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Publisher: Taylor & Francis

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## Journal of Vertebrate Paleontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/ujvp20>

### Taxonomy and phylogeny of the turtle *Tropidemys langii* Rüttimeyer, 1873, based on new specimens from the Kimmeridgian of the Swiss Jura Mountains

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Published online: 04 Mar 2014.

To cite this article: Christian Püntener, Jean-Paul Billon-Bruyat, Loïc Bocat, Jean-Pierre Berger & Walter G. Joyce (2014) Taxonomy and phylogeny of the turtle *Tropidemys langii* Rüttimeyer, 1873, based on new specimens from the Kimmeridgian of the Swiss Jura Mountains, *Journal of Vertebrate Paleontology*, 34:2, 353-374, DOI: [10.1080/02724634.2013.804412](https://doi.org/10.1080/02724634.2013.804412)

To link to this article: <http://dx.doi.org/10.1080/02724634.2013.804412>

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## TAXONOMY AND PHYLOGENY OF THE TURTLE *TROPIDEMYS LANGII* RÜTIMEYER, 1873, BASED ON NEW SPECIMENS FROM THE KIMMERIDGIAN OF THE SWISS JURA MOUNTAINS

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**ABSTRACT**—The fossil turtle *Tropidemys langii* is a representative of Plesiochelyidae, a traditionally recognized group of Late Jurassic turtles diagnosed by the presence of three cervical scutes and adapted to life in the sea. *Tropidemys langii* was previously only known from fossilized carapaces and, possibly, plastra from Europe, most notably the famous 'Solothurn Turtle Limestone' of Switzerland. Due to the sparse fossil record of *Tropidemys langii*, several questions concerning its taxonomy and phylogeny have remained unanswered. Here, new material of *Tropidemys langii* is reported from the Kimmeridgian of Porrentruy, Canton Jura, Switzerland. In addition to three well-preserved carapaces, associated plastra and limb bones (humerus and femur) are described for the first time. The type specimens of '*Tropidemys valanginiensis*' and '*Pelobatochelys blakii*' lack diagnostic characters, but can nevertheless be referred to *Tropidemys*. A potential extension of the lineage into the Early Cretaceous is uncertain, however, because the type locality of '*Tropidemys valanginiensis*' is dubious. A cladistic analysis shows that *Tropidemys langii* is sister to *Plesiochelys solodurensis*, thereby tentatively confirming for the first time the monophyly of Plesiochelyidae using cladistic arguments.

**SUPPLEMENTAL DATA**—Supplemental materials are available for this article for free at [www.tandfonline.com/UJVP](http://www.tandfonline.com/UJVP)

### INTRODUCTION

*Tropidemys* is a Late Jurassic turtle from Western Europe (Lapparent de Broin, 2001). It is traditionally placed within Thalassemydidae (e.g., Bräm, 1965; Antunes et al., 1988; Bardet, 1995) or Plesiochelyidae (e.g., Broin, 1994; Lapparent de Broin et al., 1996; Lapparent de Broin, 2001), but the circumscription of these two higher taxonomic units is somewhat unclear (Bardet, 1995; Billon-Bruyat et al., 2005; Joyce, 2007), mostly because the phylogenetic relationships of many Late Jurassic turtles from Europe remain unresolved. For the purpose of this contribution, we restrict the term Plesiochelyidae to the clade of turtles diagnosed by the presence of three cervical scutes homologous with those developed in *Plesiochelys solodurensis* Rüttimeyer, 1873. Plesiochelyidae have long featured as quintessential eucryptodires (Gaffney, 1975), but recent phylogenies hint at the possibility that they may actually represent basal paracryptodires (Sterli, 2010).

The study of *Tropidemys* began in the second and third decades of the 19th century, when Prof. Franz Joseph Hugi (1791–1855) established a collection of fossil turtles that were discovered in a quarry in the vicinity of Solothurn, Canton Solothurn, Switzerland (Bräm, 1965). The lithostratigraphic unit from which these turtles originated later became known as the 'Solothurn Turtle Limestone' member, which forms the uppermost part of the Kimmeridgian (Late Jurassic) Reuchenette Formation (Meyer, 1994a). Rüttimeyer (1873) studied the fossil turtles from Solothurn and erected the three species: *Tropidemys expansa*, *T. gibba*, and *T. langii*. Additionally, Rüttimeyer (1873) transferred the Valanginian (Early Cretaceous) *Chelonia valanginiensis* Pictet and Campiche, 1858–1860, of Sainte-Croix,

Canton Vaud, Switzerland, to *Tropidemys*, thereby creating the new combination *Tropidemys valanginiensis*.

Some 80 years after the fundamental work of Rüttimeyer (1873), Bräm (1965) reviewed the fossil turtles of Solothurn. He had access to a well-preserved *Tropidemys* specimen that was found in 1895 and preliminarily described by Bloch (1902). Bräm (1965) believed that the differences used by Rüttimeyer (1873) to create three Solothurn species of *Tropidemys* were individual particularities. He therefore merged the three Solothurn species into one and retained the name *Tropidemys langii*, which he considered to be the type species. The holotype of *T. langii* (NMS 8554) consists of the posterior part of a carapace and is stored at the Naturmuseum Solothurn, Canton Solothurn, Switzerland.

Furthermore, we refer to *Tropidemys* two isolated neurals from the collection of the Musée Jurassien des Sciences Naturelles (MJSN), Porrentruy, Switzerland. These two neurals come from the Kimmeridgian of the Porrentruy region and were mentioned as turtles by Thurmann and Etallon (1861–1864).

In addition to the Swiss material, *Tropidemys* is also known from localities in Germany, France, and England. Portis (1878) erected *Tropidemys seebachi* on a few carapacial and plastral elements from the Kimmeridgian (Late Jurassic) of Hannover, Lower Saxony, Germany. These turtle fragments were erstwhile described under the name *Styemys lindenensis* by Maack (1869) and were later reviewed by Oertel (1924). Lydekker (1889) reported *Tropidemys* material (costals, a neural, and a left hyoplastron) from the Kimmeridge Clay of Weymouth, Dorset, England. According to Benton and Spencer (1995), the fossil reptiles from the Kimmeridge Clay of Weymouth come from the three earliest Kimmeridgian zones and probably also from the latest Oxfordian. Finally, Sauvage (1902) mentioned two carapace fragments of *Tropidemys* from Fumel, Département Lot-et-Garonne,

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France. These fragments, dated to the *Autissiodirensis* ammonite zone (late Kimmeridgian) (Lapparent de Broin et al., 1996), were later reviewed by Bergounioux (1935), but are today considered to be lost (Lapparent de Broin et al., 1996). Herein, we also refer the fragmentary type material of *Pelobatochelys blakii* Seeley, 1875, from the Kimmeridge Clay of Weymouth, Dorset, England, to *Tropidemys*, although we remain uncertain about the specific identity of these fragments.

More recent discoveries of *Tropidemys* were reported from the earliest Kimmeridgian of Hildesheim, Lower Saxony, Germany (Böttcher, 1977), from the Kimmeridgian of the Boulonnais, Département Pas-de-Calais, France (Cuny et al., 1991), and from Nettelstedt/Wallücke, North Rhine-Westphalia, Germany (Karl, 1997). Undetermined fragments of Plesiochelyidae from Fumel, Département Lot-et-Garonne, France, that resemble *Tropidemys* were discussed in Lapparent de Broin et al. (1996). Studies on *Tropidemys* remains from the Kimmeridgian of Le Havre, Département Seine-Maritime, France, are currently in progress (F. Lapparent de Broin, pers. comm., January 2012).

In February 2000, a new paleontological project was established in Porrentruy, Canton Jura, Switzerland, to rescue the paleontological heritage found during construction of the Transjurane highway A16 through fossiliferous formations (Marty and Billon-Bruyat, 2009). Excavations led by this project, named Paleontology A16 (PAL A16), resulted in a rich and diverse collection of fossils, notably dinosaur footprints (Marty and Hug, 2003; Marty et al., 2007; Marty, 2008) and numerous Kimmeridgian turtles (Billon-Bruyat, 2005). This turtle fauna also contains new material of *Tropidemys langii*, including well-preserved carapaces and the first known associated plastra and limb bones (a femur and a humerus).

Prior to the discoveries at Porrentruy, *Tropidemys langii* was only known from carapacial and plastral elements of questionable affinities. This made it difficult to determine the systematic position of this taxon (Bräm, 1965). Numerous cladistic studies have included Late Jurassic turtles (e.g., Dryden, 1988; Gaffney and Meylan, 1988; Gaffney et al., 1991; Gaffney, 1996; Hirayama et al., 2000; Joyce, 2007), but none has ever tested the phylogenetic relationships of *Tropidemys langii*.

The aims of this work are (1) to describe the new material from Porrentruy and compare it with that from the type locality Solothurn; (2) to update the diagnosis of Bräm (1965); (3) to determine the species present in Porrentruy and Solothurn; and (4) to test the phylogenetic position of *Tropidemys langii* in a global phylogenetic framework.

**Institutional Abbreviations**—MCG, Musée Cantonal de Géologie, Lausanne, Switzerland; MJSN, Musée Jurassien des Sciences Naturelles, Porrentruy, Switzerland; NMS, Naturmuseum Solothurn, Switzerland.

**Locality Abbreviations**—BSY, Courtedoux—Bois de Sylleux; CRE, Courtedoux—Creugenat; SCR, Courtedoux—Sur Combe Ronde; TCH, Courtedoux—Tchâfouè; TLB, Porrentruy—Tunnel du Banné; VTT, Courtedoux—Vâ Tche Tchâ.

## GEOLOGIC SETTING

The majority of the *Tropidemys langii* remains were collected by Paleontology A16 from the Vâ Tche Tchâ (VTT) site near the village of Courtedoux during the 2006 field season (Fig. 1). Further discoveries originate from the Tunnel du Banné (TLB), Bois de Sylleux (BSY), Sur Combe Ronde (SCR), and Creugenat (CRE) sites. All excavation sites are situated along the route of the future Transjurane highway A16 in the Ajoie Region, Canton Jura, Switzerland (Fig. 1).

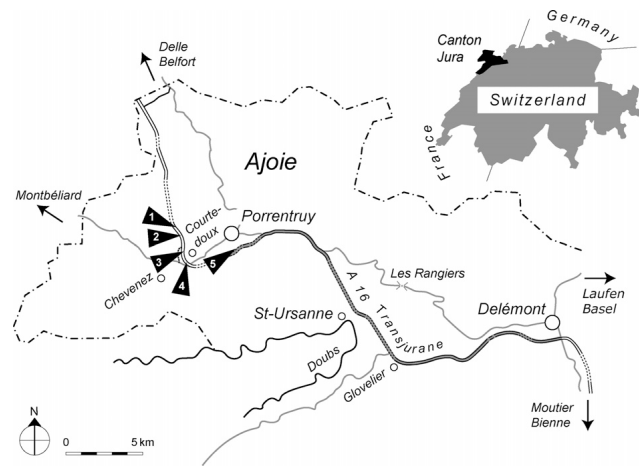


FIGURE 1. Map of the Ajoie Region, Canton Jura, Switzerland, with the excavation sites that yielded *Tropidemys langii* remains. 1, Courtedoux—Vâ Tche Tchâ (VTT); 2, Courtedoux—Bois de Sylleux (BSY); 3, Courtedoux—Tchâfouè (TCH); 4, Courtedoux—Sur Combe Ronde/Creugenat (SCR/CRE); 5, Porrentruy—Tunnel du Banné (TLB).

Most of the Ajoie Region belongs to the tabular portion of the Jura Mountains (Marty et al., 2007), which are composed of flat-lying Jurassic limestones (Trümpy, 1980). The Kimmeridgian is represented in the western part of Swiss Jura Mountains by the Reuchenette Formation (Thalmann, 1966; Gygi, 1995; Colombié and Strasser, 2005; Jank et al., 2006; Comment et al., 2011), which is on average 140 m thick (Colombié, 2002; Colombié and Strasser, 2005). Ammonites of the Tethyan realm dominate at the base of the formation, but are replaced by ammonites of the boreal realm in the late Kimmeridgian (Schweigert and Callomon, 1997; Hardenbol et al., 1998; Colombié and Strasser, 2005).

A more regional subdivision of the Reuchenette Formation is based upon lithology (Fig. 2). In ascending stratigraphic order, these are the Banné Marls (Gygi, 2000a; Jank et al., 2006), the Nerinean Limestones (Jank et al., 2006; Waite et al., 2008) with dinosaur footprint bearing layers (Marty and Hug, 2003; Marty et al., 2007; Marty, 2008), and the Virgula Marls (Jank et al., 2006). Most of the *Tropidemys langii* specimens were found in the ~10-m-thick Banné Marls, which consist of “grey, decimeter-thick layers of marlstones, calcarenitic marls, and marly limestones” (Jank et al., 2006:178). The Banné Marls are assigned to the *Divisum* ammonite zone of the Tethyan realm (Jank et al., 2006).

During the Kimmeridgian, the Ajoie Region was part of the southwest-northeast trending Jura platform, which was situated between the Paris Basin to the northwest, the Massif Central to the southwest, the Tethys to the southeast, and the London Brabant and Rhenish massifs to the north (Fig. 3) (Ziegler, 1988; Thierry et al., 2000; Marty and Hug, 2003; Colombié and Strasser, 2005). Various depositional environments can be recognized within the platform, such as tidal flats, more- or less-restricted lagoons, channels, barriers, reefs, or islands (Marty and Hug, 2003; Colombié and Strasser, 2005; Marty, 2008). The dinosaur tracks of the Nerinean Limestone and the fossil woods of the Virgula Marls (Philippe et al., 2010) indicate a nearby coast. The sedimentation of the Banné and Virgula marls was influenced by lagoons, channels, and the littoral zone (Marty and Hug, 2003). These rapidly changing sedimentation systems led to a diverse fossil invertebrate assemblage in the Banné Marls of the Courtedoux—Vâ Tche Tchâ site (Marty and Hug, 2003).

