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Solnhofia parsonsi, a New Cryptodiran Turtle from the Late Jurassic of Europe

EUGENE S. GAFFNEY[1]

ABSTRACT

Solnhofia parsonsi is a new genus and species of turtle based on skull material from the Late Jurassic of Germany and Switzerland. One of the specimens has been described (but not named) elsewhere (Parsons and Williams, 1961); new information on the palate and basicranium is presented herein. *Solnhofia* possesses the shared derived characters diagnostic of the Cryptodira and within the Cryptodira of a group I have termed the Eucryptodira. More specific hypotheses of relationship are difficult to make for *Solnhofia* because most of the characters that are useful in comparing turtles are either primitive or uniquely derived in *Solnhofia*.

INTRODUCTION

Parsons and Williams (1961, p. 89) described two Jurassic turtle skulls (called by them the Solnhofen skull and the Portland skull) because "interest in this case attaches to the antiquity of the fossil itself" and "it could be hoped that it would reveal a stage or step in the evolutionary line which stretches from the most ancient turtle to those of the Recent." And they wrote, "we are therefore disappointed to discover that two skulls of Upper Jurassic age tell us astonishingly little about the evolution of turtles, next to nothing about features primitive for turtles, and nothing at all that in any way points to the group from which turtles have been derived." My own interest in turtle phylogeny has involved an examination of Jurassic turtles, and I think that a meaningful hypothesis of relationships can be developed for the "Solnhofen" skull (the Portland skull is dealt with in Gaffney, 1975). Furthermore, I have located what appears to be another specimen of this species and this new skull supplies information not available in the original specimen. I also include a comparison of the secondary palate in this species and other turtles and a more detailed description of the canals and foramina in the basicranium.

I have elsewhere (Gaffney, In press) proposed a phylogeny reconstruction and classification of turtles. The discussion of relationships presented for *Solnhofia* presupposes some familiarity with that work but some of that material is summarized here for clarity. Nonetheless, the important

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arguments concerning the relationships of chelonian higher categories are given elsewhere and are not repeated here.

The turtle skull nomenclature I use is explained and illustrated in a glossary (Gaffney, 1972b).

Acknowledgments

I am particularly indebted to Dr. C. O. van Regteren-Altena, Teyler Museum, Haarlem, Netherlands, and Dr. H. Ledermann, Solothurn Museum, Solothurn, Switzerland, for allowing me to borrow and study two specimens of *Solnhofia*, and for the time and resources they freely gave to aid my research. Financial support for a European study trip was obtained from the Osborn Research Fund, Department of Vertebrate Paleontology, and the Scientific Council Fund of the American Museum of Natural History. Chester Tarka, Lorraine Meeker, Jennifer Emry, and Robin Ingle are responsible for the high quality of the figures, and the Graphics Department of the American Museum for the labeling and diagram. Charlotte Holton helped type the manuscript and checked references. I am grateful to all for their help.

Institutional Abbreviations

AMNH, Department of Herpetology, the American Museum of Natural History
SM, Mineralogy-Geology Collection of the Solothurn Museum, Solothurn, Switzerland
TM, Teyler Museum, Haarlem, Netherlands

Anatomical Abbreviations Used in Figures

ang, angular
art, articular
bo, basioccipital
bs, basisphenoid
cor, coronoid
den, dentary
epi, epipterygoid
ex, exoccipital
fr, frontal
ju, jugal
mx, maxilla
na, nasal
op, opisthotic
pa, parietal
pal, palatine
pf, prefrontal
pm, premaxilla
po, postorbital
pr, prootic
pra, prearticular
pt, pterygoid
qj, quadratojugal
qu, quadrate
so, supraoccipital
sq, squamosal
sur, surangular
vo, vomer

SYSTEMATICS

DIVISION TETRAPODA

COHORT AMNIOTA

SUPERORDER SAUROPSIDA

ORDER TESTUDINES LINNAEUS, 1758[1]

SUBORDER CASICHELYDIA GAFFNEY, 1975

INFRAORDER CRYPTODIRA (COPE, 1871)

PARVORDER EUCRYPTODIRA GAFFNEY, 1975

SUPERFAMILY AND FAMILY *INCERTAE SEDIS*

SOLNHOFIA, NEW GENUS[2]

Type Species. S. parsonsi.[3]

Known Distribution. Late Jurassic of (?) Germany and Switzerland.

Diagnosis. Cryptodire with complete secondary palate, elongate snout, and limited temporal emargination; nasals, prefrontals, frontals, and parietals meet in midline of skull roof; secondary palate comparable in extent with living cheloniids but not so extensive as in osteopygine toxochelyids; palate composed primarily of maxilla, vomer nearly hidden, palatines reduced compared with cheloniids; *processus pterygoideus externus* reduced as in living cheloniids, pterygoid lacking "waist," *foramen palatinum posterius* reduced to one or two small foramina; triturating surfaces smooth, broadly concave ventrally, lingual ridge absent; premaxillae extend anteriorly beyond edge of *apertura narium externa*; jugal widely exposed in orbital floor; *foramen supramaxillare* in jugal-palatine suture; *processus trochlearis oticum* more extensive than in most cryptodires, obscures *foramen nervi trigemini* in lateral view; basioccipital enters *foramen magnum*; exoccipital does not contact pterygoid; *tuberculum basioccipitale* better developed than in *Chelydra*, but not so extensive as in living cheloniids; *foramen stapedio-temporale* about twice the diameter of *foramen posterior*

[1]See Hunt, 1958, for discussion of the ordinal name for turtles.

[2]The type specimen has been referred to by Parsons and Williams, 1961, as "the Solnhnofen skull."

[3]For Dr. Thomas S. Parsons, University of Toronto, in recognition of his work in chelonian cranial anatomy.

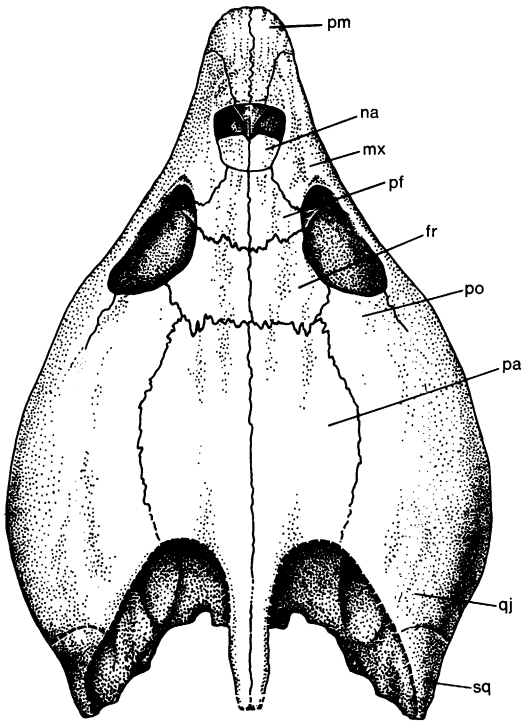


FIG. 1. *Solnhofia parsonsi*, new genus and new species. Dorsal view of restored skull based on TM 4023 and SM 137.

canalis carotici interni, agreeing with testudinoids but differing from trionychoids; *foramen anterior canalis carotici interni* joined into common opening before entering *cavum cranii* in posterior part of *sella turcica*; *canalis caroticus lateralis* with posterior opening on ventral surface of the skull not found in other turtles; *rostrum basisphenoidale* short compared with *Chelydra* and cheloniids but similar to trionychoids; symphysis of lower jaw about one-half length of lower jaw; elongate median trough on dorsal surface of lower jaw symphysis; lower jaw labial ridge sharp but low, lingual ridge absent; *sulcus cartilaginis meckelii* relatively short compared with *Chelydra*, splenial well developed.

Solnhofia parsonsi, new species

Type Specimen. TM 4023, a partially damaged skull with lower jaw.

Locality. Not known, probably Bavaria.

