

A new Late Jurassic turtle specimen and the taxonomy of *Palaeomedusa testa* and *Eurysternum wagleri*

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A new fossil turtle specimen from the Late Jurassic of Solnhofen, Germany, provides new insights into the validity of the species *Palaeomedusa testa*. The new specimen exhibits a number of characters in the carapace, such as the absence of well-developed fontanelles and the presence of three cervicals, five pleurals, and narrow vertebrae, which are present in *Palaeomedusa testa*, but not in *Eurysternum wagleri*. These characters warrant the tentative placement of the new turtle in *Palaeomedusa testa* and the refutation of the traditionally accepted synonymy between *Eurysternum wagleri* and *Palaeomedusa testa*. An additional taxon, *Thalassemys marina*, is also cautiously placed in *Palaeomedusa testa*, thus synonymizing *Thalassemys marina* with *Palaeomedusa testa*. The presence of three cervicals and a wide, trapezoidal nuchal is currently thought to be diagnostic of the Plesiochelyidae and Eurysternidae, respectively, but both characters occur simultaneously in *Palaeomedusa testa*. Consequently, one of these characters must have been lost during phylogeny or evolved twice and therefore is not useful in diagnosing a monophyletic group of turtles. Finally, the fossil taxon *Eurysternum wagleri*, which is primarily diagnosed by its deep pygal notch, is based on the description of an illustration of an incomplete and now missing fossil turtle specimen. Although the designation of a neotype may be useful, this study demonstrates that no eligible specimen is available, and as such, the type illustration will have to suffice until a neotype is found.

INTRODUCTION

One of the most notable, yet markedly misunderstood, turtles from the Late Jurassic of Europe is *Eurysternum wagleri*. Herman von Meyer (1839b) erected this taxon based on a highly fragmentary skeleton from the platy limestone quarries of Solnhofen, Germany (Fig. 1). Interestingly, he never saw the holotype, but rather described this species based on an illustration by the artist C. Hohe. Although this illustration has great aesthetic value, its scientific information is limited and its accuracy questionable. The validity of the type description is thus suspect, as later admitted by Meyer (1861) himself. To augment the dilemma, the holotype was destroyed in Munich during World War II (Wellnhofer 1967). As such, it will never be possible to verify the original description of this species or to observe new traits through further study or preparation. In this investigation, an extensive search was undertaken for casts of the *E. wagleri* holotype, which yielded only a poorly manufactured replication that is now housed in the Sedgwick Museum in Cambridge, England. This replica demonstrates only few of the details that are described in the type description or depicted in the type illustration (Meyer 1839b).

The fossil taxon *Palaeomedusa testa*, in contrast, was first described by Meyer (1860) based on a relatively well-preserved anterior half of a fossil turtle from the lithographic limestone quarries of Kelheim, Germany (Fig. 1). The original description of the type specimen was also accompanied by a beautifully crafted illustration. A comparison of the illustration with the holotype reveals considerable discrepancies between the two, especially in the cranial region. For instance, according to the type illustration *Pal. testa* is characterized

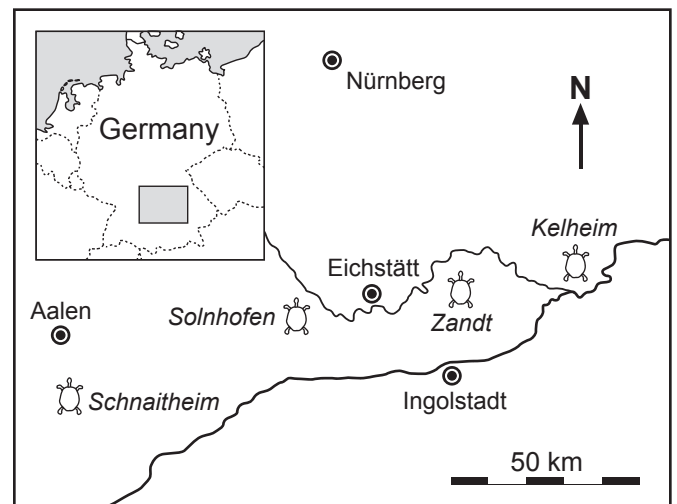


Fig. 1. Map of southern Germany showing location of several Late Jurassic fossil turtle sites.

by extensive upper temporal emarginations. Close study of the holotype, however, reveals that the temporal region of *Pal. testa* is almost completely ossified, similar to *Solnhofia parsonsi* (Gaffney 1975). This demonstrates that incongruities exist between holotypes and their illustrations, which is of particular significance when assessing the true morphology of *Eurysternum wagleri*.

