3D model presented with the Radiance Scaling (Lit Sphere) shader enabled; A_4–A_6, closeups of the regions indicated in A_1. **B**. Restoration of the plastron. Scale bars 10 mm.

(metischial) process is thorn-like, narrow, triangular, and relatively long, and projects predominantly posteriorly with a slight (presumed lateral) skew. As exposed, the medial branch which contacted the contralateral ischium appears to be short and narrow, but it is unclear if that is an accurate representation of its original shape, or if it is damaged or still partially embedded in the matrix. Autopodial elements and vertebrae, due to their lack of articulation and generalized morphology, provide no useful information.

Overall, the bones are mostly consistent morphologically with corresponding elements of *Glarichelys knorri*. The main difference is the bridge index, which is significantly larger than the bridge index of approximately 70 (in reality between about 65 and 80) observed by Zangerl (1958) for *Glarichelys knorri*. However, we disregard this character for several reasons:

The specimen includes remains of one than more individual (three scapulae) possibly slightly differing in size, so it is not certain if the preserved plastral elements allow a reliable measurement.

There is no complete hyoplastron and estimation of the length of its lateral branch (which is longer than the hypoplastral and thus determines the width of the plastron; see Zangerl 1958) based on the preserved remains may yield some error.

The elements are disarticulated and thus, e.g., the size of the central plastral fontanelle (impacting the breadth of the plastron) is uncertain.

The specimen is much smaller than the described individuals of *Glarichelys knorri* allowing the measurement of the bridge index, and thus may be differently proportioned (there is clear variability of the plastral index in the Cheloniidae documented by Zangerl 1958), especially that ossification of plastral bones might have been still in progress.

The specimen may simply represent a different species of *Glarichelys* or an ontogenetic stage of *G. knorri* characterized by a different plastral index.

Other potential differences (e.g., the angle between the mandibular rami) may also possibly result from preservational or ontogenetic factors. On the other hand, proportions of the scapulocoracoid and morphology of the carapacial bones and girdles allow refereal of MZM Ge 27364 to the genus *Glarichelys*. In the end, we consider the material not sufficiently diagnostic to allow its specific determination, therefore it is referred here solely to the genus, as *Glarichelys* sp.

Remarks.—The black and white photograph of the specimen published by Gregorová and Młynarski (1992) is not particularly legible and the drawings are schematic and only present outlines of selected bones but it seems that since its description the specimen underwent some minor additional preparation. In the original description, Gregorová and Młynarski (1992) only mentioned some of the now identifiable bones and the labels for the hyo- and hypoplastra in their fig. 1 are switched relative to the description.

Discussion

Taxonomic identity and ontogeny.—ISEA FR/WNC-1, MRJ 70.1P.-P, UR/1055, and UR/1056 are here considered to belong to the same taxon based on their generally consistent morphology. Although they represent immature individuals and only partially overlap regarding the preserved structures, they share the same general morphology of the shell and general proportions. Moreover, they all converge in their overall similarity to *Glarichelys knorri*, expressed in a very similar form of the shell (all specimens) and skull (ISEA FR/WNC-1 and MRJ 70.1P.-P), proportions of the limbs (ISEA FR/WNC-1, MRJ 70.1P.-P, and UR/1055), and body size (all specimens), differentiating them from other named cheloniod genera (e.g., Zangerl 1958; Młynarski 1959; Lapparent de Broin et al. 2018), but also differ from the known larger individuals of *G. knorri* in details of anatomy of various body parts. At the same time, the observed differences between individual specimens were shown (Zangerl 1958) to be ontogenetically dependent in cheloniids (small differences in proportions between limb bones) or explicitly variable within *Glarichelys knorri* (outline of the posterior part of the carapace). For that reason, they are referred herein to *Glarichelys knorri* but with a notion that their status must be reassessed once more specimens are recovered.

It must be stressed that due to the limited sample size, large morphological variability in cheloniids, and parallelisms between their juvenile and derived adult morphology (highly adapted to marine environment), pinpointing the ontogenetic stages represented by the known representatives of the genus *Glarichelys* is difficult (e.g., Zangerl 1958; Młynarski 1959; Lapparent de Broin et al. 2018). The most in-depth consideration of that issue was presented by Zangerl (1958) who concluded that the specimens of *G. knorri* available to him were too large to be hatchlings. He also noted a disparity between the degree of ossification of the shell (which he considered consistent with that observed in similarly sized extant cheloniids) and the distal parts of the limbs (particularly mani, comparatively more advanced than in the shell and even the stylopodia). The most significant feature, according to his evaluation, is that the phalanges are fully ossified and articulated, and not separated by gaps corresponding to unossified proximal and distal parts, which in extant turtles characterizes individuals at least one third the maximum (terminal) size (Zangerl 1958). Overall, Zangerl (1958) considered the hypodigm of *Glarichelys knorri* (at the time including two to five specimens) to consist of young but not completely juvenile individuals, a notion still true today (Table 1). Młynarski (1959, 1984) generally considered the individual from Winnica to be ontogenetically younger, consistent with its smaller size. We agree with that observation but also note that even in the smallest specimen available to us (UR/1055) the digits are well ossified and lack articular gaps. This is significant for several reasons. Firstly, it is uncertain whether the ossification of the autopodia at such an early stage of shell development and small body size was

Table 1. Comparison of carapace lengths (in mm) of specimens of *Glarichelys* spp. and other possibly related turtles. e, estimated.

Species	Specimen	Carapace length [mm]	Locality	References
Glarichelys knorri	ISEA FR/WNC-1, MRJ 70.1P.-P	70	Winnica, Poland	Młynarski 1959, 1984; this study
Glarichelys knorri	UR/1055	40e	Hermanowa, Poland	Přikryl et al. 2016; this study
Glarichelys knorri	UR/1056	70e	Hermanowa, Poland	Přikryl et al. 2016; this study
Glarichelys knorri	PIMUZ A/III 596	100e	Engi, Glarus, Switzerland	Knorr 1755; Gessner 1756; Andreae 1776; Gmelin 1778, 1793; Cuvier 1809, 1810a, b, 1812, 1824; Gray 1831; Keferstein 1834; Buckland 1836b, a; Meyer 1856; Peyer 1950; Zangerl 1958; Leu 1998; Furrer 1998; this study
Glarichelys knorri	NWSGL-EF-100789, NWSGL-EF-100790	125e	Engi, Glarus, Switzerland	Steinmüller 1802; Heer 1865; Zangerl 1958; Furrer 1998; Leu 1998
Glarichelys knorri	PIMUZ A/III 594	133	Engi, Glarus, Switzerland	Zangerl 1958; Furrer 1998; Leu 1998; this study
Glarichelys knorri	PIMUZ A/III 593	> 210	Engi, Glarus, Switzerland	Zangerl 1958
"*Chelonia*" *gwinneri*	SMF-R 263	670	Flörsheim, Hesse, Germany	Wegner 1911, 1914
Glarichelys sp.	MZM Ge 27363	60–70e	Litenčice, Moravia, Czechia	Gregorová and Młynarski 1992; this study
cf. *Glarichelys knorri*	NKM 82, NKM 83	150	Siegsdorf, Bavaria, Germany	Darga et al. 1999; Karl 2002a
Cheloniidae indet.	SMNK-PAL 6608	700–750e	Rauenberg, Baden-Württemberg, Germany	Alexander and Frey 2010; Maxwell et al. 2016
Cheloniidae indet.	SMNK-PAL 6609	300	Rauenberg, Baden-Württemberg, Germany	Alexander and Frey 2010; Maxwell et al. 2016
Chelonia oligocena	MNSPN Cz. (unnumbered)	70	Cozla, Piatra Neamț, Romania	Ciobanu 1977
?*Puppigerus* sp.	FUM N 15877	79	Færker Hede, Fur island, Denmark	Nielsen 1959; Madsen 2008; Karl and Madsen 2012; Garza et al. 2021

autapomorphic for *Glarichelys knorri,* or if it is an autapomorphy indicative of a taxonomic distinctiveness of the specimens from Poland. All the published specimens from Switzerland attributable to *G. knorri* that preserve limbs have already well-ossified autopodia, and so is true for the limb-preserving specimens from Poland, so if the ossification of articular ends of phalanges is indeed a good signifier of the body size reaching one third of the maximum size, the exact size at which that happened remains unknown. Secondly, it is unclear whether the correlation between the body size and degree of autopodial development, observed in extant cheloniids, was also true for *Glarichelys knorri*. Either an ontogenetic shift of autopodial ossification to an earlier developmental stage or postponing of shell ossification is potentially possible for that species. Finally, we cannot exclude specific differences or sexual dimorphism regarding terminal body size, ossification tempo, etc.