Horizon. Not known, probably Late Jurassic (see van Regteren-Altena, 1967).

Collector. Not known, first recognized in the private collection of Dr. Häberlein, Pappenheim, in 1839 (*ibid*).

Specific Diagnosis. Same as for genus.

Hypodigm. The type specimen and SM 137, a skull without lower jaws, mentioned by Bräm (1965, pp. 186-187). Locality: Limestone quarry within or around the city of Solothurn, Switzerland. Horizon: "Kimmeridge, *Pseudomutabilis* zone" (label). Late Jurassic.

DISCUSSION

The higher categories I use here may be unfamiliar to some readers but a few words of explanation may clarify my intentions. It seems to me that a classification should be a written version of a phylogenetic hypothesis, in the sense of geneology or kinship, and consist only of strictly monophyletic groups to the extent that this is possible. The taxon "Reptilia" is clearly unsatisfactory by these criteria and I have adopted a more phyletic classification. The supraordinal categories and taxa used are modified from a classification suggested by Nelson (1969). Tetrapoda and Amniota are in the sense of Goodrich (1930), whereas Sauropsida is from Goodrich (1916). The chelonian categories are from a phylogeny and classification of turtles (Gaffney, In press) in which fossil and recent forms are related on the basis of skull criteria predominantly.[1]

When Parsons and Williams (1961, p. 43) described the "Solnhofen skull" they could not identify it with a known taxon but preferred not to erect a new species for the following reasons: "At present the higher taxonomy of Jurassic turtles is based exclusively upon shells. It would be necessary to have shells associated with these skulls in order to place them as to family. To devise or use skull genera for these forms, when these skull genera will most probably in the not distant future be sunk in the synonymy of shell

[1]Although the higher categories are diagnosed and discussed in a paper still in press, the names have already appeared (Gaffney, 1975) due to the vagaries of printing.

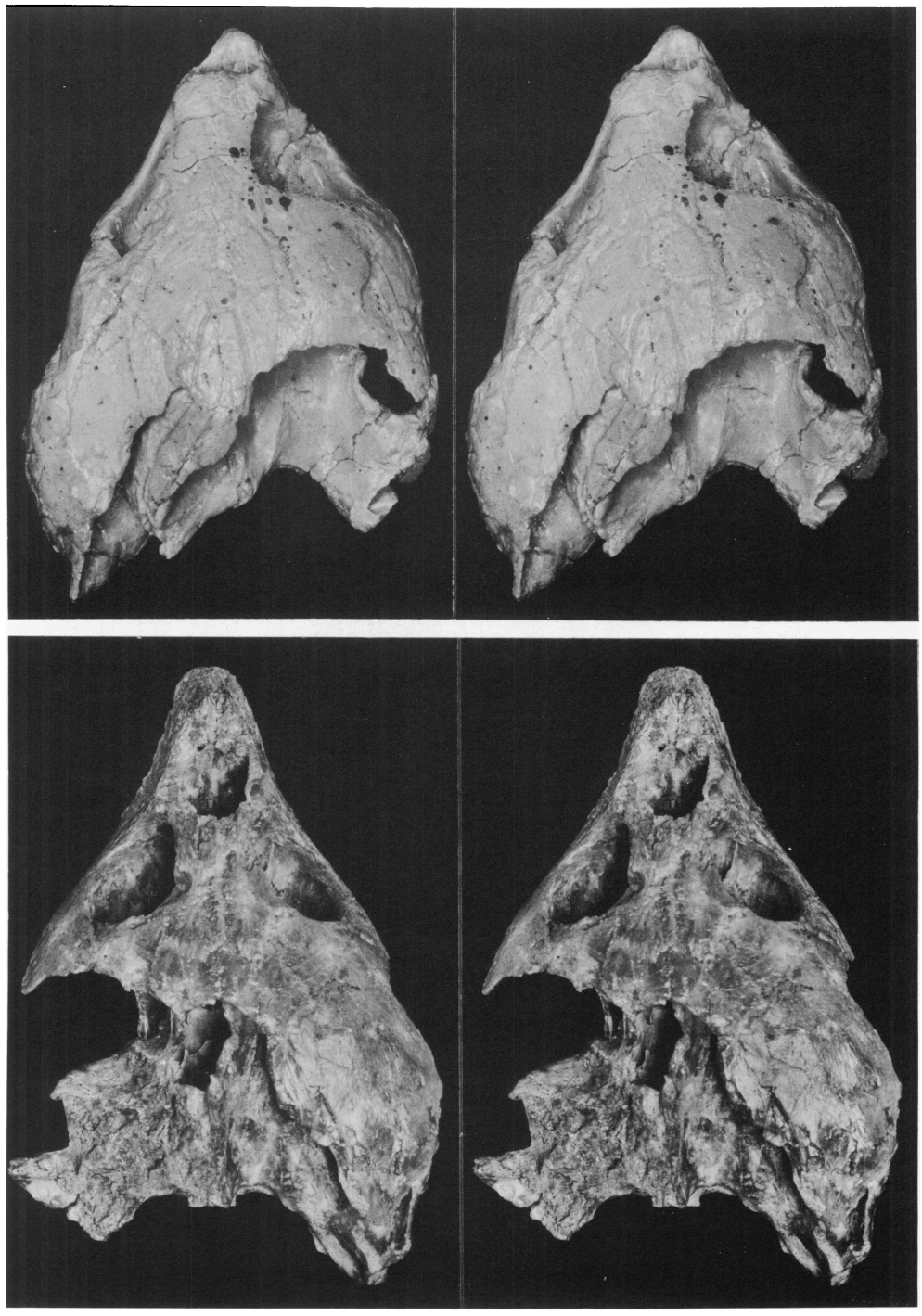


FIG. 2. *Solnhofia parsonsi*, new genus and new species. Dorsal stereophotographs. *Upper*, SM 137; *lower*, TM 4023. (See figs. 3, 4.)

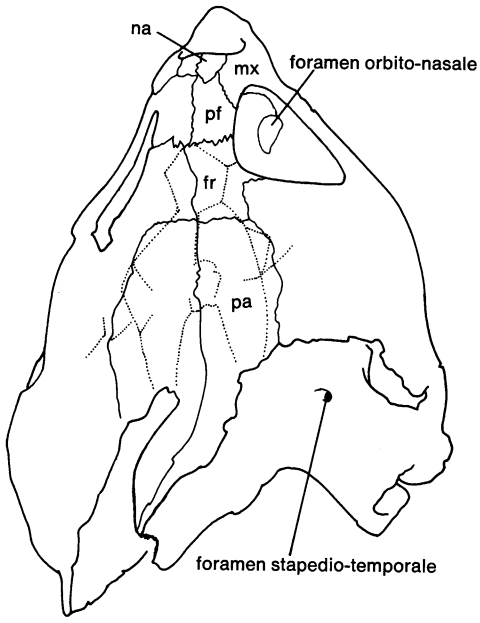


FIG. 3. *Solnhofia parsonsi*, new genus and new species. Dorsal view of SM 137. (See fig. 2.)

genera, would, we believe, serve no useful purpose."

I offer the following argument in favor of naming this form:

1. I have examined most of the major European Jurassic turtle collections and have not been able to find a skull-shell association identifiable with this form. Although such a specimen may very well be in a collection at present or one may be discovered soon, I believe that the probability of either is fairly low.
2. Although the taxonomy of Jurassic turtles, and many other turtle groups, is presently based primarily on shell morphology, this is not necessarily a satisfactory or even tolerable situation. In fact, I believe that turtle systematics has been and is hampered by an emphasis on shell morphology.