One year after the publication of *Palaeomedusa testa*, Wagner (1861a) redescribed the holotype and claimed authorship to this species because he had mentioned the holotype under the name *Eurysternum crassipes* in an earlier publication (Wagner 1859). In a passionate response, Meyer

(1861) defended the validity of his authorship, pointing out that Wagner (1859) had listed neither any characters nor a specimen in his earlier paper. Wagner's *Eurysternum crassipes* is clearly a *nomen nudum*, because even the most liberal interpretation of the ICZN (1999) cannot support the availability of a name without a description, diagnosis, or illustration. However, as the official rules of availability were not established until the 20th century, many early authors arrived at a different conclusion and granted Wagner's (1859) *E. crassipes* priority over Meyer's (1860) *Pal. testa* (e.g., Maack 1869, Rüttimeyer 1873, Zittel 1889, Lortet 1892).

Despite the fragmentary nature of the *Eurysternum wagleri* holotype, an extensive list of turtles from the Late Jurassic of Germany and France has been synonymized with it. This list includes such taxa as *Aplax oberndorferi* Meyer 1843, *Achelonia formosa* Meyer 1860, *Acichelys redenbacheri* Meyer 1854, *Parachelys eichstaettensis* Meyer 1864, and most notably for this study, *Palaeomedusa testa*, as successively proposed by Wagner (1861a, b), Rüttimeyer (1873), Zittel (1877), Fraas (1903), and Oertel (1915). Although all of these authors suggested synonymies after consulting the type material, few of them agree upon the exact list of synonyms. Furthermore, the characters used to consolidate these many taxa into one species (e.g., outline of the carapace, presence of fontanelles) are trivial, especially if one considers the number of diagnostic characters that some of the synonymized taxa exhibit. As an unfortunate result, the current understanding of *E. wagleri* is not based on our knowledge of the holotype but rather on the morphologies displayed in its alleged synonyms.

A new fossil turtle from the Late Jurassic of Solnhofen, Germany, displays a number of previously neglected characteristics, which are clearly visible in the holotype of *Palaeomedusa testa* but appear to be absent from *Eurysternum wagleri*, thereby refuting the traditionally accepted synonymy between these two taxa. Given the problematic status of *Eurysternum wagleri*, it is almost impossible to objectively compare morphologies and evaluate synonymies. The primary goal of this study, consequently, is to review the holotype morphology of this taxon and to evaluate the availability of a specimen that may serve as a neotype. The second goal is focused on describing the new specimen and to explore its impact on the taxonomy of Late Jurassic turtles.

Abbreviations: BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; MB, Museum für Naturkunde, Berlin, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

SYSTEMATIC PALEONTOLOGY

REPTILIA Linnaeus 1758 (sensu Gauthier et al. 1988)

TESTUDINES Batsch 1788 (sensu *Testudo* Linnaeus 1758)

Eurysternum wagleri Meyer 1839b

Fig. 2a

Holotype—Holotype lost (Wellnhofer 1967); incomplete skeleton in ventral view, only fragmentary remains of the cra-

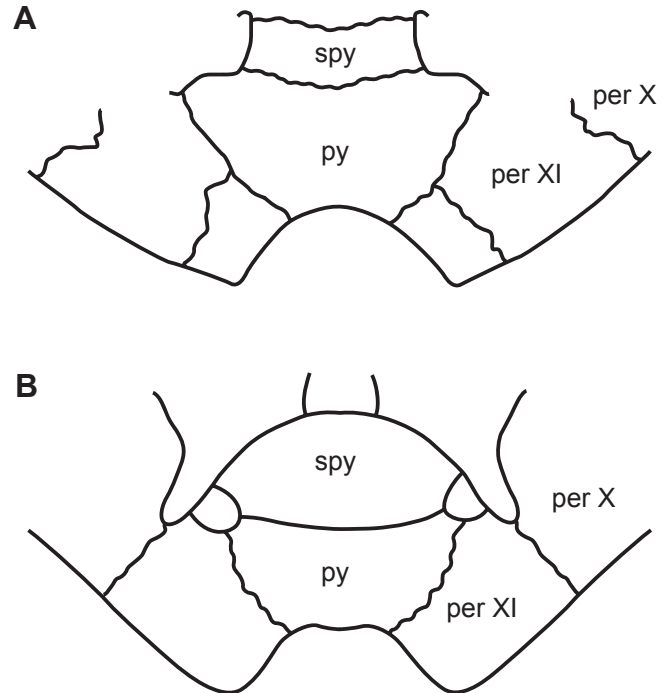


Fig. 2. Schematic drawings of the pygal region of two Late Jurassic turtles. **A.** Holotype of *Eurysternum wagleri*, specimen lost, illustration based on Meyer 1839b, pl. 19; specimen partially reconstructed by duplication of morphological information from one side of the individual to the other. **B.** BSPG AS I 921, illustration based on Zittel 1877, pl. 28, *personal observations*. co, costal bone; per, peripheral bone; py, pygal bone; spy, suprapygal bone.