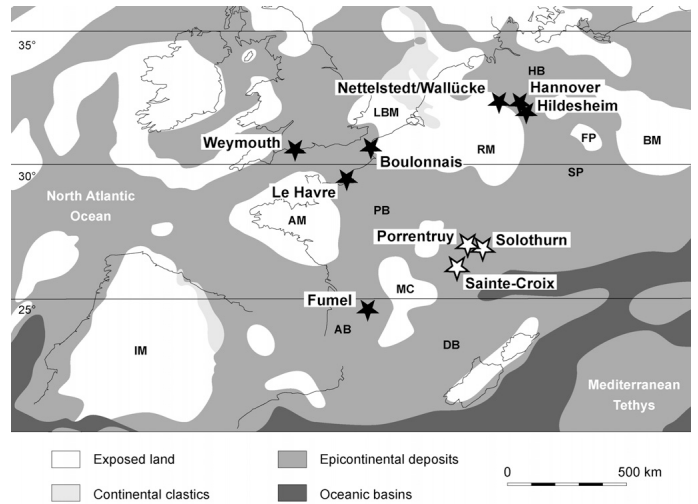
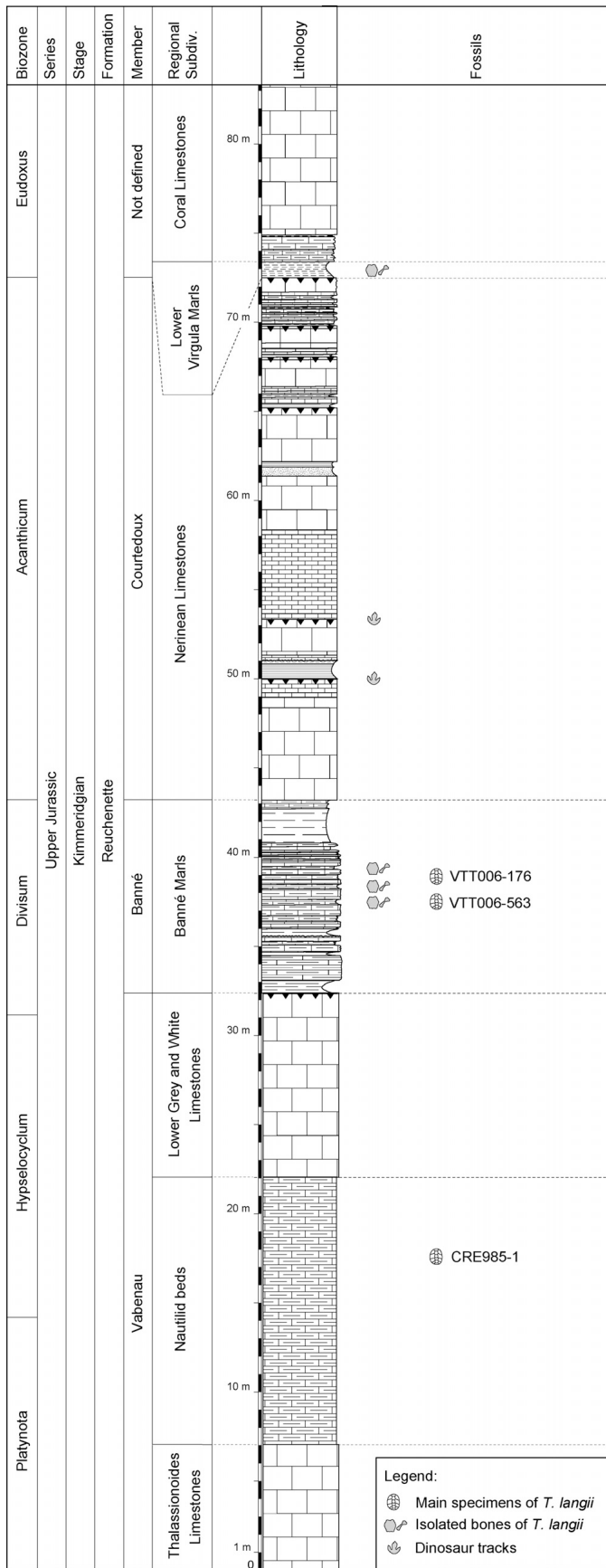


FIGURE 3. *Tropidemys* localities in Switzerland (white stars) and in other European countries (Germany, France, and England) (black stars) on the early Kimmeridgian paleoenvironmental map of Western Europe (modified after Thierry et al., 2000). **Abbreviations:** AB, Aquitaine Basin; AM, Armorican Massif; BM, Bohemian Massif; DB, Dauphinois Basin; FP, Franconian Platform; HB, Hannover Basin; IM, Iberian Massif; LBM, London Brabant Massif; MC, Massif Central; PB, Paris Basin; RM, Rhenish Massif; SP, Swabian Platform.

All other *Tropidemys* remains from Western Europe also occur within epicontinental deposits (Fig. 3).

MATERIALS AND METHODS

The *Tropidemys langii* material from Porrentruy comprises 22 numbered specimens that were collected between 2001 and 2010 (Appendix 1). VTT006-176 and VTT006-563 are the most complete specimens, but their elements are fully disarticulated. In order to understand the original geometry of the shell, they were arranged on a bed of sand and then measured and photographed. CRE985-1, an almost complete carapace of a juvenile, was donated to the collection Paleontology A16 by Pierre Bigler (preparation team Paleontology A16). Special attention was paid to a humerus (VTT006-253) and a femur (VTT010-13) that were found associated with carapace remains of *T. langii* (VTT006-253 and VTT010-13, respectively). All of this material is presently part of the collection Paleontology A16 (Office de la Culture, République et Canton du Jura), but will be stored by the end of 2018 at the Musée Jurassien des Sciences Naturelles (MJSN; Office de la Culture, République et Canton du Jura) in Porrentruy, Switzerland.

The primary comparative material used in this study is stored at the Naturmuseum Solothurn (NMS) and is composed of 17 cataloged *T. langii* fossils that were described and studied by Rütimyer (1873), Bloch (1902), and Bräm (1965). The best-preserved specimen is an almost complete carapace (NMS 8648). To better understand the stratigraphic distribution of *Tropidemys*, we furthermore studied the holotype of ‘*Tropidemys*

← FIGURE 2. Bio-, chrono-, and lithostratigraphic intervals of the Reuchenette Formation in Porrentruy, indicating *Tropidemys langii*-bearing levels and dinosaur tracks. Regional subdivisions are from Gygi et al. (2000a, 2000b) and Jank et al. (2006), chronostratigraphic members are from Comment et al. (2011).

*valanginiensis*' (MCG GEOLREG 16849), which was described by Pictet and Campiche (1858–1860). Unpublished material of *Plesiochelys* sp. of the collection Paleontology A16 was furthermore used for comparisons, including a humerus (BSY007-140), a femur (BSY008-668), and three carapaces (TCH005-42, TCH007-272, and VTT006-299).

#### SYSTEMATIC PALEONTOLOGY

TESTUDINES Batsch, 1788

PANCRYPTODIRA Joyce, Parham, and Gauthier, 2004

PLESIOCHELYIDAE Baur, 1888

*TROPIDEMYS* Rüttimeyer, 1873

**Emended Diagnosis**—*Tropidemys* can be diagnosed as a representative of Pancryptodira based on the absence of mesoplastra and as a representative of Plesiochelyidae by the presence of three cervicals. Within Plesiochelyidae, *Tropidemys* exhibits the following list of characters: carapace roundish-oval; nuchal notch sometimes present; high carapace with a tectiform posterior part; neurals wide and hexagonal; middle and posterior neurals wider than long with no short anterior sides; midline keel present and more distinct posteriorly; a crest-like axillary buttress present on the ventral side of costal I; inguinal buttress forms a strong ridge on costal V and peripheral VIII; relatively narrow vertebrals and wide pleurals.

**Referred Material**—Holotype of '*Tropidemys valanginiensis*' Pictet, 1858, in Pictet and Campiche, 1858–1860; all specimens referred by Bräm (1965) to *Tropidemys langii* Rüttimeyer, 1873, including the holotypes of *T. expansa* and *T. gibba*, but to the exception of the plastral material; holotype of *Tropidemys seebachi* Portis, 1878; type series of '*Pelobatochelys blakii*' Seeley, 1875.

**Stratigraphic Distribution**—Early Kimmeridgian (Böttcher, 1977) to late Kimmeridgian (Rüttimeyer, 1873; Bräm, 1965; Meyer, 1994a); perhaps even Valanginian (Pictet and Campiche, 1858–1860).

**Geographic Distribution**—Switzerland, Germany, France, and England.

**Note**—The holotypes of '*Tropidemys valanginiensis*' and '*Pelobatochelys blakii*' possess features that allow their referral to *Tropidemys*, but none that allow them to be referred to any of the valid species. Hence, they should be regarded as *Tropidemys* sp.

*TROPIDEMYS LANGII* Rüttimeyer, 1873  
(Figs. 4–14)

**Diagnosis**—*T. langii* can be distinguished from the only other valid species of *Tropidemys*, *T. seebachi*, by being significantly larger (carapace length up to 60 cm) and by having five vertebrals. *Tropidemys seebachi* is much smaller (carapace length 40 cm) and has more than five vertebrals.

**Referred Specimens**—BSY007-128, CRE985-1, SCR010-482, SCR010-1100, TLB001-55, VTT001-579, VTT004-114, VTT006-1, VTT006-52, VTT006-55, VTT006-157, VTT006-175, VTT006-176, VTT006-204, VTT006-224, VTT006-244, VTT006-253, VTT006-288, VTT006-290, VTT006-563, VTT006-573, VTT010-13 (see also Appendix 1).

#### DESCRIPTION AND COMPARISON

##### General Preservation

**VTT006-176**—The specimen is composed of carapacial and plastral shell bones (Figs. 4, 7, and 11). Well-developed sulci indicate that the shell was once covered by keratinous scutes, like in

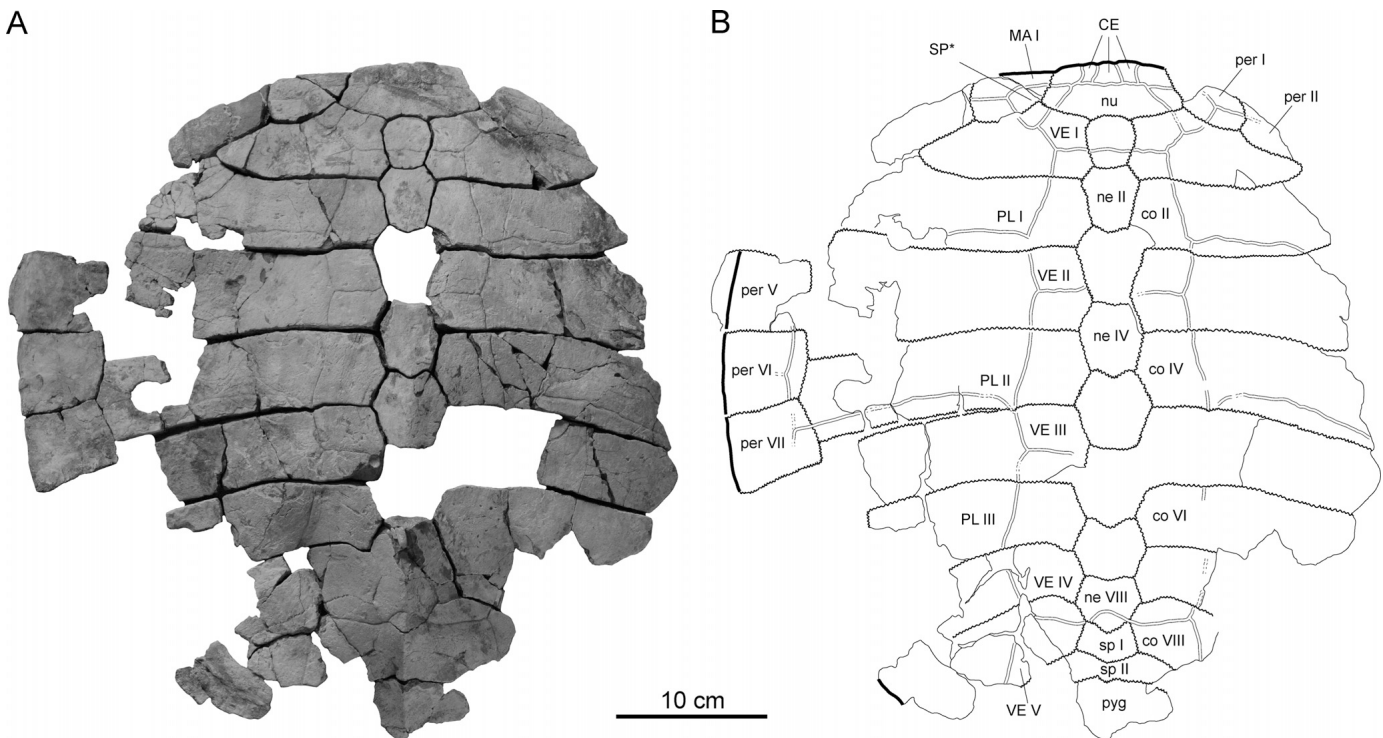


FIGURE 4. Specimen VTT006-176 of *Tropidemys langii* (Kimmeridgian, Porrentruy, Switzerland). Carapace in dorsal view. **A**, photograph; **B**, illustrative drawing showing bone sutures (zigzag line); scute sulci (double line); the preserved outline of the carapace (thick line); and fractures (thin line). **Abbreviations**: CE, cervical; co, costal; MA, marginal; ne, neural; nu, nuchal; per, peripheral; PL, pleural; pyg, pygal; sp, suprapygals; SP\*, supernumerary pleural; VE, vertebral.

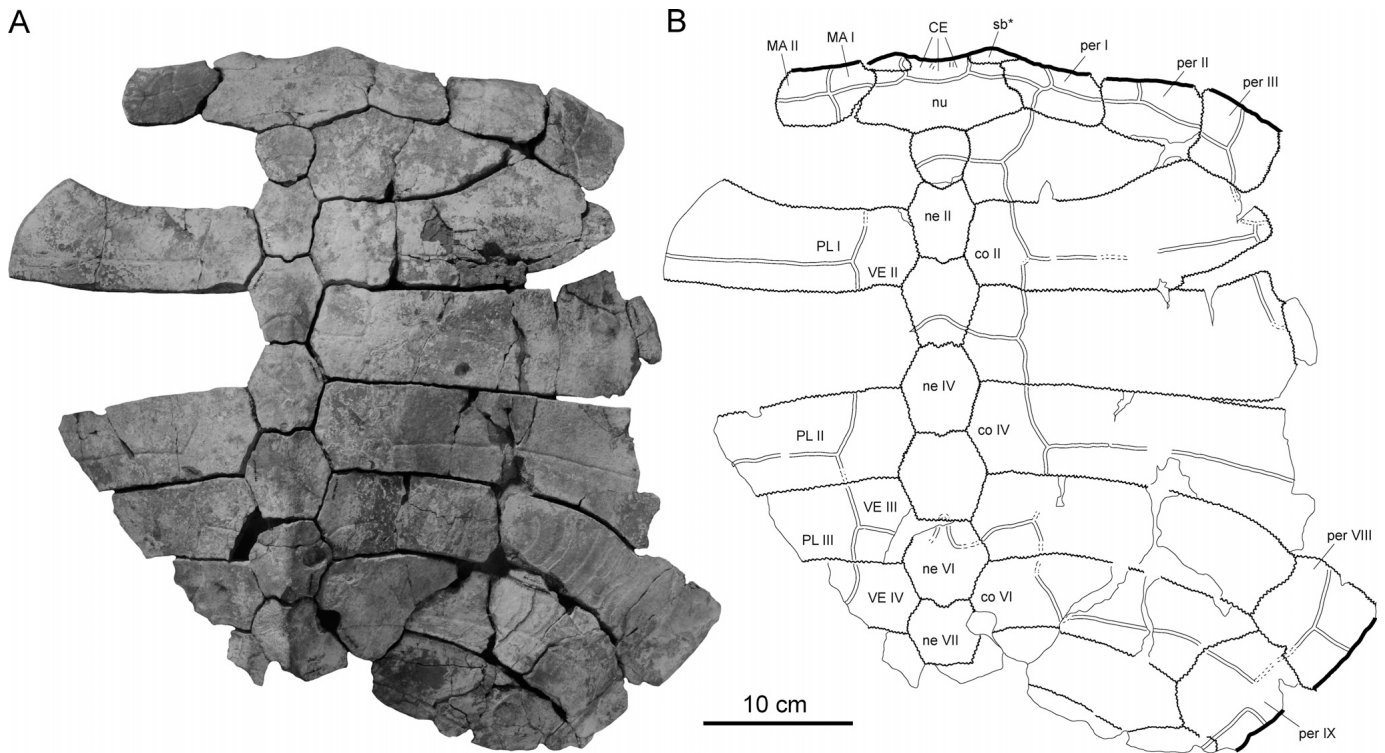


FIGURE 5. Specimen VTT006-563 of *Tropidemys langii* (Kimmeridgian, Porrentruy, Switzerland). Carapace in dorsal view. **A**, photograph; **B**, illustrative drawing showing bone sutures (zigzag line); scute sulci (double line); the preserved outline of the carapace (thick line); and fractures (thin line). **Abbreviations:** CE, cervical; co, costal; MA, marginal; ne, neural; nu, nuchal; per, peripheral; PL, pleural; sb\* = supernumerary bone; VE, vertebral.

most other turtles (Joyce, 2007; Scheyer, 2007). However, sutures and sulci are better preserved on the carapace than on the plastron. Whereas the midline of the carapace is only missing two neurals, the lateral portions of the costals and most peripherals are absent (Fig. 4). The bones are disarticulated, impeding direct observation on the original shell shape.

**VTT006-563**—This specimen includes elements of the carapace and plastron (Figs. 5, 8, 9, 10, and 12). The midline of the carapace is rather well preserved, but the entire pygal region is missing. Whereas the medial parts of the costals are often well preserved, the lateral parts are not and only a few peripherals are preserved. Most bones of the carapace were found disarticulated. Taphonomic compaction on the right side of the carapace was made visible by a three-dimensional reconstruction of the shell on an artificial sandbed. Sutures and scute sulci of the plastral bones are better preserved than those of VTT006-176.