Similar as in the larger *Glarichelys knorri*, the interorbital bridge of the juvenile individual from Winnica is very narrow, equal to about 0.6 of the prefrontal length in the narrowest place. While this value seems to be extreme compared to other known cheloniids, it must be noted that the width of the interorbital bridge is subject to ontogenetic change. In the juvenile (KU-H269218, premaxillary-occipital length about 24 mm, Fig. 15F) and adult (NHMUK 1938.1.9.1, premaxillary-occipital length about 146 mm, Fig. 15G) skulls of *Caretta caretta* examined by us the ratio of the interorbital width to prefrontal length is about 0.75 and 1.16, respectively. The seemingly proportionally larger contribution of the frontal to the orbital rim, likewise, is an ontogenetically-dependent character, as evidenced by *Caretta caretta*. The juveniles have the frontals contributing to the orbit, but in older individuals this contact is precluded by the prefrontals and postorbitals (Zangerl 1958; Jones et al. 2012; Fig. 5F, G). This, together with the rounded and elevated cranial scales and small body size suggests an early juvenile age for the Polish individuals of *Glarichelys knorri* and a later juvenile age for the known Swiss individuals of that species. On the contrary, the xiphiplastra of the Polish juveniles of *Glarichelys knorri* are relatively broad compared to those of the larger individuals of *Glarichelys knorri* from Switzerland, despite the smaller size of the individuals of the former. This stands in contrast to the general trend observed in extant cheloniids, in which the xiphiplastra retain similar proportions or widen throughout ontogeny (Zangerl 1958), and thus may be a potential taxonomic character.

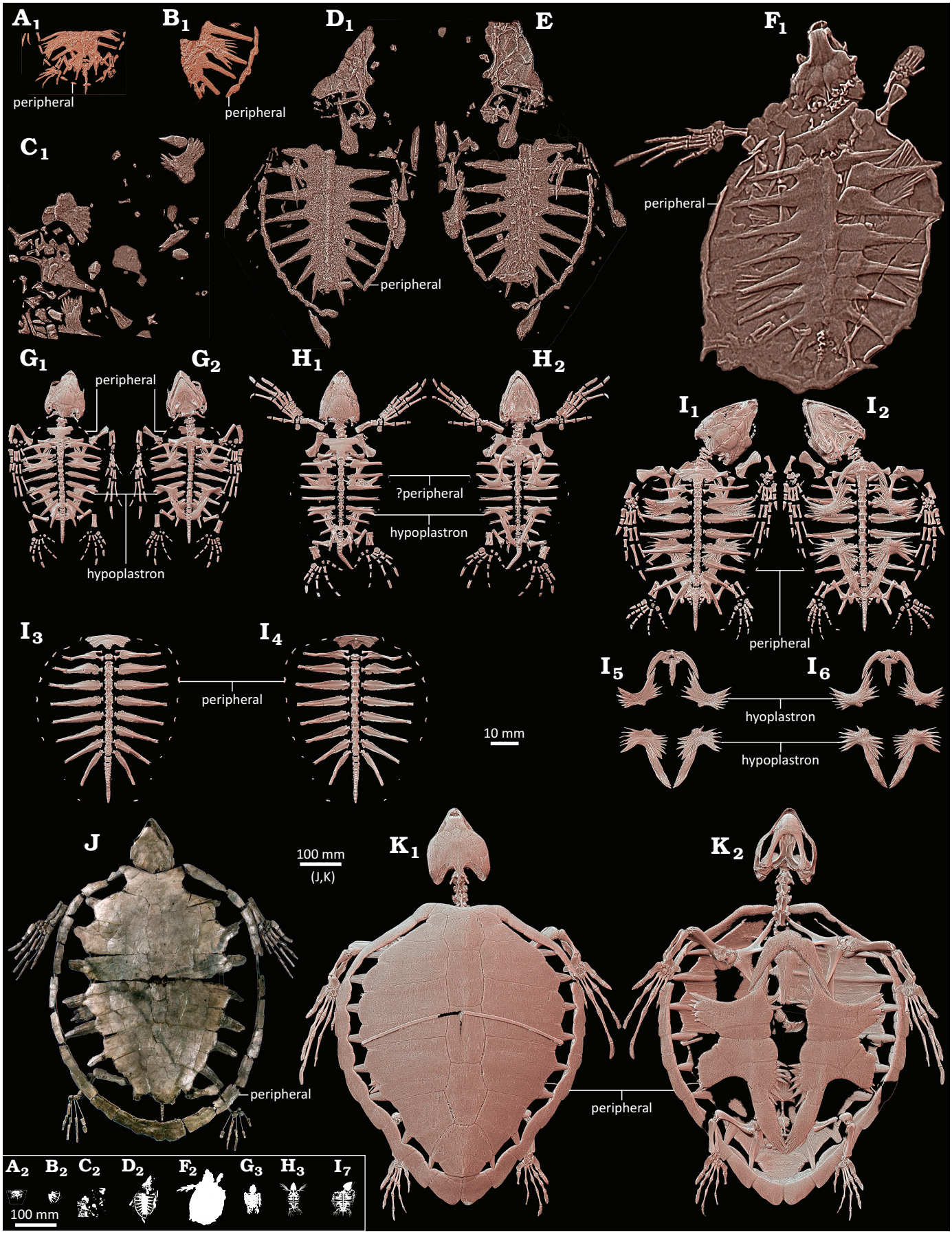
Probably the most puzzling aspect of the taxonomic identity of *Glarichelys knorri* is its relation to "*Chelonia*" *gwinneri*. Both taxa have a number of shell features in common, but at the same time exhibit a number of differences and significantly differ in size, allowing a possibility of a significant ontogenetic change (Zangerl 1958; Lapparent de Broin et al. 2018). As noted above, the significantly larger width of the interorbital bridge in the latter taxon may be explained ontogenetically. However, if the holotype (PIMUZ A/III 596, Fig. 16F) of *Glarichelys knorri* (10 cm of carapace length)

is indeed one third of the maximum size, then the holotype (SMF-R 263, Fig. 16J) of "*Chelonia*" *gwinneri* at 67 cm of carapace significantly exceeds the expected maximum body size for the species, and this disparity is even more striking when the specimens from Poland are considered. Moreover, SMF-R 263 exhibits larger shell fontanelles than somatically more adult extant cheloniids (Fig. 16K), suggesting the possibility that it does not represent a fully grown and somatically developed individual. Furthermore, the juvenile *Caretta caretta* KU-H269218 (Fig. 16I; carapace about 6 cm long, 1.5 times the size of UR/1055, Fig. 16A; about the size of *Glarichelys* sp. MZM Ge 27363, Fig. 16C; and almost 0.9 the size of UR/1056, Fig. 16B, and the Winnica individual, Fig. 16D–E) reveals not only a less advanced ossification of the limbs, but also of the shell (no anteroposterior contact between the hyo- and hypoplastra, almost no peripherals and no pygal) than in even the smallest available *Glarichelys knorri* specimen (UR/1055). Similarly less advanced stages of ossification are also observed in the examined similarly-sized individuals of *Chelonia mydas* YPM Herr 004058 (Fig. 16H) and *Lepidochelys olivacea* KU-H319112 (Fig. 16G). Adult *Caretta caretta* reach on average 90 cm of straight carapace length (about 1.4 times as large as the "*Chelonia*" *gwinneri* holotype SMF-R 263) and their hatchlings span between about 4 and 5 cm of straight carapace length (e.g., Ernst and Lovich 2009). Therefore, assuming a roughly linear correspondence between the relative size and osteological development (which is, obviously, and approximation, because various species or even populations may exhibit different growth curves), if the known juveniles of *Glarichelys knorri* indeed reached about 70 cm of carapace length (as suggested by SMF-R 263), they would be expected to be less ossified. Finally, "*Chelonia*" *gwinneri* does not fit the known representatives of the genus *Glarichelys* in its coracoid exceeding the acromion in length and proportionally shorter manual digits but more elongated ultimate phalange (Wegner 1914; Zangerl 1958). Karl (2002b) attempted to explain these differences as either intraspecific or ontogenetic variability, with the exaggerated ultimate phalange of the first digit being sexually dimorphic, but these assumptions seem to be unfounded based on available data. Zangerl (1958) additionally mentioned paired parietal scales as differentiating *Glarichelys knorri* from "*Chelonia*" *gwinneri*. However, the parietal scale seems to be also paired in "*Chelonia*" *gwinneri* (Wegner 1911, 1914; Drevermann 1914; Aslanova et al. 1979; Karl 2007). Conversely, Lapparent de Broin et al. (2018) proposed the presence of an additional, mesially positioned parietal (or interparietal) scale in *Glarichelys knorri*, an observation we agree with. The presence of the interparietal scale in "*Chelonia*" *gwinneri* is uncertain due to the quality of available documentation, but even if present, it did not invade the area of the frontoparietal scales (Wegner 1911, 1914; Drevermann 1914; Karl 2007). In summary, we see no justification for the specific synonymy between *Glarichelys knorri* and "*Chelonia*" *gwinneri*. Although we consider referral of the species "*Chelonia*" *gwinneri* to the genus *Glarichelys* more plausible, given the current scarcity of information on the Flörsheim specimen, an absence of intermediate specimens bridging the morphological gaps between both species, even considering the largest historically proposed hypodigm, and no previous attempts of framing of the involved taxa in a phylogenetic context, we believe making judgments regarding their beta taxonomy to be premature.

