

# THE FIRST COMPLETE SKELETON OF *SOLNHOFIA PARSONSI* (CRYPTODIRA, EURYSTERNIDAE) FROM THE UPPER JURASSIC OF GERMANY AND ITS TAXONOMIC IMPLICATIONS

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**ABSTRACT**—A complete skeleton of *Solnhofia parsonsi* (Cryptodira, Eurysternidae) from the Kimmeridgian/Tithonian boundary of Schamhaupten, Germany provides the first complete understanding of the postcranial morphology of this genus. The here newly described postcranial characters are important in distinguishing *Solnhofia* from shell-based genera and thus help in resolving part of the parataxonomic conflict between shell-based and cranium-based turtle genera. This disparity originated during the last 150 years due to the history of fossil finds, preparation, and changing interests of researchers. Synonymies of *Solnhofia* with such turtle genera as *Eurysternum*, *Idiochelys*, *Plesiochelys*, *Thalassemys*, and *Euryaspis* can now be refuted. Similarities with *Hydropelta* are apparent, but not considered sufficient to support a synonymy. Newly observed or confirmed characters include the relatively large head (40 percent of the carapace length), the pentagonal carapace, the unique arrangement of bones and fontanelles in the pygal region, and the absence of mesoplastra, epiplastra, and an entoplastron.

The carcass of the new specimen was embedded in finely laminated limestones and shows little sign of disintegration or scavenging, suggesting hostile bottom conditions with very low water energy during deposition. This taphonomy agrees with recent published models for the origin of the lithographic limestones of southern Germany. Tooth marks along the posterior margin of the carapace are evidence of predation by a broad-nosed crocodylian. This is the first clear example for this type of predatorial interaction from the Upper Jurassic of Germany.

## INTRODUCTION

**S**OLNHOFIA PARSONSI is an eucryptodiran turtle from the Upper Jurassic of Western Europe (Gaffney, 1975b; Lapparent de Broin et al., 1996). Parsons and Williams (1961) described the holotype in detail which is an isolated cranium from the Solnhofen limestone, Germany. They were hesitant to assign it to a known taxon because, at that time, the taxonomy of previous workers relied entirely upon shell morphology. A second isolated skull was described by Bräm (1965) who again did not assign a name to it for the same reason. After visiting most major collections in Europe, Gaffney (1975b) concluded that no other specimens of such a turtle was present or likely to be found in the near future. Based on this assumption, he erected *Solnhofia parsonsi* based on the two crania. Additional, but fragmentary, specimens have since been described and tentatively assigned to *Solnhofia* (Broin, 1994; Lapparent de Broin et al., 1996). Lapparent de Broin et al. (1996) also noted that a beautifully preserved and complete turtle, JM SCHA 70, depicted in Frickhinger (1994) should be assigned to *Solnhofia*. In general, complete turtle skeletons from the Jurassic are extremely rare and provide valuable information that help resolve taxonomy and phylogeny. Consequently, this exquisite fossil is the focus of this paper, the purpose of which is: 1) to describe the anatomy of JM SCHA 70 in detail; 2) to discuss its placement in the genus *Solnhofia*; and 3) to consider synonymies and differences to other genera. Anatomical terms of the cranium are used as defined by Gaffney (1972), those of the shell are used as defined by Zangerl (1969).

**Abbreviations.**—The following acronyms are used in the body of the text: JM, Jura-Museum, Eichstätt, Germany; TM, Teyler Museum, Haarlem, Netherlands; SM, Naturmuseum Solothurn, Solothurn, Switzerland; MNHN, Muséum National d'Histoire Naturelle, Paris, France.

## HISTORY OF RESEARCH

The lithographic limestones of southern Germany and France have yielded many remains of Upper Jurassic turtles. Classic turtle localities include the lithographic limestone quarries of Cerin (Thiollière, 1851; H. v. Meyer, 1860; Jourdan, 1862), Eichstätt (H. v. Meyer, 1864), Kehlheim (H. v. Meyer, 1839a, 1860, 1843), and Solnhofen (H. v. Meyer, 1839a; Wagner, 1859).

These turtles were considered among the oldest known representatives of the order Testudines until Baur (1887) described the genus *Proganochelys* from the Upper Triassic of Germany (Kuhn, 1961; Gaffney, 1990).

H. v. Meyer (1839a, 1839b, 1843, 1852, 1854, 1860, 1864) alone erected eight different turtle genera from the lithographic limestones, typically based on highly fragmentary material such as isolated limbs, plastra, and partial carapaces. Additional genera were added by others (Wagner 1859, 1861a; Jaekel, 1904). Most of these authors distinguished their genera from each other by minute differences in postcranial morphology. Only little to no attention was ever paid to the not infrequently preserved skulls. Subsequent authors typically recognized *Platychelys* Wagner, 1859 as a valid genus and included *Chelonemys* Jourdan, 1862 in *Idiochelys* H. v. Meyer, 1839a, as proposed by Rüttimeyer (1873). Most of the other genera were lumped one by one into *Eurysternum* H. v. Meyer, 1839b, as done by Wagner (1861a, 1861b), Rüttimeyer (1873), Zittel (1877), Oertel (1915), and Kuhn (1961).

Other fossil turtles from the Upper Jurassic and the lowermost Cretaceous were found during the last century in northern Germany (Maack, 1869), England (Owen, 1853), and Switzerland (e.g., Rüttimeyer, 1873). The taxa described from this material were again based entirely on postcranial characters. Interestingly, these localities contain faunas that are rather different from the lithographic limestones, with genera such as *Plesiochelys* Rüttimeyer, 1873; *Thalassemys* Rüttimeyer, 1859; and *Tropidemys* Rüttimeyer, 1873. Lapparent de Broin et al. (1996) interpreted these genera as coastal forms and those of the lithographic limestones as lagoon inhabitants. Only *Platychelys* Wagner, 1859 is found both in Bavaria and Switzerland, and was interpreted as a terrestrial form by Lapparent de Broin et al. (1996).

Parsons and Williams (1961) were the first to describe in detail turtle skulls from the Upper Jurassic of Europe, one from the Isle of Portland, Great Britain, the other from the Solnhofen region. However, as stated previously, they were reluctant to name the specimens without associated shell material. Bräm (1965), in his comprehensive overview of the turtles from Solothurn, Switzerland, described a skull he attributed to *Plesiochelys etalloni* (Pictet and Humbert, 1857) and, briefly, an additional but unidentified skull.

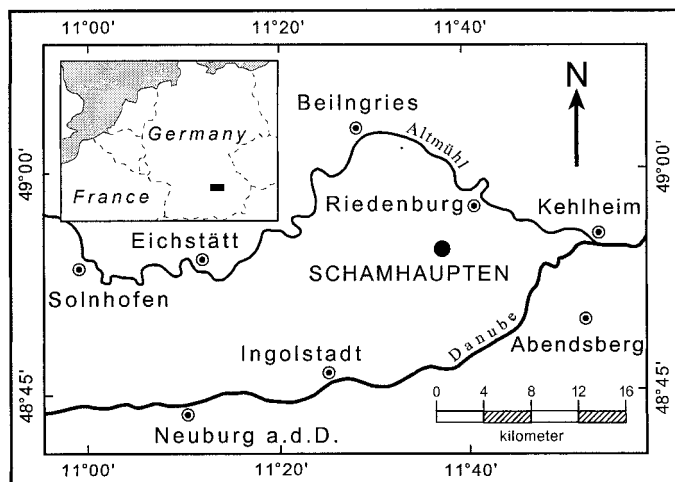


FIGURE 1—Geographic location of the Stark quarry.

Gaffney (1975a, 1975b) was confident enough to create *Portlandemys mcdowelli*, based on the “Portland skull” described earlier by Parsons and Williams (1961), and *Solnhofia parsonsi*, based on the “Solnhofen skull” of Parsons and Williams (1961) and Bräm’s (1965) unidentified “Solothurn skull.” He then integrated the newly acquired cranial data into his cladistic phylogeny of turtles (Gaffney, 1975c). An additional skull was described by Rieppel (1980) and assigned to *Thalassemys moseri* Bräm, 1965. However, Gaffney and Meylan (1988) questioned the specimen’s affiliation with *Thalassemys* because they doubted whether the identification of the fragmentary shell associated with the skull was valid. This was later confirmed by Lapparent de Broin et al. (1996).

Prior to this paper *Plesiochelys* was the only turtle from the Jurassic of Europe with a described cranium clearly associated with a name-bearing shell (Gaffney, 1975a, 1976). Most other genera are primarily based on either shell or cranial characters. This parataxonomic conundrum vividly illustrates the need for new specimens that link both classificatory systems.

#### COLLECTING AND PREPARATION

The new *Solnhofia* specimen (JM SCHA 70) was collected in the Stark quarry during the 1990 field season of the Jura-Museum, Eichstätt (Röper, 1992). The Stark quarry is situated 0.5 km northwest of the village of Schamhaupten, in the center of Bavaria, southern Germany (Fig. 1), with the Gauss-Krüger Coordinates of R4469650/H5420160 (Thies and Zapp, 1997). Other finds include beautifully preserved fossils such as *Lepidotes* sp. (Thies and Zapp, 1997) or *Leptosaurus* sp. (Renesto and Viohl, 1997).

The turtle specimen broke into several pieces during recovery from the quarry. The slabs were later glued together and mechanically prepared. Only parts of the dorsal but most of the ventral view were freed from the matrix, leaving the skeleton partially embedded and retaining a range of taphonomic information. X-ray photographs reveal that the few elements, especially of the appendicular skeleton, that are missing, are unlikely to be still hidden in the matrix. The ring of marginal carapace elements can be observed in ventral view but is partially covered by matrix on the dorsal side. The central carapace, in contrast, is dorsally exposed but covered ventrally by the plastron and some matrix. Collectively, both views provide a nearly complete picture of the carapace.

JM SCHA 70 is housed together with a set of its X-ray photographs at the Jura-Museum, Eichstätt, Germany. Röper (1992,

pl. 1, fig. 1) attributed the specimen to *Plesiochelys* sp., whereas Frickhinger (1994, fig. 511, 512) mentioned it as an undescribed turtle. Lapparent de Broin et al. (1996) were the first to correctly attribute JM SCHA 70 to the genus *Solnhofia*.

#### GEOLOGY AND STRATIGRAPHY

During the Oxfordian, an epicontinental sea covered most of southern Germany. Under shallow marine conditions sponge-algae mounds formed along paleogeographically elevated areas, such as the Franconian carbonate platform. The massive spongiolithic facies of the mounds (*Massenfazies*) is in contrast to the surrounding bedded facies (*Bankfazies*). The initially isolated mounds slowly merged during the Oxfordian and Kimmeridgian, rising above the retreating bedded facies, subsequently forming isolated basins of bedded limestone (R. K. F. Meyer and Schmidt-Kaler, 1989). The Stark quarry lies at the southeastern margin of one of these basins, the Schamhaupten basin (Bausch, 1963). The sedimentation of bedded limestone continued during the upper Kimmeridgian and Tithonian. An exceptional type of bedded limestone is the famous lithographic limestone of Solnhofen and Eichstätt. This finely laminated micritic limestone is quarried because of its platy nature and homogeneity (Bartel et al., 1992). The facies exposed in the Stark quarry differs from the Solnhofen facies in containing a coarser, more heterogeneous limestone that can contain high levels of silica and does not split evenly along bedding planes when quarried (Röper, 1992).