**CRE985-1**—CRE985-1 is the only specimen from Porrentruy with most of the carapace bones still in articulation (Fig. 6). The carapace offers both a dorsal and a ventral view. In the latter, a part of the vertebral column is visible. Most peripherals and the posterior part of the pygal region are missing. Compaction distorted the original shell shape. An undetermined fragment of the plastron, probably a part of a hyo- or hypoplastron, is associated with the carapace.

#### Carapace

**VTT006-176**—Only a small portion of the pygal is missing and the carapace is estimated to have measured approximately 450 mm along the midline (Fig. 4). The width of the carapace is similarly estimated at about 500 mm. Because the carapace was flattened during compaction, it is likely that it was about as long

as wide originally and roundish in outline. Three-dimensional reconstruction using industrial sand shows that the carapace was well domed in anteroposterior and mediolateral directions. The doming is rather flat in the anterior part of the shell but becomes gradually more tectiform towards the posterior. The doming, however, is developed independently from the keel (see keel below).

**VTT006-563**—The length of the reconstructed carapace measures about 410 mm along the midline, excluding the missing posterior neurals, the suprapygals, and the pygal (Fig. 5). The greatest preserved but incomplete width measures about 490 mm. The outline was probably roundish and the carapace vaulting resembles that of VTT006-176.

**CRE985-1**—The carapace is much smaller than those of VTT006-176 and VTT006-563. It has a preserved length of 302 mm (without the missing suprapygals and pygal) and a preserved width of 267 mm (without the missing peripherals and lateral parts of the costals). The outline would have been oval (Fig. 6). The three-dimensional shape is similar to specimens VTT006-176 and VTT006-563. The vaulting in anteroposterior direction matches with the reconstruction of VTT006-176. In mediolateral direction, the specimen is relatively flat in the anterior part and tectiform in the posterior part.

#### Nuchal

**VTT006-176**—The well-preserved nuchal (Fig. 7) is trapezoidal in outline and almost two times wider than long. The anterior border is slightly convex towards the anterior. The posterior border is convex posteriorly, with an embayment to hold the first neural.

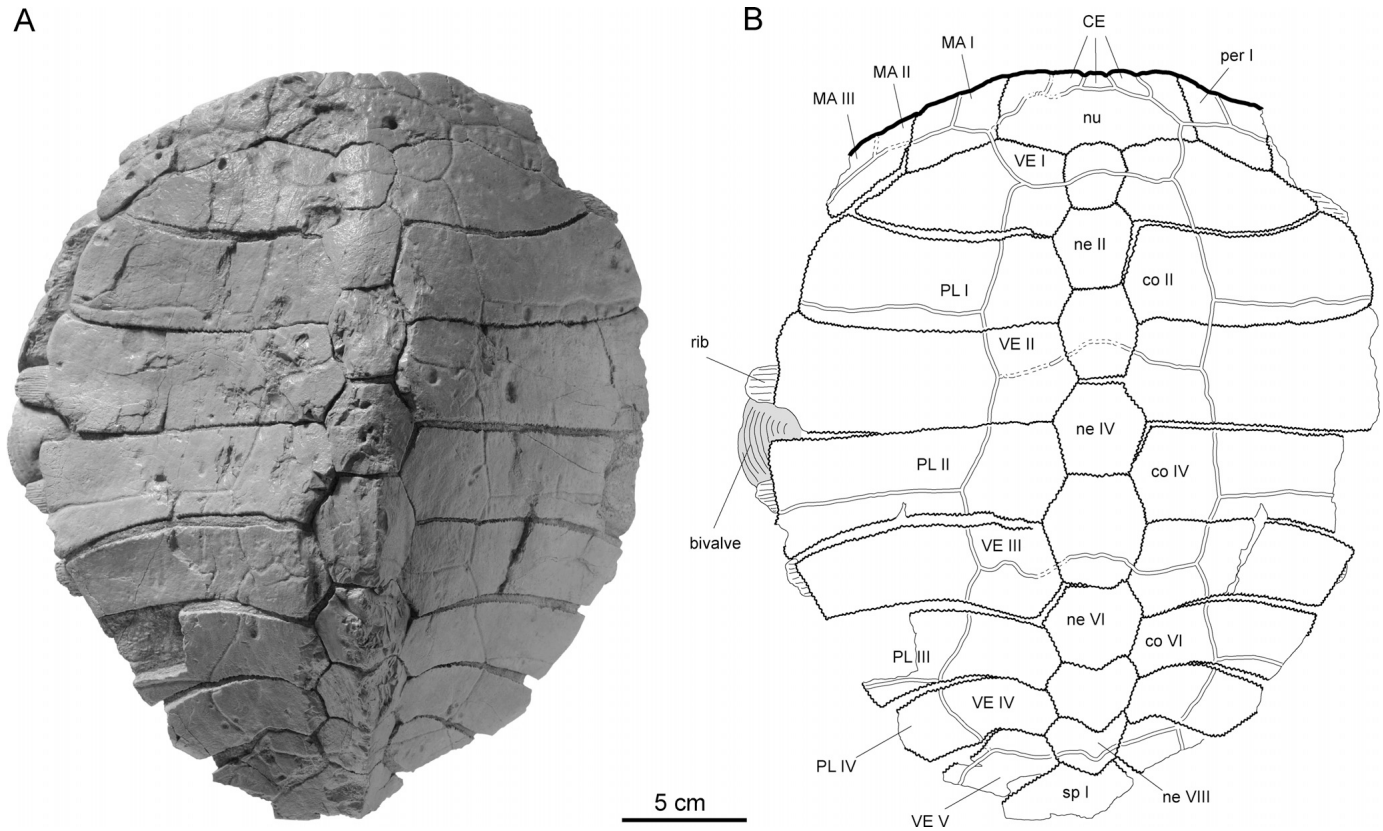


FIGURE 6. Specimen CRE985-1 of *Tropidemys langii* (Kimmeridgian, Porrentruy, Switzerland). Carapace in dorsal view. **A**, photograph; **B**, illustrative drawing showing bone sutures (zigzag line); scute sulci (double line); the preserved outline of the carapace (thick line); and fractures (thin line). **Abbreviations:** CE, cervical; co, costal; MA, marginal; ne, neural; nu, nuchal; per, peripheral; PL, pleural; sp, suprapygal; VE, vertebral.

**VTT006-563**—The shape of the well-preserved nuchal (Fig. 8) is influenced by two unusual, supernumerary bones that occupy the anterolateral edges of the nuchal. These small, somewhat oval bones form the anterior-most margin of the carapace (Fig. 5). The supernumerary bones and the nuchal form a nuchal notch that stretches about 60 mm between the apices that are formed by the supernumerary bones. The posterior border of the nuchal is similar to that of VTT006-167 by exhibiting a rounded notch for articulation with neural I. The nuchal is almost twice as wide than long.

**CRE985-1**—The outline of the nuchal is somewhat trapezoidal, but more rectangular than that of VTT006-176. Its anterior rim forms a moderate notch that is slightly less distinctive than in VTT006-563. The nuchal is almost twice as wide than long.

### Neurals

**VTT006-176**—Although the third and sixth neurals are missing, it is apparent that the specimen had eight neurals (Fig. 4). With the exceptions of neurals I and VIII, all are hexagonal. The first neural is somewhat oval, longer than wide, and narrows posteriorly. Neurals II and IV are clearly longer than wide, whereas neural V is slightly wider than long, and neurals VII and VIII clearly wider than long. A correlated pattern can be observed in the length of the lateral borders. Neurals II and IV have narrow anterior sides, whereas neurals VII and VIII have wide anterior sides. Neural V appears to be transitional, but nevertheless has short anterior sides, though less distinctively than neurals II and IV. The neurals tend to have a convexity along the

posterior border, with the exception of neural V, which has a straight posterior border, for articulation with the anterior border of the subsequent neural. The posterior border of neural VIII is extremely convex and the bone therefore has a pentagonal to heptagonal outline. The thickness of the neurals increases from the first (10 mm) to the fourth (17 mm) neural. Neurals V and VII are a bit thinner at 15 and 16 mm, respectively. The thickness of neural VIII could not be measured.

**VTT006-563**—Neurals II–V are complete, but small parts of neurals I, VI, and VII as well as most of neural VIII are missing (Fig. 5). With the exception of the first neural, all preserved neurals are hexagonal. Neural I is longer than wide and narrows towards the posterior. Neurals II, III, and IV are longer than wide, whereas neurals V and VI are slightly wider than long. The shape cannot be identified for neurals VII and VIII. The anterior sides of neurals II and III are clearly narrower than the posterior sides. The anterior and posterior sides of neurals IV and V are approximately the same width, whereas neurals VI and VII have wider anterior sides. Neural V is the transition point for both length:width ratio and the position of the narrow side. This is not apparent in Figure 5, however, due to distortions caused by the perspective. The posterior borders of the neurals tend to have a convexity for articulation with the anterior border of the succeeding neural. However, there is considerable variation in the expression of this convexity (Fig. 5). The thickness of the neurals ranges from 7 (neural VI) to 13 (neurals III and IV) mm.

**CRE985-1**—With the exception of the first neural, all neurals are hexagonal in outline (Fig. 6). The first neural is roundish to oval in outline, but slightly more angular than in specimens VTT006-176 and VTT006-563. Neurals I through III are longer

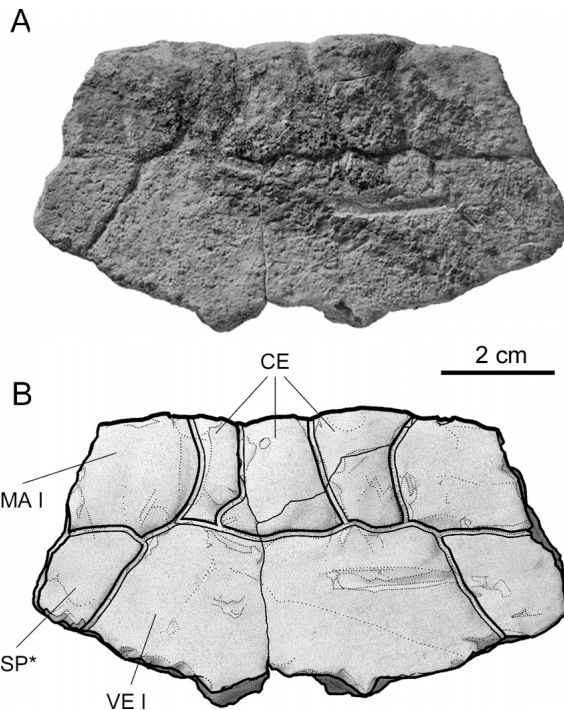


FIGURE 7. Specimen VTT006-176 of *Tropidemys langii* (Kimmeridgian, Porrentruy, Switzerland). Nuchal in dorsal view. **A**, photograph; **B**, drawing. **Abbreviations:** CE, cervical; MA I, marginal; SP\*, supernumerary pleural; VE I, vertebral. [planned for column width]

than wide, neurals IV and V about as long as wide, and neurals VI through VIII wider than long. Neurals I through III have narrow anterior sides. This is also the case for neurals IV and V, but less distinctively so. Neurals VI and VII have wide anterior

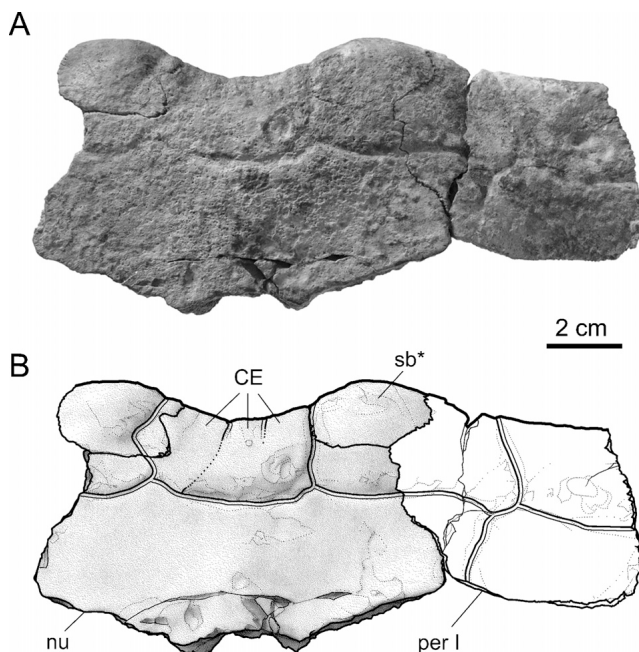


FIGURE 8. Specimen VTT006-563 of *Tropidemys langii* (Kimmeridgian, Porrentruy, Switzerland). Nuchal in dorsal view. **A**, photograph; **B**, drawing. **Abbreviations:** CE, cervical; nu, nuchal; per, peripheral; sb\*, supernumerary bone.

sides, whereas neural VIII exhibits anterior and posterior margins that are equal in width. In contrast to specimens VTT006-176 and VTT006-563, the posterior borders of the neurals are rather straight. This is not correctly reflected for the posterior neurals in Figure 6 because of distortion caused by the perspective.

### Suprapygals and Pygal

**VTT006-176**—The midline bone posterior to neural VIII is interpreted as the first suprapygal (Fig. 4), because its ventral side has no trace of a neural spine, as can be observed on the visceral side of all neurals. The bone has a trapezoidal outline with a concave anterior and a convex posterior border. The second suprapygal is much wider than long and boomerang-shaped, with the two lateral arms directed posteriorly. Anteromedially, however, it is concave for articulation with the first suprapygal. The lateral half of the left side is broken, but the right side is intact. The outline of the pygal is unclear because the posterior and lateral portions are missing. It is nevertheless apparent that the pygal was larger than suprapygal I.

**CRE985-1**—Only the first suprapygal is present (Fig. 6). It is much wider than long and somewhat resembles the second suprapygal of VTT006-176. The anterior border is concave and the lateral arms are directed posteriorly.

### Keel

**VTT006-176**—A keel is developed along the midline of the carapace (Fig. 4). The nuchal and the first neural are slightly vaulted. The keel is slightly visible on the second neural (angle of  $167^\circ$ ) and is fully recognizable on neural V ( $141^\circ$ ). The keel is sharply developed on neurals VII ( $122^\circ$ ) and VIII ( $114^\circ$ ), but flatly developed on the first suprapygal ( $130^\circ$ ). The keel is slightly developed along the anterior half of the pygal, but absent along the posterior half. The keel is clearly offset from the doming of the remainder of the carapace. The angle of the keel is therefore not propagated laterally by the costals.

**VTT006-563**—Like in specimen VTT006-176, the nuchal and first neural are slightly vaulted (Fig. 5). The keel is slightly visible on the second neural ( $164^\circ$ ) and gradually becomes more distinct towards the posterior (neural VII =  $121^\circ$ ). The most dramatic change occurs between neurals V ( $143^\circ$ ) and VI ( $123^\circ$ ). In contrast to the specimen VTT006-176, the inclination between the neurals and costals is continuous.

**CRE985-1**—The keel along the midline of the carapace (Fig. 6) has a similar evolution to that of specimens VTT006-176 and VTT006-563, but it is more sharply developed. The nuchal and neurals I and II are slightly vaulted. The keel is better visible on neural III ( $140^\circ$ ) and gradually sharpens towards the posterior (neural VIII =  $98^\circ$ ). As in specimen VTT006-176, the keel is flat on the suprapygal and the inclination between the neurals and costals is not continuous.