The only published photograph of the holotype of *Chelonia oligocena* from Piatra Neamţ (Ciobanu 1977) is overcontrasted, making the details of the anatomy difficult to read. However, the specimen is roughly the size of ISEA FR/WNC-1, MRJ 70.1P.-P, and UR/1056, yet presents a clearly less advanced stage of shell ossification and apparently less elongated manus than *Glarichelys knorri*. For that reason, we consider it to represent an indeterminate cheloniid and thus tentatively exclude it from *Glarichelys knorri*.

We see no justification for the synonymy of the genera *Chelyopsis* and *Glarichelys* proposed by Karl and Tichy (1999) and Karl (2002b, 2007). In particular, shell fragments referred to *Chelyopsis* spp. appear to provide little diagnostic value beyond their substantial thickness (Smets 1888; Karl 1989, 1995; Karl and Tichy 1999), unlike the relatively thin carapacial bones in *Glarichelys knorri*. At least in "*Chelyopsis*" *halleri*, the nuchal bears ventrally a distinct articulation knob for the last cervical vertebra (Karl 1989), but such a structure is absent in *Glarichelys knorri* MRJ 70.1P.-P (Fig. 9A$_2$). The humeri referred by Karl (2007) differ from the humeri of the all the known Swiss and Polish representatives of *Glarichelys knorri* in the taller medial process separated from the humeral head by a notch, and less radially

Fig. 16. Size and developmental comparison of sea turtle taxa. **A**, **B**. *Glarichelys knorri* (Gray, 1831), juvenile specimens from Hermanowa, Poland, Rupelian. → **A**. UR/1055, partial skeleton in dorsal aspect (digital positive). **B**. UR/1056, partial shell in ventral aspect (digital positive). **C**. *Glarichelys* sp. from Litenčice, Czechia, Rupelian, MZM Ge 27364, juvenile specimen, disarticulated skeletons of at least two juvenile individuals. **D**, **E**. *Glarichelys knorri* from Winnica, Poland, Rupelian. **D**. ISEA FR/WNC-1, partial skeleton in dorsal aspect (digital positive). **E**. MRJ 70.1P.-P, partial skeleton in ventral aspect (digital positive). **F**. *Glarichelys knorri* from Glarus, Switzerland, Rupelian, PIMUZ A/III 596, holotype, skeleton in dorsal aspect. **G**. *Lepidochelys olivacea* (Eschscholtz, 1829), Recent, KU-H319112, extant juvenile: G_1, dorsal view; G_2, ventral view. **H**. *Chelonia mydas agassizi* Bocourt, 1868, from Equador, Recent, YPM Herr 004058, extant juvenile: H_1, dorsal view; H_2, ventral view. **I**, **K**. *Caretta caretta* (Linnaeus, 1758). **I**. KU-H269218, extant juvenile from Leticia, Colombia, Recent: I_1, skeleton in dorsal view; I_2, skeleton in ventral view; I_3, isolated carapace and vertebral column (except the neck) in dorsal view; I_4, isolated carapace and vertebral column (except the neck) in ventral view; I_5, isolated plastron in dorsal (visceral) view; I_6, isolated plastron in ventral (external) view. **K**. MSNUP B 32, extant adult (Recent): K_1, skeleton in dorsal view; K_2, skeleton in ventral view. **J**. "*Chelonia*" *gwinneri* Wegner, 1911, from Flörsheim, Germany, Rupelian, SMF-R 263, holotype, skeleton in dorsal view (photograph courtesy of Krister Smith and Sven Tränkner, Senckenberg Gesellschaft für Naturforschung). All 3D models of *Glarichelys* spp. and juveniles of extant cheloniids at the same scale. White silhouettes to scale with adult specimens to show the size difference. Note the less advanced ossification stage of juvenile extant cheloniids (little to no dermal carapacial elements, lack of contact between the hyo- and hypoplastra, unossified articular ends of appendicular bones) compared to similarly sized *G. knorri*.


A1
peripheral
B1
peripheral
D1
E
C1
peripheral
F1
peripheral
G1
G2
peripheral
hypoplastron
H1
H2
?peripheral
hypoplastron
I1
I2
peripheral
I3
I4
peripheral
10 mm
I5
I6
hyoplastron
hypoplastron
J
100 mm
(J,K)
K1
K2
peripheral
peripheral
A2 B2 C2 D2 F2 G3 H3 I7
100 mm

projected lateral process (Figs. 1–3, 6, 8, 9A, B, 11A_3, B_3; Zangerl 1958). Although such differences are expected due to ontogeny, the specimens in question simply show no morphological basis for their referral to the genus *Glarichelys*. The scapular material presented by Karl (2007) is mostly incomplete and thus not diagnostic enough to warrant correct attribution, except of the uncatalogued NML specimen, which presents coracoids significantly longer than the scapular processes, inconsistent with the diagnosis of the genus (Zangerl 1958). The most morphologically congruent specimens from Germany, from the pool referred by Darga et al. (1999), Karl and Tichy (1999), and Karl (2002b, a, 2007), are the scapula and coracoid from Galon-Graben (Darga et al. 1999; Karl 2002a) and mandibles of "*Chelyopsis*" *raabei* described in Schleich et al. (1994). However, the Galon-Graben specimens were variably stated to come from a single horizon and possibly represent a single individual (Darga et al. 1999), or to come from two different horizons (Karl 2002a), so their relative proportions, or even conspecificity, are uncertain. A reasonable validation of the taxonomical referrals of isolated mandibulae would require a more in-depth review of mandibular anatomy of various cheloniid taxa at various ontogenetic stages and possibly CT scanning of the available slabs of *Glarichelys knorri*. Other specimens from Germany possibly representing or related to the genus (Alexander and Frey 2010; Micklich and Hildebrandt 2010; Maxwell et al. 2016) need further study to determine their taxonomic identity. In summary, the presence of *Glarichelys knorri* in the region of current-day Germany seems plausible but should be treated as yet unconfirmed.

Regarding the FUM N 15877 from Fur (Nielsen 1959; Madsen 2008; Karl and Madsen 2012; Garza et al. 2021), we agree with the most recent conclusion (Karl and Madsen 2012; Garza et al. 2021) that it is not a member of the genus *Glarichelys*. Likewise, we agree with the conclusion of Danilov et al. (2017) that the material from Azerbaijan and Kazakhstan is currently not referrable to that genus (Chkhikvadze 1969, 1983; Aslanova et al. 1979; Averianov 2002; Danilov et al. 2017).

Digestive tract contents.—Preservation of digestive tract contents of marine turtles is rare. Kear (2006) described phosphatic nodules containing fragmented inoceramid bivalve shells preserved inside the shells (cololites) of protostegids (cf. *Notochelone* sp.) and associated coprolites/bromalites from the Cretaceous Toolebuc Formation (Australia). Alexander and Frey (2010) noted the presence of small concretion-like globules embedded in white, phosphatic material with a crystalline structure scattered between the remains of a cheloniid from the Rupelian (lower Oligocene) Bodenheim Formation of Germany. They interpreted those globules as probable mineralized gut contents and ruled out the possibility of them being gastroliths based on no records their presence in sea turtles known at the time. However, the occurrence of gastroliths (either carbonatic or carbonatic and siliceous) in those animals was recently documented by Serafini et al. (2024) based on a study of extant cheloniids and a protostegid from the Cretaceous Scaglia Rossa Formation of Italy. A possible cololite was also noticed within the shell of the Late Jurassic thalassochelydian *Thalassemys bruntrutana* Püntener et al., 2015 from Germany (Joyce et al. 2021b). The structures in UR/1055 appear to be most similar structurally to the polituberculate elements of regurgitalite B (capsulate type) described and figured by Brustur and Chitea (2021) from the Oligocene Valea Caselor Facies of Romania, with the obvious differences consisting of their negative character of preservation (consistent with the remainder of the fossil), and location within the body cavity (making them impressions of gastrolites or cololites rather than regurgitalites). The exact interpretation of their original identity is difficult. Firstly, the structures may potentially represent gastroliths contained within the stomach or gut of the animal, which, depending on their mineral composition, could be dissolved together with bone material due to diagenetic factors, or possibly lost prior to or during recovery, when the impression of the body was exposed either by erosion or mechanical splitting of the slabs. However, while there is evidence for the presence of gastroliths in sea turtles, we know no reports of their occurrence in such small individuals and the specimen showed no evidence of gastroliths on recovery (Tomáš Přikryl, personal communication 2024). Secondly, the structures may be impressions of organic contents of the gut (fecal matter) that were dense enough to register on the sediment surface but could then be dissolved or otherwise decomposed together with the soft tissues of the animal. This scenario seems more plausible as it requires no additional explanation for the absence of any mineral content of the observed concavities.