The exact age of the sediments exposed in the Stark quarry is somewhat unclear. Bausch (1963) dated the strata of the Schamhaupten basin with ammonites. He concluded the age of a 30 m thick unit of silicic limestone, also exposed in the Stark quarry, to be Malm Epsilon 2 (*setatus*-zone/upper Kimmeridgian) or slightly younger. However, the actual index fossil of the *setatus*-zone was not found.

More recent, unpublished investigations challenge this age. The ammonite fauna unearthed during the excavations of the Jura-Museum, for instance, tentatively hints at a slightly younger age (Schweigert, personal commun., 1999) as does the occurrence of the radiolarian *Vallupus hopsoni* (Kiessling, personal commun., 1999). If these speculations are true, the Stark quarry is stratigraphically closer in age to the actual Solnhofen Limestone than previously thought.

Röper (1992) described a measured section of the Stark quarry in detail. He distinguishes between finely laminated limestones and non-laminated limestones. The non-laminated limestone may contain particularly high amounts of silica. Based on the faunal assemblages and sediment marks, Röper (1992) suggested that the finely laminated sediments were of intertidal origin and that the non-laminated ones were subtidal. This interpretation seems unlikely because characteristic sediment structures of a tidal flat, such as break up clasts, teepees, dolomite caps, signs of subareal exposure, channel deposits, etc., cannot be found. Renesto and Viohl (1997) preferred the more widely accepted model of a permanently submerged, shallow marine basin with hostile bottom conditions (Viohl, 1985, 1998), arguing that the non-laminated sediments are tempestites and that the finely laminated sediments correspond to the normal background sedimentation.

JM SCHA 70 was found in a 124 mm thick, finely laminated layer which was labeled E/23 by Röper (1992). The shell was preserved in a silicic concretion, the cranium and the extremities in the surrounding soft limestone matrix. The accompanying fauna includes teleost scales, coprolites, and aptychs (Röper, 1992).

#### TAPHONOMY

The partial disarticulation of the skeleton suggests that the carcass of JM SCHA 70 must have had time to decay before

being fully buried by sediment (Figs. 2, 3). The mandible became detached and came to rest next to the cranium. The hyoids separated, one now lying at the ventral surface of the basicranium and the other in the vicinity of the left manus. The forelimbs are heavily disarticulated, with only three digits and some carpals of the left hand remaining in association with another. Other elements of the manus are lost. The long bones of the forelimbs were sorted in a peculiar fashion: the radii are lying parallel to one another near the mandible, whereas the ulnae are imbricating with a coracoid and the right scapula. The hind limbs are relatively complete. Showing only few signs of disintegration, the left foot is intact and articulates with the fibula. The right foot is articulated with the tibia and fibula but many phalanges are missing. The right femur is positioned where the left normally should be, and the left femur overlies both feet. The cervical vertebrae are articulated and form a slightly arched string. The tail coiled up and was disarticulated into two strings. The larger portion contains twelve caudals and lies in situ. Four distal caudals are tucked next to the left femur. Altogether, the scattering of the limb bones indicates currents that were strong enough to move bones but too weak to remove larger bones from the carcass. Scavengers potentially could also have played a role in disintegrating the skeleton, but this seems unlikely in the context of the depositional model of Renesto and Viohl (1997).

The dorsal part of the carapace, the cranium, and the plastron were heavily crushed during diagenesis. Nevertheless, they remain in rather good condition. The exact determination of the sutures is sometimes extremely difficult due to the abundance of small cracks and fissures. Furthermore, many small foramina were filled with calcite during diagenesis, obscuring their position. The spongy articular ends, and some of the long bone shafts, were crushed during compaction. This is clearly illustrated by the right femur. Its distal end, including the shaft, was flattened by the outer rim of the carapace. The proximal end, in contrast, stayed fully intact inside the shell.

The posterior rim of the carapace shows several small and round indentations (2–3 mm in diameter) as well as protuberances (Fig. 7.3). These may be interpreted as tooth marks because small indentations on the dorsal side correspond to wide knobs on the ventral side and vice versa. C. A. Meyer (1984, 1989, 1994) interpreted similar marks on turtle shells from Solothurn as being caused by predators such as the broad-nosed crocodylian *Machimosaurus*. Similarly built modern crocodylians are known to have diets that include turtles (C. A. Meyer, 1984). The tooth marks on JM SCHA 70 were probably not produced during a single attack nor did they lead to the animal's death. Rather, the turtle was under attack several times and escaped with only minor injuries. This is demonstrated by the fact that all bite marks are located only along the posterior edge of the carapace and that some bite marks appear to be healed.

#### SYSTEMATIC PALEONTOLOGY

Order CRYPTODIRA Cope, 1871  
Suborder EUCRYPTODIRA Gaffney, 1975a  
Family EURYSTERNIDAE Dollo, 1886  
Genus SOLNHOFIA Gaffney, 1975b

*Type species.*—*Solnhofia parsonsi* Gaffney, 1975b, by monotypy.

*Emended diagnosis.*—Skull 40 percent of carapace length;

carapace pentagonal; wide nuchal notch; cervical scute as wide as nuchal posteriorly, but narrower anteriorly; pygal well developed, rectangular, and with waist; plastron with central fontanelle and semilunate lateral fontanelles; carapace with small lateral fontanelles and relatively large pygal fontanelles; mesoplas- tra absent. A detailed diagnosis of the skull was given by Gaffney (1975b).

*Occurrence.*—Upper Kimmeridgian of Lot, France (Lapparent de Broin et al., 1996) and Solothurn, Switzerland (Gaffney, 1975b); Kimmeridgian/Tithonian boundary of Schamhaupten, Germany; lower Tithonian of the Solnhofen region, Germany (Gaffney, 1975b) and Canjuers, France (Broin, 1994).

#### SOLNHOFIA PARSONSI Gaffney, 1975b

Figures 2–9

*Diagnosis.*—As for genus.

*Material examined.*—JM SCHA 70.

*Occurrence.*—As for genus.

*Referred specimens.*—TM 4023 (holotype), partially eroded skull with lower jaw (Parsons and Williams, 1961, fig. 2, 7, 10, 11, pl. 4; Gaffney, 1975b, fig. 1, 2, 4–17); JM SCHA 70, complete and only partially disarticulated skeleton, identified as *Plesiochelys* sp. by Röper (1992, pl. 1, fig. 1) and figured as an “undescribed turtle” by Frickhinger (1994, fig. 511, 512).

The following specimens were assigned to, or close to, the genus *Solnhofia*, but they either are too fragmentary to be included in the species *S. parsonsi* or display variations from the holotype that were considered sufficient by Lapparent de Broin et al. (1996) to exclude them from *S. parsonsi*, or even *Solnhofia*: SM 137 (hypodigm), partially eroded skull, “uncertain systematic position” in Bräm (1965, pp. 186–187), *S. parsonsi* in Gaffney (1975b, fig. 2, 3, 7, 8, 13), *Solnhofia* sp. in Lapparent de Broin et al. (1996); MNHN CNJ 82, disarticulated and crushed skeleton with skull, *Solnhofia* sp. (Broin, 1994, pl. 1, fig. 2–6); Coll. Dutrieux n° 7D, skull fragment, *Solnhofia* aff. *parsonsi* in Lapparent de Broin et al. (1996, fig. 2); MNHN CNJ 76, heavily crushed and incomplete skeleton, aff. *Solnhofia* in Fabre et al. (1982, pl. 3, fig. 4), and Broin (1994, pl. 1, fig. 1).

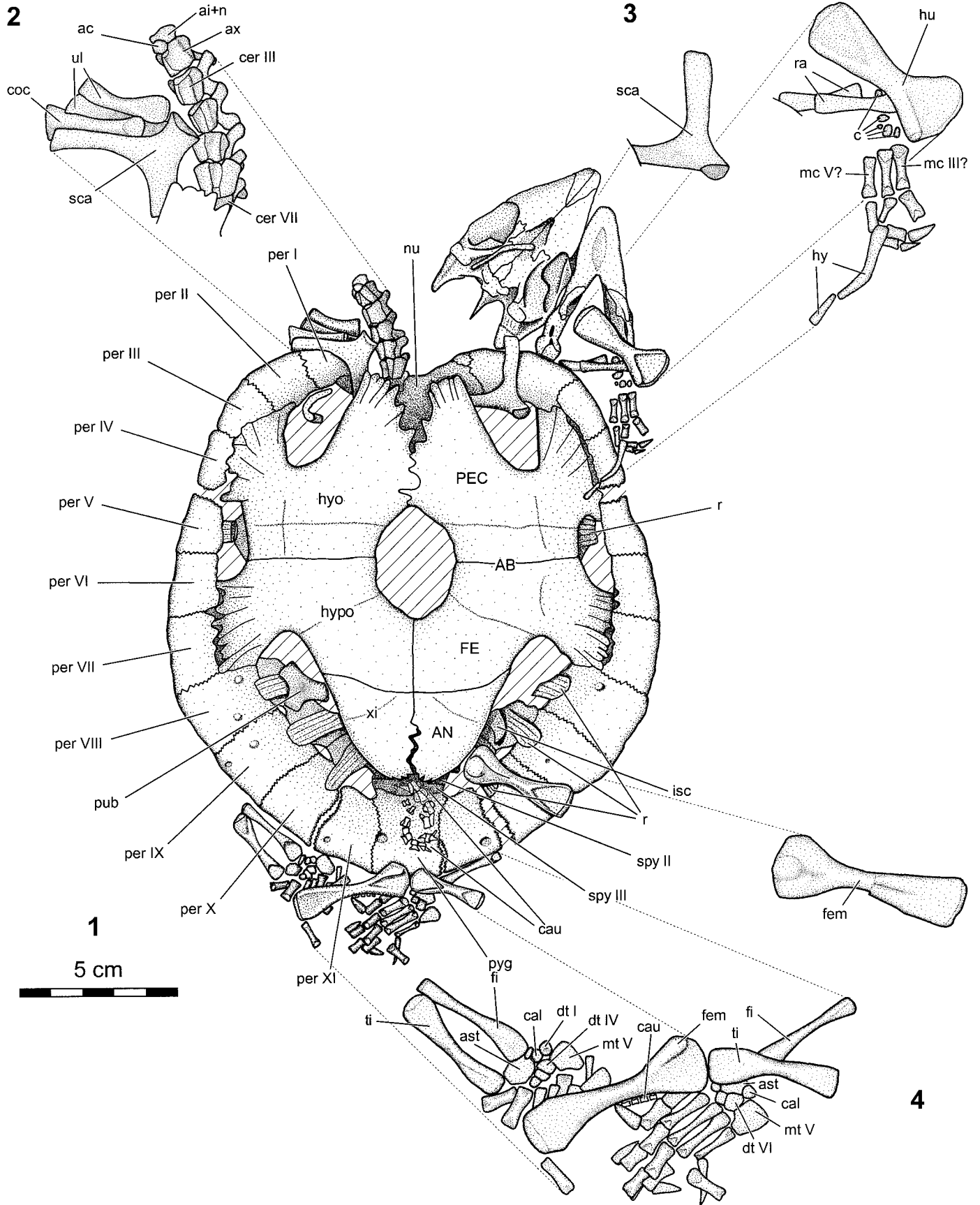
#### DESCRIPTION OF JM SCHA 70

*Cranium* (Figs. 4–6, 8.2; Table 1).—Only a few crania of European Upper Jurassic turtles have been recovered in good condition and in association with a shell. The discovery of a cranium with shell is important because the assignment to a genus relies traditionally almost entirely on postcranial characters. Unless noted otherwise, the cranium of JM SCHA 70 will be compared to that of *Plesiochelys*, as described by Gaffney (1975a, 1976), to that of “*Thalassemys*” (sensu Rieppel, 1980, non Rüttimeyer, 1873), as described by Rieppel (1980), and to that of *Solnhofia*, as described by Gaffney (1975b).