nium and limbs, pygal region moderately preserved (Meyer 1839b, pl. 19; fig. 2a).

Referred specimens—Holotype only.

Diagnosis—Moderately large turtle with thin carapace; vertebrals very wide and with radiating pattern; moderate nuchal notch; deeply notched pygal region, which includes a twelfth pair of peripherals, a wide, trapezoidal pygal, and at least one slim suprapygal; small pygal fontanelles present; cranium relatively small (ca. 25 per cent of carapace length).

Occurrence—Late Jurassic (Tithonian) of Solnhofen, Germany (Meyer 1839b, fig. 1).

Palaeomedusa testa Meyer 1860

Fig. 3

Synonymies—*Eurysternum crassipes* Wagner 1859 (*nomen nudum*), *Palaeomedusa testa* Meyer 1860, *Eurysternum crassipes* Wagner 1861a, *Thalassemys marina* Fraas 1903.

Holotype—BSPG AS I 818; anterior half of a skeleton in dorsal view, including the cranium, articulated cervical vertebral, and the entire right forelimb (Meyer 1860, pl. 10, fig. 1; Frickhinger 1994, fig. 503).

Referred specimens—SMNS 10817, holotype of *Thalassemys marina* Fraas 1903, partial carapace and plastron, (Fraas 1903, figs. 1–3, pls. 1–3); MB R 2894, nearly complete