Paddle evolution.—*Glarichelys knorri* UR/1055 provides some data regarding the shape of the paddles, particularly in the hindlimb (Figs. 7A, 12A_3, A_4, 13). In extant cheloniids, the autopodia and zeugopodia are united into stiffened flippers or paddles, elongate in the forelimbs and shorter in the hindlimbs, usually with two first claws protruding beyond their margin (Wyneken 2001; Joyce et al. 2021b). A similar morphology is observed in *Dermochelys coriacea* (Vandelli, 1761), although the skin surface of the autopodia is scaleless (Garza et al. 2021; Joyce et al. 2021b). Among extant freshwater turtles, the carettochelyid autopodia are flexible, soft, also elongated in forelimbs but broad and shorter in hindlimbs, with only two first digits bearing claws and no scales (Delfino et al. 2010; Garza et al. 2021). Other freshwater turtles have broader, shorter paddles on the forelimbs and more claws, with the skin being devoid of scales in trionychids and other primarily aquatic species, but finely scaled in those that leave water often (Delfino et al. 2010; Garza et al. 2021; Joyce et al. 2021b). Preservation of outlines of autopodial soft tissues in the fossil record of turtles were thus far recorded in some Jurassic thalassochelydian turtles from Germany (Joyce et al. 2021b), Early Cretaceous pleurodire *Araripemys barretoi* Price, 1973 (*Araripemys ar-*

turi Fielding et al., 2005) SMNK-PAL 3979 from Brazil, Cretaceous protostegid *Rhinochelys nammourensis* Tong et al., 2006 MIM F50 (former ESC-2) from Lebanon (Tong et al. 2006; Kear et al. 2025), and in the Eocene (Fur Formation of Denmark) indeterminate pan-cheloniid DK 807 (Garza et al. 2021) and cheloniine *Tasbacka danica* Karl & Madsen, 2012, NHMD 141598 (Madsen 2008; Lindgren et al. 2017).

Interestingly, some Jurassic thalassochelydians had stiff, derived flippers with no interdigital notching and a cover of well-keratinized, large scales, apparently developed independently from crown cheloniids (Joyce et al. 2021b). A similar outline of flippers was also present in *Rhinochelys nammourensis*—although scales are not discernible, the pedes of several specimens are preserved in a fixed position, suggesting their immobility (Tong et al. 2006) or only partial mobility (Kear et al. 2025). In the case of *Tasbacka danica* NHMD 141598 only a small part of the posterior paddle is exposed, precluding meaningful comparisons with UR/1055. DK 807, however, showcases wonderfully preserved folds of loose, seemingly scaleless skin connecting the digits of the pes, differing in that respect from extant cheloniids and resembling *Dermochelys coriacea* or freshwater turtles (Garza et al. 2021). In UR/1055 only a discolored outline of soft tissues is preserved so the observable detail is limited, but the deeply posteriorly notched outline of the posterior paddle with partially distinct digits may, likewise, indicate a more flexible and softer skin (Fig. 12A$_4$). It should be noted that Joyce et al. (2021b) observed a correlation between the scalation of the autopodia and their preservation: paddles likely covered with soft, scaleless skin tend to be preserved in a curled state with the digits overlying each other (consistent, e.g., with the morphology observed in *Araripemys barretoi* SMNK-PAL 3979, Fielding et al. 2005), whereas those that were stiffer and had well-developed scales, are typically preserved flattened and with digits spread out. The position of the pes of UR/1055 fits the latter category better, however, the feet of DK 807 are preserved both in a spread out state (right) and with digits straight but grouped together (left), indicating that some variability in that regard may result from taphonomic factors and, perhaps, that the stiffening of the autopodia was a gradual process in the evolution of pan-cheloniids. If correct, that would indicate that scaleless or at least softer feet were still present in at least some cheloniids as late as the Oligocene.

Conclusions

The small-bodied Oligocene sea turtle genus *Glarichelys* is represented by some of the historically oldest specimens known to vertebrate paleontology. Despite the fact that the available material includes several nearly complete skeletons and skulls, the taxon remains relatively poorly understood. This is mostly caused by the fact that all of its unquestionable representatives seem to be juveniles. Moreover, over the years the hypodigm of the genus *Glarichelys* accumulated a large sample of questionable and poorly documented finds from numerous localities in Europe and Asia. New and historical specimens from Poland and Czechia represent even younger juveniles, but at the same time they allow to clarify some of the confusion and to observe additional anatomical and developmental characters, informing about the ontogenetic variability and growth of *Glarichelys knorri*. A detailed description and documentation of those specimens is presented here. Both the genus and its type species are considered valid and diagnosable. Although it seems reasonable that the geographic range of the genus *Glarichelys* spanned across the western and central Europe, with occurrences documented in Czechia and possibly Germany, diagnostic and informative specimens of *Glarichelys knorri* are currently confirmed only in Switzerland and Poland.

Acknowledgements

This work is dedicated to Professor Marian Młynarski (1926–2024)—one of the leading Central European paleoherpetologists specializing in turtle evolution in the second half of the 20th century, a long time employee of the Institute of Systematics and Evolution of Animals and collaborator of the Institute of Paleobiology, PAS, and the author of the original descriptions of the specimens from Winnica and Litenčice, among his numerous other contributions. Professor Młynarski would be 100 years old this year, and although he is no longer with us, his legacy lives on. We thank Torsten Scheyer, Dennis Hansen, Christian Klug, and the staff of the Department of Paleontology of the University of Zurich (PIMUZ) for the photographs of and information on PIMUZ AIII/85, 593, 594, 596, and 1034 (copyright Paläontologisches Institut, Universität Zürich, PIMUZ A/III 593, 594, and 596 reproduced here with permission) and for the access to those specimens. Heinz Furrer (former PIMUZ) is thanked for additional information on the Swiss material and photographs of *Glarichelys knorri* NWSGL-EF-100789 and 100790 (copyright Canton Glarus, reproduced here with permission), and additional photographs of PIMUZ A/III 593, 594, and 596 (copyright Paläontologisches Institut, Universität Zürich, PIMUZ A/III 593 reproduced here with permission). Christophe Ferrante (NWSGL) is thanked for granting us access to those specimens. Tomáš Příkryl (Institute of Geology of the Czech Academy of Sciences, Prague, Czechia) is thanked for additional information on the Polish and Czech material. Růžena Gregorová (MZM) is thanked for the access to MZM Ge 27363. Katarzyna Janiszewska (ZPAL) is thanked for CT scanning of UR/1055 and UR/1056. Paweł Bącal (ZPAL) is thanked for the SEM imaging of UR/1055 and UR/1056 and discussion. Krister Smith and Sven Tränkner (both Senckenberg Gesellschaft für Naturforschung) are thanked for photographs of the holotype SMF-R 263 of "*Chelonia*" *gwinneri*. Finally, we thank the editor Daniel E. Barta (Oklahoma State University, Tahlequah, USA), the reviewers Ray Chatterji (University of Texas at Arlington, USA), and one anonymous. This research project was supported by the NCN POLONEZ BIS project No. 2022/45/P/NZ8/00600 co-funded by the National Science Centre, Poland (NCN), and the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement no. 945339. Digitization of the Swiss material of *Glarichelys knorri* was performed as part of a research trip funded by the National Science Centre, Poland (NCN) grant 2020/39/B/NZ8/01074 awarded to TS. GLG acknowledges funding from the research project no. 2023/49/B/ST10/02631 financed by the National Science Center of Poland (Narodowe Centrum Nauki). This research was supported by the Minister of Science of the Republic of Poland

under the Programme “Regional initiative of excellence”, Agreement No. RID/SP/0010/2024/1 and the institutional support RVO 67985831.

Authors’ contributions

TS, digitization and photography of the Polish material, preparation of figures, literature review, anatomical comparisons and descriptions, writing of the first draft of the manuscript, revisions and editing of the text; MC, digitization and photography of the Czech material, anatomical comparisons, revisions and editing of the text; MCz, digitization of the Swiss material, logistics of the trips to NWSGL and PIMUZ; RP, digitization of the Swiss material; GLG, revisions and editing of the text, curating of material; IKK, description of geology, revisions and editing of the text; PW, revisions and editing of the text, curating of material.

Editor: Daniel Barta

References

Ahrens, J., Geveci, B. and Law, C. 2005. ParaView: an end-user tool for large data visualization. *In*: C.D. Hansen and C.R. Johnson (eds.), *Visualization Handbook*, 717–731. Elsevier, Amsterdam.

Alexander, S. and Frey, E. 2010. Zwei Meeresschildkröten (Cheloniidae) aus der Tongrube Unterfeld bei Rauenberg (Unteroligozän, Rupelium). *Kaupia* 17: 73–105.

Andreae, J.G.R. 1776. *Briefe aus der Schweiz nach Hannover geschrieben, in dem Jare 1763*. 248 pp. Joh. Gaspar Fůekli Sohn, Zürich.

Aslanova, S.M. 1969. Perekiškyul’skaâ fauna vyssih pozvonočnyh majkopskoj svity. 22 pp. Baku State University, Baku.

Aslanova, S.M., Pronin, V.G., and Chkhikvadze, V.M. 1979. Remains of sea turtles from the Oligocene deposits of Absheron and northern Ustyurt [in Russian]. *Vestnyk Zoolohyy* 13 (6): 17–22.