*Premaxilla.*—The premaxilla is a large element forming much of the elongate, flat snout. Together with the maxilla and the palatine it forms a secondary palate. This derived structure separates the nasal passage from the oral cavity, enabling the living animal to breathe through its nose while handling food in the oral cavity. In palatal view, along with its counterpart, the premaxilla forms a wedge between the maxillae. Many small vascular openings result in a serrated appearance of the labial margin. The triturating surface is smooth and without labial or lingual ridges, giving the snout the appearance of a duckbill. In

FIGURE 2—*Solnhofia parsonsi* (JM SCHA 70), Upper Jurassic, Germany. Complete skeleton as seen in 1, ventral and 2, dorsal view. Scale bars equal 2 cm.





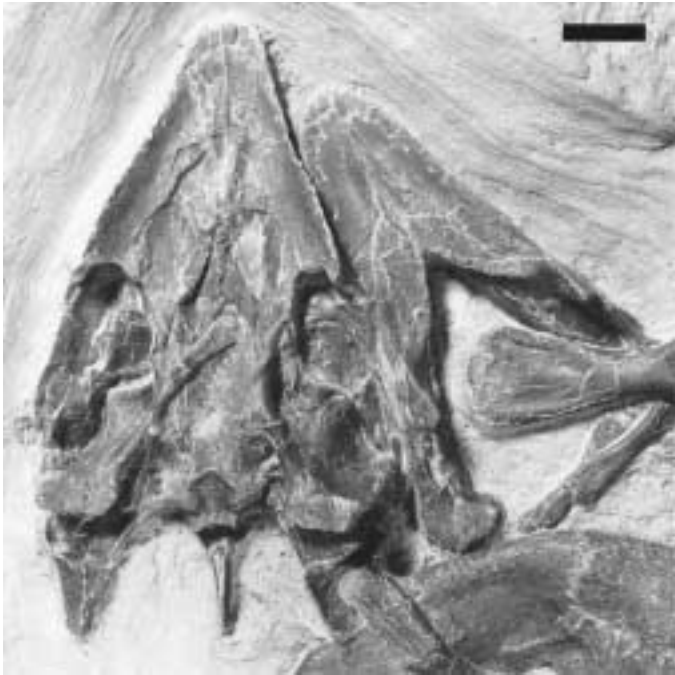


FIGURE 4—*Solnhofia parsonsi* (JM SCHA 70), Upper Jurassic, Germany. Ventral view of the cranium and dorsal view of the mandible. Scale bar equals 1 cm.



FIGURE 5—*Solnhofia parsonsi* (JM SCHA 70), Upper Jurassic, Germany. Dorsal view of the cranium and ventral view of the mandible. Scale bar equals 1 cm.

dorsal view, only the heavily vascularized posterior part of the premaxilla is exposed which forms the anterior rim of the apertura narium externa. In all features, the premaxilla of JM SCHA 70 corresponds to *Solnhofia*. The premaxilla of *Plesiochelys*, on the other hand, is considerably shorter, does not form a secondary palate, and is characterized by high lingual and labial ridges.

**Maxilla.**—The ventral horizontal plate of the maxilla, together with the premaxilla, forms a smooth triturating surface and an extensive secondary palate. This is considered a key character of *Solnhofia*. The maxilla meets the premaxilla anteromedially, the palatine posteromedially, the pterygoid posteriorly, and the jugal posterolaterally. The medial contact is somewhat unclear. As opposed to other fossil turtles such as *Eretmochelys* and *Erquelinnesia* (Gaffney, 1975b), it appears that the vomer is submerged underneath the articulating maxillae. The maxillae of *Plesiochelys* do not meet at all, nor do they form a secondary palate, or contact the pterygoid. They are additionally sculptured with high lingual and labial ridges.

The vertical plate of the maxilla can only be partially observed in dorsal view. Anteriorly it meets the premaxilla and forms the lateral rim of the apertura narium externa. Towards the back it forms the anterior and lateral wall of the orbit. Posteriorly the maxilla meets the jugal and sends an ascending process medially to form part of the posterior wall of the orbit. This condition is only seen in *Solnhofia*. The ascending nasal process

and the postorbital process shifted during compaction, allowing the nasal processes to meet in the middle and cover the nasals, making the apertura narium externa and the orbit seem smaller than they are. Inside the orbit the maxilla forms the posterolateral rim of the foramen orbito-nasale and sends a process between the palatine and the jugal.

**Nasal.**—Only the posterior border of the nasals can be observed because diagenesis has slightly crushed the skull, pushing the ascending processes of the maxillae over the nasals. From what can be seen, the nasals probably are rectangular elements and about half the length of the prefrontals. Well developed nasals are clearly present in many primitive eucryptodires. The posterior border of these elements in JM SCHA 70 is similar to *Plesiochelys* and *Solnhofia*, both of which have rectangular nasals. In comparison, "*Thalassemys*" has much smaller and triangular nasals.

**Prefrontal.**—The dorsal plate of the prefrontal is small and rectangular. The lateral border forms part of the dorsal margin of the orbit. Like in most turtles, a small vertical plate extends anteroventrally forming the anterior wall of the orbit (Gaffney, 1976). Anteriorly and posteriorly the prefrontal meets along transverse sutures with the nasal and frontal, respectively. As in *Solnhofia*, the prefrontals meet over their entire length along the

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FIGURE 3—*Solnhofia parsonsi* (JM SCHA 70), Upper Jurassic, Germany. 1, Complete skeleton as seen in ventral view; 2, enlarged view of the cervical vertebrae, the ulnae, and the right coracoid and scapula; 3, enlarged view of the left humerus and scapula, the radii, and parts of the left manus; 4, enlarged view of the hind limbs. Abbreviations: AB, abdominal scute; ac, atlas centrum; ai+n, atlas intercentrum and neural arch; AN, anal scute; ast, astragalus; ax, axis; c, carpal; cal, calcaneum; cau, caudal vertebra; cer, cervical vertebra; coc, coracoid; dt, distal tarsal; FE, femoral scute; fem, femur; fi, fibula; hu, humerus; hy, hyoid; hyo, hyoplastron; hypo, hypoplastron; isc, ischium; mc, metacarpal; mt, metatarsal; nu, nuchal bone; PEC, pectoral scute; per, peripheral; pub, pubis; pyg, pygal bone; r, rib; ra, radius; sca, scapula; spy, suprapygal bone; ti, tibia; ul, ulna; xi, xiphoplastron.

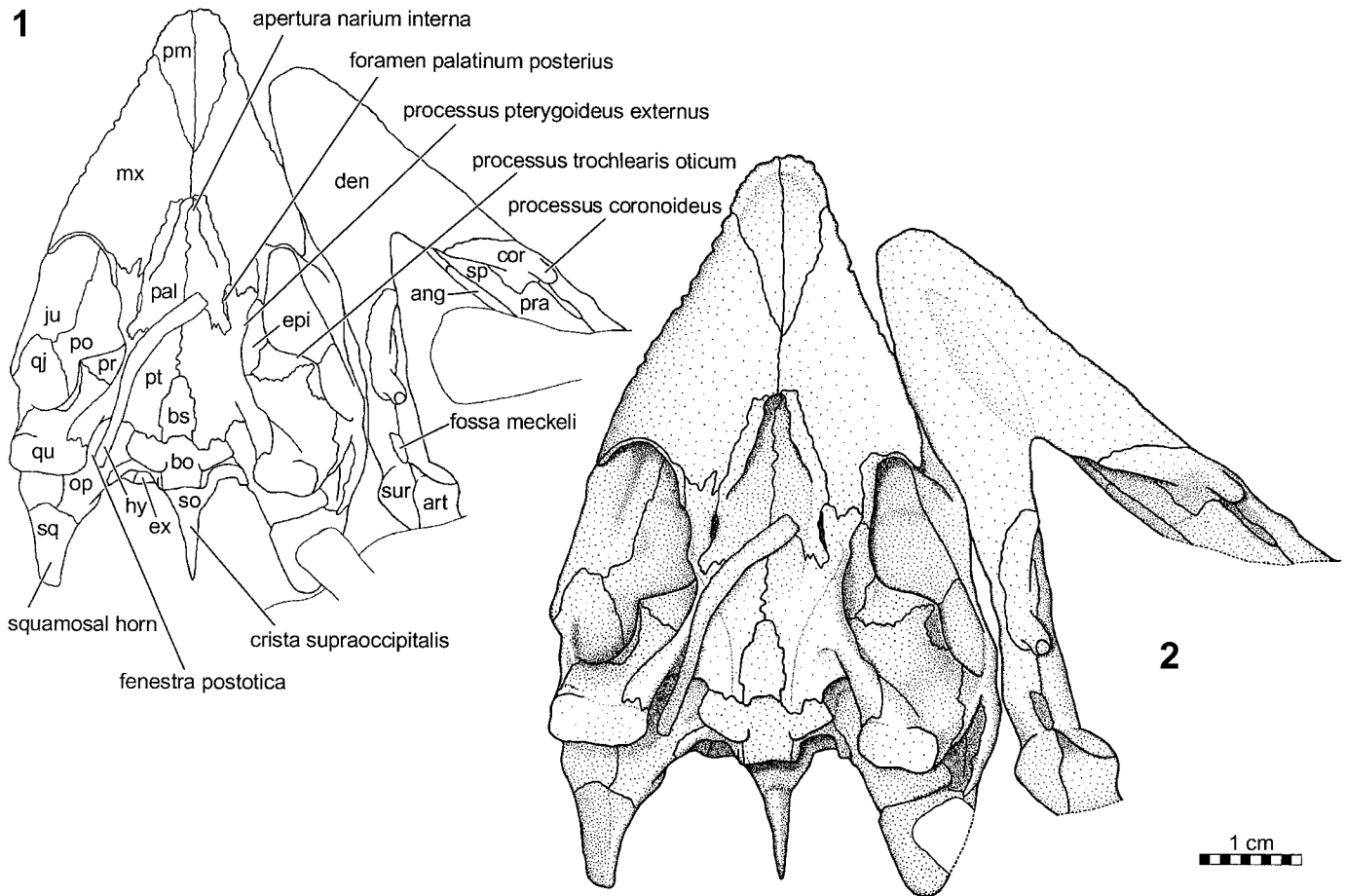


FIGURE 6—*Solnhofia parsonsi* (JM SCHA 70), Upper Jurassic, Germany; 1, 2, ventral view of the cranium and dorsal view of the mandible. Abbreviations: ang, angular; art, articular; bo, basioccipital; bs, basisphenoid; cor, coronoid; den, dentary; epi, epipterygoid; ex, exoccipital; hy, hyoid; ju, jugal; mx, maxilla; op, opisthotic; pal, palatine; pm, premaxilla; po, postorbital; pr, prootic; pra, prearticular; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; sp, splenial; sur, surangular.

skull mid line. This condition differs from that in *Plesiochelys* and “*Thalassemys*” in which the prefrontals only meet partially, if at all.