The specific identity of the two skulls is not immediately apparent because of preservational differences between them. The area around the *apertura narium externa* is markedly dissimilar. TM 4023 has the anterior portions of the premaxillae preserved intact but lacks the nasals and much of the dorsal and lateral rim of the *apertura narium externa*. SM 137 has retained the nasals and most of the margin of the *apertura* but the anterior prolongation of the premaxillae is eroded. Furthermore, TM 4023 is largely undistorted but SM 137 is quite distorted. SM 137, therefore, appears to have a much shorter preorbital snout and a relatively smaller *apertura narium externa*. The restored dorsal view corrects for these preservational differences. The two skulls differ in size; TM 4023 is 73 mm. from condyle to anterior tip of premaxillae, whereas SM 137 is 58 mm. Other biological variations are difficult to determine because of the relatively poor preservation of SM 137. The right orbits in both skulls seem to have uneroded edges and are the same length. This suggests that the smaller specimen has relatively larger orbits; however, it is probably due to distortion of the orbital margin in SM 137. The *condylus mandibularis* in SM 137 has a more expanded lateral half when compared with TM 4023. All other differences that I have seen can be ascribed to poor preservation.

SECONDARY PALATE

The secondary palate in *Solnhofia* is a quite

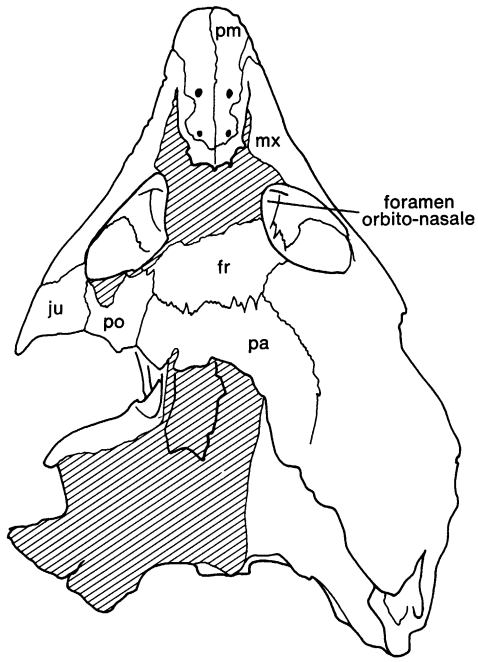


FIG. 4. *Solnhofia parsonsi*, new genus and new species. Dorsal view of TM 4023. (See fig. 2.)

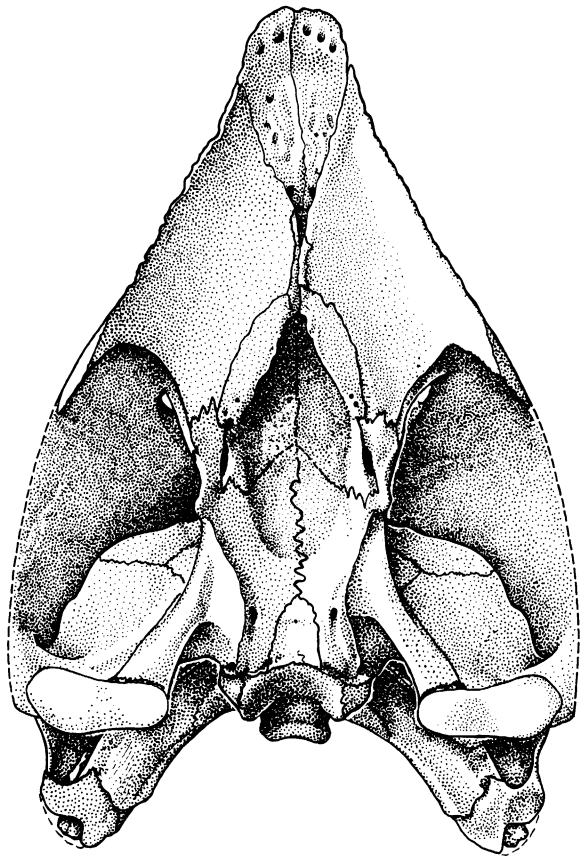


FIG. 5. *Solnhofia parsonsi*, new genus and new species. Ventral view of restored skull, based primarily on TM 4023. Modified from Parsons and Williams, 1961.

distinctive feature of the skull and is different in construction from other turtles with partial or complete secondary palates. The triturating or feeding surfaces of the mandible and maxilla show a considerable diversity. In order to evaluate the morphology of the palate in *Solnhofia* I give below a brief summary of this region in some selected groups. The term secondary palate has been used for a varied mixture of palatal conditions in turtles. I am using a more conservative sense of the term by restricting it to a condition in which the bony expansion of the lateral triturating surfaces meet medially to completely close off at least some portions of the primary palate. The condition in such forms as *Ctenochelys* (Zangerl, 1953, fig. 61), *Eubaena* (Gaffney, 1972a, fig. 19), and *Shweboemys* (Wood, 1970, fig. 1, as preserved) is not considered to be a true secondary palate in my usage. These forms may be described as having an incipient or partial secondary palate. In life, the horny covering of the jaws may close the medial gaps in an incipient secondary palate to form a functionally complete secondary palate, but this is not determinable from the bones. The function of secondary palates is diverse among vertebrates, and there are no detailed functional studies showing that secondary palates of turtles are correlated with

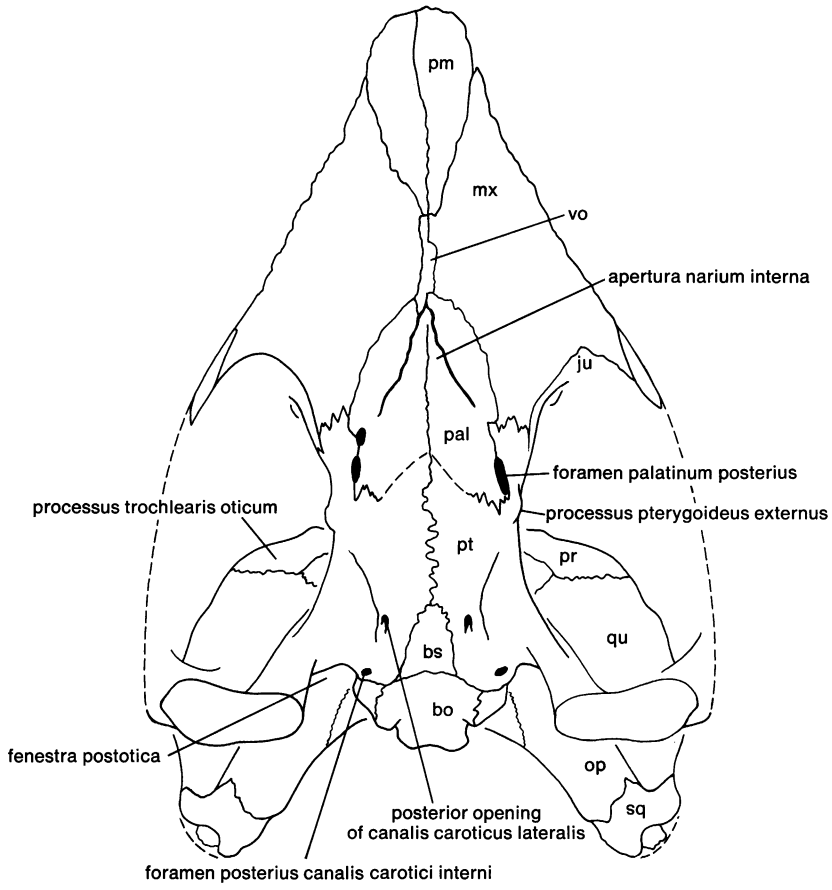


FIG. 6. *Solnhofia parsonsi*, new genus and new species. Restored ventral view. (See fig. 5.)

particular biological roles, although such studies would be extremely useful.

The secondary palate of *Solnhofia* is formed mostly by the maxillae. The ventral exposure of the vomer is extremely reduced but contrary to statements in Parsons and Williams (1961) I think it does have a limited exposure on the palate, thus barely preventing the medial maxillary expansions from meeting in the midline. The palatines form a limited portion of the secondary palate and border the *apertura narium interna*.