Averianov, A.O. 2002. Review of Mesozoic and Cenozoic sea turtles from the former USSR. *Russian Journal of Herpetology* 9 (2): 137–154.

Bajdek, P. and Bienkowska-Wasiluk, M. 2020. Deep-sea ecosystem revealed by teleost fish coprolites from the Oligocene of Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 540: 109546.

Batsch, A.J.G.C. 1788. *Versuch Einer Anleitung, zur Kenntniß und Geschichte der Tiere und Mineralien*. 528 pp. Akademische Buchhandlung, Jena.

Van Beneden, P.-J. 1883. Note sur des ossements de *Sphargis* trouvés dans la terre à brique du pays de Waas. *Bulletins de l’Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique* 3 (6): 665–684.

Bienkowska-Wasiluk, M., Bajdek, P., and Granica, M. 2025. Vertebrate coprolites reveal diversity of prey fishes in the Oligocene Carpathian Basin of the Paratethys. *Diversity* 17 (8): 507.

Bochenski, Z. and Bochenski, Z.M. 2008. An Old World hummingbird from the Oligocene: A new fossil from Polish Carpathians. *Journal of Ornithology* 149 (2): 211–216.

Bochenski, Z.M., Tomek, T., Wertz, K., Happ, J., Bujoczek, M., and Swidnicka, E. 2018. Articulated avian remains from the early Oligocene of Poland adds to our understanding of passerine evolution. *Palaeontologia Electronica* 21 (2): 32A.

Bocourt, M.F. 1868. Description de quelques chéloniens nouveaux appartenant à la faune Mexicaine. *Annales des Sciences Naturelles, Zoologie et Paléontologie* 10: 121–122.

Brustur, T. and Chitea, F. 2021. Oligocene digestichnia in the lower part of the Valea Caselor facies from Fieni (Romania)—a preliminary report. *Geo-Eco-Marina* 27: 137–151.

Buckland, W. 1836a. *The Bridgewater Treatises on the Power Wisdom and Goodness of God as Manifested in the Creation. Treatise VI. Geology and Mineralogy Considered with Reference to Natural Theology. Vol. 1*. 618 pp William Pickering, London.

Buckland, W. 1836b. *The Bridgewater Treatises on the Power Wisdom and Goodness of God as Manifested in the Creation. Treatise VI. Geology and Mineralogy Considered with Reference to Natural Theology. Vol. 2*. 128 pp. William Pickering, London.

Casale, P., Freggi, D., Basso, R., and Argano, R. 2005. Size at male maturity, sexing methods and adult sex ratio in loggerhead turtles (*Caretta caretta*) from Italian waters investigated through tail measurements. *Herpetological Journal* 15 (3): 145–148.

Chkhikvadze, V.M. 1969. New turtles from the Paleogene deposits of the Zaysan Basin and Central Kazakhstan [in Russian]. *Byulleten’ Geologii* 6: 145–146.

Chkhikvadze, V.M. 1977. Review of knowledge on fossil turtles of the Northern Caucasus [in Russian]. *Voprosy Gerpetologii* 4: 226–227.

Chkhikvadze, V.M. 1983. *Iskopayemye čerepahi Kavkaza i Severnogo Pričernomorâ*. 149 pp. Georgian Academy of Sciences, Tbilisi.

Chroust, M. and Szczygielski, T. 2025. TED (Turtle Evolution Database), an online database of fossil turtles from Czechia and Poland with images and 3D models. *Swiss Journal of Palaeontology* 144 (1): art. 68.

Cignoni, P., Callieri, M., Corsini, M., Dellepiane, M., Ganovelli, F., and Ranzuglia, G. 2008. MeshLab: An open-source mesh processing tool. *In*: V. Scarano, R. De Chiara, and U. Erra (eds.), *Sixth Eurographics Italian Chapter Conference*, 129–136. European Association for Computer Graphics, Salerno.

Ciobanu, M. 1977. *Fauna fosilă din oligocenul de la Piatra Neamț*. 159 pp. Editura Academiei Republicii Socialiste România, Bucharest.

Cope, E.D. 1868. On the origin of genera. *Proceedings of the Academy of Natural Sciences of Philadelphia* 20: 242–300.

Cosmovici, L. 1887. Păturele cu Pești din Munžii Petricica și Cozla, Districtul Neamtz orașul Peatra (România). *Buletinul Societăžii de medici și naturaliști din Iași, an I* 3: 96–105.

Cuvier, G. 1809. Sur les ossements fossiles de tortues. *Annales du Museum d’Histoire Naturelle* 14: 229–244.

Cuvier, G. 1810a. Sur les tortues fossiles. *Journal des Mines* 157: 79–80.

Cuvier, G. 1810b. Sur les tortues fossiles. *Nouveau Bulletin des Sciences* 2: 7–8.

Cuvier, G. 1812. *Recherches sur les ossemens fossiles, où l’on rétablit les caractères de plusieurs animaux dont les révolutions du globe ont détruit les espèces. T. IV. Contenant les ruminans, les onguiculés et les reptiles fossiles*. 684 pp. Deterville, Paris.

Cuvier, G. 1824. *Recherches sur les ossemens fossiles, où l’on rétablit les caractères de plusieurs animaux dont les révolutions du globe ont détruit les espèces. Nouvelle édition. T. 5, Pt. II*. 547 pp. G. Dufour et ed. d’Ocagne, Paris.

Cuvier, G. 1836a. *Recherches sur les ossemens fossiles, où l’on rétablit les caractères de plusieurs animaux dont les révolutions du globe ont détruit les espèces. Quatrième edition. Atlas. T. 2*. 106 pp. Edmond d’Ocagne, Paris.

Cuvier, G. 1836b. *Recherches sur les ossemens fossiles, où l’on rétablit les caractères de plusieurs animaux dont les révolutions du globe ont détruit les espèces. Quatrième edition. T. 9*. 494 pp. Edmond d’Ocagne, Paris.

Czernicki, J. 1981. Stanisław Kadyi (1900–1980). *Annales Societatis Geologorum Poloniae* 51: 597–599.

Dames, W. 1894. Die Chelonier der norddeutschen Tertiärformation. *Palaeontologische Abhandlungen* 4 (4): 197–219.

Danil’chenko, P.G. 1950. The genus *Paleogadus* and its development [in Russian]. *Trudy Paleontologičeskogo Instituta Akademii Nauk SSSR* 25: 1–25.

Danilov, I.G. 2005. Die fossilen Schildkröten Europas. *In*: U. Fritz (ed.), *Handbuch Der Reptilien Und Amphibien Europas. Band 3/IIIB: Schildkröten (Testudines) II (Cheloniidae, Dermochelyidae, Fossile Schildkröten Europas)*, 329–441. AULA-Verlag GmbH, Wiebelsheim.

Danilov, I.G., Syromyatnikova, E.V., and Sukhanov, V.B. 2017. Subclass Testudinata [in Russian]. *In*: A.V. Lopatin and N.V. Zelenkov (eds.), *Iskopaemye pozvonočnye Rossii i sopredel’nyh stran. Iskopayemye reptilii i ptitsy. Vypusk 4*, 27–395. GEOS, Moskva.

Darga, R., Böhme, M., Göhlich, U.B., and Rössner, G.E. 1999. Reste höherer Wirbeltiere aus dem Alttertiär des Alpenvorlandes bei Siegsdorf/Oberbayern. *Mitteilungen der Bayerischen Staatssammlung für Palaontologie und Historische Geologie* 39: 91–114.

Delfino, M., Fritz, U., and Sánchez-Villagra, M.R. 2010. Evolutionary and developmental aspects of phalangeal formula variation in pig-nose and soft-shelled turtles (Carettochelyidae and Trionychidae). *Organisms Diversity and Evolution* 10 (1): 69–79.

Deraniyagala, P.E.P. 1939. *Tetrapod Reptiles of Ceylon. Volume I. Testudinates and Crocodilians*. 412 pp. Colombo Museum, Dulau & Co., Colombo, London.

Dollo, L. 1903. *Eochelone brabantica*, tortue marine nouvelle du Bruxellien (Éocène moyen) de la Belgique. *Bulletin de la Classe des Sciences* 5: 725–727.

Dollo, L. 1909. The fossil vertebrates of Belgium. *Annals of the New York Academy of Sciences* 19 (4.1): 99–119.

Drevermann, F. 1914. Die Meersaurier im Senckenbergischen Museum. *Bericht der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt am Main* 45: 35–48.

Ernst, C.H. and Lovich, J.E. 2009. *Turtles of the United States and Canada. Second Edition Revised and Updated with New Species Names*. 840 pp. The Johns Hopkins University Press, Baltimore.

Eschscholtz, F. 1829. *Zoologischer Atlas: enthaltend Abbildungen und Beschreibungen neuer Thierarten, während des Flottcapitains v. Kotzebue zweiter Reise um die Welt, auf der russisch-kaiserlichen Kriegsschlupp Predpriaetië in den Jahren 1823–1826. Ertes Heft*. 15 pp. G. Reimer, Berlin.