**Frontal.**—The frontal of JM SCHA 70 is an elongate, rectangular to triangular bone with a blunt anterior tip. Anteriorly it meets the prefrontal, posterolaterally the postorbital, posteriorly the parietal, and medially with its counterpart. Laterally it forms the posterior half of the dorsal rim of the orbit. The small lateral process that forms the posteromedial border of the orbit, as in *Plesiochelys* or *Solnhofia*, seems to have been eroded on the right side but is present on the left.

**Parietal.**—The dorsal surface of the skull’s posterior region is not fully prepared. The exposed bones are shattered and the sutures are faint to invisible. This makes the shape and contacts of the parietal quite unclear. It can be seen, however, that the parietal meets the prefrontal anteriorly and the postorbital anterolaterally. The lateral, medial, and posterior contacts are unclear which leads to a number of additional uncertainties. It is impossible, for instance, to assess to what extent the parietals are engaged in the formation of the crista supraoccipitalis.

**Postorbital.**—In dorsal view the postorbital is only partially exposed behind the orbit. It meets the frontal posteromedially and forms the posterior rim of the orbit. The lateral contact with the jugal seems to be disrupted. The posterior extension of the

postorbital can be estimated by looking through the fenestra subtemporalis. In this view, the postorbital contacts the jugal at a long lateral suture and extends further posteriorly contacting the quadratojugal posterolaterally. This arrangement of the postorbital is essentially the same as in *Solnhofia* and *Plesiochelys*.

**Jugal.**—The dorsal exposure of the jugal is limited to a fragment of the right jugal, which is exposed between the postorbital process of the maxilla and the postorbital. Like in *Solnhofia* and *Plesiochelys*, it probably forms part of the posterior rim of the orbit. In palatal view, the jugal forms much of the lateral roof and rim of the fossa temporalis inferior. The bone meets the postorbital medially and the quadratojugal posteromedially. Anteriorly it sends a process ventrally to meet the maxilla, pterygoid, and probably even the epipterygoid, forming the antero-medial rim of the fenestra subtemporalis. This configuration can be observed in *Solnhofia*, but is not developed in *Plesiochelys*.

**Quadratojugal.**—The quadratojugal of JM SCHA 70 is a tri-radiate bone which can only be seen in ventral view. Anteriorly it forms the posterolateral roof and rim of the fossa temporalis inferior and sends a wide process between the jugal and postorbital. Posteriorly the quadratojugal meets the quadrate and frames the anterior half of the cavum tympani by sending a process ventrally towards the articular surface of the quadrate, and another process dorsally to meet the squamosal. There is a



likely contact with the postorbital on the dorsal surface; however, this contact cannot be observed due to matrix cover.

*Squamosal.*—The squamosal is partially exposed in dorsal view but its contacts are obscure because of fractures and faint sutures. In palatal view, the squamosal contacts the quadrate anterolaterally and the opisthotic anteromedially. It meets the quadratojugal ventral to the cavum tympani. The squamosal extends posteriorly to form a pronounced squamosal horn. *Plesiochelys* and *Solnhofia* have not been described to possess such pronounced horns. The type specimen of *Solnhofia*, however, is heavily eroded in the temporal area, and thus cannot be ruled out to have squamosal horns.

*Vomer.*—The vomer of *Plesiochelys* is a slim bone, fully exposed in palatal view and in contact with the palatine posteriorly. In JM SCHA 70 the extensive secondary palate covers the vomer. The vomer pillar, however, seems to have been crushed between the articulating maxillae during compaction, creating a small mound surrounded by many cracks and fissures. This generally agrees with the condition seen in *Solnhofia*. Like in JM SCHA 70, Parsons and Williams (1961) were not able to find a palatal exposure of the vomer in the type specimen of *Solnhofia*. In contrast, Gaffney (1975b) was able to find a slim palatal exposure of the vomer that prevents a medial contact of the maxillae.

*Palatine.*—The palatines of JM SCHA 70 are unique in that they meet medially in palatal view over their full length forming the entire floor of the apertura narium interna. This is also seen in *Solnhofia* but not in *Plesiochelys* where the vomer completely separates the palatines. Posteromedially the palatine meets the pterygoid. Laterally it meets the anterior process of the pterygoid and forms the medial rim of the foramen palatinum posterius (Gaffney, 1975b). Anterolaterally, a ventral process of the palatine meets the maxilla to form part of the secondary palate and the rim of the apertura narium interna. Dorsally the palatine is visible inside the orbit, forming the posterior rim of the foramen orbito-nasale and contacting the maxilla and jugal laterally.

*Pterygoid.*—The pterygoid of JM SCHA 70 can only be observed in palatal view. It meets along a sinuous suture with the other pterygoid over the first two thirds of its medial margin, and with the triangular basisphenoid over the remaining one third. Posteriorly the pterygoid contacts the basioccipital, forms the ventral margin of the fenestra postotica, and sends a long process posteroventrally towards the articular surface of the quadrate. The lateral part of the pterygoid forms the concave medial rim of the fenestra subtemporalis. In comparison to *Plesiochelys*, the processus pterygoideus externus is not a large projection that intrudes the fossa temporalis interior, but rather a small reduced process similar to that of *Solnhofia* and living chelonians (Gaffney, 1975b). The faint attachment site of the pterygoideus jaw musculature starts along the pterygoid articulation with the maxilla and then extends from the processus pterygoideus externus towards the basioccipital in a concave arch (Gaffney, 1976). The pterygoid sends a process anteriorly to meet the maxilla and jugal, enclosing the foramen palatinum posterius, as seen in *Solnhofia*. In *Plesiochelys* the foramen palatinum posterius is an open concavity surrounded only medially by the palatine and the pterygoid. Anteriorly the pterygoid of JM SCHA 70 meets the palatine. In *Solnhofia* the pterygoids form a blunt wedge between the palatines. It is difficult to assess to what extent this occurs in JM SCHA 70 because the region is covered by one of the hyoids.

*Basisphenoid.*—The flat basisphenoid is shaped like a blunt equilateral triangle. It meets the pterygoid anterolaterally and the basioccipital posteriorly along a convex suture. The size of the basisphenoid relative to the pterygoid is similar in *Solnhofia* and

JM SCHA 70. *Plesiochelys* has a comparatively larger basisphenoid.

*Prootic.*—Only the anteroventral part of the prootic can be seen in palatal view through the fenestra subtemporalis. The bone contacts the epipterygoid laterally along a vaguely visible suture and posteriorly meets the quadrate. As in *Solnhofia*, the prootic forms the entire ventral surface of the processus trochlearis oticum. In contrast, the processus trochlearis oticum of *Plesiochelys* is formed by the quadrate and prootic together.

*Epipterygoid.*—Only the left epipterygoid can be partially observed in palatal view. Its sutures, however, are rather unclear, due to the recrystallization of the bones. Nevertheless, it can be inferred that the epipterygoid meets the prootic and quadrate posterolaterally and the pterygoid ventromedially. Tentatively, the epipterygoid also touches the jugal anteriorly.

*Opisthotic.*—The opisthotic is only visible in palatal view. It is roughly rectangular and oriented diagonally. Medially it meets the exoccipital, posterolaterally the squamosal, and anterolaterally the quadrate beneath the condylus mandibularis. Anteriorly it forms the dorsal rim of the fenestra postotica and the posteromedial edge of the cranium.

*Quadrate.*—The quadrate of JM SCHA 70 generally resembles that of *Plesiochelys*, but is most similar to that of *Solnhofia*. Laterally it forms the kidney-shaped cavum tympani. Anteriorly the quadrate extends dorsally into the fossa temporalis inferior, almost reaching the processus trochlearis oticum. Inside the fossa temporalis inferior, it meets the pterygoid medially, the epipterygoid and prootic anterodorsally, and the jugal laterally. Posteriorly the quadrate meets the squamosal and posteromedially the opisthotic. Parallel to the border of the opisthotic it forms the incisura columella auris, and sends a process ventrally to form the condylus mandibularis.

*Basioccipital.*—The basioccipital forms the tubercula basioccipitale and the central portion of the condylus occipitalis. Similar to *Solnhofia*, the basioccipital meets the pterygoids and basisphenoid anteriorly along a sinuous border. In contrast, the basioccipital of *Plesiochelys* anteriorly meets the basisphenoid only. Posterolaterally the basioccipital of JM SCHA 70 contacts the exoccipital.

*Exoccipital.*—Most of the exoccipital is not visible because the occiput is not fully prepared. Medially the exoccipital meets the basioccipital and forms the lateral rim of the condylus occipitalis. Anteriorly it meets the pterygoid and anterolaterally the opisthotic. The posterior rim is free.

*Supraoccipital.*—Only the posterior projection of the supraoccipital, which forms the crista supraoccipitalis, can be observed in palatal view. The anterior contact with the exoccipital is concealed by the condylus occipitalis. The crista extends posteriorly to the same level as the squamosal horns. An elongate crista supraoccipitalis is known from *Plesiochelys planiceps* (Gaffney, 1975a). Other members of the genera *Plesiochelys* and "*Thalassemys*", however, have a comparably short crista supraoccipitalis (Gaffney, 1975b, Rieppel, 1980). The crista of the type specimen of *Solnhofia* is heavily eroded, making it impossible to estimate its length.

*Mandible (Figs. 4–6, 8.2).*—Only the genera *Plesiochelys*, *Portlandemys*, and *Solnhofia* have adequately described mandibles (Gaffney, 1975a, 1975b, 1976), which can be compared to the lower jaw of JM SCHA 70.

*Dentary.*—The ramus of the lower jaw are medially fused in an extensive symphysis, which is similar to that of *Solnhofia*. The triturating surface is large and smooth, sculptured only by a flat medial trough. High lingual and tomial ridges, as seen in *Plesiochelys*, are absent in JM SCHA 70. Posterolaterally the dentary meets the coronoid and the surangular. On the medial surface of each ramus, the dentary encloses the splenial dorsally



TABLE 1—Measurements of *Solnhofia parsonsi* (JM SCHA 70) from the Upper Jurassic of Germany. All measurements are given in millimeters.

skull, from tip of snout to occipital condyle	59
skull, length including crista supraoccipitalis	71
skull width between the lateral margins of the quadrates	36
skull, maximum width	40
carapace, length along midline	184
carapace, maximum width (between peripherals seven and eight)	167
humerus, length	36
radius, length	18
ulna, length	19
metacarpal, length of the longest element (metacarpal IV?)	10
coracoid, length	21
femur, length	41
tibia, length	28
fibula, length	27
metatarsal, length of the longest elements (metatarsal II and III)	13

and ventrally. The posteroventral contact with the angular is only partially visible in ventral view.

**Angular.**—The angular is only partially exposed in dorsal and ventral view, and its contacts are mostly hidden by matrix. It meets the dentary on the ventral surface and the splenial and prearticular on the medial surface.

**Surangular.**—The surangular of JM SCHA 70 forms most of the posterolateral surface of the mandible. Anteriorly it meets the dentary and medially, from front to back, the coronoid, the prearticular, and the articular. The surangular also forms the lateral rim of the fossa Meckeli. As seen in *Plesiochelys* and *Solnhofia*, the posterior part of the surangular together with the articular and the posterior part of the prearticular form a flat and expanded area articularis mandibularis.

**Coronoid.**—The coronoid contacts the dentary anterolaterally, the splenial and prearticular lateroventrally, and the surangular posterolaterally. The processus coronoideus is well developed and points posterodorsally.