### Costals

**VTT006-176**—Eight pairs of costals are present (Fig. 4). On the right side of the carapace, the medial part of costal V is missing. With the exception of costals I and left costal IV, all costals lack their lateral parts. Costal I has three slightly concave notches on the anterior border for articulation with the nuchal and the two first peripherals. The anterior border of the second costal is concave, its posterior border slightly convex. Although the lateral part is missing, it is clear that the costal is anteroposteriorly longer laterally than medially. This is true for all other costals, except for costals I and V. The third costal separates the anterior costals that curve anteriorly (i.e., they have a convex posterior border) from the posterior costals that curve posteriorly (i.e., they have a concave anterior border). Costal III is therefore the only costal with a concave anterior and a concave posterior border. Medially, the costals are considerably thicker where they



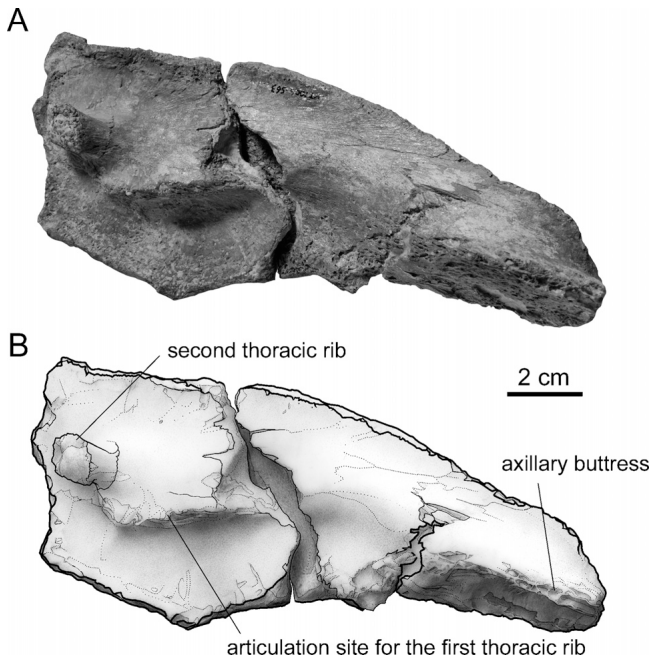


FIGURE 9. Specimen VTT006-563 of *Tropidemys langii* (Kimmeridgian, Porrentruy, Switzerland). Right costal I in ventral view (180° rotation). **A**, photograph; **B**, drawing.

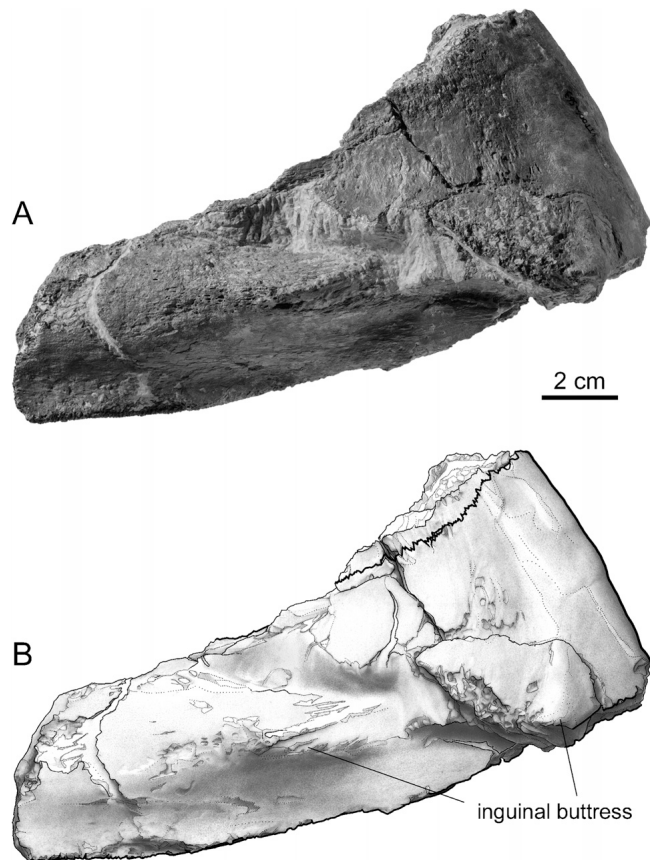


FIGURE 10. Specimen VTT006-563 of *Tropidemys langii* (Kimmeridgian, Porrentruy, Switzerland). Right costal V and peripheral VIII in ventral view (180° rotation). **A**, photograph; **B**, drawing.

meet the thick neurals than laterally where they meet the thinner peripheral bones. In ventral view, the medially emerging heads of the ribs are only poorly preserved and the first costal has a short articulation site for the displaced first thoracic rib.

**VTT006-563**—Eight pairs of costals are evident (Fig. 5). With the exception of costals IV and VIII, the series is almost complete on the right side of the carapace. On the left side, only the medial parts of costals II, IV, V, VI, and VII are preserved. Costal I is similar in outline to that of VTT006-176. Costals II, III, IV, and VII are anteroposteriorly longer laterally than medially. As in VTT006-176, costals I and V make the exception and decrease in anteroposterior length towards the lateral. The third costal separates the anterior costals, which curve anteriorly, from the posterior costals, which curve posteriorly. The costal thickness decreases laterally, though less distinctively than in VTT006-176.

In visceral view, the medially emerging heads of the ribs are partially preserved. The ribs are laterally fused with the costals, forming a flat ridge. In costals I and V, this ridge laterally expands to a crest that contacts the distal end of the axillary and inguinal buttresses, respectively (Figs. 9, 10). A short (40-mm-long) articulation site for the first thoracic rib is visible on the medial end of the first costal (Fig. 9).

**CRE985-1**—Whereas the medial portions of the costals are intact, the lateral extent of the posterior costals are not preserved (Fig. 6). The outline of the first costal matches that of specimens VTT006-176 and VTT006-563, but the notches for the first and second peripherals are less marked. Costals I and V are the only costals where a decrease in anteroposterior length can be observed laterally. Costal VIII is too incomplete to clarify this characteristic. The third costal separates the anterior costals, which curve anteriorly, from the posterior costals, which curve posteriorly. Costal III itself has a concave anterior border and a convex posterior border, similar to VTT006-563. The free rib ends protrude beyond the lateral margin of some costals (Fig. 6).

In ventral view, the axillary buttress is visible on right costal I. Unfortunately, most of this is obscured by matrix. The strong

inguinal buttresses are in contact with the lateral quarter of the fifth costal.

### Peripherals

**VTT006-176**—The first and second peripherals are preserved on both sides and the fifth through seventh peripherals on the left side (Fig. 4). The first peripheral is irregular in outline. The dorsal portions of peripherals V, VI, and VII are somewhat squarish, of similar size, and form obtuse angles (‘V’-shaped) with their respective ventral laminae. There is no peripheral gutter.

**VTT006-563**—Peripherals I, II, III, VIII, IX, and a small part of peripheral X are preserved on the right side, whereas only peripheral I is preserved on the left side (Fig. 5). As in specimen VTT006-176, the first peripheral is irregular in outline. The anteroposterior length decreases from the first to the third peripheral, but the width remains about the same. Peripherals VIII and IX are wider than the anterior peripherals and have irregular sutures with the adjacent costals. There is no peripheral gutter.

**CRE985-1**—Peripheral I is preserved on both sides, with peripheral II preserved only on the left (Fig. 6). The first peripheral has the outline of a parallelogram and therefore differs from VTT006-176 and VTT006-563 by having an angular posteromedial border. There is no peripheral gutter.

### Scutes of the Carapace

**VTT006-176**—Three cervicals are visible on the medial margin of the nuchal (Fig. 7). The median cervical is irregularly trapezoidal in outline and wider than the lateral ones.

Five vertebral scutes can be discerned (Fig. 4). Vertebral I is hexagonal in outline. The anterior border is irregular and lies entirely on the nuchal. Vertebrae II, III, and IV are hexagonal and widest where they meet the interpleural scute sulci. Vertebrae I–IV are wider than long and this was likely also the case for the incomplete vertebral V. The intervertebral scute sulci cross neurals I (straight sulcus), III (neural missing), VI (neural missing), and VIII (sulcus curving anteriorly).

Four regular pleural scutes are present (Fig. 4). The interpleural scute sulci meet the widened posterior part of the vertebrae and are situated on the posterior part of costals II and IV. The placement of the interpleural III/IV scute sulcus cannot be discerned. Pleural I covers approximately half of the dorsal width of peripheral I, whereas pleural II only covers about one-fifth of the dorsal width of peripherals VI and VII. A particularity of VTT006-176 is a supernumerary pleural scute that is situated anteromedial to the first pleural (Figs. 4, 7). This triangular scute is positioned on the intersection of costal I, peripheral I, and the nuchal and is present on both sides of the carapace.

The marginal scutes are very poorly preserved. They cover about half the width of the first peripheral and the better part of the sixth and seventh peripheral. It is unclear if the marginals lapped onto the plastron.

**VTT006-563**—Vague sulci indicate the presence of three cervicals (Fig. 8). Portions of the first four vertebral scutes are visible, whereas the fifth is not preserved (Fig. 5). Vertebral I has a broad, trapezoidal outline. The anterior sulcus crosses the nuchal and peripheral I and is longer than the posterior sulcus. Vertebrae II, III, and IV are the widest where they meet the interpleural scute sulci. Whereas vertebral I is clearly wider than long, vertebrae II and III are about as wide as long. The vertebral I/II scute sulcus is slightly curved anteriorly and crosses neural I and the vertebral II/III sulcus strongly curves anteriorly and crosses neural III. The vertebral V/VI sulcus exhibits a distinct midline inflection and therefore crosses the anterolateral part of neural VI but encroaches medially onto neural V.

Four pleural scutes can be discerned. The interpleural scute sulci meet the vertebrae at their lateral apices and are situated on the posterior parts of costals II, IV, and VI. Pleural I covers two-fifths of the first peripheral, about half of the second peripheral, and one-fourth of the anterior part of the third peripheral. The pleural I/marginal IV scute sulcus encroaches onto costal II and the pleural II/marginal V scute sulcus onto costals II and III (Fig. 5B). Pleural III covers about half of the dorsal width of peripheral VIII.

The only more or less complete marginal scutes are left marginal I and right marginals I through III and IX. These scutes are rectangular in outline and almost twice as long as wide. Marginals IV and V encroach onto costals II and III.

**CRE985-1**—The nuchal possesses three cervicals on its anterior rim (Fig. 6). The one in the middle is trapezoidal in outline and smaller than the adjacent ones.

There are five vertebral scutes. Vertebral I is irregular in outline. Its anterior border is restricted to the nuchal on the right side of the carapace but encroaches onto peripheral I on the left side. Vertebrae II, III, and IV meet the interpleural scute sulci along apices on costals II, IV, and the limit of VI/VII, respectively. All preserved vertebral scutes are wider than long. The intervertebral scute sulci cross neurals I (sulcus slightly curving anteriorly), III (sulcus strongly curving anteriorly), V (sulcus strongly curving anteriorly), and VIII (sulcus slightly curving anteriorly).

Four pleural scutes can be distinguished. The pleural scute sulci meet the lateral apices of the vertebrae and are situated on the posterior part of costals II, IV, and VI (medially on the limit costal VI/VII). Pleural I covers approximately half of peripherals I and II.

Only marginals I and II are preserved. Whereas the first marginal is very irregular in outline, the second is rectangular and exactly twice as long than wide.

### Plastron

**VTT006-176**—The hyo- and hypoplastra are partially preserved (Fig. 11). The four disarticulated bones are in rather poor condition, with only few original borders and almost no scute sulci preserved. The central portion of the plastron reveals a concavity visible in ventral view that is consistent with the individual being male. The possible presence of a central fontanelle cannot be determined with confidence. Ento-, epi-, xiphi-, and mesoplastra are not preserved. The latter were probably absent, because there are no indications for supplementary bones between the hyo- and hypoplastra.

**VTT006-563**—The right hypoplastron is almost complete, the left hypoplastron is laterally broken, whereas the right hypoplastron is damaged posteriorly (Fig. 12). The three bones are disarticulated. As in specimen VTT006-176, the hyoplastra and the hypoplastra are not flat, but depressed towards the center of the plastron, as is typical for male individuals. However, the presence of a central fontanelle is clearly visible. About a quarter of the margin of the central fontanelle (25 mm) is formed by the hypoplastra and about three quarters (70–80 mm) by the hyoplastra. At the common border of the hyo- and hypoplastron, the central fontanelle is about 70 mm wide, but it broadens further posteriorly.

As in specimen VTT006-176, ento-, epi-, and xiphiplastra are missing and there is no evidence for the presence of mesoplastra. The partially preserved anteromedial parts of the hypoplastra do not preserve a notch for articulation with the entoplastron. No sutural articulation sites are apparent for epiplastra.

### Hyoplastra

**VTT006-176**—The suture between the right and left hyoplastra is not preserved, nor are their anterior and lateral borders. The preserved posterior border of the right hyoplastron is concave and thins toward both lateral and medial margins. The bridge of the right hyoplastron is approximately 80 mm long measured

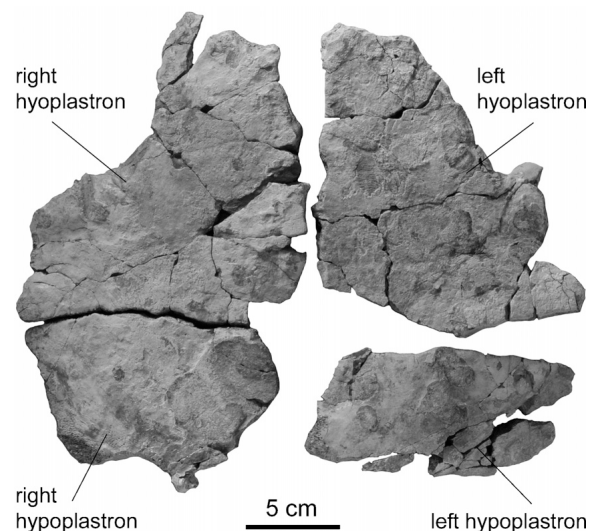


FIGURE 11. Specimen VTT006-176 of *Tropidemys langii* (Kimmeridgian, Porrentruy, Switzerland). Photograph of the plastron in ventral view.

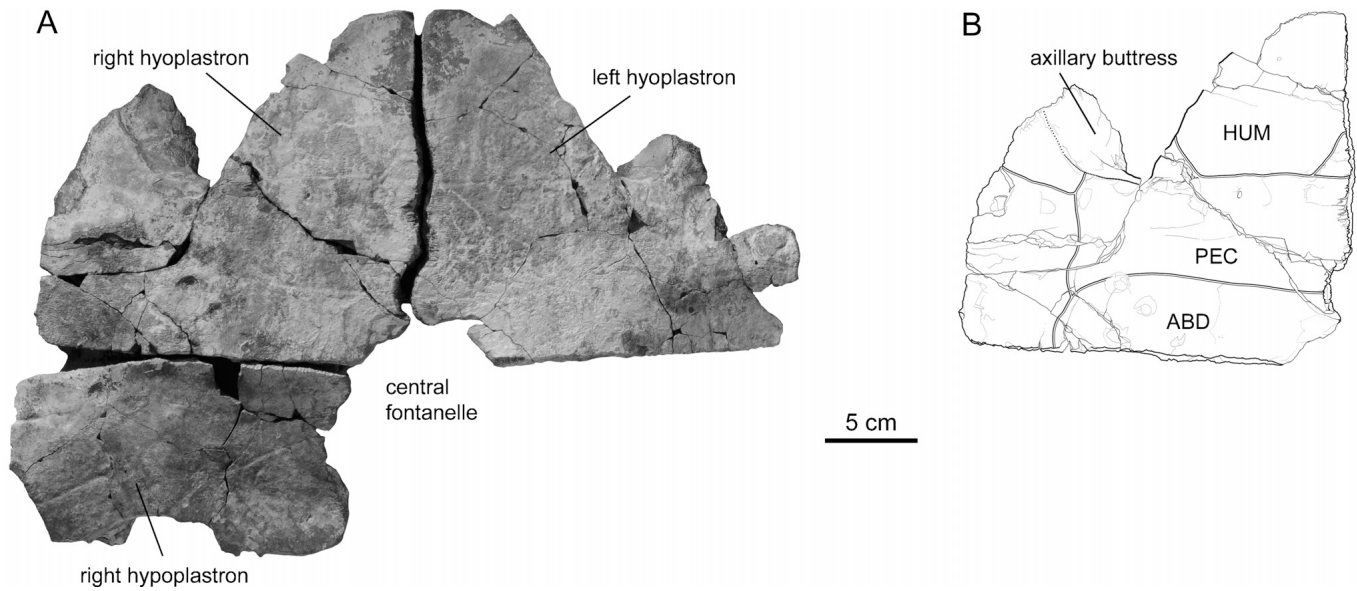


FIGURE 12. Specimen VTT006-563 of *Tropidemys langii* (Kimmeridgian, Porrentruy, Switzerland). **A**, photograph of the plastron in ventral view; **B**, drawing of the right hyoplastron in ventral view. **Abbreviations:** ABD, abdominal scute; HUM, humeral scute; PEC, pectoral scute.

from the posterior border of the element to the deepest point of the axillary notch. A crest-like structure that is apparent on the visceral part of the first costal served as the terminal attachment site for the axillary buttress.