Fedorov, A., Beichel, R., Kalpathy-Cramer, J., Finet, J., Fillion-Robin, J.-C., Pujol, S., Bauer, C., Jennings, D., Fennessy, F.M., Sonka, M., Buatti, J., Aylward, S.R., Miller, J. V., Pieper, S., and Kikinis, R. 2012. 3D Slicer as an image computing platform for the quantitative imaging network. *Magnetic Resonance Imaging* 30 (9): 1323–1324.

Fielding, S., Martill, D.M., and Naish, D. 2005. Solnhofen-style soft-tissue preservation in a new species of turtle from the Crato Formation (Early Cretaceous, Aptian) of north-east Brazil. *Palaeontology* 48 (6): 1301–1310.

Fitzinger, L. 1835. Entwurf einer systematischen Anordnung der Schildkröten nach den Grundsätzen der natürlichen Methode. *Annalen des Wiener Museums der Naturgeschichte* 1: 103–128.

Fitzinger, L. 1846. Entwurfe einer systematischen Anordnung der Schildkröten nach den Grundsätzen der natürlichen Methode. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 1846: 379–381.

Furrer, H. 1998. Fossilien und Geologie. *In*: H. Furrer and U.B. Leu (eds.), *Der Landesplattenberg Engi. Forschungsgeschichte, Fossilien und Geologie*, 74–119. Siftung Landesplattenberg Engi, Engi.

Gard, H.J.L. and Fordyce, R.E. 2017. A fossil sea turtle (Testudines: Pan-Cheloniidae) from the upper Oligocene Pomahaka Formation, New Zealand. *Alcheringa* 41: 134–140.

Garman, S. 1880. On certain species of Chelonioidae. *Bulletin of the Museum of Comparative Zoology at Harvard College* 6: 123–126.

Garza, R.G.D. La, Madsen, H., Eriksson, M.E., and Lindgren, J. 2021. A fossil sea turtle (Reptilia, Pan-Cheloniidae) with preserved soft tissues from the Eocene Fur Formation of Denmark. *Journal of Vertebrate Paleontology* 41 (3): e1938590.

Gessner, J. 1756. *Dissertatio physica de petrificatorum variis originibus praecipuarum telluris mutationum testibus*. 36 pp. Officina Gessneriana, Zürich.

Giebel, C.G.A. 1856. *Fauna der Vorwelt mit steter Berücksichtigung der lebenden Thiere. Bd. 2*. 218 pp. F.A. Brockhaus, Leipzig.

Gmelin, J.F. 1778. *Des Ritters Carl von Linne' vollständiges Natursystem des Mineralreichs nach der zwölften lateinischen Ausgabe. T. III*. 486 pp. Gabriel Nicolaus Rafpe, Nürnberg.

Gmelin, J.F. 1793. *Caroli a Linne systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis. T. III. Editio decima tertia, aucta, reformata*. 476 pp. Beer, Leipzig.

Godley, B.J., Broderick, A.C., Frauenstein, R., Glen, F., and Hays, G.C. 2002. Reproductive seasonality and sexual dimorphism in green turtles. *Marine Ecology Progress Series* 226: 125–133.

Gray, J.E. 1831. *Synopsis Reptilium; or Short Descriptions of the Species of Reptiles. Part I. Cataphracta. Tortoises, Crocodiles, and Enaliosaurs*. 85 pp. Treuttel, Wurtz, and Co., London.

Gregorová, R. 2006. A new discovery of a seabird (Aves: Procellariiformes) in the Oligocene of the „Menilitic Formation" in Moravia (Czech Republic). *Hantkeniana* 5: 90.

Gregorová, R. 2011. Fossil fish fauna (Teleostei, Selachii) from the Dynów marlstone (Rupelian, NP 23) of the Menilitic Formation at the locality of Litenčice (Czech Republic). *Acta Musei Moraviae, Scientiae Geologicae* 96 (2): 3–33.

Gregorová, R. and Młynarski, M. 1992. Première découverte de *Glarichelys knorri* (Gray), tortue marine (Cheloniidae) dans l'Oligocène des couches à ménilite en Moravie (Tchécoslovaquie). *Acta Musei Moraviae. Scientiae Naturae* 77 (1–2): 63–69.

Heckel, J.J. 1850. Beiträge zur Kenntnis der fossilen Fische Österreichs. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathe-matisch-Naturwissenschaftliche Klasse* 1: 201–242.

Heckel, J.J. 1856. Beiträge zur Kenntniss der Fossilen Fische Österreichs. II. Abhandlung. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathe-matisch-Naturwissenschaftliche Klasse* 11: 187–274.

Heer, O. 1865. *Die Urwelt der Schweitz*. 622 pp. Friedrich Schulhteß, Zürich.

Hendrickson, J.R. 1958. The green sea turtle, *Chelonia mydas* (Linn.) in Malaya and Sarawak. *Proceedings of the Zoological Society of London* 130: 455–535.

Hermanson, G., Arnal, F.A.M., Szczygielski, T., and Evers, S.W. 2024. A systematic comparative description of extant turtle humeri, with comments on humerus disparity and evolution based on fossil comparisons. *Anatomical Record* 307: 3437–3505.

ICZN (International Commission on Zoological Nomenclature) 1999. *International Code of Zoological Nomenclature. Fourth edition*. 306 pp. The International Trust for Zoological Nomenclature, London.

International Turtle Nomenclature Committee, Joyce, W.G., Parham, J.F., Anquetin, J., Claude, J., Danilov, I.G., Iverson, J.B., Kear, B.P., Lyson, T.R., Rabi, M. and Sterli, J. 2020a. Testudines. *In*: K. de Queiroz, P.D. Cantino, and J.A. Gauthier (eds.), *Phylonyms. A Companion to the PhyloCode*, 1049–1051. CRC Press, Boca Raton.

International Turtle Nomenclature Committee, Joyce, W.G., Parham, J.F., Anquetin, J., Claude, J., Danilov, I.G., Iverson, J.B., Kear, B.P., Rabi, M. and Sterli, J. 2020b. Cryptodira. *In*: K. de Queiroz, P.D. Cantino, and J.A. Gauthier (eds.), *Phylonyms. A Companion to the PhyloCode*, 1061–1063. CRC Press, Boca Raton.

Jerzmańska, A. 1968. Ichtyofaune des couches a ménilite (flysch des Karpathes). *Acta Palaeontologica Polonica* 13: 379–488.

Jirman, P., Geršlová, E., Pupp, M., and Bubík, M. 2018. Geochemical characteristics, thermal maturity and source rock potential of the Oligocene Šitbořice Member of the Menilite Formation in the Ždánice Unit (Czech Republic). *Geological Quarterly* 62 (4): 858–872.

Jones, M.E.H., Werneburg, I., Curtis, N., Penrose, R., O'Higgins, P., Fagan, M.J., and Evans, S.E. 2012. The head and neck anatomy of sea turtles (Cryptodira: Chelonioidea) and skull shape in Testudines. *PLoS ONE* 7 (11): 352–354.

Jonet, S. 1958. *Contributions à l'étude des schistes disodyliques oligocènes de Roumanie. La fauna ichthyologique de Homorâciu District de Prahova*. 112 pp. Sociedade Tipográfica, Lda, Lisboa.

Joyce, W.G., Anquetin, J., Cadena, E.A., Claude, J., Danilov, I.G., Evers, S.W., Ferreira, G. de S., Gentry, A.D., Georgalis, G.L., Lyson, T.R., Pérez-García, A., Rabi, M., Sterli, J., Vitek, N.S., and Parham, J.F. 2021a. A nomenclature for fossil and living turtles using phylogenetically defined clade names. *Swiss Journal of Palaeontology* 140 (1): 5.

Joyce, W.G., Mäuser, M., and Evers, S.W. 2021b. Two turtles with soft tissue preservation from the platy limestones of Germany provide evidence for marine flipper adaptations in Late Jurassic thalassochelydians. *PLOS ONE* 16 (6): e0252355.

Joyce, W.G., Parham, J.F., and Gauthier, J.A. 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically de-

fined clade names, as exemplified by turtles. *Journal of Paleontology* 78: 989–1013.

Joyce, W.G., Werneburg, I., and Lyson, T.R. 2013. The hooked element in the pes of turtles (Testudines): A global approach to exploring primary and secondary homology. *Journal of Anatomy* 223: 421–441.

Kadyi, S. 1958. O znaleziskach paleontologicznych na terenie województwa rzeszowskiego. *Rocznik Województwa Rzeszowskiego* 1 (2): 13–26.

Kapuścińska, A. and Machalski, M. 2015. Upper Albian chelonioid turtles from Poland. *Geobios* 48: 385–395.

Karl, H.-V. 1989. Die Schildkröten aus dem marinen Mitteloligozän der DDR (Reptilia, Testudines). *Mauritiana* 12: 225–242.

Karl, H.-V. 1995. Über neue fossile Seeschildkrötenreste (Testudines, Cheloniidae) vom Doberg bei Bünde. *Mauritiana* 15: 349–356.