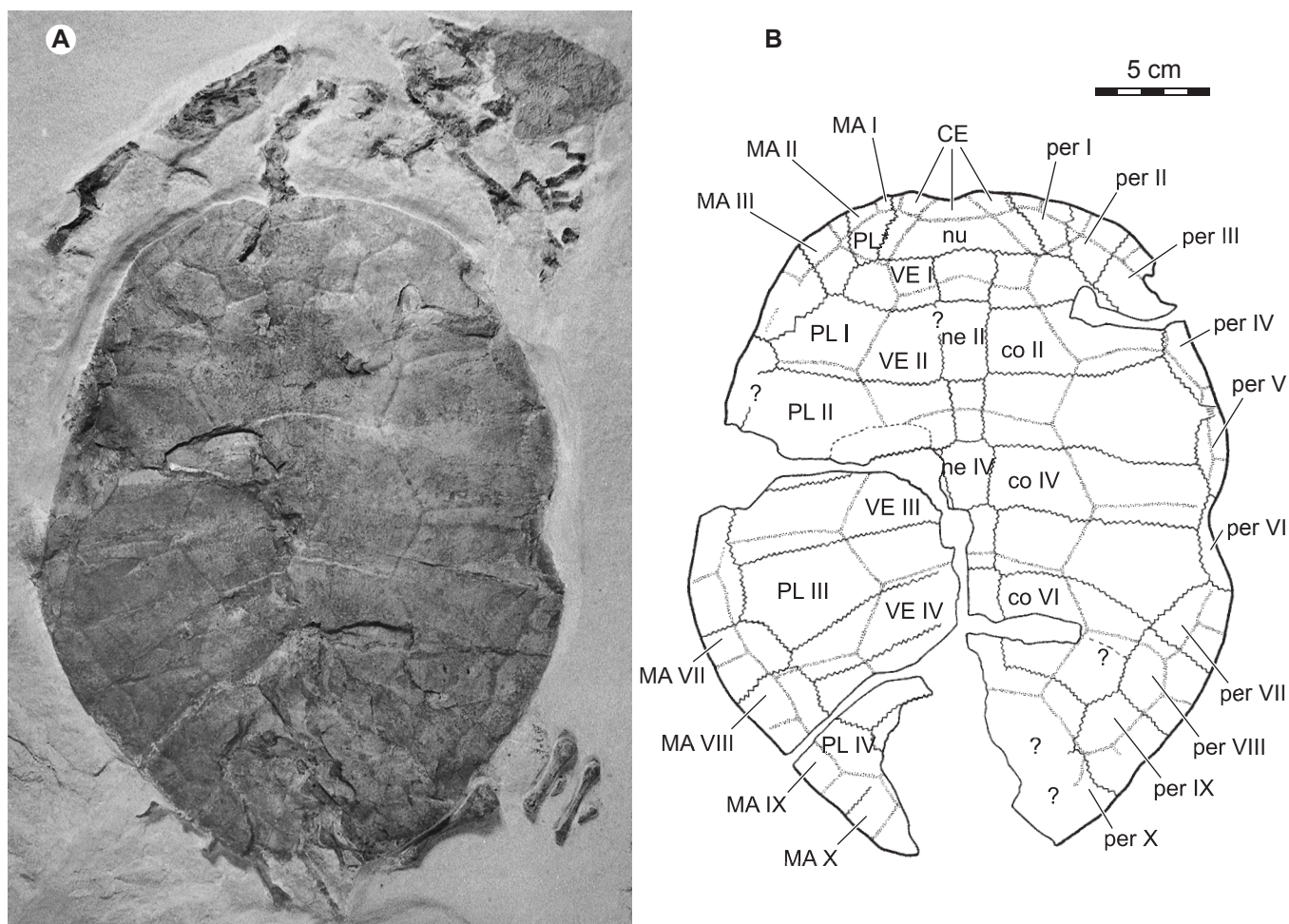


Fig. 3. *Palaeomedusa testa* Meyer 1860 (MB R 2894), Late Jurassic, Solnhofen, Germany. A. Specimen in dorsal view. B. Illustrative drawing of the carapace only. CE, cervical scute; co, costal bone; MA, marginal scute; ne, neural bone; nu, nuchal bone; per, peripheral bone; PL, pleural scute; PL*, supernumerary pleural scute; VE, vertebral scute.

carapace and minor other remains (Fig. 3).

Diagnosis—Large turtle with a thin shelled carapace and clearly observable sulci; carapacial fontanelles very small or absent; five pleurals and three cervicals present; vertebrae covering less than one third of costals; the first vertebral only in contact with the central cervical; nuchal trapezoid in outline; plastron loosely attached to carapace by ligaments; mesoplastra absent; large lateral and central fontanelles present; cranium relatively small (ca. 20 to 25 per cent of carapace length).

Occurrence—Late Jurassic (Tithonian) of Kelheim (Meyer 1860), Schnaitheim (Fraas 1903), and Solnhofen, Germany (Fig. 1).

TAXONOMIC REVIEW OF *EURYSTERNUM WAGLERI*

Among fossil turtles, *Eurysternum wagleri* is somewhat unique because its description is based solely on an illustration. Despite the inconsistencies that may arise from this type of name designation, the ICZN (1999) makes no statements

against this practice. Consequently, the name *Eurysternum wagleri* must be considered available and the illustrated specimen (not the illustration) the holotype. To further complicate the matter, the holotype was housed in Munich (see Wagner 1853, 1861b; Maack 1869; Rüttimeyer 1873; Zittel 1877; Oertel 1915) and was destroyed during World War II (Wellnhofer 1967). Finally, because Meyer (1839b) only referred to a single specimen (the illustrated holotype), no syntypes or lectotypes exist. During this investigation, a poorly made cast of the holotype was discovered in the Sedgwick Museum in Cambridge, England. However, according to rules of the ICZN (1999), casts may not be designated as type specimens. Given the great importance of *Eurysternum wagleri* for the taxonomy of Jurassic turtles, the designation of a neotype is nevertheless desirable.

The greatest problem with designating a neotype of *Eurysternum wagleri* is our uncertain knowledge of the morphology displayed in the holotype. Nevertheless, a number of features of the shell can be inferred from the type description, the type illustration, and the cast of the

holotype. In particular, the carapace has a moderate nuchal notch, wide vertebral scutes with strong radiating patterns, and a distinct pentagonal outline due to its greatest width being at the sixth to seventh peripheral. The single most diagnostic feature of *Eurysternum wagleri* is the presence of a deep and rounded pygal notch. This characteristic has been observed in a number of other turtles from the Late Jurassic of Europe. However, it is unclear if this feature is diagnostic for a single species, or a more inclusive clade that contains several species.