A number of turtles have secondary palates as extensive as that in *Solnhofia*, but all differ in the method of formation. The cheloniid sea turtles have a secondary palate with a greater contribution of the palatines and a prominent exposure of the vomer. *Erquelinnesia*, redescribed by Zangerl (1971), is an Eocene toxochelyid sea turtle with the most advanced secondary palate known in turtles. *Erquelinnesia* differs from *Solnhofia* in having the vomerine exposure quite well developed and the *apertura narium interna* well posterior to the level of the *processus pterygoideus externus*. The premaxillae of *Erquelinnesia*, although fused, are similar to those in *Solnhofia* in that they are large and extensive compared with the condition in most other toxochelyids and cheloniids. The living Cheloniidae and the toxochelyids *Erquelinnesia* and *Osteopygis* have secondary palates formed by expan-

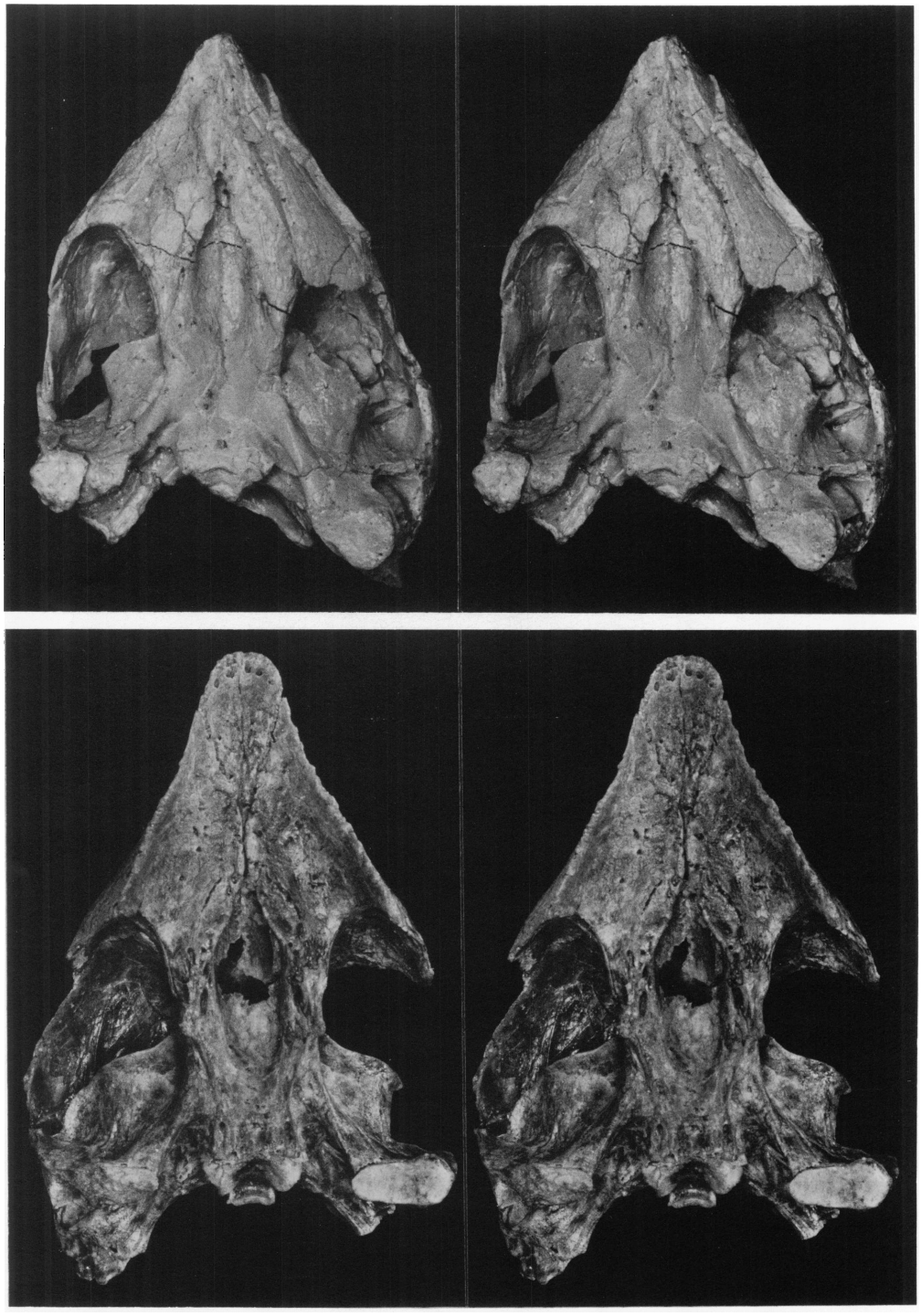


FIG. 7. *Solnhofia parsonsi*, new genus and new species. Ventral stereophotographs of skulls. *Upper*, SM 137; *lower*, TM 4023.