**VTT006-563**—The hyoplastra (Fig. 12) once articulated with one another along a suture that is straight anteriorly and sinuous posteriorly. The medial fontanelle, however, separated the posterior eighth of the hyoplastra from one another. The hyoplastra are wider than long and have straight posterior borders. The bridge of the right hyoplastron measures 95 mm from the deepest part of the axillary notch to the posterior rim and 95 mm from the deepest part of the axillary notch to the lateral rim. In dorsal view, the crest-like axillary buttress extends anteriorly from the deepest point of the axillary notch while increasing in height. The distal end of the axillary buttress is dislocated from the rest of the hyoplastron and remains in connection with the lateral portion of the first costal (Fig. 9). The axillary buttress was in contact with peripherals II and III.

### Hypoplastra

**VTT006-176**—The anterior portion of the right hypoplastron is preserved and articulates well with the posterior portion of the right hyoplastron (Fig. 11). The bridge of the hypoplastron measures approximately 76 mm from the anterior border of the hypoplastron to the deepest point of the inguinal notch. The inguinal buttress is flat and broad proximally and expands into a crest-like structure distally. A well-developed articular site for the inguinal buttress is developed on the visceral side of costal V.

**VTT006-563**—The right hypoplastron (Fig. 12) is 187 mm wide (including the fontanelle). The anterior border is convex and therefore does not correspond with the straight posterior border of the adjacent hyoplastron. This is likely the result of compaction. The bridge of the hypoplastron is 83 mm from the anterior border to the deepest point of the inguinal notch and 72 mm from the lateral border to the deepest point of the inguinal notch. The posterior border of the hypoplastron is preserved (only slightly fractured). The inguinal buttress begins flat

and broad at the inguinal notch and terminates in a distinctive ridge that articulated with costal V and peripheral VIII (Fig. 10).

### Scutes of the Plastron of VTT006-563

Because the epiplastra are missing, it is unclear if gular and extragular scutes were present with only the posterior portion of humeral scutes preserved. The posterior border of the humeral is situated at the same level as the deepest point of the axillary notch (Fig. 12B). However, laterally and medially the sulcus curves anteriorly. A supernumerary scute is apparent along the midline between the humeral and pectoral. The preserved portion of the humeral has a length of 90 mm (measured along the midline). The pectoral scute is short (60 mm, measured along the midline) in comparison with the humeral. Medially, the abdominal scute is about 75 mm long, with the anterior 35 mm lying on the hypoplastron. Laterally, the abdominal is much longer (about 110 mm). Without the missing part on the xiphoplastron, the femoral scute is 60 mm long along the midline. There are no signs of anal scutes on the hypoplastron. Four inframarginals can be discerned along the bridge, the second one being clearly longer anteroposteriorly than the other three (Fig. 12).

### Comparisons between *Tropidemys* Specimens from Porrentruy and Solothurn

These comparisons are mainly based on the three main specimens described above (VTT006-176, VTT006-563, and CRE985-1), but other, fragmentary specimens are also taken into account (cf. Appendix 1 and Fig. 2). Most information from Solothurn is provided by specimens NMS 8554 (holotype of *T. langii*), NMS 8648 (main specimen of Bräm, 1965), and NMS 8665 (holotype of '*T. gibba*'). Table 1 provides a comparative overview between these six specimens. In order to verify their validity, the three species named by Rüttimeyer (1873), i.e., '*T. expansa*,' '*T. gibba*,' and *T. langii*, are noted together with the specimen number. Additionally, the studied material of *Tropidemys* is compared with other Plesiochelyidae. Given that we agree with Bräm that only a single species of *Tropidemys*, *T. langii*, is present at Solothurn,

TABLE 1. The main specimens from Porrentruy and Solothurn in comparison.

Anatomy	Character	<i>Tropidemys langii</i> from Porrentruy			<i>Tropidemys langii</i> from Solothurn		
		VTT006-176	VTT006-563	CRE985-1	NMS 8554	NMS 8648	NMS 8665
Carapace Nuchal	Outline	Roundish	Roundish	Oval		Oval	
	Outline	Trapezoidal	Irregular	Trapezoidal to rectangular		Trapezoidal to rectangular	
	Anterior notch	No	Yes	Yes		No	
	Supernumerary bone	No	Yes	No		No	
Neurals	Number of neurals	8		8	8	8	
	Neurals preserved	I, II; IV, V, VII, VIII	I–VII	I–VIII	VI–VIII	I–VIII	II–V
	Wider than long	V, VII, VIII	V, VI	VI–VIII	VI–VIII	II–VIII	
	Wider anterior side	VII–VIII	VI, VII	VI, VII	VI–VIII	VII	
Crest angle	Neural II	167°	164°	155°		151°	148°
	Neural III		160°	140°		134°	130°
	Neural V	141°	143°	120°		93°	105°
	Neural VII	114°	121°	99°	96°	90°	
Scutes	Number of cervicals	3	3	3		3	
	Neurals crossed by vertebrales	I-III-VI-VIII	I-III-V/VI-VIII	I-III-V-VIII	?-?-?-VIII	I-III-V-VIII	?-III-V-?
	Supernumerary pleural	Yes	No	No		No	

we place ‘*T. expansa*’ and ‘*T. gibba*’ in quotes where appropriate in this section to highlight their invalid status.

**Carapace Size**—There is much variation in carapace size among available *Tropidemys* specimens. Bräm (1965) measured a length of 615 mm for NMS 8648 without the missing pygal region. This is clearly longer than the 450 mm of VTT006-176 (a specimen missing only a small part of the pygal). Rütimeyer (1873) differentiated the three species, ‘*T. gibba*’, ‘*T. langii*’, and ‘*T. expansa*’ among others by their size, with ‘*T. gibba*’ being the smallest and ‘*T. expansa*’ the larger, and by comparing the dimensions of the neurals (e.g., in particular neural III). According to this criterion, specimens VTT006-176, VTT006-253, and VTT006-563 are in the range of ‘*T. gibba*’ (Table 2). However, the remains of CRE985-1 and some other fragments from Porrentruy (e.g., VTT006-224, VTT006-244) belong to distinctively smaller animals.

In Solothurn, *Plesiochelys solodurensis* and *Craspedochelys picteti* are of similar size to the adult specimens of *Tropidemys* spp., whereas ‘*Thalassemys moseri*’ is distinctively smaller and ‘*Thalassemys hugii*’ larger (cf. Bräm, 1965).

**Carapace Shape**—The reconstructions of specimens VTT006-176 and VTT006-563 are estimated as exhibiting a subcircular outline, whereas CRE985-1 is rather oval. Bräm (1965) recon-

structed an oval outline on the basis of specimen NMS 8648 (Table 1).

All specimens from Solothurn and Porrentruy are only slightly domed anteriorly, but clearly tectiform posteriorly. Specimens VTT006-563 and CRE985-1 are more strongly vaulted than VTT006-176, but all three are flatter than NMS 8665 (holotype of ‘*T. gibba*’), the specimen from Solothurn with the best-preserved three-dimensional structure. The anteroposterior vaulting of the three specimens from Porrentruy is similar to one another and less distinctive than that of NMS 8665 (holotype of ‘*T. gibba*’).

The carapaces of other Plesiochelyidae are distinctively flatter than those of *Tropidemys* spp. (Bräm, 1965).

**Nuchal**—The five preserved nuchals (four in Porrentruy and one in Solothurn) can roughly be described as trapezoidal with a convex posterior border in which a medial notch receives the first neural (Table 1). The shape nevertheless exhibits some variation. CRE985-1 and NMS 8648 approach a rectangular outline, but VTT006-244 is hexagonal in outline due to a strongly convex posterior border. The nuchal of VTT006-563 is irregular in outline due to the presence of two symmetrical supernumerary bones. The nuchals of VTT006-563 and CRE985-1 have concave anterior borders. By contrast, VTT006-176 and NMS 8648 exhibit convex anterior borders whereas the anterior border of VTT006-244 is straight. All five nuchals are wider than long.

Some authors (Lapparent de Broin et al., 1996; Joyce, 2000, 2003) describe the nuchals of plesiochelyids as being rectangular in order to distinguish them from the wide and trapezoidal nuchal of eurysternids. However, this distinction does not apply to *Tropidemys*, a taxon exhibiting a trapezoidal nuchal, but which is nonetheless herein diagnosed as belonging to Plesiochelyidae on the basis of the presence of three cervical scutes.

**Neurals**—Bräm (1965) concluded that nine neurals are present in NMS 8648 (Bräm, 1965:pl. 8, fig. 5) and eight neurals in NMS 8554 (holotype of *T. langii*; Rütimeyer, 1873:pl. VII, fig. 1). Specimens VTT006-176 and CRE985-1 both have eight neurals. A comparison between VTT006-176 and NMS 8648 suggests that the ninth neural of the latter specimen is in fact the first suprapygal, followed by a second suprapygal and pygal. The first suprapygals of CRE985-1 and NMS 8554 (*T. langii*) are clearly widening

TABLE 2. Comparison of the medial length of the third neural of *Tropidemys*.

Specimen/Species after Rütimeyer (1873)	Medial length of neural III (mm)	References
VTT006-176	45 (estimated)	This work
NMS 8665/ <i>T. gibba</i>	49	Bräm (1965)
VTT006-253	50	This work
VTT006-563	52	This work
NMS 8666/ <i>T. gibba</i>	55	Bräm (1965)
NMS 8648	55	Bräm (1965)
<i>T. langii</i> (specimen unknown)	56	Rütimeyer (1873)
NMS 8556/ <i>T. expansa</i>	66	Rütimeyer (1873); Bräm (1965)

posteriorly, in contrast to the rather narrow first suprapyrgals of VTT006-176 and NMS 8648.

All neurals (except the first one) of NMS 8648 are wider than long (Bräm, 1965:pl 8, fig. 1). This seems to be an exception, because all other specimens from Porrentruy and Solothurn have anterior neurals that are longer than wide (Table 1).

Bräm (1965) utilized the geometry of the neurals, mostly based on NMS 8648, to diagnose *Tropidemys langii*. In particular, the second and third neurals have distinctively narrower anterior margins (relative to the posterior margin). The fourth to sixth neurals exhibit approximately equal anterior and posterior margins, with the seventh and eighth neurals exhibiting relatively wide anterior sides. We observe approximately the same pattern in the three main specimens from Porrentruy.

**Keel**—The main specimens from Porrentruy have less distinctively angled neurals than those from Solothurn (Table 1). The anterior neurals are more angled in Solothurn specimens, giving the impression of a keel that originates more anteriorly. Our observations of additional materials support the tendency that keels are more distinct in Solothurn than in Porrentruy. However, CRE985-1 and VTT010-13 have more distinctive keels than VTT006-176 and VTT006-563, and approach the values of NMS 8554 (holotype of *T. langii*). According to Bräm (1965), *Tropidemys langii* has a continuous inclination between the neurals and costals. Our own observations can confirm this for two specimens (VTT006-563 and NMS 8665). In four other specimens, however, the inclination is offset between the neurals and costals (CRE985-1, VTT006-176, NMS 8554, and NMS 8648).

No other plesiochelyid exhibits such wide and keeled neurals as the representatives of *Tropidemys* (Bräm 1965).

**Pygal**—The only preserved pygals from Porrentruy (VTT006-176 and VTT006-204) are incomplete and lack the lateral portions of the element. Thus, their shape remains unclear. Bräm (1965) described the strongly deformed pygal of NMS 8554 (holotype *T. langii*) as being wide and rectangular. The keel ends within the pygal of VTT006-176 and VTT006-204, but continues until the very end in another isolated pygal from Solothurn (NMS 8991).

**Costals**—Costal III separates the anterior costals, which curve anteriorly, from the posterior costals, which curve posteriorly. This applies to the three main specimens from Porrentruy in addition to NMS 8648. Apart from the uniquely shaped first costal, costal V is the only element of the costal series in the three main specimens from Porrentruy that is shorter laterally than medially. Costal V of NMS 8554 (holotype of *T. langii*) and NMS 8648 is only slightly longer laterally, contrary to condition of the succeeding costals in which they are clearly longer laterally. An exception to this pattern is costal II of NMS 8648, which is clearly shorter laterally than medially (Bräm, 1965:pl. 8, fig. 1).

**Peripherals**—Peripheral I of CRE985-1 is more angular than the irregular peripherals I of VTT006-176 and VTT006-563. In NMS 8648, the width increases from the first through the eighth peripheral and decreases again along the posterior elements of the series (Bräm, 1965). The few preserved peripherals from Porrentruy neither confirm nor contradict this observation.

**Cervicals**—Bräm (1965) reconstructed *Tropidemys langii* with three cervicals on the nuchal. He could not observe them on the only preserved nuchal (NMS 8648) from Solothurn, but instead referred to Bloch (1902), who documented them with a photograph. Three cervicals are present on specimens CRE985-1, VTT006-176, VTT006-244, and VTT006-563. In CRE985-1, VTT006-176, and VTT006-244, the median cervical is trapezoidal in outline and expands posteriorly. According to the reconstruction of Bräm (1965:177), this is also the case in NMS 8648. In contrast to NMS 8648, VTT006-176, and VTT006-244, the median cervical of CRE985-1 is smaller than the lateral ones.

The presence of three cervicals is considered to be a diagnostic trait of Plesiochelyidae (Bräm, 1965; Lapparent de Broin et al.,

1996; Joyce, 2003). However, a specimen of *Palaeomedusa testa* (MB R 2894) also has three cervicals, but at the same time exhibits a wide and trapezoidal nuchal that was thought to be diagnostic for the Eurysternidae (Joyce, 2003). Other eurysternids (sensu Lapparent de Broin et al., 1996) such as *Eurysternum wagneri*, *Idiochelys fitzingeri*, and *Solnhofia parsonsi* have only a single cervical (Joyce, 2003), similar to *Thalassemys hugii* (Bräm, 1965).

**Vertebrales**—Two specimens from Porrentruy (VTT006-176 and VTT006-563) and one from Solothurn (NMS 8648) have vertebrales that are clearly narrower than the pleurals. The three main specimens from Porrentruy have vertebrales with varying widths. The same range of variation can be observed in Solothurn.

The vertebral scute sulci of NMS 8648 cross neurals I, III, V, and VIII (Bräm, 1965). The same is true for CRE985-1 (Table 1). In VTT006-176, it is neural VI instead of V, and in VTT006-563 the vertebral III/IV scute sulcus encroaches from neural VI onto neural V. The fossils from Solothurn remain within the I-III-V-VIII pattern.

As in NMS 8648, the vertebral II/III and vertebral III/IV scute sulci of the three main specimens from Porrentruy are anteriorly curved. The same condition is present for the vertebral IV/V scute sulcus in VTT006-176.

Lapparent de Broin et al. (1996) compared the length of the pleural II/III scute sulcus and the width of vertebral III (pleural II/III–vertebral III ratio) in representative plesiochelyids (Table 3). The specimens from Porrentruy are in the range of other *Tropidemys* and are clearly different from other plesiochelyids.

**Pleurals**—The interpleural scute sulci of specimens VTT006-176, VTT006-563, and CRE985-1 are situated on the posterior part of the second, fourth, and sixth costals. The same is true for NMS 8648.