A review of deeply pygal-notched turtles from the Solnhofen region reveals two morphotypes of the pygal region. The first morphotype (Fig. 2a) is only seen in the type illustration of *Eurysternum wagleri*. The posterolateral margin of the carapace is formed by an elongate pair of eleventh peripherals. A set of two smaller bones of uncertain homology form the flanks of the notch, a trapezoidal medial bone of uncertain homology forms the concavity of the notch, and at least one, slim suprapygal connects the peripheral bones with the neurals. For simplicity, the elements with unknown homology are referred to as the peripherals XII and the pygal. A small pygal fontanelle is apparent in this large specimen indicating that fontanelles were present even in large individuals. The second morphotype (Fig. 2b) can be observed in a well-preserved specimen from Zandt, Germany (Fig. 1) that was originally described by Zittel (1877) as another individual of *Eurysternum wagleri* and which still resides in Munich to this day (BSPG AS I 921). The morphology of this specimen generally resembles that observed in the *Eurysternum wagleri* type illustration, but the posterolateral border of the carapace is solely formed by enlarged eleventh peripherals. *Acichelys redenbacheri* Meyer 1854 also appears to be notched, but until the only existing syntype (MB R 2440) has been prepared and restudied, its morphology must be regarded as uncertain, because parts of the pygal region are still covered by sediment (*personal observation*).

Despite the great correspondence between the morphology observed in the *Eurysternum wagleri* type illustration and the specimen described by Zittel (1877), there is a significant difference in the presence of supernumerary bones that form the apices of the pygal notch in *Eurysternum wagleri*. As the holotype is lost, however, it is impossible to judge if this difference truly exists. If these supernumerary bones were accurately depicted by the artist, the differentiation between the two taxa is warranted. Alternatively, if these supernumerary bones were misidentified by the artist, both specimens could be assigned to *Eurysternum wagleri*, justifying the designation of the Zittel (1877) specimen as the neotype. In the absence of evidence, it is reasonable to conclude that the artistic observations are correct and that the Zittel specimen indeed belongs to a different, unnamed species. Additionally, given that no other specimen is currently known with the same morphology, a neotype cannot be designated for *Eurysternum wagleri* and the type illustration must suffice until one is found.

DESCRIPTION AND COMPARISON OF MB R 2894

To avoid propagating misconceptions regarding the morphology and taxonomy of Jurassic turtles, MB R 2894 will primarily be compared to the holotypes or holotype descriptions of a number of fossil taxa from the Late Jurassic of southern Germany. This list includes *Eurysternum wagleri* Meyer 1839b (as described and depicted by Meyer 1839b), *Palaeomedusa testa* Meyer 1860 (as described by Meyer 1860, Wagner 1861a, *personal observations*), and *Thalassemys marina* Fraas 1903 (as described and depicted by Fraas 1903, *personal observations*). In addition, MB R 2894 is compared to a relatively complete fossil turtle that was described by Zittel (1877), which is herein considered very closely related to *Eurysternum wagleri*, but which must be regarded as the representative of a separate, unnamed species (see discussion above). Finally, MB R 2894 will also be compared to a series of better understood taxa from the Late Jurassic of Europe in general, such as *Idiochelys fitzingeri* Meyer 1839a (as described and depicted by Meyer 1839a and Rüttimeyer 1873), *Plesiochelys solodurensis* Rüttimeyer 1873 (as described and depicted by Bräm 1965), *Solnhofia parsonsi* Gaffney 1975 (as described by Joyce 2000, *personal observations*), *Platycheilus oberndorferi* Wagner 1853 (as described and depicted by Bräm 1965, *personal observations*), and *Tropidemys langi* Rüttimeyer 1873 (as described and depicted by Bräm 1965, *personal observations*).

Geological setting—The exact provenance of MB R 2894 is not known, because it arrived at its current location via private collections. The platy limestones of the Solnhofen region have been quarried at a large scale for several hundred years (Barthel et al. 1990) and quarrying remains active to this day. Unfortunately, many fossils found during the quarrying process are sold into private hands and are typically associated with unreliable locality data. According to its label, MB R 2894 was found near the village of Solnhofen. The accuracy of this information remains uncertain. However, the lithographic limestone in which the fossil is preserved is at least consistent with this locality and implies a middle Tithonian age (see Barthel et al. 1990).