**Articular.**—In dorsal view the articular is a triangular bone that forms the posterior part of the area articularis mandibularis. It meets the prearticular anteromedially and the surangular anterolaterally. The quadrate articulated with both the articular and surangular, as can be seen from the two articular surfaces. This condition is also developed in *Plesiochelys* and *Solnhofia*.

**Prearticular and splenial.**—The suture between the prearticular and splenial is unclear due to strong recrystallization and compaction of the bones. However, it probably was positioned as seen in *Solnhofia*. Together these bones form the flat medial surface of the jaw ramus. Anteriorly the splenial is embraced by the dentary. Dorsally it meets the coronoid and the surangular and forms the medial border of the fossa Meckeli. Ventrally the splenial meets the dentary and the angular.

**Carapace and plastron (Figs. 2, 3, 1, 8, 1, 9, 3; Table 1).**—The list of European Upper Jurassic turtle genera based on carapaces and plastra of varying completeness is seemingly endless. To simplify, the shell of JM SCHA 70 will mainly be compared to the following, sufficiently understood species and genera: *Eurysternum wagleri* H. v. Meyer, 1839b, as described by H. v. Meyer (1839b) and Zittel (1877); *Eurysternum ignoratum* Bräm, 1965, as described by Bräm (1965); *Idiochelys* H. v. Meyer, 1839a, as described by H. v. Meyer (1839a) and Rüttimeyer (1873); *Plesiochelys "etalloni"* (Pictet and Humbert, 1857), as described by Bräm (1965); and *Thalassemys hugii* Rüttimeyer,

1873, as described by Bräm (1965). According to Lapparent de Broin et al. (1996) the material described by Bräm (1965) as *Plesiochelys "etalloni"* actually represents *Plesiochelys solodurensis* Rüttimeyer, 1873.

**Carapace.**—In general, the outline of the carapace strongly resembles *Eurysternum wagleri*. Instead of having an oval outline, as seen in *Plesiochelys "etalloni"* and *Idiochelys*, the carapace steadily widens from the third to the seventh peripheral, creating a peculiar, almost pentagonal appearance. A sinuous nuchal notch characterizes the anterior end. The posterior end differs from *Eurysternum wagleri* in lacking a pronounced pygal notch, but rather shows a smooth and rounded margin.

**Fontanelles of the carapace.**—Some costals are not fully ossified in JM SCHA 70 which results in open peripheral fontanelles and in uncovered distal ends of the corresponding ribs. Especially the ribs belonging to costals two to four are not covered dorsally by dermal bone. It is hard to evaluate how large the fontanelles were in the living animal as the ribs were drawn from their sockets in the peripherals during compaction. Thus the fontanelles appear larger than they probably were. Several minor peripheral fontanelles are situated between the costals six through eight. Two more major fontanelles are present between the suprapygal, the pygal, the terminal costals, and the terminal peripherals. Peripheral fontanelles, a juvenile feature retained in some adults (Rüttimeyer, 1873), are known from all European Upper Jurassic turtles except for *Plesiochelys*, *Craspedochelys*, *Tropidemys*, and *Thalassemys*.

**Neurals.**—The neurals resemble those of *Eurysternum wagleri* and *Thalassemys hugii*. Although they vary in shape, they are all roughly hexagonal. The first neural is the largest in the series. Despite the fact that compaction has greatly distorted its shape, it can be seen that the first neural formed a roughly equilateral hexagon with a concavity along the anterior border. The second through fifth neurals are similar in length to the first but narrow increasingly towards the posterior end of the carapace, forming elongate irregular hexagons. Neural six through eight are shorter than the previous ones. Neurals seven and eight form equilateral hexagons. The neurals of *Plesiochelys "etalloni,"* in comparison, are more regular in shape while the neurals of *Idiochelys* are reduced both in number and size.

**Costals.**—The central part of the carapace was crushed during diagenesis, shattering the costals into many pieces and disturbing their position. From what can be seen, the eight pairs of costal bones show no special characters. Like in most other turtles, their borders lie parallel to one another and perpendicular to the longitudinal axis. Only the two posteriormost pairs are wedge-shaped and curve backwards. The first through third elements are the longest, the following steadily decrease in length.

**Nuchal.**—The anterior margin of the very wide and short nuchal is approximately half as wide as the posterior margin. Both borders are smooth and curve posteriorly. This trapezoidal outline can also be observed in *Idiochelys* and some specimens assigned to the genus *Eurysternum*. Other genera, such as *Plesiochelys*, typically have a rectangular nuchal with a small posterior notch for articulation with the first neural.

**Peripherals.**—Most of the eleven pairs of peripherals are still articulated, forming the pentagonal outline of the carapace described above. A small, supernumerary bone can be clearly seen in ventral view between the nuchal and the first left peripheral. The peripherals one through seven are longer than wide, while

FIGURE 7—*Solnhofia parsonsi* (JM SCHA 70), Upper Jurassic, Germany. 1, Right coracoid and scapula, cervical vertebrae, and ulnae; 2, left humerus and scapula, radii, and parts of the left manus; 3, hind limbs. Scale bars equal 1 cm.



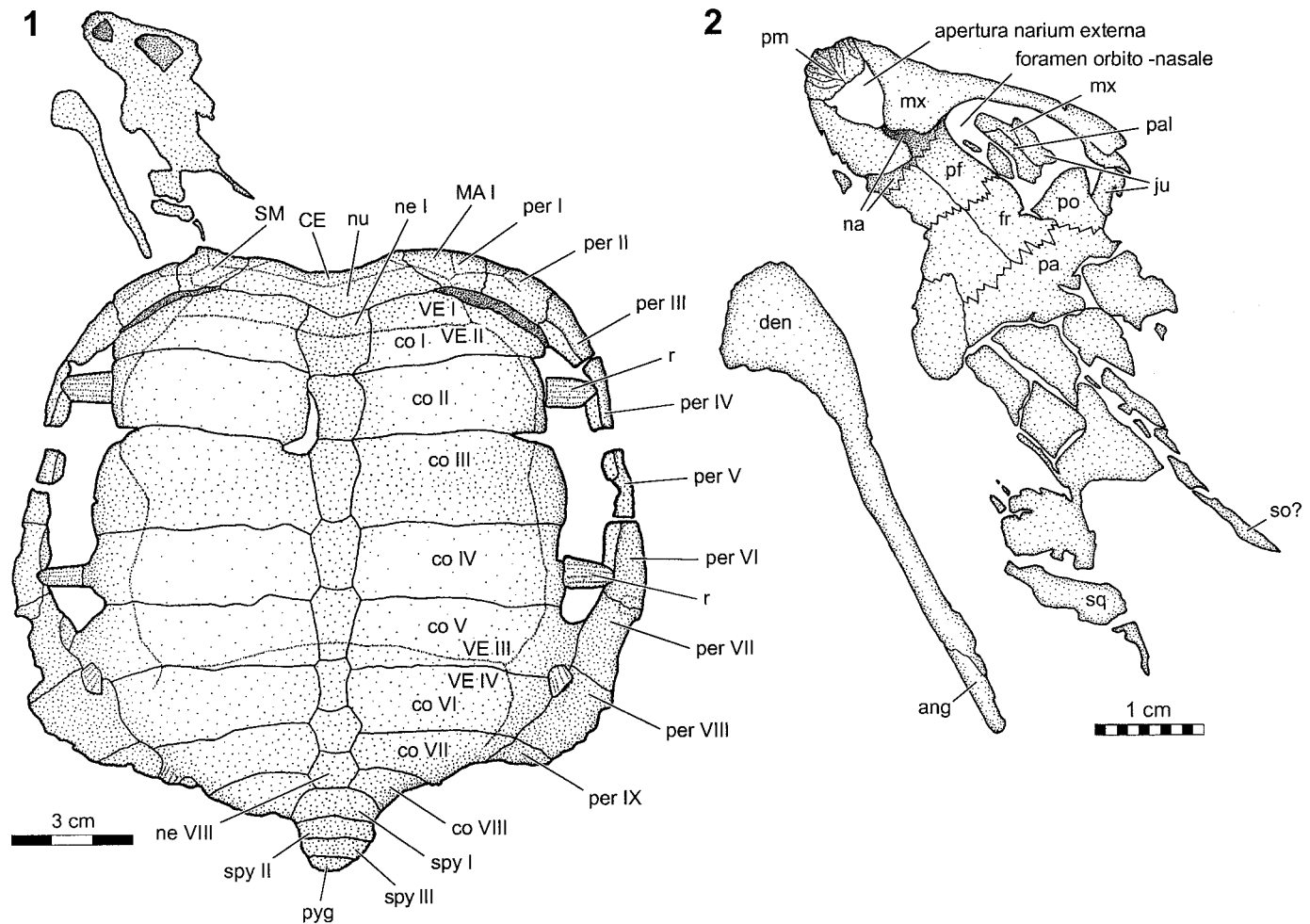


FIGURE 8—*Solnhofia parsonsi* (JM SCHA 70), Upper Jurassic, Germany; 1, complete skeleton as seen in dorsal view; 2, enlargement of the dorsal view of the cranium and ventral view of the mandible. Abbreviations: ang, angular; CE, cervical scute; co, costal bone; den, dentary; fr, frontal; ju, jugal; MA, marginal scute; mx, maxilla; na, nasal; ne, neural bone; nu, nuchal bone; pa, parietal; pal, palatine; per, peripheral bone; pf, prefrontal; pm, premaxilla; po, postorbital; pyg, pygal bone; r, rib; SM, supramarginal scute; so, supraoccipital; spy, suprapygal bone; sq, squamosal; VE, vertebral scute.

peripherals eight through eleven are wider than long. The second, third, sixth, and seventh peripherals have small vacuities along their ventromedial edge that serve as loose articulation sites for the plastron. *Plesiochelys "etalloni"* has a more strongly fused bridge than JM SCHA 70. The bridges of *Idiochelys* and *Eurysternum wagleri* are less, or equally as well, developed as that of JM SCHA 70.

**Pygal region.**—The pygal region of JM SCHA 70 is characterized by three slim suprapygals and by a large and rectangular pygal with a waist. The pygal is integrated into a continuous belt of similar sized rectangular peripherals. The tightly fused suprapygals firmly connect the central elements with the peripheral ring of the carapace.

The pygal region offers diagnostic characters in many Jurassic turtle genera (Fig. 9). In *Idiochelys* the contact between the most posterior suprapygal and the pygal is not very firm or even absent. In *Plesiochelys* the suprapygals are larger than the pygal, which contrasts the opposite arrangement in JM SCHA 70. The pygal region of *Thalassemys hugii* is not very well known. Nevertheless, it can be inferred that the suprapygal elements are relatively larger than in JM SCHA 70.

The pygal region of *Eurysternum wagleri* is also not well

understood. Unfortunately, the holotype to this genus and species was destroyed, making it impossible to verify either the description given by H. v. Meyer (1839b) or the included figure drawn by the artist C. Hohe. Consequently, the specimen described by Zittel (1877) should be favored as this original can still be seen in Munich, Germany. Unlike H. v. Meyer (1839b), Zittel (1877) only described the presence of one pygal element instead of several (Lapparent de Broin et al., 1996). Instead, the specimen exhibits at least two pygal elements. One is interpreted here as a large pygal and the other as a rather narrow suprapygal. The most apparent feature that distinguishes *Eurysternum wagleri* from JM SCHA 70 is the well-developed pygal notch.