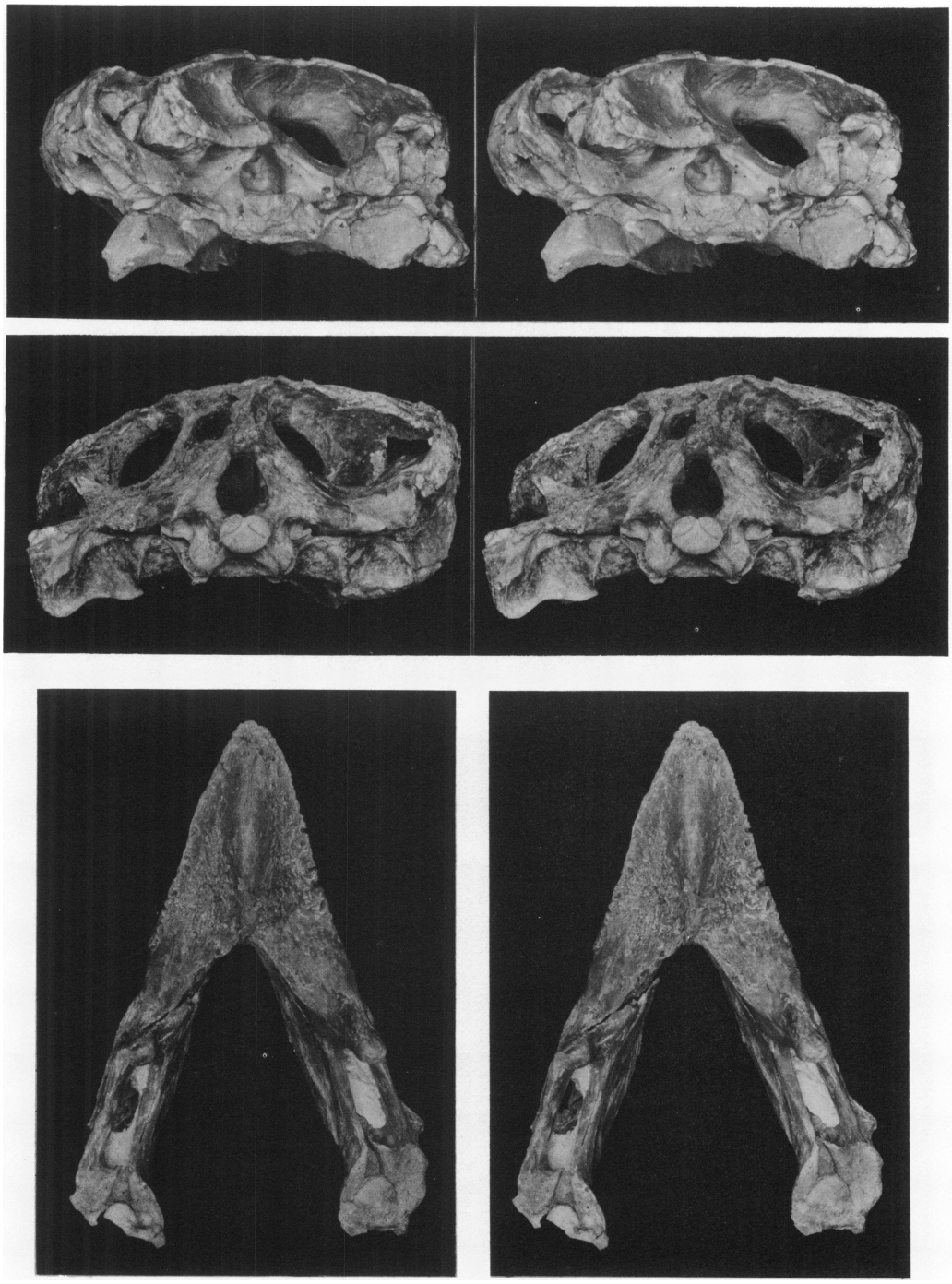


FIG. 8. *Solnhofia parsonsi*, new genus and new species. *Upper*, occipital stereophotograph of SM 137; *middle*, occipital stereophotograph of TM 4023 (see fig. 9); *lower*, stereophotograph of lower jaw of TM 4023.

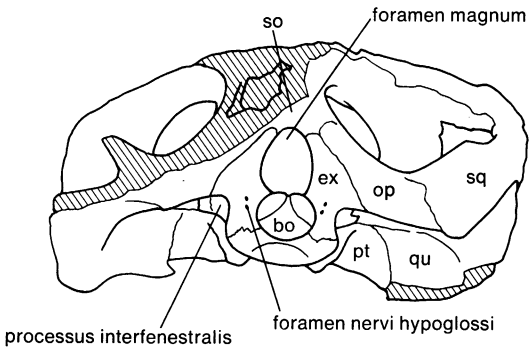


FIG. 9. *Solnhofia parsonsi*, new genus and new species. Occipital view of TM 4023. (See fig. 8.)

sion not only of the maxillae but of the ventral plates of the vomer and the palatines as well. *Solnhofia*, on the other hand, has a secondary palate formed primarily by maxillary expansion with relatively minor contributions from the palatines and vomer.

Although no turtle with a complete secondary palate has the condition seen in *Solnhofia*, two other turtles, *Ctenochelys* and *Eubaena*, possess incipient secondary palates that may be structurally antecedent to the condition in *Solnhofia*. The triturating surfaces of *Ctenochelys* are more advanced than the condition seen in *Toxochelys* in that the maxillae and palatines are expanded medially, but a true secondary palate, where the elements completely enclose the in-

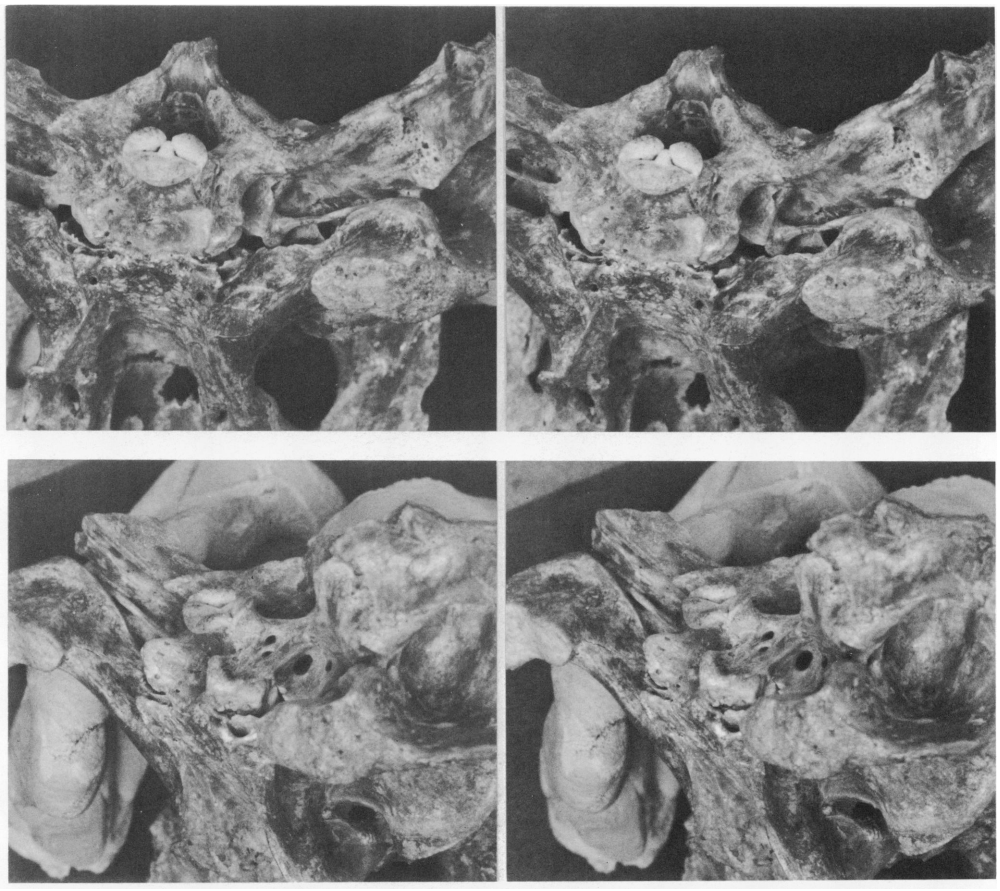


FIG. 10. *Solnhofia parsonsi*, new genus and new species. Stereophotographs of occiput in TM 4023. *Upper*, right half of posterior end of skull. Anterior end of skull is tilted ventrally. *Lower*, posterior end of skull taken obliquely from the right side of the specimen. Axis of skull is oriented somewhat ventrally. (See figs. 11, 12.)

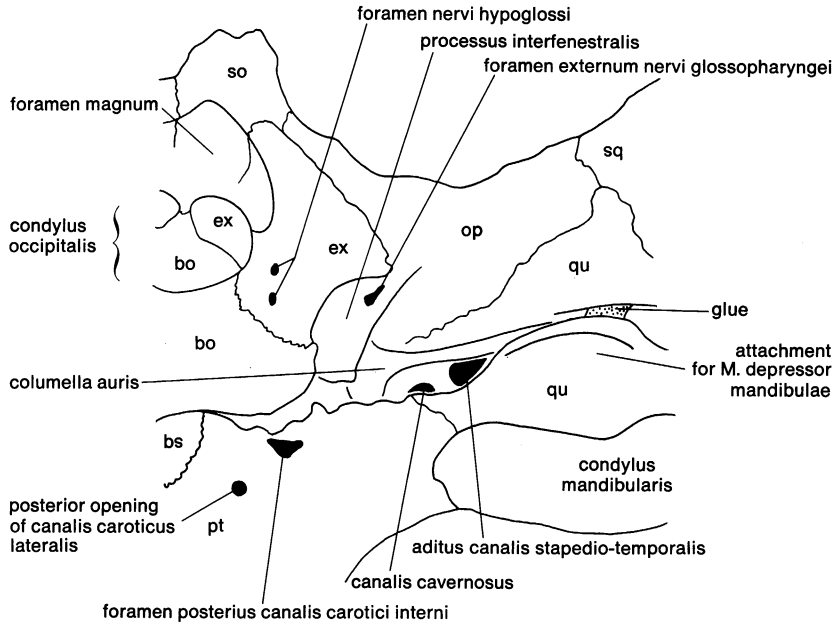


FIG. 11. *Solnhofia parsonsi*, new genus and new species. Occiput of TM 4023. (See fig. 10, upper.)