Preservation—As typical for Solnhofen turtles, MB R 2894 is preserved as a relatively complete skeleton situated on the underside of a single limestone slab (Wellnhofer 1967). The shell is seen in dorsal view, thus impeding the study of its underside. The carapace is rather complete, but its left posterior third is damaged. Several major fractures are present, which fully isolate two larger portions of the carapace. Most bones of the pygal region are missing. This is attributed to the quarrying process because the missing bones left faint impressions in the matrix. Unlike many Solnhofen turtles, the limbs are fully disarticulated and lie scattered around the shell. A significant number of elements are missing and the remaining ones were typically split during recovery, obscuring their morphology. Given the disarray of the limbs, it is assumed that currents or scavengers moved them. At least five cervical vertebrae are present and articulated, but

they were also split in half during the recovery of the fossil, making it impossible to determine their exact identity or observe diagnostic morphologies. The cranium also appears to be present; however, like the neck and limbs, it was split during quarrying and later not prepared, leaving it presently useless for anatomical studies. Therefore, these elements are not described herein. As a novelty among fossil turtles, an impression of the dorsal cranial skin is preserved in detail just anterior to the cranial remains. Due to their uniqueness, these impressions will be described otherwise. Most of the bony sutures and sulci of the carapace are easily observed. Only the pygal region cannot be reconstructed.

Fontanelles—The size and number of fontanelles are commonly used among Late Jurassic turtles to help diagnose taxa even though their size and shape are known to change drastically during the ontogeny of some turtles (e.g., Lang and Rüttimeyer 1867). Fontanelles, nevertheless, can be somewhat useful if their presence is set in relation to the size of an individual, which can be used as a rough proxy for the relative age of an individual. Among Solnhofen turtles, MB R 2894 may be considered intermediate in size (carapace length ca. 270 mm), but it possesses no carapacial fontanelles. In comparison, *I. fitzingeri* is a much smaller turtle and exhibits no fontanelles. *Ple. solodurensis*, *Pal. testa*, *Th. marina*, and *Tr. langi* are significantly larger, but only *Pal. testa* and *Th. marina* appear to possess relatively minor fontanelles. It is not clear if carapacial fontanelles were present in *E. wagleri*, but they are generously developed in the closely related specimen described by Zittel (1877) even though this specimen is similar in size to MB R 2894.

Neurals—Only the anterior seven neurals are preserved. They are flat and have somewhat irregular outlines due to heavily interdigitating sutures. The first neural is the shortest among the preserved elements and rather square. The second neural is rectangular and appears to be the longest. Unlike all other neurals, the second neural is in contact with three pairs of costals. Most of the neural elements exhibit the same width, but the third neural is rectangular and significantly narrower. The remaining neurals appear to be of equal size and are hexagonal with short anterior sides. In comparison, the neurals of *I. fitzingeri* are reduced both in number and in size. The neural column of *Tr. langi* exhibits a distinct ridge.

Costals—At least eight pairs of costals are present in MB R 2894. An additional pair is known to exist in some Solnhofen turtles (*Idiochelys wagneri* Meyer 1840), but this may be an abnormality. Unlike *I. fitzingeri*, all neurals are present and the costals do not meet along the midline. As in most Solnhofen turtles, the anterior costals curve slightly to the front whereas the posterior ones curve to the back. The costals of MB R 2894 exhibit a unique articulation pattern in the anterior region of the carapace. Unlike most turtles, the first costal is very small relative to all other costals and does not articulate with the third peripheral but is separated from it by an articulation of the second peripheral with the second

costals. In addition, the costals are about equal in length along their medial contact with the neurals, but widen and narrow distally in an alternating fashion, giving the costals a wedge shape. This is most prevalent among the third and fifth costals that widen, and the fourth and six that narrow distally. Wedge-shaped costals are also known from several members of the Testudinidae; however, in these taxa the third, fifth, and seventh costals narrow distally. Meyer (1854) noted such an arrangement in some less well preserved turtles from the Solnhofen region and created the taxon *Acichelys redenbacheri* to encompass such individuals. However, although the pygal region of MB R 2894 is not fully preserved, a number of characters can be identified that are different from *Acichelys redenbacheri*, such as the significantly narrower vertebrals of MB R 2894.

Nuchal—The nuchal of MB R 2894 forms a moderate nuchal notch anteriorly and possesses an embayment posteriorly that holds the first neural. Similar to *I. fitzingeri*, *S. parsonsi*, *Pal. testa*, and *Th. marina*, the nuchal of MB R 2894 is trapezoidal in outline and about two times wider than it is long. This character was considered by Lapparent de Broin et al. (1996) to be diagnostic for the Eurysternidae, but it is not visible in the holotype of *Eurysternum wagleri*. The nuchal of *Ple. solodurensis* and *Tr. langi* is rectangular in outline.