**Plastron.**—The plastron is less ossified than in *Plesiochelys* and *Idiochelys*, but more heavily ossified than in *Eurysternum wagleri*. Its general outline is somewhat similar to that of *Plesiochelys "etalloni"*, differing in that it is shorter and lacks the epiplastra and the entoplastron. These plastral elements were likely present in the living animal but are not preserved either because they were not ossified or not firmly attached to the rest of the plastron. Mesoplastra are also absent, a character considered a synapomorphy of eucryptodires (Gaffney and Meylan, 1988).

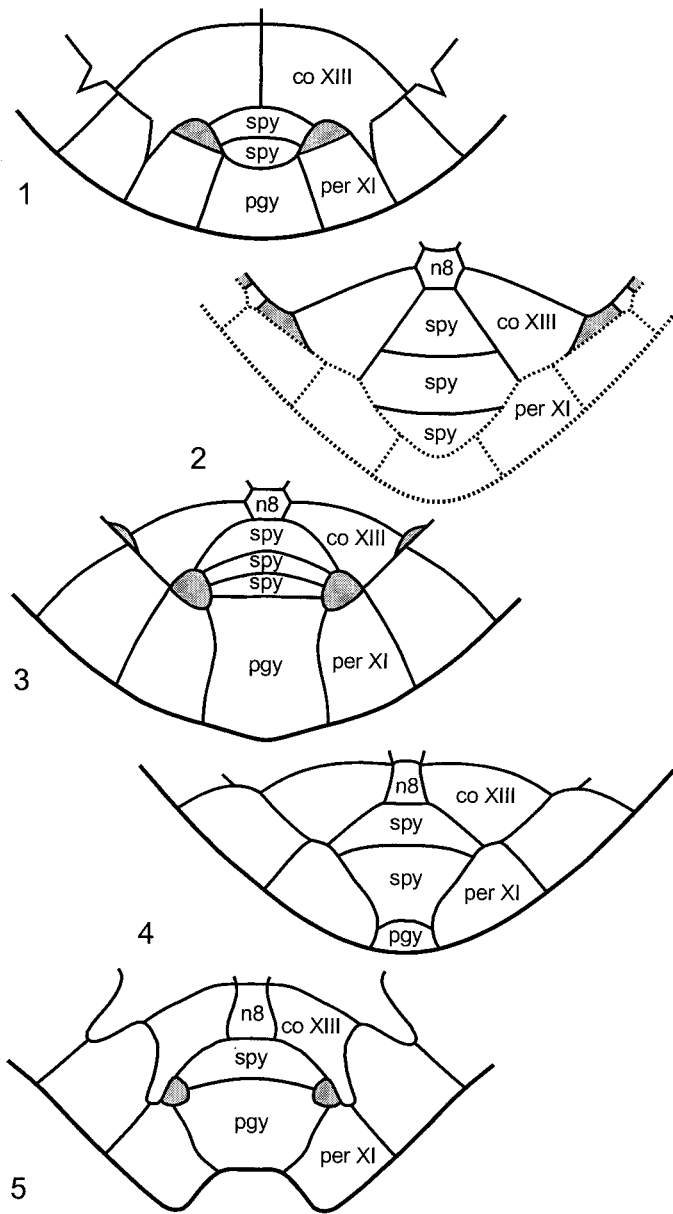


FIGURE 9—Pygal region of 1, *Idiochelys* (from Rüttimeyer, 1873); 2, *Thalassemys hugii* (from Bräm, 1965); 3, JM SCHA 70; 4, *Plesiochelys "etalloni"* (from Bräm, 1965); and 5, *Eurysternum wagleri* (after Zittel, 1877). Grey fields are fontanelles. Abbreviations: co, costal; n8, neural 8; per, peripheral; pyg, pygal; spy, supra-pygals.

The anteromedial border of the hyoplastron is lined by a row of free processes. The missing entoplastron created a wide notch between the hyoplastra. The posterior edge of the xiphiplastra is lined by a similar, but much shorter, row of small processes. However, the opening between the xiphiplastra is likely due to compaction.

The central plastral fontanelle is similar in shape to that of *Plesiochelys "etalloni,"* but it is larger and lies more anteriorly, partially separating the hyoplastron from the hypoplastron and the pectoral from the abdominal scutes. Bridge fontanelles are also present, semilunate in shape, and located roughly at the same level as the central fontanelles. The fifth and sixth peripherals form their lateral border.

The axillary buttress of the hyoplastron terminates at the posterior half of the second peripheral, and the inguinal buttress of the hypoplastron terminates between the seventh and the eighth peripheral. In *Plesiochelys "etalloni"* the axillary buttresses terminate at the third and the inguinal buttress at the beginning of the eighth peripheral.

*Scutes of the carapace (Figs. 2, 3.1, 8.1).*—The sulci of the anteriorly positioned scutes are well developed, whereas those of the more posterior ones are less developed to invisible. The area of the cervical scute is still partially covered by matrix. The posterior margin of the cervical scute paralleled the outline of the carapace across the entire nuchal. Anteriorly the outline of the cervical scute decreases more abruptly in width than the nuchal, creating a trapezoid outline. In *Thalassemys hugii* and *Eurysternum (Palaeomedusa)*, the cervical scute was considerably narrower than the nuchal, whereas in *Idiochelys* the cervical scute was wider than the nuchal. *Plesiochelys* had three cervical scutes.

The sulci of the vertebral scutes of JM SCHA 70 are poorly preserved. Only the outline of the first vertebral scute can be identified with confidence. It contacted the cervical scute anteriorly and expanded posteriorly onto the middle of the first costal forming a trapezoid. Anterolaterally, it met with the marginal scutes and laterally with the pleural scutes. The outlines of the succeeding vertebral scutes are very vague. They only can be inferred to have been very wide, almost covering the entire dorsal surface of the carapace like in most other European Upper Jurassic turtles. Unlike in *Eurysternum wagleri* and *Idiochelys*, the vertebral scutes of JM SCHA 70 and of *Plesiochelys* were more rectangular than hexagonal. *Eurysternum ignoratum* is defined by having had very narrow vertebral scutes.

The sulci of only the three anteriormost pairs of marginal scutes can be traced in the dorsal view of JM SCHA 70. Ventrally they are invisible. On the right side, the first marginal scute was triangular with the blunt apex contacting the first pleural scute. Posteromedially it met the cervical and first vertebral scute. On the left side a small, supernumerary, submarginal scute was squeezed in between the marginal ring and the first vertebral scute. According to Zangerl (1957), shield abnormalities like this occur quite commonly in modern turtles.

*Scutes of the plastron (Figs. 2.1, 3.1).*—Gular and intergular scutes, as well as humeral scutes, cannot be traced due to the lack of the epi- and entoplastron, which normally contain their sulci. The posterior sulcus of the humeral scute should normally be found on the hyoplastron, but it either lies anteriorly to the hyoplastron or its impressions are too vague to be detected. The arrangement of the remaining scutes was similar to that of *Plesiochelys "etalloni."* The sulcus between the pectoral and abdominal scute runs anterior and parallel to the border between the hypo- and hypoplastron. The abdominal and femoral scutes articulated along a line that extends from the deepest point of the inguinal notch to the posterior quarter of the central fontanelle. The border between the anal and femoral scutes takes a similar course to that of *Plesiochelys "etalloni."* However, it cannot be observed if it crosses the border between the hypo- and xiphiplastron medially.

Inframarginal scutes are not discernible in ventral view. The position of the faint lateral border of the pectoral and abdominal scutes, however, strongly resembles *Plesiochelys* in its position and suggests either extremely wide marginal scutes or, more likely, a row of inframarginals similar to those of *Plesiochelys*.

*Vertebral column (Figs. 3.2, 3.4, 7.1, 7.3).*—The vertebrae of Upper Jurassic turtles are occasionally preserved but have been poorly described in the literature. Rather, early workers concentrated on the morphology of the shell, reducing their observations to the general shape of the vertebrae and the number of

elements found in each vertebral region. The cervicals of *Idiochelys* were briefly described by Rüttimeyer (1873) and the caudals by H. v. Meyer (1839a) and Rüttimeyer (1873). The cervicals of *Eurysternum wagleri* are preserved in the "*Palaeomedusa*" specimen (H. v. Meyer, 1860). Zittel (1877) mentions the cervicals and caudals of an additional specimen of *Eurysternum wagleri*. The only detailed descriptions of vertebrae were given by Bräm (1965), who described four cervical vertebrae of the genus *Plesiochelys* and three more of the genus *Thalassemys* (sensu Rüttimeyer, 1873, non Rieppel, 1980) and by Wellnhofer (1967), who described the caudals of a turtle loosely attributed to the family Thalassemydidae. Due to the scarcity of comparative material, the vertebrae of JM SCHA 70 will also be compared to the primitive Triassic turtle *Proganochelys* as well as to the extant forms *Macrolemys* and *Podocnemis*, all of which have been described in detail by Gaffney (1990).

**Cervical vertebrae.**—It is assumed that, like in all other turtles (Romer, 1956; Gaffney, 1990), JM SCHA 70 has eight cervical vertebrae, of which only the first seven can be observed in ventrolateral view. The eighth and most of the seventh cervical are still covered by the matrix underneath the plastron.

The atlas of turtles generally consists of an intercentrum, a centrum, and the neural arch elements (Gaffney, 1990). In JM SCHA 70 these elements are well fused, the suture between the centrum and the surrounding elements being the weakest. Most of the dorsal part of the neural arch is still buried in matrix. The posteriorly directed flange that articulates with the prezygapophyses of the axis (Gaffney, 1990) is not visible. It is consequently either covered by matrix or has been damaged by taphonomic processes or preparation. Anteroventrally the neural arch is tightly fused with the intercentrum, posteroventrally it connects with the centrum. The centrum is a small wedge between the intercentrum of the atlas and the centrum of the axis.

The axis mediates morphologically between the atlas anteriorly and the following cervicals posteriorly. In modern turtles, the axial prezygapophyses differ from the others in facing dorsolaterally, whereas the following ones face dorsomedially (Gaffney, 1990). The outline of the axial prezygapophyses of JM SCHA 70 cannot be clearly observed. However, it is likely that they were oriented as in modern turtles. As in *Proganochelys*, the axis has a notch anteroventrally for the attachment with the atlas centrum.

The size ratio between the atlas and axis is strikingly similar to some extant turtles. In *Proganochelys* these two vertebrae are roughly the same size. In contrast, the atlas is only half the size of the axis in JM SCHA 70, *Macrolemys*, and *Podocnemis*.

Cervicals three through seven of JM SCHA 70 are only slightly larger than the axis, the posterior elements being the largest. They generally resemble the cervical vertebrae of *Plesiochelys* as described by Bräm (1965) in being short but very wide (including the zygapophyses). The centra, including that of the axis, are ventrally constricted to form a keel, as also can be seen in *Proganochelys*. Although the articular surfaces are not fully prepared, they seem to be amphicoelous, which is a primitive trait of early turtles (Gaffney and Meylan, 1988).

The prezygapophyses protrude anterodorsally and laterally and the postzygapophyses posterodorsally and laterally, giving the vertebrae their short and wide shape. Because the vertebrae were crushed during diagenesis, it is difficult to assess to what extent the articular plane of the zygapophyses was tilted medially from the horizontal plane, which is a characteristic of modern turtles (Gaffney, 1990).