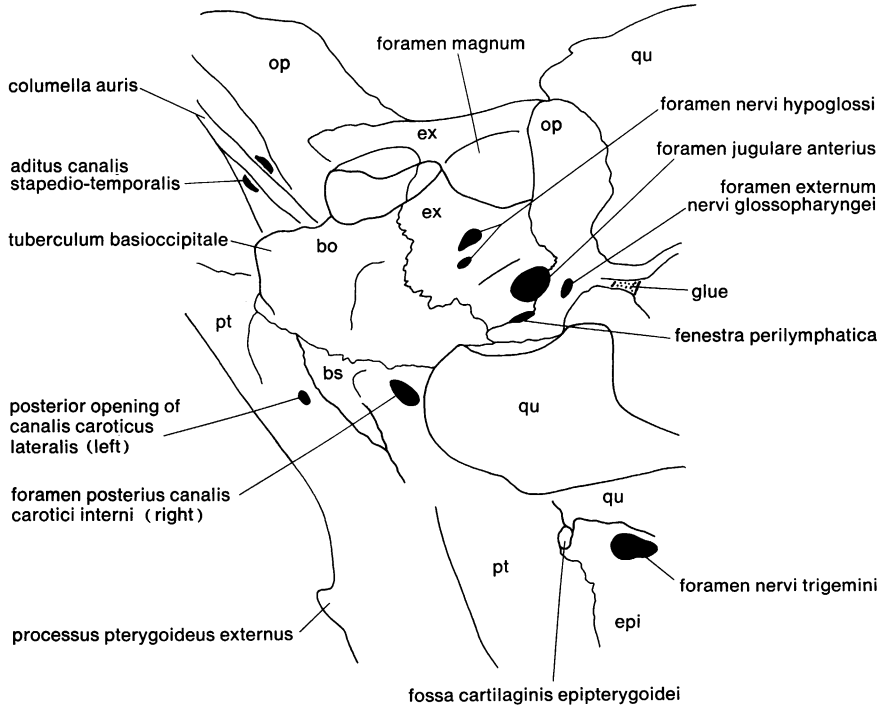
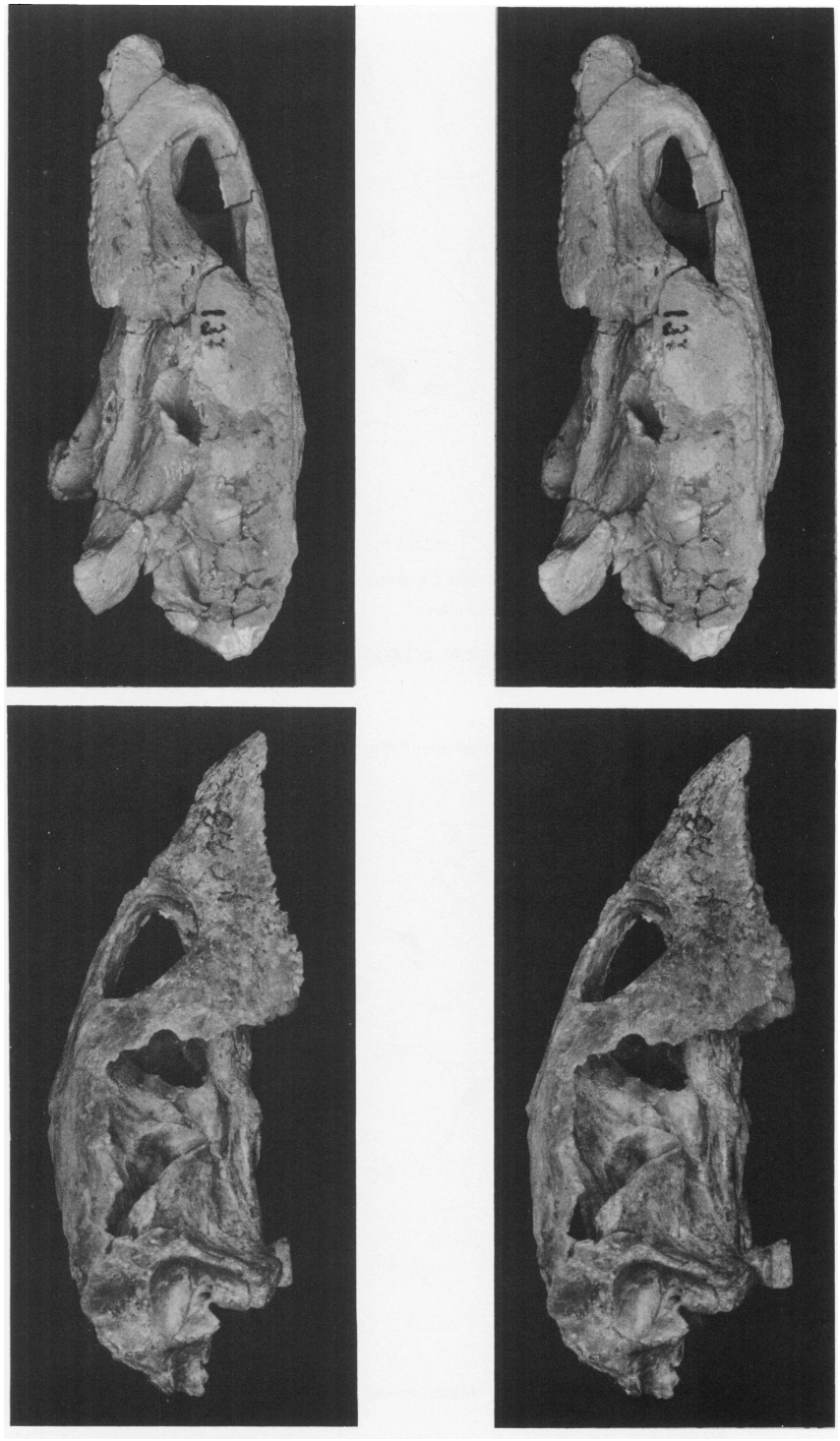


FIG. 12. *Solnhofia parsonsi*, new genus and new species. Occiput of TM 4023. (See fig. 10, lower.)



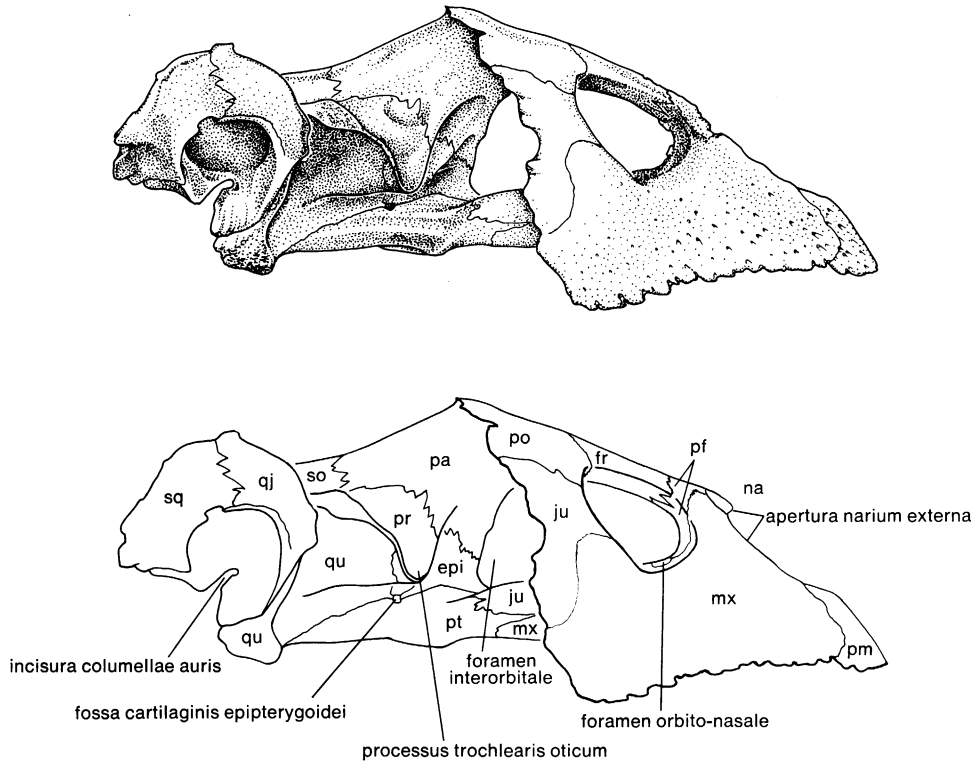
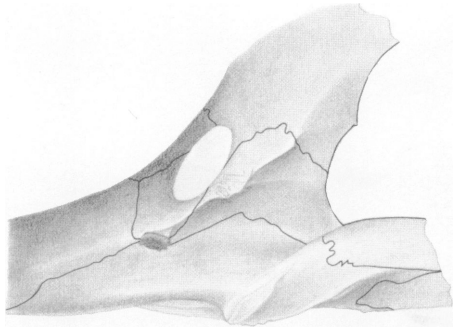