Peripherals—Only the anterior ten pairs of peripherals are preserved in MB R 2894. An additional bone is visible just posterior to the tenth left peripheral that may represent an eleventh peripheral, but the poor preservation of the pygal region precludes the positive identification of this bone. No fossil turtle from the Late Jurassic of Europe is known to have only ten pairs of peripherals. Similar to *E. wagleri* and *S. parsonsi*, the outer rim of the peripherals is smooth and gives the carapace a pentagonal shape with the greatest width at the sixth peripheral. Due to the trapezoid outline of the nuchal, the first peripheral is somewhat triangular in shape, a condition also seen in *I. fitzingeri*, *Pal. testa*, *S. parsonsi*, and *Th. marina*. Unlike *Ple. solodurensis*, the medial articular suture between the peripheral and costals is irregular in outline. As noted above, there is a unique articulation between the second peripheral and the second costal.

Vertebrals—The presence and outlines of five vertebrals can be clearly inferred from the sulci of MB R 2894. Only the posterior border of the fifth vertebral is unclear. Similar to *Pal. testa*, the vertebrals were distinctly hexagonal with straight lateral edges and covered about one half of the carapace. The anterior borders of the second, third, and fourth vertebrals were clearly convex. Radiating vertebral striations, a feature typical of many primitive turtles, are present but faint. Unlike *Ple. solodurensis* where all vertebrals are roughly equal in width, the vertebrals of MB R 2894 varied in width, with the first and fifth the narrowest and the third the widest. The sulci between the vertebrals are situated on the same bones as in most turtles, thus lacking any notable features.

Pleurals—A prominent feature of MB R 2894 is a pair

of supernumerary pleurals just anterior to the regular first pleurals. Given the large size and symmetric development of these scutes, they are not considered shield abnormalities (sensu Zangerl 1957), but rather a well-developed feature of the taxon it represents. Although this morphology is unusual, supernumerary pleurals are known to have existed in other Late Jurassic turtles such as *Pal. testa*, *S. parsonsi*, *P. oberndorferi*, and *Th. marina*. However, this character has not received much attention from taxonomists. Whereas the supernumerary scute of *S. parsonsi* occurred only on one side, and thus may be considered a shield abnormality, those of *Pal. testa*, *P. oberndorferi*, and *Th. marina* were well developed and clearly regular. Overall, the triangular and flat supernumerary pleurals of MB R 2894 closely resemble those of *Pal. testa* and *Th. marina*. Due to their small size, the supernumerary scutes did not contact the second vertebral as in *Pal. testa*. Instead, there was a broad contact between the first vertebrals and the first regular pleurals, as seen in *Th. marina*. The sulci between the pleurals and marginals are situated on the peripherals.

Cervicals—Another feature of MB R 2894 is the development of three cervicals, a diagnostic character that unites all members of the genus *Plesiochelys* (Bräm 1965, Lapparent de Broin et al. 1996). However, whereas the first vertebral of *Plesiochelys* is very wide and anteriorly contacts all three cervicals and the first marginal, the first vertebral of MB R 2894 was narrow anteriorly and just barely contacted the outer pair of cervicals at their posteromedial corner. *Pal. testa* also exhibits this unique arrangement. In contrast, *E. wagleri*, *I. fitzingeri*, and *S. parsonsi* only have a single, wide cervical. Three cervicals may have also been present in *Tr. langi*, but this is not certain (Bräm 1965).

Marginals—The sulci of most marginals can be clearly discerned as a slight zigzag line on the peripherals along the rim of the carapace. No unique features are noticeable.

DISCUSSION

Specific assignment of MB R 2894

Based on the combination of three discrete characters (presence of three cervicals, five pleurals, and the absence of lateral carapacial fontanelles), MB R 2894 can be clearly distinguished from all currently known Jurassic and Cretaceous turtles. Nevertheless, two Late Jurassic turtle taxa, *Palaeomedusa testa* Meyer 1860 and *Thalassemys marina* Fraas 1903, exhibit a number of similarities that may warrant ascribing MB R 2894 to one or the other taxon.

Like MB R 2894, *Pal. testa* possesses three cervicals and five pleurals, characters that were noticed by Meyer (1860) and Wagner (1861b) but not considered for taxonomic studies by later authors. Furthermore, both MB R 2894 and *Pal. testa* possess rather small heads (estimated at 20 to 25 per cent of the carapace length), flattened shells (as apparent from their taphonomy), minor nuchal notches, and crisply developed sulci. *Pal. testa* differs from MB R 2894 by exhibiting much larger supernumerary pleurals that inhibit

a broad contact between the first vertebral and first regular pleural and give the first vertebral a trapezoidal shape. In addition, even though *Pal. testa* is almost twice as large as MB R 2894 and thus presumably ontogenetically older, *Pal. testa* exhibits modest, yet clear, lateral carapacial fontanelles, a juvenile feature, which may warrant the placement of MB R 2894 in a species other than *Pal. testa*.