Short and stout transverse processes are developed along the anterolateral edge of the cervicals. These appear not to be involved in the articulation of any ribs. Cervical ribs are only known from primitive turtles such as *Proganochelys* (Gaffney,

1990), *Meiolania* (Gaffney, 1985), *Ordosemys* (Brinkman and Peng, 1993), and *Eubaena* (Brinkman and Nicholls, 1993).

**Dorsal and sacral vertebrae.**—Dorsal and sacral vertebrae cannot be observed in JM SCHA 70.

**Caudal vertebrae.**—A string of twelve poorly preserved proximal caudal vertebrae are exposed in ventral view, just posterior to the plastron. An additional four distal vertebrae lie next to the right femur. A caudal count totaling only sixteen vertebrae is rather low in comparison to other Upper Jurassic taxa. *Idiochelys*, for instance, has 22 to 23 long and slender vertebrae (H. v. Meyer, 1839a; Rüttimeyer, 1873). *Eurysternum* possesses a short and stout tail with at least 19 caudal vertebrae (Zittel, 1877). Therefore it is likely that several vertebrae are missing in JM SCHA 70. This hypothesis is supported by the significant size difference between the terminal vertebrae of the proximal string and the size of the distal vertebrae. It is possible that additional elements were preserved but remain hidden underneath the plastron. The density of the bone of the shell makes it impossible to verify this on X-ray photographs. The total length of the tail was presumably intermediate between *Idiochelys* and *Eurysternum*. To simplify the description, the proximal caudals of JM SCHA 70 will be numbered one through twelve.

The caudals decrease rapidly in size, the first being roughly double the size of the twelfth. The proximal four caudals are only one third of the length of the first. The centra are elongate and show a moderately developed keel. The pre- and postzygapophyses are adequately preserved only in caudals four through six. Like in the cervicals, the zygapophyses are well developed and greatly extend dorsolaterally and ventrolaterally. Similar to *Idiochelys*, the caudals have well-developed transverse processes which are only preserved in caudals one and five. In caudal one these processes are directed anterolaterally and in caudal five posterolaterally.

**Pectoral girdle (Figs. 3.2, 3.3, 7.1, 7.2; Table 1).**—H. v. Meyer (1839b) described the pectoral girdle of *Eurysternum*, while Bräm (1965) described material from the Solothurn quarries that he attributed to *Plesiochelys*, *Thalassemys* (sensu Rüttimeyer, 1873, non Rieppel, 1980), and *Eurysternum ignoratum*. In JM SCHA 70 the right coracoid and the scapulae are present, but it is rather difficult to assess their original shape as they have been crushed during diagenesis and are partially covered by other bones and matrix.

**Scapula.**—The left scapula of JM SCHA 70 can be observed in lateral view and the right one in medial view. The scapula basically resembles that of modern turtles. It is triradiate with a long, dorsally projecting scapular process, a well developed, ventromedially projecting acromial process, and a laterally facing glenoid on top of an elongate "neck". The scapular process is long and slender and hidden by the plastron on both sides. However, the scapular process of the left scapula can be faintly traced on a radiograph. The acromial process is rather flat and roughly 75 percent of the length of the scapular process. Bräm (1965) measured ratios of 80 percent for *Thalassemys*, 75 percent for *Eurysternum*, and 60–80 percent for *Plesiochelys*, concluding that lower ratios were typical for ontogenetically younger specimens. The angle between these two processes is hard to determine in JM SCHA 70 as the scapulae have been heavily crushed during diagenesis, but it can be estimated to be around 115 degrees. This value is more comparable to *Thalassemys* (117 degrees) and *Eurysternum ignoratum* (118 degrees) than to *Plesiochelys* (102–104 degrees).

The glenoid and articular surface of the coracoid can be best observed in the left scapula. As in *Thalassemys*, *Eurysternum*, and *Plesiochelys*, the glenoid is set on a "neck" that helps the turtle to extend its limbs further laterally. This is a characteristic typical for extant turtles adapted to swimming (Bräm, 1965).

*Coracoid*.—Only the right coracoid can be clearly identified, squeezed between the left scapula and the ulnae. Anteriorly it was in contact with the scapula and formed part of the glenoid. Posteriorly it is expanded, as in other turtles, although the extent of the expansion cannot be estimated as it is covered by the scapula. The coracoid is much shorter than the scapular process of the scapula, a character typical of modern fresh water turtles and tortoises and also seen in *Thalassemys*, *Eurysternum*, and *Plesiochelys*.

*Pelvic girdle* (Figs. 2.1, 3.1).—Pelvic girdles have only been described in a thalassemydid turtle (Wellnhofer, 1967), *Plesiochelys*, *Thalassemys*, and *Eurysternum ignoratum* (Bräm, 1965). The pelvic girdle of JM SCHA 70 suffers from extensive disarticulation. Of the bones that make up the pelvic girdle, only the pubis and part of the ischium can be identified. The comparison of the fragmentary pelvic elements of JM SCHA 70 to the scanty descriptions in literature requires some interpretation.

*Pubis*.—The disarticulated pubis lies in the right inguinal notch. Like in most other European Upper Jurassic turtles it is a triradiate bone with three short and stout processes. The distal ends are either eroded or show no specific features, such as articular surfaces. As a consequence, defining the orientation is speculative.

*Ischium*.—A curved, pointed process can be observed just anterior to the right femur. This is interpreted to be the caudal process of the ischium. It is more curved than the caudal process of thalassemydid described by Wellnhofer (1967). As with the pubis, however, this interpretation is tentative.

*Forelimbs* (Figs. 3.3, 7.2; Table 1).—Several limbs of European Jurassic turtle genera have been completely preserved in the lithographic limestones of southern Germany and France. Forelimbs are well known from *Idiochelys fitzingeri* H. v. Meyer, 1839a (H. v. Meyer, 1839a). The forelimbs of *Aplax oberndorferi* H. v. Meyer, 1843, *Achelonia formosa* H. v. Meyer, 1860, *Palaeomedusa testa* H. v. Meyer, 1860, and *Parachelys eichstaettensis* H. v. Meyer, 1864, are either known from juvenile or fragmentary material and, at various times, have been associated with *Eurysternum* (Wagner, 1861a, 1861b; Rüttimeyer, 1873; Zittel, 1877) or *Idiochelys* (Wagner, 1861b).

*Humerus*.—Only the left humerus of JM SCHA 70 is preserved and can be seen in ventral view. Its shaft is slightly sinuous in anterior and posterior view and forms a round, narrow waist at the proximal third. The lateral process expands anteriorly and is topped by a strong ventrally projecting crest. The medial process, in contrast, only extends posteriorly along the horizontal plane. Together these processes form a rounded, proximal articular surface. Only the lateral process clearly defines the boundary of the intertubercular fossa. Distally the humerus expands less prominently along the horizontal plane, forming a rounded articular surface.

*Radius*.—Both radii are positioned parallel to one another with the ends partially covered by the humerus and the shell. They are rather short, slim elements with only very slight terminal expansions. It is not clear which of the elements is the right and the left and how they are oriented.

*Ulna*.—Both ulnae are closely packed between the cervical vertebrae and the right scapula. Again, left and right cannot be distinguished. Only the more anteriorly located ulna can be fully observed. It is slightly curved and has moderate expansions at both ends. Proximally, no clear olecranon fossa is developed. Distally, the bone has two equally sized articular surfaces for the carpal articulation.

*Carpus*.—Only five carpal elements of the left carpus are present. Since they are poorly preserved and disarticulated from one another, their identification is highly speculative. The carpals

are round to oval. The largest are roughly half the size of the largest phalanx.

*Manus*.—Three metatarsals and some phalanges are all that remains of the left manus. The most laterally positioned metatarsal is associated with one proximal phalanx, the other two are each associated with three. All metatarsals are long and narrow. The middle metatarsal is the longest, being roughly twice the length of the phalanges. In *Eurysternum*, *Achelonia*, and *Palaeomedusa*, the third, fourth, and fifth metatarsal are slender elements, the fourth always being the longest. Consequently, the elements of JM SCHA 70 can tentatively be assigned to digits three, four, and five, resulting in a digital formula of least ?-?-?-3-3.

*Hind limbs* (Figs. 3.4, 7.3; Table 1).—Hind limbs are known in *Eurysternum wagleri* H. v. Meyer, 1839b, were described by H. v. Meyer (1839b) and Zittel (1877), and reviewed by Wellnhofer (1967). The hind limbs of *Idiochelys fitzingeri* H. v. Meyer, 1839a were described by H. v. Meyer (1839a) and Jourdan (1862). Unfortunately, most descriptions are not very precise and the accompanying drawings are schematic, making a close comparison of these genera difficult. The position of the hind limbs of JM SCHA 70 and the degree of disarticulation are described in the taphonomy section.

*Femur*.—The right femur can be seen in dorsal view, and the left femur in ventral view. The femoral shaft is round in cross section and slightly arched dorsally. The hemispherical articular head projects dorsally from the shaft, away from the long axis of the bone. The proximal third of the femur expands towards the trochanter minor anteriorly and the strongly developed trochanter major posterodorsally. Between the trochanters lies the V-shaped intertrochanteric fossa. The distal half of the femur is less expanded than the proximal end. Articular surfaces are not clearly developed.

*Tibia and fibula*.—The tibia and fibula are of roughly the same length. The tibia has a short cylindrical shaft and is slightly curved. It expands at both ends to roughly twice the width of the shaft. The fibula is a long, slightly curved, slender element with a wide distal expansion. Together with the tibia it encloses a fusiform spatium interosseum. Only the distal articular surfaces of the zeugopodium are clear. The expanded fibula bears the articular surfaces of the laterally positioned calcaneum and the medially located astragalus. As in all turtles, the distal end of the tibia articulates with the calcaneum only.

*Tarsus*.—The astragalus is the largest element in the tarsus. In ventral view it is roughly hexagonal. Proximally it articulates with the tibia and fibula. Medially it tightly articulates with the calcaneum. In modern turtles these two elements are commonly fused (Romer, 1956). Distally the astragalus articulates with the second, third, fourth, and presumably also with the first, tarsal. The calcaneum is a small, square bone. Medially it meets the astragalus, proximally the fibula, and distally the fourth tarsal.

The distal row of tarsals contains four elements. The position of the first distal tarsal is unclear as it is covered by the left tibia in the left foot and is disarticulated in the right foot. It likely lines up in a row together with the other three tarsal elements as is seen in most turtles. The tarsals increase in size from the first to the fourth. The first two are roughly isometric, whereas the other two are elongate distally. All four bones articulate with the astragalus proximally. The fourth tarsal additionally meets the calcaneum proximally and the fifth metatarsal laterally.

*Pes*.—The second through fifth metatarsals are well preserved and in articulation in the left pes. The first metatarsal is also in place but concealed by the right tibia. Turtles have a special arrangement in the foot where the fifth metatarsal has a unique shape that resembles and functions as a tarsal element. As a substitute for the true metatarsal the first phalanx of the fifth

digit is elongate and thus resembles a metatarsal. The same arrangement is seen in JM SCHA 70. The fifth metatarsal is roughly rectangular with a small mediiodistal notch for the fourth metatarsal. This permits the fifth digit to freely extend and flex, enlarging or decreasing the surface of the foot (Wellnhofer, 1967). From what can be seen in the left pes, the first metatarsal is rather short and strong. The left femur conceals its proximal articulation. The second metatarsal is longer than the first, the third and fourth metatarsals are the longest, i.e., twice as long as most phalanges. The functional fifth metatarsal, which actually is the first phalanx, is as long as the second metatarsal but is much slimmer.