The pleural I/II scute sulcus on the second costal of NMS 8648 laterally encroaches onto the third costal. Bräm (1965) judged this as an individual anomaly. Curiously, a similar ‘anomaly’ can be observed on the same costals in VTT006-253. However, the ‘anomaly’ of the latter is the result of a supernumerary scute, in contrast to the condition in NMS 8648 in which the pleural I/II scute sulcus is displaced. Another paired supernumerary pleural scute is observed immediately lateral of vertebral I in VTT006-176.

Supernumerary pleural scutes like that in VTT006-176 also appear in a specimen of *Palaeomedusa testa* (Joyce, 2003).

**Marginals**—The outline of only a few marginals can be discerned in the specimens from Porrentruy. They are usually rectangular in outline and about two times longer than wide. This is consistent with the marginals of NMS 8648, which Bräm (1965:179) described as “mostly long-rectangular and about two times as long as wide” (translation from German by the authors).

TABLE 3. Comparison of the ratio between the pleural II/III length and vertebral width of Plesiochelyidae (modified after Lapparent de Broin et al., 1996).

Taxa/Specimen	Pleural II/III– vertebral III ratio (%)
<i>Craspedochelys picteti</i>	67
<i>Plesiochelys</i> s.s.	25–47
<i>Plesiochelys etalloni</i>	38
<i>Plesiochelys solodurensis</i>	46
<i>Thalassemys</i>	78
<i>Tropidemys</i> from Le Havre	100
<i>T. langii</i> from Solothurn	158
<i>T. langii</i> from Porrentruy (VTT006-176)	121
<i>T. langii</i> from Porrentruy (VTT006-563)	156 (estimated)
<i>T. langii</i> from Porrentruy (CRE985-1)	183 (estimated)

Encroachment of the marginals onto the costals can be observed in VTT006-253 and VTT006-563, both in the region of costal II.

**Plastron**—The main plastral element for comparison in Solothurn is the hypoplastron of NMS 8651, an element discussed in Bräm (1965).

**Central Fontanelle**—In most turtles, the centrally located plastral fontanelle closes during ontogeny, with some taxa retaining a patent fontanelle even in the adult stage (Joyce, 2007). In Porrentruy, a central fontanelle can be observed in VTT006-290 and VTT006-563. The latter shows that the majority of the fontanelle is situated between the hypoplastra (Fig. 12A). If VTT006-52 has a fontanelle, it must be much smaller (at least the part between the hypoplastra) than the one of VTT006-563. The central fontanelle of NMS 8651 is either much bigger than the one of VTT006-563 or the better part of it is situated between the hypoplastra and only a small part between the missing hypoplastra.

A central fontanelle is retained in adult specimens of *Thalassemys hugii*, *Plesiochelys etalloni*, and *Craspedochelys jaccardi*, but not in *Plesiochelys solodurensis* (Bräm, 1965).

**Hypoplastra**—The right hypoplastra of VTT006-563 and NMS 8651 have about the same length (both 190 mm), but differ from one another greatly in width (205 and 160 mm, respectively). This difference is mainly due to the broader bridge in VTT006-563 (95 mm, vs. only 50 mm in NMS 8651). VTT006-52 and VTT006-290 have also relatively large bridges.

A wide hypoplastron and a wide bridge can also be observed in *Thalassemys hugii* and ‘*Plesiochelys jaccardi*’, whereas *Plesiochelys etalloni* and *P. solodurensis* are much narrower in this respect (Bräm, 1965).

Following Bräm (1965), the axillary buttress of *Craspedochelys jaccardi* expresses a rounded ridge on the first costal (ventral view), with a shallow groove positioned anteriorly. By contrast, the ridge is crest-like and the groove deeper in *Tropidemys langii*. VTT006-563 develops indeed a crest-like structure laterally (contacting costal I and peripherals II and III), but only a very shallow anterior groove can be observed.

**Hypoplastra**—A strong inguinal buttress can be observed in VTT006-563 and CRE985-1. It forms a distinct ridge on the lateral part of costal V and peripheral VIII.

The inguinal buttress of *Plesiochelys* spp. is less developed than in *Tropidemys langii* and contacts costals V and VI and peripherals VII and VIII, with the better part on peripheral VII (e.g., TCH005-42, TCH007-272, VTT006-299). In *Craspedochelys jaccardi*, the inguinal buttress is in contact with peripherals VI and VII and with the better part of peripheral VII.

**Scutes of the Plastron**—The posterior border of the humeral has a similar course in specimens VTT006-52, VTT006-563, and NMS 8651, and is situated at the same level as the deepest point of the axillary notches, but curves anteriorly at the lateral margin. The humerals of these three specimens do not preserve the anterior margin, but even the incomplete humerals are longer than the pectorals. The abdominal portion of the hypoplastron is longer in NMS 8651 than in the specimens VTT006-52 and VTT006-563.

Humeral that clearly exceed pectorals in length are present in *Craspedochelys jaccardi* and *Thalassemys hugii*, whereas in *Plesiochelys etalloni* and *P. solodurensis* the humerals are only slightly longer than the pectorals (Bräm, 1965).

### Description and Comparison of the Limb Bones

The humerus and femur described herein were found in the Banné Marls, closely associated with carapacial bones of *Tropidemys langii* (VTT006-253 and VTT010-13, respectively).

**Humerus (VTT006-253)**—In anterior view, the left humerus is only slightly sigmoid (Fig. 13B, F). The humeral head is not preserved. The processes are similarly incomplete. The anteriorly expanding lateral process seems to be the smaller one (Fig. 13A, C, E, G), as in most cryptodires (Gaffney, 1990). It thins proxi-

mally and ventrally forms a narrow deltopectoral crest. The narrowing shaft forms a flattened and broad waist at approximately one-third of the total humeral length. Towards the distal end, the bone gets thicker again, with epicondyles expanding along a horizontal plane. The ectepicondyle is broken. Epicondylar foramina and facets for the radius and ulna cannot be observed on the altered surface.

A humerus of *Plesiochelys* (BSY007-140) from Porrentruy is also slightly sigmoid. Its lateral process expresses a stronger crest ventrally and the medial process is less prominently expanded posteriorly than in *Tropidemys*. In contrast to *Tropidemys*, the shaft of *Plesiochelys* is more circular in section and narrower. The expansion of the epicondyles is less expressed than in *Tropidemys*.

**Femur (VTT010-13)**—Only the proximal part of the right femur is preserved (Fig. 14). The articular head is hemispherical, not elongated, and projects dorsally at about 45° from the long axis of the bone. Trochanters on either side of the head expand along the horizontal plane. In ventral view (Fig. 14C, G), the intertrochanteric fossa is widely ‘V’-shaped and rounded at its base. The shaft is circular in cross-section.

The large and ovoid-to-elongate head of a *Plesiochelys* (BSY008-668) from Porrentruy projects from the long axis at an angle of approximately 25°. The trochanters of BSY008-668 are less expanded along the horizontal plane and the ‘V’-shaped intertrochanteric fossa is narrower than in *Tropidemys*. The shaft is circular in cross-section, similar to *Tropidemys*.

## DISCUSSION

### Taxonomy

**Alpha Taxonomy of *Tropidemys***—According to Rüttimeyer (1873), three species of *Tropidemys* are present in Solothurn (*T. expansa*, *T. gibba*, and *T. langii*) and these differ in size, the extent of the carapace vaulting along the anteroposterior axis, and in the form of the vertebral scutes. Our study of all available neurals reveals that they do not cluster into size classes (see Table 2). It is therefore apparent that size alone cannot be used to diagnose Rüttimeyer’s three species. Rüttimeyer (1873) described the vertebrals of *T. expansa* as being much less cambered than those of *T. langii*, but our observations again fail to confirm a clear pattern of differentiation. Finally, although differences in the vaulting are apparent among various *Tropidemys* specimens, it is clear that taphonomic compaction is responsible for the observed variation in this feature. We therefore agree with Bräm (1965) that only a single species of *Tropidemys* (*T. langii*) is present at Solothurn, and that *T. expansa* and *T. gibba* should be treated as its junior synonyms.

Portis (1878) erected *Tropidemys seebachi* based on fragmentary carapacial and plastral materials from the Kimmeridgian (Late Jurassic) of Hannover, Germany. In contrast to *T. langii*, *T. seebachi* is a relatively small turtle (carapace length approximately 40 cm) and exhibits the highly derived presence of up to eight vertebral scutes. It therefore seems that this represents a valid taxon. The available material is too incomplete to allow its inclusion in a phylogenetic analysis, but the development of a midline keel suggests that it likely represents a close relative of *T. langii*.

*Chelonia valanginiensis* from the Cretaceous (Valanginian) of Sainte-Croix, Canton Vaud, Switzerland (Pictet and Campiche, 1858–1860), was transferred to *Tropidemys* by Rüttimeyer (1873) to produce the new combination *Tropidemys valanginiensis*. Our observations of the type material of this taxon (MCG GEOL-REG 16849) confirm the presence of a midline keel and we therefore agree with Rüttimeyer (1873) that the specimen is diagnostic of *Tropidemys*. Rüttimeyer (1873) noted additional similarities with *T. langii*, such as bone striations, the arrangement of scute sulci, and the presence of imbricated neurals. However, given

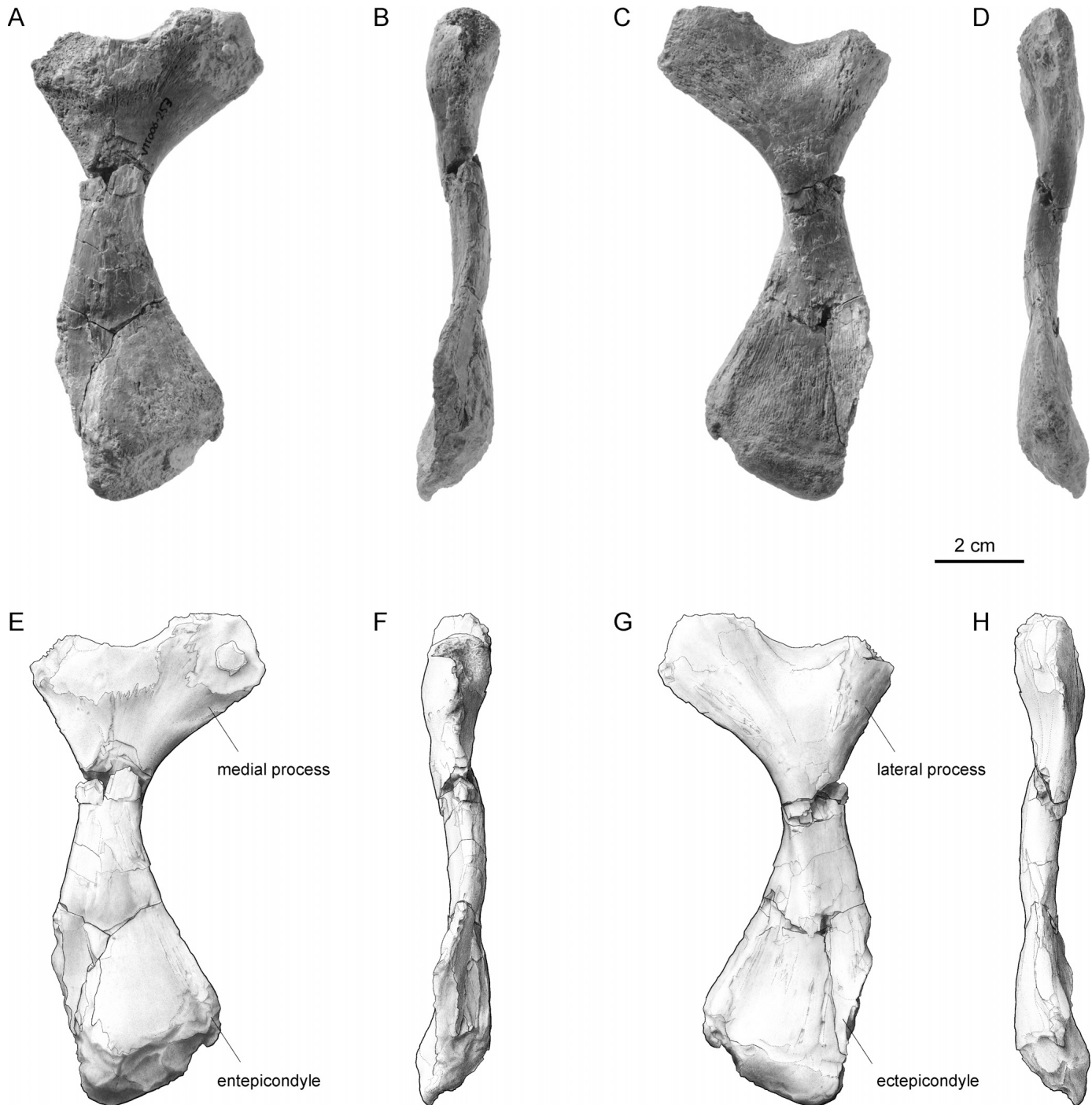


FIGURE 13. Left humerus (VTT006-253) of *Tropidemys langii* (Kimmeridgian, Porrentruy, Switzerland). **A, E**, dorsal view; **B, F**, anterior view; **C, G**, ventral view; **D, H**, posterior view.

that all apparent characters of '*Tropidemys valanginiensis*' are either diagnostic of *Tropidemys*, or must be interpreted as symplesiomorphies (i.e., the presence of five vertebrals), and given a lack of autapomorphies, it is apparent that this taxon does not exhibit any diagnostic characters that would distinguish it from *T. langii* and *T. seebachi*. We therefore designate it herein *Tropidemys* sp.

The presence of *Tropidemys* sp. in Valanginian sediments implies that this lineage crossed the Jurassic/Cretaceous boundary. However, Rittener (1902) pointed out that the original owner

of the specimen, the physician Campiche, was a collector and not a geologist, and therefore purchased fossils from fossil collectors who did not particularly care about distinguishing different fossiliferous layers. Campiche mixed up various excavation sites and some can be demonstrated to not belong to the locality of Sainte-Croix (Rittener, 1902). Moreover, the historical (Rittener, 1902) and current (Rigassi and Jaccard, 1995) geological maps of Sainte-Croix do not agree entirely in the distribution of Valanginian units and both show Kimmeridgian strata in the

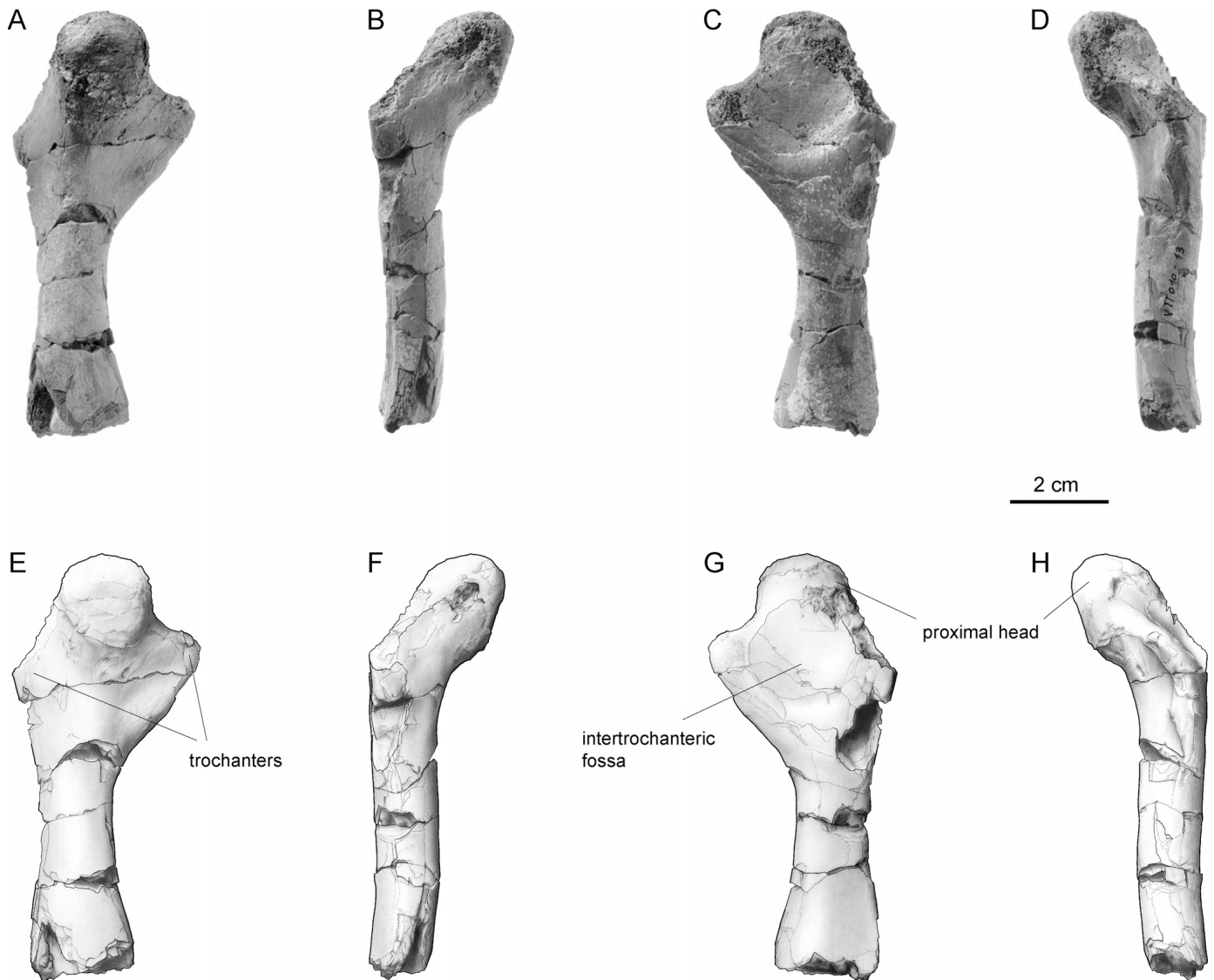


FIGURE 14. Right femur (VTT010-13) of *Tropidemys langii* (Kimmeridgian, Porrentruy, Switzerland). **A, E**, dorsal view; **B, F**, posterior view; **C, G**, ventral view; **D, H**, anterior view.

region of Sainte-Croix. Hence, the stratigraphic extension of *Tropidemys* and of the Plesiochelyidae into the Cretaceous cannot be supported at the moment based on this find.