Thalassemys marina is a poorly known turtle based on a partial carapace and plastron from the Late Jurassic of Schnaitheim, Germany (Fraas 1903, fig. 1). In a recent review of this species, Maisch (2001) noted that the type material exhibits morphologies that stand in contrast to those described and reconstructed by Fraas (1903). Based on the photographs provided by Fraas (1903), it is apparent that the holotype of *Th. marina* is similar to MB R 2894 in being rather flat and exhibiting clear sulci. Furthermore, but in contrast to the observations made by both Fraas (1903) and Maisch (2001), the holotype distinctly shows the former presence of supernumerary pleurals and a first vertebral that had a significant contact with the second pleural. The anterior rim of the carapace is incomplete, making it impossible to assess the former presence of three cervicals. Unlike in MB R 2894, the lateral margins of the vertebrals of *Th. marina* are somewhat rounded and, like *Pal. testa*, *Th. marina* possesses clear lateral fontanelles despite being significantly larger than MB R 2894. Even though MB R 2894 is more similar to *Th. marina* than to *Pal. testa*, the differences listed above may again be significant enough to warrant a new species. Interestingly, none of the characters discussed in this section are observed in the type material of *Thalassemys hugii* Rüttimeyer 1873, *Thalassemys gresslyi* Rüttimeyer 1873, or *Thalassemys moseri* Bräm 1965 thus warranting the exclusion of *Th. marina* from this genus as already proposed by Bräm (1965).

Among Jurassic and Cretaceous turtles, MB R 2894 is most similar to *Palaeomedusa testa* and *Thalassemys marina*, but still exhibits enough differences that may demand placing it in its own, new species. However, given that some extant turtles show considerable variation in the distribution of their scutes and that only three specimens are known to date that exhibit this general morphology, it seems more appropriate to cautiously place MB R 2894 within *Pal. testa* and to synonymize *Pal. testa* with *Th. marina* thus maintaining only one species. If additional material systematically shows the same differences listed above, the creation an additional species for MB R 2894 and the placement of *Th. marina* as a valid species within *Palaeomedusa* may be warranted. At the very least, it seems reasonable to place all three specimens within their own, exclusive taxon.

Monophyly of the Eurysternidae and Plesiochelyidae

A further result of this investigation is the presence of two unique characters in *Palaeomedusa testa*: the wide trapezoidal nuchal, a diagnostic character of the Eurysternidae (Lapparent de Broin et al. 1996), and the presence of three

cervicals, a key character in the identification of members of the Plesiochelyidae (Bräm 1965, Lapparent de Broin et al. 1996). From a simple three-taxon statement, using Plesiochelyidae, Eurysternidae, and *Pal. testa* as the terminal taxa, it becomes apparent that at least one of these characters must have been lost during phylogeny or that one of them evolved twice, thus not being developed homologically. At the very least, it seems plausible to assert that the simple presence of both characters is not sufficient to diagnose two exclusive groups, because *Pal. testa* would belong to both. A cladistic analysis is necessary to test these hypotheses. However, the morphology and basic alpha-level taxonomy of a significant number of Late Jurassic turtles must first be reviewed before such an analysis is undertaken.

CONCLUSIONS

The following six points summarize this investigation: (1) *Eurysternum wagleri* is an available taxon name, but the holotype has been lost; (2) no specimens are known that precisely replicate the morphology depicted in the illustrated holotype of *Eurysternum wagleri*. Consequently, a specimen that may serve as a neotype is not present and the illustrated holotype must suffice until one is found; (3) *Palaeomedusa testa* is not a junior synonym of *E. wagleri*; (4) the new Solnhofen turtle (MB R 2894) is assigned to *Pal. testa*, but may prove to be a new species; (5) *Thalassemys marina* is tentatively placed in *Pal. testa*, but may also prove to be a valid species within *Palaeomedusa*; (6) *Pal. testa* exhibits characteristics of both of Plesiochelyidae and Eurysternidae, thus calling into question the traditional diagnoses of both taxa.

Future work should focus on reviewing all Solnhofen turtles with a pygal notch in order to designate a neotype for *E. wagleri*. Once this has been accomplished, it will be possible to reevaluate the morphology and proposed synonymies of the Solnhofen turtles, integrate them into a comprehensive phylogenetic framework, and more confidently assess the true diversity of Late Jurassic turtles.

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