The phalanges are complete but somewhat scattered in the left foot. The digital formula adds up to 2-3-3-3-3. The distal elements are claw bearing. The intervening phalanges are rather short and stout. Only the elements of the fifth digit appear to be very delicate. The first phalanx of which is elongate and slender, and functions as the metatarsal as mentioned previously. The two distal elements are quite short and fragile, together only attaining to the length of one normal phalanx.

The pes of *Idiochelys* differs from other European Jurassic turtles in having a digital formula of 2-3-3-3-2 and a long, narrow fifth metatarsal (H. v. Meyer, 1839a). H. v. Meyer (1839b) also determined a digital formula of 2-3-3-3-2 for *Eurysternum wagneri*, believing the functional fifth metatarsal to be a true metatarsal. Wellnhofer (1967) corrected this mistake. It is obvious that H. v. Meyer (1839a) and Jourdan (1862) made the same mistake with *Idiochelys*. Therefore, *Eurysternum*, *Idiochelys*, and JM SCHA 70 all have similar hind limbs, with *Idiochelys* being notably smaller. A close reexamination of the hind limb morphology of *Eurysternum* and *Idiochelys* may help to further distinguish the morphology of these two genera from that of JM SCHA 70.

#### DISCUSSION

*Generic attribution of JM SCHA 70.*—Lapparent de Broin et al. (1996) were the first to assign JM SCHA 70 to the genus *Solnhofia*, based on the photographs published in Frickhinger (1994). Their assignment was rooted in the overall resemblance of the cranium of JM SCHA 70 to that of the *Solnhofia* type specimen. However, they were not able to determine the exact species of JM SCHA 70 based on the photographs.

JM SCHA 70 can be confidently assigned to *Solnhofia* due to the unique development of the extensive secondary palate. Other attributes, such as the elongation of the snout beyond the apertura narium externa, the limited temporal emargination, the greatly reduced vomer that does not separate the palatines, the long suture between the ramus of the mandible, the smooth triturating surfaces, the extensive processus trochlearis oticum, and the reduction of the processus pterygoideus and foramen palatinum posterius are all characters of *Solnhofia* which can be seen in JM SCHA 70. These clearly observable features substantiate the attribution of JM SCHA 70 to *Solnhofia* and distinguish the cranium of JM SCHA 70 from those of *Plesiochelys*, *Thalassemys* (non Rüttimeyer, 1873, sensu Rieppel, 1980), and *Portlandemys*.

Other Jurassic turtle genera, such as *Eurysternum* and *Idiochelys*, have occasionally been preserved with crania but have not been sufficiently described to differentiate them from *Solnhofia* based on morphological characters. However, Lapparent de Broin et al. (1996) noticed that these genera differ from *Solnhofia* by the relative size of their cranium. *Idiochelys* has a relatively small head by comparison to its carapace (23 percent in the specimens from Cerin), as does *Eurysternum* (20–25 percent in the specimens from Solnhofen). In contrast, *Solnhofia* has a considerably larger head relative to the carapace (40 percent in

JM SCHA 70, 44 percent in a crushed specimen from Canjuers, France), making it possible to distinguish *Solnhofia* from these other genera. The new specimen now allows the genus *Solnhofia* to also be distinguished from other genera in much greater detail based on postcranial characters. Of the postcranium, the pygal region offers the most distinctive characters.

*Plesiochelys* not only differs from *Solnhofia* in the cranium, but also in the absence of bridge and peripheral fontanelles and in the presence of three cervical scutes, well attached epiplastra and an entoplastron, a rectangular nuchal, and a small pygal bone. *Thalassemys* (sensu Rüttimeyer, 1873, non Rieppel, 1980) differs in having well developed suprapygal. Both *Plesiochelys* and *Thalassemys* have substantially larger carapaces than *Solnhofia* (*Thalassemys*: ca. 60 cm; *Plesiochelys* 40–60 cm; *Solnhofia*: ca. 20 cm).

Lapparent de Broin et al. (1996) grouped *Solnhofia* together with *Eurysternum* and *Idiochelys* within the family Eurysternidae. Characters that these taxa share with one another are the presence of a central, plastral fontanelle, bridge fontanelles, and peripheral fontanelles even in adult specimens. Furthermore, they are united by the presence of a trapezoidal nuchal (and consequently a triangular peripheral I), only one cervical, a clear nuchal notch, and very wide vertebral scutes.

Within the Eurysternidae, *Eurysternum* differs from *Solnhofia* not only in the relative size of the head but also in the more strongly developed fontanelles, a less attached bridge, and the development of a pygal notch (Lapparent de Broin et al., 1996). Additional differences can now be observed in the pygal region. The pygal of *Solnhofia* is very large, rectangular, has a waist, and connects to the neurals via three slim suprapygal. Furthermore, *Solnhofia* had rectangular vertebral scutes, compared to the hexagonal ones of *Eurysternum*.

*Idiochelys* differs from *Solnhofia* by being smaller, having reduced neurals, a closed central fontanelle and more rectangular bridge fontanelles (Lapparent de Broin et al., 1996). This can be confirmed and underscored by differences in the pygal region. *Idiochelys*, like *Solnhofia*, has an even ring of posterior peripherals and the pygal; however, the peripheral ring is narrower than in *Solnhofia*, and the suprapygal contact the pygal only slightly, if at all.

*Specific attribution of JM SCHA 70.*—Lapparent de Broin et al. (1996) were able to point out characters in the hypodigm of *Solnhofia parsonsi*, SM 137, that may be considered significant enough to create a new species of *Solnhofia*. SM 137, for instance, is more robust and has a shorter snout than the holotype. By contrast, Gaffney (1975b) considers all the differences between SM 137 and the holotype to be due to poor preservation.

The cranium of JM SCHA 70 shows only minor differences from the holotype. It is slightly smaller (holotype: 73 mm from occipital condyle to the tip of the snout, JM SCHA 70: 59 mm), the exposure of the palatine along the posteromedial rim of the secondary palate is narrower, the basisphenoid is relatively longer, and the squamosal horn and the crista supraoccipitalis are better developed. The skull also looks narrower, but this is probably due to differences in compaction. In summary, the skull of JM SCHA 70 shows no major differences from the holotype of *S. parsonsi*, but differs from the hypodigm SM 137 in the same ways as the holotype does. JM SCHA 70 is thus considered to be the first known complete skeleton of the species *Solnhofia parsonsi*. The size difference to the holotype is credited to the younger ontogenetic stage of the new specimen. The incomplete squamosal horns and crista supraoccipitalis of the type specimen were likely eroded.

*Synonymies.*—Prior to the discovery of JM SCHA 70, Broin (1994) had argued that *Solnhofia* might be the junior synonym of *Euryaspis radians* Wagner, 1859. This species is based on a



fragmentary carapace and differentiated from others by having a domed shell, a wide nuchal, and clearly defined vertebral scutes decorated with a radial pattern. The shell of JM SCHA 70 is relatively domed and has a wide nuchal. However, the vertebral scutes are neither defined by clear sulci nor do they show a radial pattern. Therefore, a synonymy between *Solnhofia parsonsi* and *Euryaspis radians* cannot be confirmed.

Based on what was apparent in the photographs of Frickhinger (1994), Lapparent de Broin et al. (1996) proposed a possible synonymy of *Solnhofia* and *Eurysternum ignoratum* Bräm, 1965. This again cannot be confirmed. *Eurysternum ignoratum* was described by Bräm (1965) based on an incomplete specimen from Solothurn, Switzerland. The specimen consists of some costal bones, the anterior part of the plastron, and remains of the girdles. Unlike *Plesiochelys* and *Thalassemys*, two commonly found genera in Solothurn, the specimen has well developed bridge fontanelles like *Eurysternum*. Unlike *Eurysternum wagneri*, however, the Solothurn specimen has much narrower vertebral scutes, which only cover a quarter to half of the costals. This persuaded Bräm to erect a new species of *Eurysternum*. JM SCHA 70 does not show this character of *Eurysternum ignoratum*. Instead, though not exactly traceable, the vertebral scutes cover more than 75 percent of the costal bones.

Lapparent de Broin et al. (1996) also brought up a possible synonymy of *Hydropelta meyeri* (Thiollière, 1851) with *Solnhofia*. This genus is based on a very fragmentary specimen from Cerin, first described by Thiollière (1851) as *Chelone? meyeri* and later reattributed by H. v. Meyer (1852) to this new genus. The drawing that H. v. Meyer included in his great work on the reptiles of the lithographic limestones (H. v. Meyer, 1860) is very schematic, showing a very incomplete shell in ventral view. Nevertheless, some resemblances with *Solnhofia* are apparent, like the far anteriorly extending axillary buttresses. A close re-examination of this species will be necessary to achieve a better understanding of their relationships. Until the results are published, a synonymy can neither be confirmed nor rejected.

*Phylogenetic position of Solnhofia*.—Gaffney and Meylan (1988) integrated the characters obtained by Gaffney (1975b) from the skull of *Solnhofia* into their phylogenetic analysis and concluded that the position of *Solnhofia* might be close to, but not within, the Plesiochelyidae. Lapparent de Broin et al. (1996) mainly used postcranial characters and grouped *Solnhofia* with *Eurysternum* and *Idiochelys* into the Eurysternidae and considered the Eurysternidae as a possible sister-group to the Plesiochelyidae, which fundamentally corresponds to the results of Gaffney and Meylan (1988). However, the exact placement of *Solnhofia* within the Eurysternidae, and the relationships of the Eurysternidae to the Plesiochelyidae and other Mesozoic turtles still remain unclear (Lapparent de Broin et al., 1996).

A reexamination of the Eurysternidae, a family that includes such genera as *Solnhofia*, *Eurysternum*, and *Idiochelys*, is required in order to better understand phylogenetic relationships of Upper Jurassic turtles.

#### SUMMARY AND CONCLUSIONS

JM SCHA 70 is the first complete skeleton of *Solnhofia parsonsi*, a genus mainly known from cranial characters. The specimen can be confidently attributed to *Solnhofia parsonsi* based on characters of the cranium. Minor variations in size and osteology from the holotype are assumed to be due to differences in ontogenetic stage, preservation, and intraspecific variation. The well preserved postcranium, particularly the pygal region of the carapace, provides anatomical information that distinguishes JM SCHA 70 and thus *Solnhofia* from all other known turtles of the Upper Jurassic. As a consequence the validity of

the genus *Solnhofia* is confirmed, and previously discussed synonymies with *Euryaspis* and *Eurysternum ignoratum* are rejected. The type material of *Hydropelta meyeri* is too fragmentary to either confirm or reject a synonymy. A close reexamination of the Eurysternidae should clarify the relationships within the Eurysternidae and the position of the Eurysternidae relative to other Upper Jurassic turtles, such as the Plesiochelyidae. For this purpose, it will be necessary to prepare and describe the skulls of species previously only known from the postcranium, such as *Eurysternum* and *Idiochelys*, and to integrate the newly acquired characters into a more comprehensive phylogeny of these turtles.

Based on the morphology of the shoulder girdle, *Solnhofia* can be inferred to have inhabited an aquatic environment. The taphonomy confirms recently proposed models for the origin of the lithographic limestones. Bite marks are present along the posterior rim of the carapace and may be the result of predation by a broad nosed crocodylian.

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