*Pelobatochelys blakii* is based on a number of disarticulated neurals from the Kimmeridge Clays of Weymouth, England, and has not received much taxonomic attention over the course of the last 100 years. Our study of the type material reveals that this taxon exhibits a midline keel identical to that of *Tropidemys* spp., but that too little is preserved to provide a definitive diagnosis. We therefore refer this material to *Tropidemys* sp. and designate *Pelobatochelys blakii* a junior subjective synonym of this genus.

**The Specific Identity of *Tropidemys* from Porrentruy**—*Tropidemys* material from Porrentruy differs from *T. langii* (sensu Bräm, 1965) of Solothurn in four main features (Table 1):

- (1) A wider and rounder carapace. This character assumes the correctness of the reconstructions of specimens VTT006-176 and VTT006-563. The outline of specimen CRE985-1 is rather oval, like Solothurn specimen NMS 8648. Given the importance of compaction in the shape of fossil turtle shells, we attribute this difference to physical factors.
- (2) A less distinctive keel. In addition to the shell outline, it appears that the angle of the keel is also deformed during compaction. We therefore attribute this difference to nonbiological factors as well.
- (3) A larger hyoplastron. Rüttimeyer (1873) attributed some hyoplastra from Solothurn to *Tropidemys*, because he could not attribute them to any other turtle from this locality. His proposal was supported, amongst others, by the size of the elements (he estimates 155–170 mm for half the plastron width), the color (brownish-reddish), and the texture of the bone (foliated). Bräm (1965) reevaluated the identity of NMS 8651 (a right hyoplastron) and supported its referral to *Tropidemys langii*. However, Bräm (1965) also used the small bridge width of NMS 8651 to distinguish it from the much wider one of *Thalassemys hugii*. The hyoplastra from Porrentruy (the only to be associated with carapacial elements) contradict this observation by having a much wider bridge. Moreover, these elements contribute less to the central fontanelle (if at all) than the ones from Solothurn.

It is apparent that the hyoplastra from Porrentruy and Solothurn do not belong to the same species. The hyoplastra



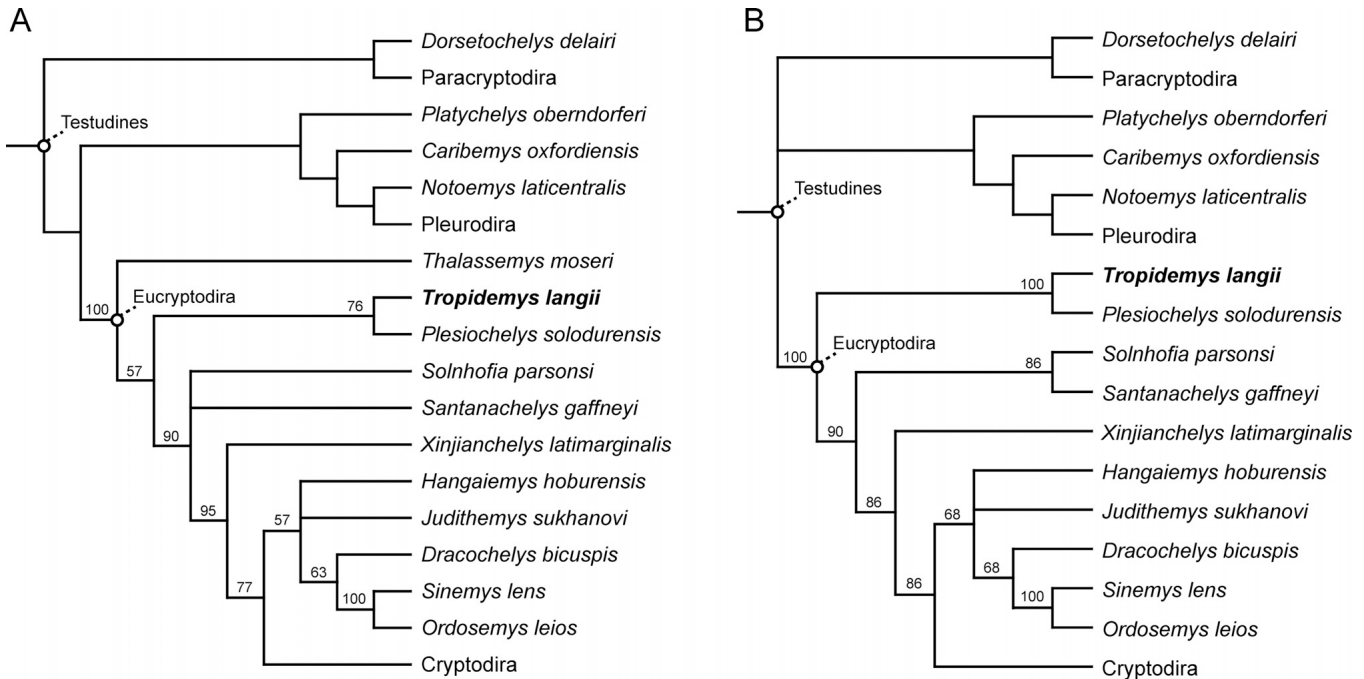


FIGURE 15. Consensus trees of the phylogenetic analyses (50% majority rule). Numbers indicate the consensus of the resulting trees in percent. **A**, first analysis (including ‘*Thalassemys moseri*’); **B**, second analysis (excluding ‘*Thalassemys moseri*’).

from Solothurn belong either to another taxon and the affiliation with *T. langii* is incorrect, or this affiliation is correct and there are two different species of *Tropidemys*. However, given how closely the carapaces from Solothurn and Porrentruy correspond with one another in shape, it appears implausible that hyoplastra with such different bridge widths could belong to carapaces of such similar outline. We therefore remove the hyoplastron from Solothurn from *T. langii* and thereby eliminate this significant difference.

- (4) Presence of supernumerary bones and a nuchal notch. Supernumerary bones or scutes occur in specimens from Porrentruy (VTT006-563 and VTT006-176, respectively), but are not observed in specimens from Solothurn. Small supernumerary bones that are intercalated between the nuchal and first peripheral have also been reported for the only known postcranial specimen of *Solnhofia parsonsi* (Joyce, 2000), but there is no evidence to date that these minute bones are of taxonomic significance. We therefore interpret them as developmental anomalies and the presence of a nuchal notch as resulting directly from the development of such supernumerary scutes. Among Late Jurassic turtles, supernumerary pleurals are present in three specimens attributed to *Palaeomedusa testa* (Joyce, 2003), but the large range of variation in their size reveals that this feature is highly variable in that taxon. Although the presence of supernumerary pleurals is of taxonomic significance for other groups of turtles (e.g., the *Baena*-lineage; Lyson et al., 2011), we herein interpret the presence of supernumerary pleurals in a single specimen as intraspecific variation because no other characters are present that corroborate the presence of a second species. We therefore conclude that all material from Porrentruy can be attributed to *T. langii*.

### Phylogeny

The phylogenetic position of *Tropidemys langii* was tested using the data matrix of Joyce (2007), a character-taxon assem-

bly focused mainly on cranial and shell features. As the skull of *Tropidemys langii* is unknown, only shell characters could be taken into account. The data matrix was assembled in MacClade 4.08 (Maddison and Maddison, 2005) and analyzed in PAUP 4.0b10 (Swofford, 2002). The expanded matrix includes 137 osteological characters, 46 fossil and 22 living representatives of turtles, and a hypothetical ancestor (see Supplemental Data 1). A new character was added, concerning the presence of a supernumerary bone between the nuchal and the first peripheral (carapace C), as observed in specimen VTT006-563 and in *Solnhofia parsonsi* (Joyce, 2000). Our scoring of *T. langii* is based on all available Swiss material. *T. langii* could be scored for 32 characters, all of which are listed in Appendix 2. The observed character states are provided in Appendix 3 along with those of a select list of basal pancryptodires.

Two principal phylogenetic analyses were performed that differ in the inclusion of ‘*Thalassemys moseri*.’ All specifications used in the analytical approach by Joyce (2007) were retained: characters were considered as reversible and equally weighted; branches were collapsed if their minimum length is zero; the most parsimonious solution was sought by using heuristic algorithms with 1000 randomly seeded replications; the retained trees were filtered for optimal solutions only; 15 multistate characters were ordered; and the rogue taxa *Portlandemys mcdowelli*, *Sandownia harrisi*, and *Mongolemys elegans* were omitted. We also omitted the testudinoid taxa *Gopherus polyphemus*, *Chrysemys picta*, and *Geoclemys hamiltonii*, because these extant turtles show convergence with basal pancryptodires by forming a thickened shell and, as a consequence, often formed a clade with *Tropidemys langii* in preliminary analyses that resulted in a large polytomy within Cryptodira.

This first analysis resulted in 317 optimal trees and a shortest tree length of 349 steps. The amount of homoplasy is given by the retention index (RI) of 0.82 and the consistency index (CI) of 0.48 (cf. Lipscomb, 1998). The 50% majority rule consensus trees proposes *Tropidemys langii* and *Plesiochelys solodurensis* as sister taxa with a consensus of 76% (Fig. 15A).

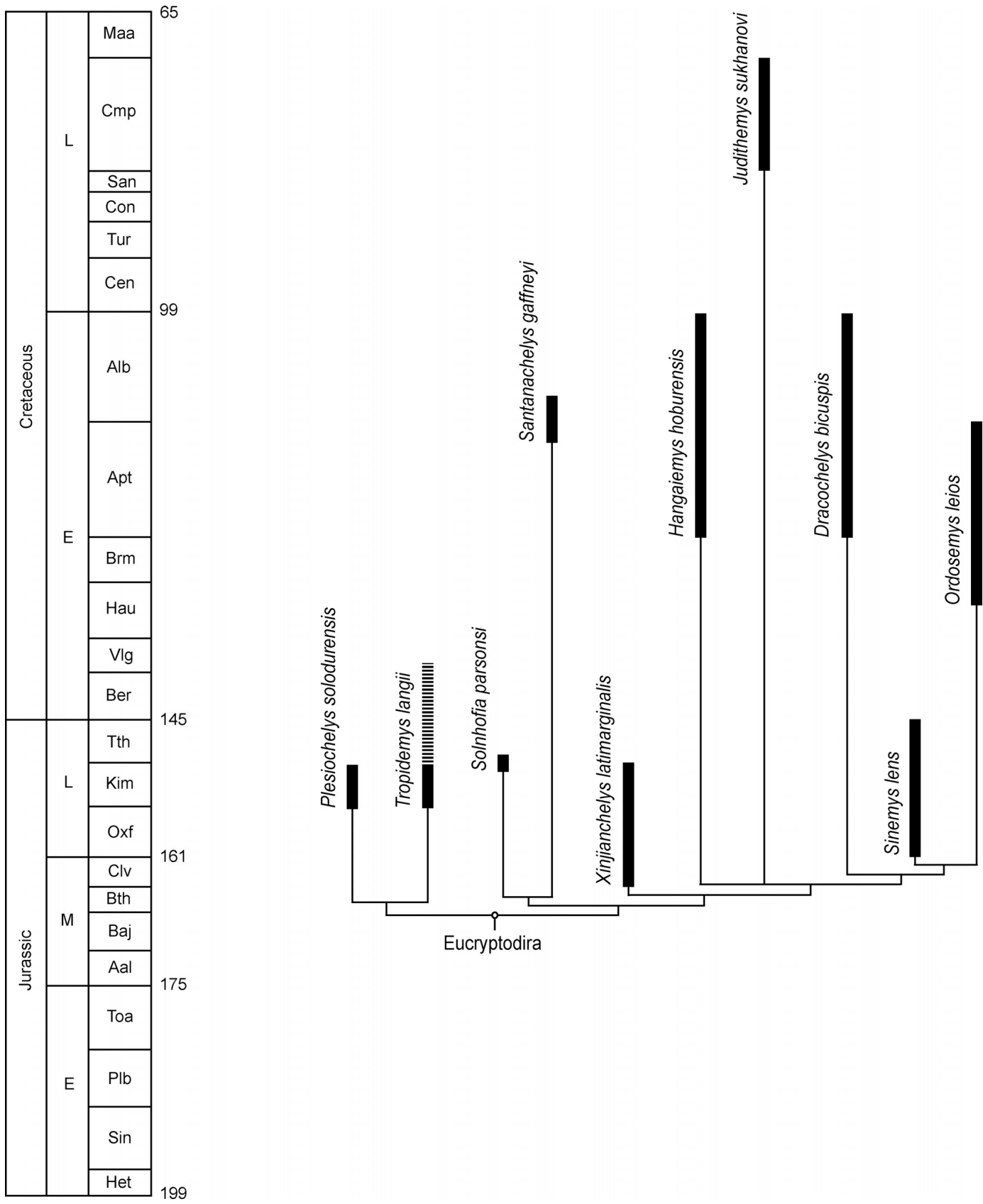


FIGURE 16. Restricted topology based on the second analysis (cf. Fig. 15B), combining phylogenetic relationships of basal pancryptodires with stratigraphic ranges. Stratigraphic ranges (black bars) are from Lang and Rüttimeyer (1867), Oertel (1924), Broin (1994), Hirayama (1998), Joyce (2000), Lapparent de Broin (2001), Parham and Hutchison (2003), and Rabi et al. (2010). Timescale is based on Gradstein et al. (2004). Numbers indicate age in millions of years.

A second analysis was performed that replicated the first analysis but omitted '*Thalassemys moseri*,' because the phylogenetic position of this taxon was unstable in the first. This reduced the number of optimal trees to 205 and the shortest tree length to 344 steps (RI = 0.82; CI = 0.49). In the 50% majority rule consensus tree, *Tropidemys langii* and *Plesiochelys solodurensis* are each other's sister taxa, with an increased consensus of 100% (Fig. 15B). Because the retention and consistency indices of both analyses remained stable with regard to the Joyce (2007) analysis, *Tropidemys langii* and *Plesiochelys solodurensis* can be considered confidently as sister taxa.