Karl, H.-V. 2002a. Über Reptilienreste aus dem Alttertiär des nördlichen Alpen-vorlandes bei Siegsdorf/Oberbayern. *Joannea Geologie und Paläontologie* 4: 69–81.

Karl, H.-V. 2002b. Übersicht über die fossilen marinen Schildkrötenfamilien Zentraleuropas (Reptilia, Testudines). *Mauritiana* 18: 171–202.

Karl, H.-V. 2007. The fossil reptiles (Reptilia: Chelonii, Crocodylia) from the marine early Oligocene of the Weisselster Basin (central Germany: Saxonia). *Studia Geologica Salmanticensia* 43: 25–66.

Karl, H.-V. and Madsen, H. 2012. *Tasbacka danica* n. sp., a new Eocene marine turtle of Denmark (Testudines: Chelonioidea). *Studia Palaeocheloniologica* 4: 193–204.

Karl, H.-V. and Tichy, G. 1999. Zur Taxonomie eines neuen Tribus von Seeschildkröten aus dem Oligozän von Deutschland (Testudines: Chelonioidea). *Joannea Geologie und Paläontologie* 1: 61–77.

Kear, B.P. 2006. First gut contents in a Cretaceous sea turtle. *Biology Letters* 2: 113–115.

Kear, B.P., Nohra, R., Lindgren, J., Rabi, M., and Bazzi, M. 2025. Cretaceous sea turtle soft tissues clarify ancestry of scale loss in chelonioids. *IScience* 28: 113641.

Keferstein, C. 1834. *Die Naturgeschichte des Erdkörpers in ihren ersten Grundzügen. T. 2. Die Geologie un Paläontologie*. 896 pp. Friedrich Fleischer, Leipzig.

Kikinis, R., Pieper, S.D., and Vosburgh, K. 2014. 3D Slicer: a platform for subject-specific image analysis, visualization, and clinical support. *In*: F.A. Jolesz (ed.), *Intraoperative Imaging Image-Guided Therapy*, 277–289. Springer Science+Business Media, New York.

Knorr, G.W. 1755. *Lapides ex celeberrimorum virorum sententia diluvii universalis testes quos in ordines ac species distribuit, suis coloribus exprimit, ariq incisos in lucem mittit et alia naturae miranda addit Georg Wolffgang Knorr Norimbergensis. Sammlung Merckwürdigkei*. 36 pp. Andreas Bieling, Rürnberg.

Kordikova, E.G. 2000. Paedomorphosis in the shell of fossil and living turtles. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 218: 399–446.

Kotlarczyk, J., Jerzmańska, A., Świdnicka, E., and Wiszniowska, T. 2006. A framework of ichthyofaunal ecostratigraphy of the Oligocene–Early Miocene strata of the Polish Outer Carpathian basin. *Annales Societatis Geologorum Poloniae* 76: 1–111.

Krhovský, J., Rögl, F., and Hamršmíd, B. 2001. Stratigraphic correlation of the Late Eocene to Early Miocene of the Waschberg Unit (Lower Austria) with the Zdanice and Pouzdrany Units (South Moravia). *In*: W.E. Piller and M.W. Rasser (eds.), *Paleogene of the Eastern Alps*, 225–254. Verlag der Österreichischen Akademie der Wissenschaften, Vienna.

Krüger, J.F. 1822. *Geschichte der Urwelt. Erster Theil*. xvi + 528 pp. Gottfried Basse, Quedlinburg.

Krüger, J.F. 1823. *Geschichte der Urwelt. Zweiter Theil*. viii + 966 pp. Gottfried Basse, Quedlinburg.

Kuhn, O. 1964. Pars 107: Testudines. *In*: F. Westphal (ed.), *Fossilium catalogus I: Animalia*. 299 pp. Dr W. Junk, Gravenhage.

Kuhn, O. 1971. *Die Amphibien und Reptilien des deutschen Tertiärs und Diluviums*. 92 pp. Verlag Gebrüder Geiselberger, Altötting.

Lapparent de Broin, F. de 2001. The European turtle fauna from the Triassic to the Present. *Dumerilia* 4 (3): 155–217.

Lapparent de Broin, F. de, Murelaga, X., Farrés, F., and Altimiras, J. 2014. An exceptional cheloniid turtle, *Osonachelus decorata* nov. gen., nov. sp., from the Eocene (Bartonian) of Catalonia (Spain). *Geobios* 47: 111–132.

Lapparent de Broin, F. de, Murelaga, X., Pérez-García, A., Farrés, F., and Altimiras, J. 2018. The turtles from the upper Eocene, Osona County (Ebro Basin, Catalonia, Spain): New material and its faunistic and environmental context. *Fossil Record* 21: 237–284.

Lednew, N.M. 1914. Die Fauna der Fischschichten derHalbinsel Apscheron. *Mémoires du Comitè Géologique (St. Petersbourg)* 80: 1–65.

Leonhard, K.C.R. von 1827. *Taschenbuch für die gesammte Mineralogie mit Hinsicht auf die neusten Entdeckungen heraugegeben. 1. Band*. 572 pp. Ludwig Reinherz, Frankfurt am Main.

Leriche, M. 1908. Sur un appareil fanonculaire de Cetorhinus trouvé à l'état fossile dans le Pliocène d'Anvers. *Comptes Rendus hebdomadaires des séances de l'Academie des Sciences* 146: 875–878.

Leu, U.B. 1998. Schieferabbau und Forschungsgescgichte. *In*: H. Furrer and U.B. Leu (eds.), *Der Landesplattenberg Engi. Forschungsgeschichte, Fossilien Und Geologie*, 11–71. Siftung Landesplattenberg Engi, Engi.

Lindgren, J., Kuriyama, T., Madsen, H., Sjövall, P., Zheng, W., Uvdal, P., Engdahl, A., Moyer, A.E., Gren, J.A., Kamezaki, N., Ueno, S., and Schweitzer, M.H. 2017. Biochemistry and adaptive colouration of an exceptionally preserved juvenile fossil sea turtle. *Scientific Reports* 7 (1): 13324.

Linnaeus, C. 1735. *Systema naturae per regna tria naturae, systematice proposita per classes, ordines, genera, & species*. 12 pp. Theodorum Haak, Leiden.

Linnaeus, C. 1758. *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata*. 824 pp. Laurentii Salvii, Holmiae.

Linnaeus, C. 1766. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. T. I. Editio duodecima, reformata*. 1364 pp. Laurentii Salvii, Holmiae.

Maack, G.A. 1869. Die bis jetzt bekannten fossilen Schildkröten und die im oberen Jura bei Kelheim (Bayern) und Hannover neu aufgefundenen ältesten Arten derselben. *Palaeontographica* 18: 193–338.

Machalski, M. 1998. Polen als fossielenland. *Gea* 3: 84–88.

Madsen, H. 2008. Luffe – En helt fantastisk skildpadde. *GeologiskNyt* 18 (3): 8–12.

Maxwell, E.E., Alexander, S., Bechly, G., Eck, K., Frey, E., Grimm, K., Kovar-Eder, J., Mayr, G., Micklich, N., Rasser, M., Roth-Nebelsick, A., Salvador, R.B., Schoch, R.R., Schweigert, G., Stinnesbeck, W., Wolf-Schwenninger, K., and Ziegler, R. 2016. The Rauenberg fossil Lagerstätte (Baden-Württemberg, Germany): A window into early Oligocene marine and coastal ecosystems of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* 463: 238–260.

Mayr, G. and Gregorová, R. 2012. A tiny stem group representative of Pici (Aves, Piciformes) from the early Oligocene of the Czech Republic. *Palaontologische Zeitschrift* 86: 333–343.

Meyer, H. von 1838. Mittheilungen, an Professor Bronn gerichtet. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde* 1838: 413–418.

Meyer, H. von 1839. Ein Vogel im Kreideschiefer des Kantons Glaris. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde* 1839: 683–685.

Meyer, H. von 1856. Schildkröte und Vogel aus dem Fischschiefer von Glarus. *Palaeontographica* 4: 84–95.

Micklich, N. and Hildebrandt, L.H. 2010. Emergency excavation in the Grube Unterfeld (Frauenweiler) clay pit (Oligocene, Rupelian; Baden-Württemberg, S. Germany): new records and palaeoenvironmental information. *Kaupia* 17: 3–21.

Młynarski, M. 1959. *Glarichelys knorri* (Gray)—a cheloniid from Carpathian menilitic shales (Poland). *Acta Palaeontologica Polonica* 4: 178–192.

Młynarski, M. 1969. *Fossile Schildkröten*. 128 pp. A. Ziemsen Verlag, Wittenberg Lutherstadt.

Młynarski, M. 1976. Teil 7/Part 7. Testudines. *In*: O. Kuhn (ed.), *Handbuch der Paläoherpetologie. Encyclopedia of paleoherpetology*. 130 pp. Gustav Fischer Verlag, Stuttgart

Młynarski, M. 1984. Fossil chelonians of Poland. *Studia Palaeocheloniologica* 1: 189–203.