FIG. 14. *Solnhofia parsonsi*, new genus and new species. Right side of TM 4023. (See also fig. 13, lower.)

ternal nares, is not present. The main element of the expansion in *Ctenochelys*, as in *Solnhofia*, is the maxilla with a small contribution from the palatine. *Eubaena*, a Cretaceous baenid, has an incipient secondary palate very similar to *Ctenochelys*. In *Ctenochelys* a portion of the vomer is part of the medial palatal expansion, whereas in *Eubaena* the vomer remains above the feeding surface. *Eubaena* and *Ctenochelys*, although not closely related to each other or to *Solnhofia*, give some indication of the method of development of this type of secondary palate, which is in sharp contrast to cheloniids and other toxochelyids.

Other incipient secondary palates are known in the Pleurodira. Wood (1970) has described new material of the African and Asian pelomedusid *Shweboemys*, which shows that the incipient secondary palate is formed by the medial expansion of maxillae and palatines with no contribution from the vomer (which is often reduced or absent in this family). A closely related genus, *Stereogenys*, from the African Eocene, has a very similar palatal modification. Andrews (1906, p. 297) has argued that *Stereogenys* had a complete secondary palate as his figure 95 indicates. It is possible that the maxillary and palatine expansions met medially in both genera and that this area is poorly preserved in most specimens. The pelomedusid palatal modifications differ from cryptodire incipient and complete secondary palates in having a

FIG. 13. *Solnhofia parsonsi*, new genus and new species. *Upper*, left side of SM 137. *Lower*, right side of TM 4023.



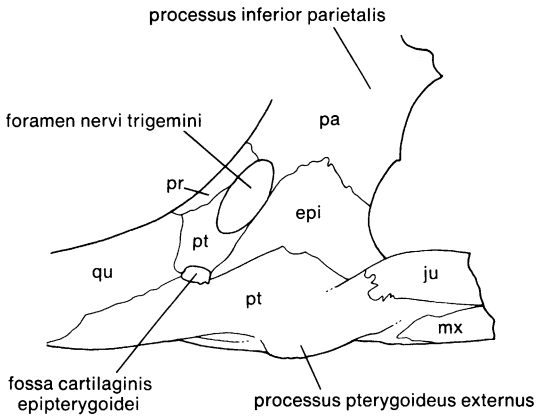


FIG. 15. *Solnhofia parsonsi*, new genus and new species. Right ethmoid region of TM 4023. *Processus trochlearis oticum* removed.

greater contribution of the palatines to the palate. In cryptodires the maxillae are usually the largest elements, whereas in *Stereogenys* and *Shweboemys* the palatines are as large or larger than the maxillae and make up the posterior half of the secondary palate.

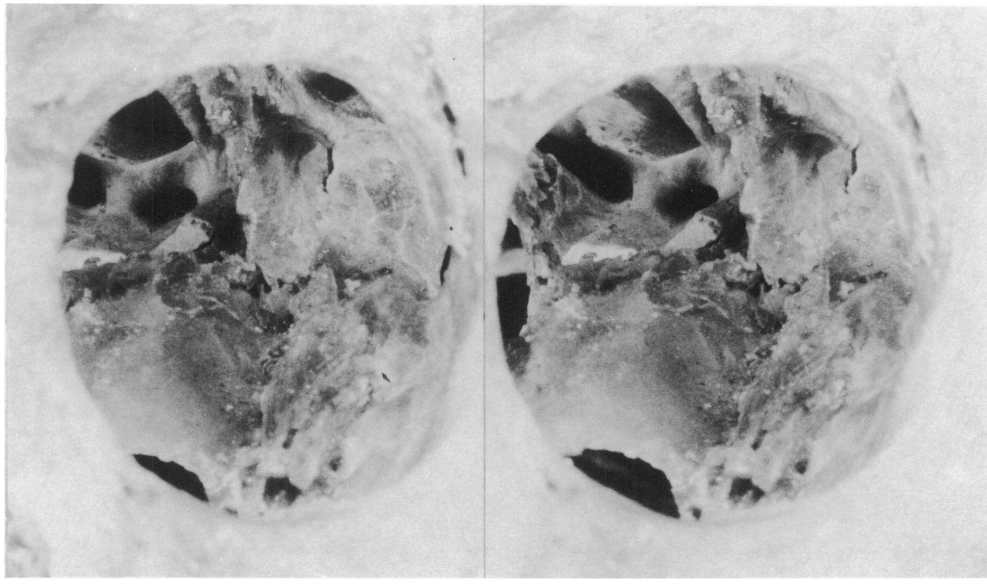
Zangerl (1971, fig. 8) has used a visual method of comparing the internal structures of secondary palates in his description of *Erquelinnesia*. *Solnhofia* seems to differ from the cheloniids illustrated by Zangerl primarily in the posterior position of the *fossa nasalis* (horizontal shading). The length of the *meatus choanae*, the nasal passages connecting the *fossa nasalis* with the *apertura narium interna*, may be used as an estimate of the degree of secondary palate development. The *meatus choanae* does not exist in forms with an incipient secondary palate, such as *Eubaena* and *Ctenochelys*. The *meatus choanae* of *Solnhofia* is relatively longer than in the recent cheloniids *Eretmochelys* and *Chelonia* and approximates the condition in *Caretta*. The vomerine pillar, which more or less separates the *meatus choanae* into two passages, is thicker and somewhat shorter in *Solnhofia* that it is in *Caretta*. These internal structures of *Solnhofia* do not reach the extreme development seen in *Erquelinnesia*.

The secondary palate of *Solnhofia*, then, is structurally comparable with the condition seen in recent cheloniids and is even advanced over some of them. *Solnhofia* does not attain the most extreme chelonian condition seen in osteopygine toxochelyids such as *Erquelinnesia*, but it is as close to this extreme as any other known turtle. It is unfortunate that no near relatives of *Solnhofia* are known so that more relevant phylogenetic comparisons may be made with the palate.

ARTERIAL CANALS AND FORAMINA

McDowell (1961, 1964) and Albrecht (1967) have investigated the use of cranial arterial patterns in phylogenetic studies of turtles. Very little of this type of work has been applied to fossil turtles although both of the above authors have argued that arterial information can be obtained with confidence from skulls lacking the actual soft parts. Albrecht (1967) has presented evidence that the size of a foramen or canal is often directly proportional to the size of the artery traversing the bony structure. Comparisons based on this assumption can be made between Recent and fossil turtle skulls and within certain limits it can be concluded that the canals reflect arterial patterns.