Only one of the 32 determined characters for *Tropidemys langii* is derived relative to *Plesiochelys solodurensis* (vertebral B; Appendices 2 and 3). According to the preferred cladogram of Joyce (2007), the acquisition of narrow vertebrals (vertebral B) occurred amongst others as a synapomorphy of the clade arising from the common ancestor of *Xinjiangchelys latimarginalis* and Cryptodira. Inclusion of *Tropidemys langii* into the analysis revealed that this character evolved independently among more basal eucryptodires.

The position of '*Thalassemys moseri*' is unstable among the 317 trees retrieved in the first analysis. In 60% of the trees, '*T. moseri*' is positioned as the sister taxon of all other pancryptodires, with 30% resulting in a polytomy consisting of *Tropidemys langii*, *Plesiochelys solodurensis*, and '*Thalassemys moseri*.' Only 10% of trees place the taxon within the clade formed by *Santanachelys gaffneyi* and *Solnhofia parsonsi*, whereas this scenario was supported by more than 50% of the trees in the analysis of Joyce (2007). Hence, inclusion of *Tropidemys langii* led to a shift of '*Thalassemys moseri*' away from Eurysternidae (sensu Lapparent de Broin et al., 1996), but its exact position remains unresolved.

On the other hand, *Solnhofia parsonsi* (Eurysternidae) is clearly separated in both analyses from the clade including *Tropidemys langii* and *Plesiochelys solodurensis*. When '*Thalassemys moseri*' is excluded from the analysis, *Solnhofia parsonsi* forms a clade with *Santanachelys gaffneyi* (Fig. 15B). The inclusion of *Tropidemys langii* did not provide any other changes to the results of Joyce (2007).

The phylogenetic relationships and stratigraphic distribution of basal pancryptodires is summarized in Figure 16. The topology is that retrieved from the second analysis. This analysis indicates that eucryptodires minimally originated in the Middle Jurassic. However, representatives of Plesiochelyidae and Eurysternidae sensu lato (*Plesiochelys solodurensis*, *Solnhofia parsonsi*, and *Tropidemys langii*) do not appear before the Late Jurassic, illustrating the relatively poor knowledge about the evolution and diversification of this paraphyletic group. Our analysis is consistent with that of Joyce (2007) by interpreting this group of turtles as a paraphyletic grade.

### Taphonomy and Paleoecology

**Taphonomy**—The specimens from Porrentruy are deformed, mainly flattened, but show no sign of transportation (e.g., abrasion), consistent with Bräm's (1965) observations for the turtles from Solothurn. Whereas the specimens from Solothurn are associated and articulated, the specimens from Porrentruy are often associated but disarticulated. This might be due to higher pressures during fossilization or to the fact that *Tropidemys langii* from Porrentruy originates from softer layers (Banné Marls, Virgula Marls), whereas those from Solothurn were found in harder limestone ('Solothurn Turtle Limestone') (cf. Meyer and Thüring, 2009). The latter suggestion is supported by CRE985-1, because it is the only articulated carapace from Porrentruy and the only specimen found in limestone.

Feeding traces of sea urchins (Echinoidea) can be observed on the hyoplastron of VTT006-563, indicating that the bone was not buried immediately. Meyer (2011) also described feeding

traces of sea urchins on carapaces of the Solothurn Turtle Limestone. An encrusting bivalve (*Camptonectes* sp.; J. Koppka, pers. comm., April 2013), which is also present in the Solothurn Turtle Limestone (Meyer, 1989, 1994a), is attached to the outer margin of CRE985-1 (Fig. 6).

VTT006-563 exhibits several aligned and round indentations (12–15 mm in diameter) on the external surface of the plastron and carapace. A puncture mark is apparent on the lateral part of costal IV of VTT006-176. Rüttimeyer (1873) and Bräm (1965) also mentioned such indentations on fossil turtles from Solothurn. Rüttimeyer (1873) assumed that they were caused by weathering pyrite, whereas Bräm (1965) suggested skin parasites. Meyer (1994b) suggested that marks found on material from Solothurn were created by marine crocodylians, such as *Machimosaurus* (also see Joyce, 2000; Karl and Tichy, 2004), the teeth of which are also present in the Banné Marls. In VTT006-563, the indentations on the carapace (right costal III, neurals VI and VII; Fig. 5A) are indeed aligned as in a crocodylian snout and correspond to those on the plastron (right hyoplastron and right hypoplastron; Fig. 12A). Moreover, the hole in VTT006-176 (left costal IV; Fig. 4A) shows clear signs of wound healing. This excludes weathering pyrite or parasite activity as cause and indicates that the animal survived the attack, as shown by Joyce (2000) for *Solnhofia parsonsi*.

**Paleoecology**—A comparison of the Porrentruy sites with those of Solothurn (Lang and Rüttimeyer, 1867; Huene, 1926; Bräm, 1965; Meyer, 1989, 1994a, 1994b; Meyer and Hunt, 1991), Hannover (Portis, 1878; Oertel, 1924; Thies and Mudroch, 1996; Thies et al., 1997; Lapparent de Broin, 2001; Fastnacht, 2005; Karl et al., 2006), Boulonnais (Cuny et al., 1991), and Fumel (Sauvage, 1902) shows that *Tropidemys langii* is always associated with *Plesiochelys* spp., marine fishes, and crocodylians (mainly Teleosauridae), indicating a coastal marine habitat for both *Tropidemys langii* and *Plesiochelys* spp. This is consistent with isotopic analyses that demonstrated the marine character of *Plesiochelys* spp. (Billon-Bruyat et al., 2005; Meyer et al., 2012).

In Porrentruy, *Tropidemys langii* is much better represented in the Banné Marls than in the Virgula Marls. The great diversity of invertebrates in the Banné Marls (especially bivalves) indicates a marine environment that provided abundant nutrient matter.

### ACKNOWLEDGMENTS

Many thanks go to the field prospectors, the preparation team, B. Migy (photographs), P. Widder (drawings), and J. Koppka (discussion on paleoecology). P. Bigler generously donated an important specimen of *Tropidemys langii* to the collection Paleontology A16. We thank D. Becker (MJSN), R. Marchand (MCG), and S. Thüring (NMS) for providing us access to the museum collections. We are also grateful for the help of R. Böttcher (Staatliches Museum für Naturkunde, Stuttgart) and H.-V. Karl (University of Göttingen). Editor P. O'Connor and reviewers D. Brinkman and C. Meyer provided very helpful comments. This study was funded by the Section d'archéologie et paléontologie, Canton Jura, Switzerland, and the University of Fribourg, Switzerland.

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Submitted September 24, 2012; revisions received April 9, 2013; accepted May 8, 2013.

Handling editor: Patrick O'Connor.

APPENDIX 1. The studied material from Porrentruy and comparative material from Solothurn and Sainte-Croix. **Abbreviations:** **BM**, Banné Marls; **Nb**, Nautilid beds; **VM**, Virgula Marls.

Location	Fossil number	Anatomy	Figures	Figure references/Remarks
Porrentruy	BSY007-128	Neural	Fig. 6	VM layer 4500
	CRE985-1	Articulated carapace		This work/Nb
	SCR010-482	Neural		VM layer 4500
	SCR010-1100	Neural		VM layer 4500
	TCH005-117	Neural		VM layer 4500
	TLB001-55	Carapace bones		BM
	VTT001-579	Neural		BM
	VTT004-114	Neural		BM
	VTT006-1	Fragments of plastron		BM layer 1400
	VTT006-52	Hyoplastra		BM layer 1100
	VTT006-55	Fragments of plastron		BM layer 1500
	VTT006-157	Neural		BM layer 1400
	VTT006-175	Costal		BM layer 900
	VTT006-176	Carapace and plastron	Figs. 4, 7, and 11	This work/BM layer 1100
	VTT006-204	Carapace bones		BM layer 1100
	VTT006-224	Neural		BM layer 800
	VTT006-244	Nuchal and neural		BM layer 1200
	VTT006-253	Carapace bones, humerus	Fig. 13	This work/BM layer 1200
	VTT006-288	Neurals, costals		BM layer 1300
	VTT006-290	Hyoplastra		BM layer 900
	VTT006-563	Carapace and plastron	Figs. 5, 8–10, and 12	This work/BM layer 700
	VTT006-573	Fragments of plastron		BM layer 800
	VTT010-13	Carapace bones, femur	Fig. 14	This work/BM
MJSN Coll.Thurm. 25 A.4.17.6 (3)	Neural	pl. LXI, fig. 1		Thurmann and Etallon (1861–1864)
MJSN Coll.Thurm. 26 A.4.17.6 (4)	Neural	pl. LXI, fig. 2	Thurmann and Etallon (1861–1864)	
Solothurn	NMS 8419 (no. 644)	Part of the carapace		
	NMS 8500 (no. 132)	Part of the carapace	pl. IX, figs. 1, 2	Rütimeyer (1873)
	NMS 8553 (no. 33)	Part of the carapace		Rütimeyer (1873)
	NMS 8554 (no. 16)	Part of the carapace	pl. VII, fig. 1	Rütimeyer (1873)/holotype
	NMS 8556 (no. 32)	Part of the carapace	pl. IX, fig. 3	Rütimeyer (1873)
	NMS 8557 (no. 22)	Part of the carapace		
	NMS 8558 (no. 21)	Part of the carapace		
	NMS 8648 (no. 15)	Carapace	pl. IX, fig. 2 pl. 6, fig. 6; pl. 8, fig. 1	Bloch (1902) Bräm (1965)
	NMS 8649	Part of the carapace		
	NMS 8650 (no. 18)	Neural	pl. VII, fig. 3	Rütimeyer (1873)
	NMS 8651 (no. 19)	Right hyoplastron	pl. X, fig. 4	Rütimeyer (1873)
	NMS 8652 (no. 20)	Right hyoplastron	pl. X, fig. 6	Rütimeyer (1873)
	NMS 8665 (no. 38)	Carapace	pl. IV, fig. 1	Rütimeyer (1873)
			pl. 8, fig. 5	Bräm (1965)
	NMS 8666 (no. 38a)	Part of the carapace	pl. VII, fig. 2	Rütimeyer (1873)
	NMS 8991 (no. 399)	Pygal		
	NMS 8994	Part of the carapace		
NMS 9215 (no. 18a)	Costal	pl. VII, fig. 4	Rütimeyer (1873)	
Sainte-Croix	MCG GEOLREG 16845	Radius?	pl. III, fig. 3	Pictet and Campiche (1858–60)
	MCG GEOLREG 16849	Part of the carapace	pls. I, II; pl. III, fig. 1	Pictet and Campiche (1858–60)
	MCG GEOLREG 16864	Part of the plastron	pl. III, fig. 2	Pictet and Campiche (1858–60)

APPENDIX 2. Description of characters used in the phylogenetic analysis. Characters from, or modified from Joyce (2007) (except for the new character 3). Number in square brackets indicates the corresponding character from Joyce (2007).

- (1) Carapacial scutes [60]: present (0); partially present (1); absent (2).
- (2) Tricarinate carapace [61]: absent (0); present, but only poorly developed (1); present and pronounced (2).
- (3) Supernumerary bone between the nuchal and the first peripheral: absent (0); present (1).
- (4) Articulation of nuchal with neural spine of eighth cervical vertebra [62]: present, along a blunt facet (0); absent (1); present, along a raised pedestal (2).
- (5) Elongate costiform processes of nuchal [63]: absent (0); present, process crosses peripheral I to contact peripheral II and sometimes even peripheral III (1).
- (6) Neural formula  $6 > 4 < 6 < 6 < 6 < 6$  [64]: absent (0); present (1).
- (7) Number of peripherals [65]: more than 11 pairs present (0); 11 pairs present (1); 10 pairs present (2); less than 10 pairs present (3).
- (8) Anterior peripherals incised by musk ducts [66]: absent (0); present (1).
- (9) Medial contact of costal I [67]: absent (0); present (1).
- (10) Medial contact of posterior costals [68]: absent (0); medial contact of up to three posterior costals present (1); medial contact of all costals present (2).
- (11) Reduction of costal ossification [69]: absent, costal fontanelles small or absent (0); present, costal fontanelles well developed (1).
- (12) Cervical [70]: one cervical present (0); cervicals absent, carapacial scutes otherwise present (1); more than one cervical present (2).
- (13) Supramarginals [71]: complete row present (0); partial row present, incompletely separating marginals from pleurals (1); absent (2).

- (14) Number of vertebrals [72]: four present (0); five or more present (1).
- (15) Shape of vertebrals [73]: vertebrals II to IV significantly broader than pleurals (0); vertebrals II to IV as narrow or narrower than pleurals (1).
- (16) Position of vertebral II/III sulcus in taxa with five vertebrals [74]: sulcus positioned on neural VI (0); sulcus positioned on neural V (1).
- (17) Connection between carapace and plastron [75]: osseous (0); ligamentous (1).
- (18) Central plastral fontanelle [76]: absent in adult individuals (0); present, even in adult individuals (1).
- (19) Plastral kinesis [77]: absent, scute sulci and bony sutures do not overlap (0); present, scute sulci coincide with hyoplastral-epiplastral contact (1).
- (20) Contacts of axillary buttresses [84]: peripherals only (0); peripherals and first costal (1).
- (21) Number and size of mesoplastra [85]: one or two pair of mesoplastra present (0); one reduced pair of mesoplastra present (1); mesoplastra absent (2).
- (22) Contacts of inguinal buttresses [86]: peripherals only (0); peripherals and costal V (1); peripherals, costal V, and costal VI (2).
- (23) Plastral scutes [89]: present (0); absent (1).
- (24) Midline sulcus [90]: straight (0); distinctly sinuous (1).
- (25) Plastral scale set 3, humerals [96]: one pair present (96); two pairs present, subdivided by a plastral hinge (1).
- (26) Plastral scale set 4, pectorals [97]: present (0); absent (1).
- (27) Plastral scale set 5, abdominals [98]: present, in medial contact with one another (0); present, medial contact absent (1); absent (2).
- (28) Plastral scale set 7, anals [99]: only cover parts of the xiphoplastra (0); anteromedially overlap onto hypoplastra (1).
- (29) Inframarginal scutes [100]: more than two pairs present (0); two pairs present (axillaries and inguinals) (1); absent (2).
- (30) Length of first dorsal rib [113]: long, extends full length of first costal and may even contact peripherals distally (0); intermediate, in contact with well-developed anterior bridge buttresses (1); intermediate to short, extends less than halfway across first costal (2).
- (31) Contact of dorsal ribs IX and X with costals [114]: present (0); absent (1).
- (32) Dorsal rib X [115]: long, spanning full length of costals and contacting peripherals distally (0); short, not spanning farther distally than pelvis (1).

APPENDIX 3. The determinable character states for *Tropidemys langii*, along with those of other basal pancryptodires in the analysis of Joyce (2007). The character states of all other taxa are given in Joyce (2007). **Abbreviations:** A, (0,1); ?, unknown.

<matrix>	10	20	30	32
Taxon				
<i>Tropidemys langii</i>	00A1001000	02211A0A01	2100000002	01
<i>Plesiochelys solodurensis</i>	0001001000	0221010A01	2100000002	01
<i>Solnhofia parsonsi</i>	001??01?00	0021011100	200000000?	?1
<i>Thalassemys moseri</i>	000100?00?	0?2?0??101	2?00000?01	??
<i>Santanachelys gaffneyi</i>	000?001000	1021001100	20?0?????0	?1
<i>Xinjiangchelys latimarginalis</i>	0001001000	00211111000	2000000102	01
<i>Hangaemys hoburensis</i>	0001001000	00211111000	2000000A02	?1
<i>Judithemys sukhanovi</i>	0001001000	00211111000	2000000A02	?1
<i>Dracochelys bicuspis</i>	???0???????	??????1???	??0???????	??
<i>Sinemys lens</i>	0001001000	0121111A?0	2000000?00	??
<i>Ordosemys leios</i>	0001001000	00211111?0	2000000100	?1

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