Moody, R.T.J. 1974. The taxonomy and morphology of *Puppigerus camperi* (Gray), an Eocene sea-turtle from northern Europe. *Bulletin of the British Museum (Natural History), Geology* 25: 155–186.

Müller, A. 1983. Fauna und Palökologie des marinen Mitteloligozäns der Leipziger Tieflandsbucht (Böhlener Schichten). *Altenburger Naturwissenschaftlische Forschungen* 2: 1–152.

Nielsen, E. 1959. Eocene turtles from Denmark. *Meddelelser fra Dansk Geologisk Forening* 14: 96–114.

Paucă, M. 1929. Fossile Fische aus dem Rumänischen Alttertiär. *Bulletin de la Section Scientifique de l'Académie Roumaine* 12 (4/5): 121–124.

Peyer, B. 1950. *Geschichte der Tierwelt*. 288 pp. Büchergilde Gutenberg, Zurich.

Pictet, F.-J. and Humbert, A. 1856. *Monographie des chéloniens de la molasse suisse*. 71 pp. J. Kessmann, Geneve.

Price, L.I. 1973. Quelônio amphichelydia no Cretáceo Inferior do nordeste do Brasilá. *Revista Brasileira de Geociências* 3 (2): 84–96.

Přikryl, T. 2013. An annotated list of the Oligocene fish fauna from the Osíčko locality (Menilitic Fm.; Moravia, the Czech Republic). *Acta Musei Nationalis Pragae, Series B, Historia Naturalis* 69 (3): 195–203.

Přikryl, T., Krzemiński, W., and Kania, I. 2011. New information about the anatomy of a peculiar fish of the genus *Hipposyngnathus* Daniltshenko, 1960. *Comptes Rendus Palevol* 10: 559–566.

Přikryl, T., Kania, I., and Krzemiński, W. 2016. Synopsis of fossil fish fauna from the Hermanowa locality (Rupelian; Central Paratethys; Poland): current state of knowledge. *Swiss Journal of Geosciences* 109: 429–443.

Přikryl, T., Bannikov, A.F., Grădianu, I., Kania, I., and Krzemiński, W. 2014. Revision of the family Propercarinidae (Perciformes, Stromateoidei) with description of a new species from the Oligocene of the Carpathians. *Comptes Rendus Palevol* 13: 691–700.

Pritchard, P.C.H., Bacon, P.R., Berry, F.H., Carr, A.F., Fletemeyer, J., Gallagher, R.M., Hopkins, S.R., Lankford, R.R., Marquez M., R., Ogren, L.H., Pringle, W.G., Reichart, H.A., and Witham, R. 1983. *Manual of sea turtle research and conservation techniques. Second edition*. *In*: K.A. Bjorndal and G.H. Balazs (eds.), Centrum for Environmental Education, Washington D.C..

Püntener, C., Anquetin, J., and Billon-Bruyat, J.-P. 2015. *Thalassemys bruntrutana* n. sp., a new coastal marine turtle from the Late Jurassic of Porrentruy (Switzerland), and the paleobiogeography of the Thalassemydidae. *PeerJ* 3: e1282.

Schleich, H.H., Vahldiek, B.W., Karl, H.-V., and Windolf, R. 1994. Neue Reptilienfunde aus dem Tertiär Deutschlands. 14. Beschreibung der fossilen Krokodil- und Schildkrötenreste der Helmstedter Mulde (Eozän) mit Beiträgen zur Geologie und Paläontologie. *Courier Forschungsinstitut Senckenberg* 173: 103–135.

Serafini, G., Gordon, C.M., Amalfitano, J., Wings, O., Esteban, N., Stokes, H., and Giusberti, L. 2024. First evidence of marine turtle gastroliths in a fossil specimen: Paleobiological implications in comparison to modern analogues. *PLOS ONE* 19 (5): e0302889.

Smets, G. 1886. Les chélonées Rupéliennes. *Annales de la Société Scientifique de Bruxelles* 10: 108–110.

Smets, G. 1887. *Chelyopsis littoreus*, Van Ben. *Annales de la Société Scientifique de Bruxelles* 11: 303–307.

Smets, G. 1888. Les chélonées Rupéliennes. *Annales de la Société Scientifique de Bruxelles* 12: 193–214.

Sönmez, B., Turan, C., Özdilek, Ş.Y., and Turan, F. 2016. Sex determination of green sea turtle (*Chelonia mydas*) hatchlings on the bases of morphological characters. *Journal of Black Sea/Mediterranean Environment* 22 (1): 93–102.

Steinmüller, J.R. 1802. *Beschreibung der schweizerischen Alpen- und Landwirthschaft nach den verschiedenen Abweichungen einzelner Kantone. Erstes Bändchen, welches die Alpen- und Landwirthschaft des alten Kantons Glarus enthält*. 276 pp. Steinerischen Buchhandlung, Winterthur.

Storms, R. 1894. Troisième note sur les poissons du terrain rupélien. *Ulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie* 8: 67–82.

Stüssi, F. 1950. La déformation des fossiles. *Schweizerische Bauzeitung* 68 (38): 523–526.

Sukhanov, V.B. 1964. Subclass Testudinata. Testudinates [in Russian]. *In*: Y.A. Orlov (ed.), *Osnovy Paleontologii. Tom 12. Zemnovodnye, Presmykaûsesâ i Ptitsy*, 354–438. Akademiâ Nauk SSSR, Moskva.

Tong, H., Hirayama, R., Makhoul, E., and Escuillie, F. 2006. *Rhinochelys* (Chelonioidea, Prostostegidae) from the Late Cretaceous (Cenomanian) of Nammoura, Lebanon. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 147 (1): 113–138.

Utkarsh, A. 2015. *The ParaView Guide: A Parallel Visualization Application*. 276 pp. Kitware, Incorporated, Clifton Park.

Vandelli, D. 1761. *Epistola de holothurio, et testudine coriacea ad celeberrimum Carolum Linnaeum*. 12 pp. Conzatti, Padova.

Vergne, R., Pacanowski, R., Barla, P., Granier, X., and Schlick, C. 2010. Radiance scaling for versatile surface enhancement. *In*: S.N. Spencer (ed.), *Proceedings of the 2010 ACM SIGGRAPH Symposium on Interactive 3D Graphics and Games*, 143–150. Association for Computing Machinery, Inc., New York

Vlachos, E. 2025. A proposal to uniquely distinguish established clade names under the PhyloCode. *Bulletin of Phylogenetic Nomentclature* 2 (1): 1–2.

Vremir, M.M. 2004. Fossil turtle found in Romania—overview. *A Magyar Állami Földtani Intézet Évi Jelentése* 2002: 143–152.

Weems, R.E. and Sanders, A.E. 2014. Oligocene pancheloniid sea turtles from the vicinity of Charleston, South Carolina, USA. *Journal of Vertebrate Paleontology* 34: 80–99.

Wegner, T. 1911. *Chelone gwinneri* n. sp., eine Meereschildkröte aus dem Rupelton von Flörsheim. *Bericht über die Senckenbergische Naturforschende Gesellschaft1* 1911: 193–195.

Wegner, T. 1914. *Chelonia gwinneri* Wegner aus dem Rupelton von Flörsheim a. M. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 36: 361–372.

Weiler, W. 1920. Die Septarientonfische des Mainzer Beckens. Eine vorläufige Mitteilung. *Jahrbücher des Nassauischen Vereins für Naturkunde* 72: 2–15.

Wettstein, A. 1886. Ueber die Fischfauna des Tertiaeren Glarnerschiefers. Untersuchung aus der geologischen Sammlung in Zürich. *Denkschriften der Schweizerischen Palaeontologischen Gesellschaft* 13: 1–103.

Wibbels, T., Owens, D.W., Morris, Y.A., and Amoss, M.S. 1987. Sexing techniques and sex ratios for immature loggerhead sea turtles captured along the Atlantic coast of the United States. *In*: W.N. Witzell (ed.), Ecology of East Florida Sea Turtles. Proceedings of the Cap Canaveral, Florida, Sea Turtle Workshop. *NOAA Technical Report NMFS* 53: 65–74.

Wyneken, J. 2001. *The Anatomy of Sea Turtles*. U.S. Department of Commerce NOAA Technical Memorandum NMFS-SEFSC-470. 172 pp. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, and Southeast Fisheries Science Center, Miami.

Zangerl, R. 1958. Die oligozänen Meerschildkröten von Glarus. *Schweizerische Paläontologische Abhandlungen* 73: 1–56.

Zangerl, R. 1969. The turtle shell. *In*: C. Gans (ed.), *Biology of the Reptilia, Vol. 1*, 311–339. Academic Press, London.

Zangerl, R. 1980. Patterns of phylogenetic differentiation in the toxochelyid and cheloniid sea turtles. *American Zoologist* 20: 585–596.

Zvonok, E.A., Udovichenko, N.I., and Bratishko, A.V. 2015. New data on the morphology and systematic position of the sea turtle *Allopleuron qazaqstanense* Karl et al. from the Middle Eocene of Kazakhstan. *Paleontological Journal* 49: 176–189.