Parsons and Williams (1961) described most of the areas of the basicranium in *Solnhofia*, but I would like to present this data in a more comparative way and add new information. The figures presented here are based primarily on the Teyler Museum skull with some additions from the Solothurn Museum specimen. The figures



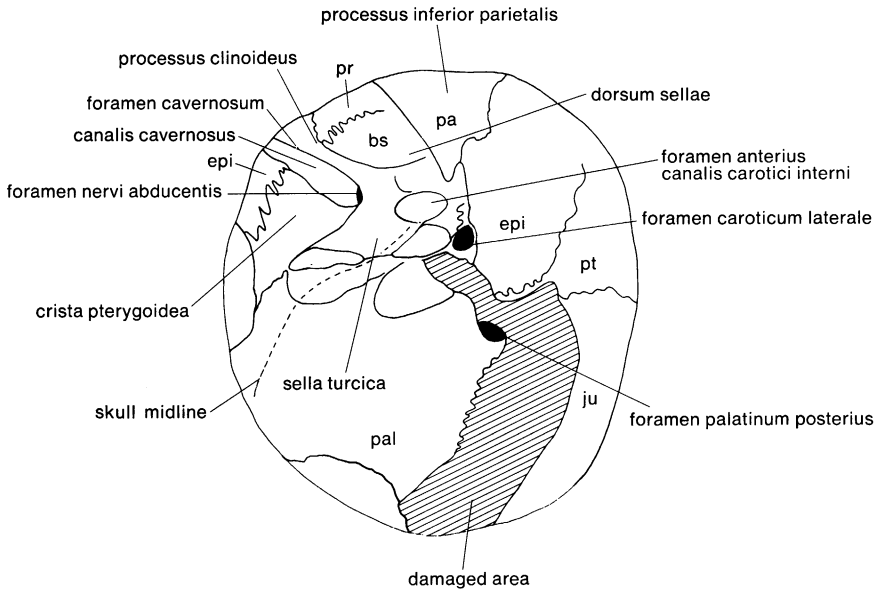


FIG. 16. *Solnhofia parsonsi*, new genus and new species. TM 4023. Stereophotograph of *sella turcica* and surrounding features taken through left orbit (camera faces posteromedially). (See fig. 17.)

are restored and partly hypothetical in that a frontal section, such as that illustrated, has never been cut. The structures in the central part of the basicranium have been drawn by looking through a hole in the skull roof, the ethmoid region, and the *foramen magnum*. Some of the dimensions may not be completely accurate but they have been controlled as much as possible. The canals

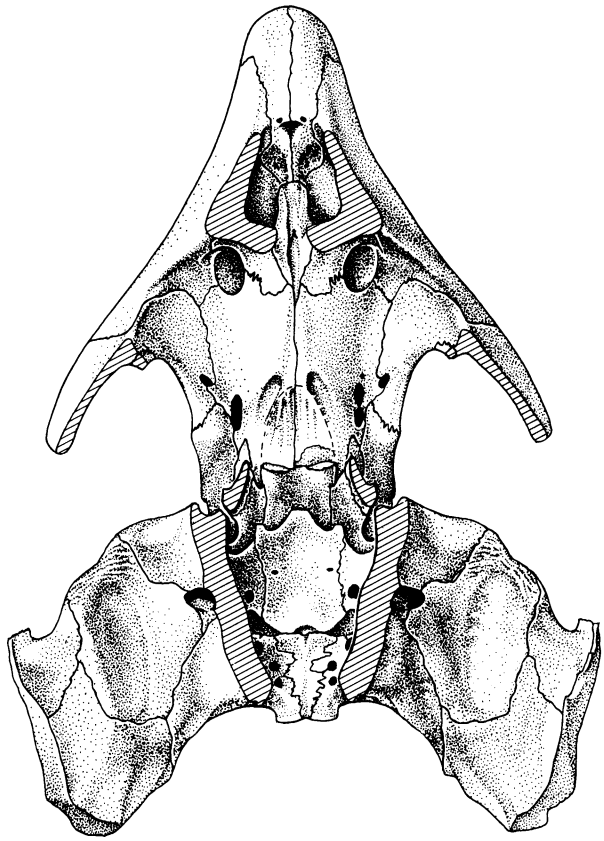


FIG. 17. *Solnhofia parsonsi*, new genus and new species. Hypothetical dorsal view of frontally sectioned skull, based on TM 4023.

have all been determined by probing with bristles. The description follows the order used by Albrecht (1967) so that comparisons can be easily made.

Canalis Stapedio-Temporalis

As noted by Albrecht (1967, p. 83), the *foramen stapedio-temporale* of *Solnhofia* is not reduced in diameter relative to the *foramen posterior canalis carotici interni* as in trionychoids (*sensu* Gaffney, In press), but has a large diameter comparable with that found in all other turtles. The diameter of the *foramen stapedio-temporale* is about twice that of the *foramen posterior canalis carotici interni.*

Canalis Caroticus Internus

I have little to add to the Parsons and Williams (1961) description of the structures related to the carotid arterial system in *Solnhofia*. As is described below, I have been able to probe a connection between the *canalis caroticus lateralis* and the *canalis caroticus internus.*

Canalis Caroticus Lateralis

This structure was first named by Albrecht in 1967 and was, therefore, not described by Parsons and Williams in 1961. Although quite small in pleurodires and most cryptodires, the *canalis caroticus lateralis* is greatly enlarged in kino-

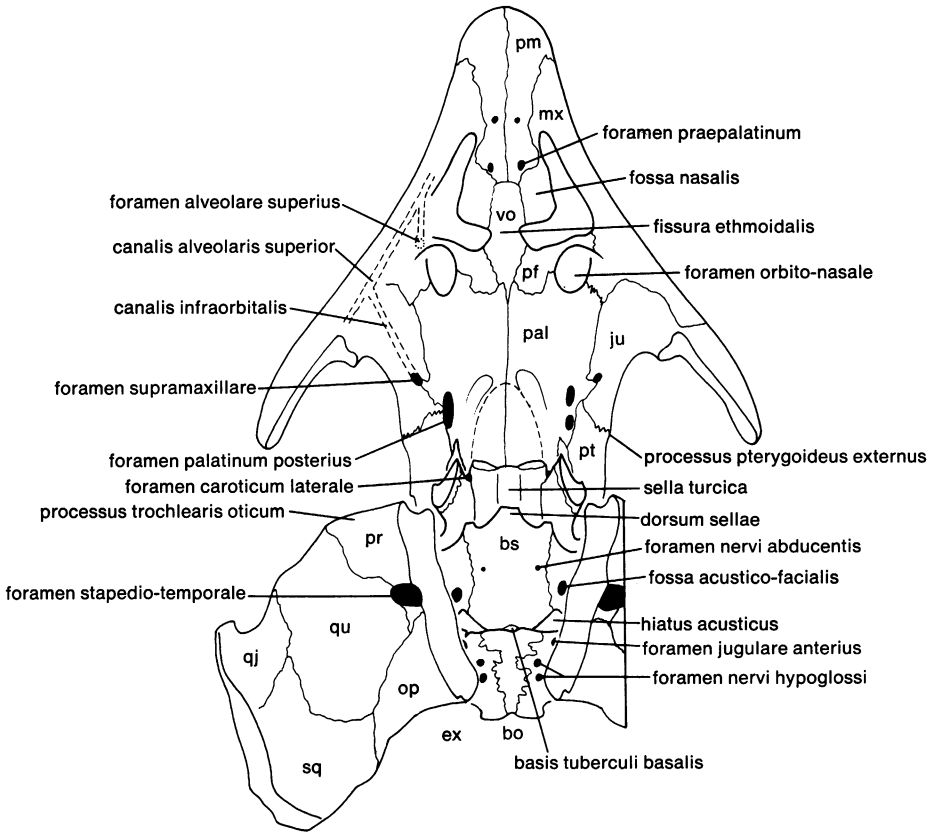


FIG. 18. *Solnhofia parsonsi*, new genus and new species. Labeled diagram of figure 17.

sternids and carries the main blood supply to the front of the skull. In *Solnhofia* the *canalis caroticus lateralis* agrees with most turtles, such as *Chrysemys* (see Albrecht, 1967, fig. 1), in which the *canalis* is relatively small. The *foramen caroticum laterale* in *Solnhofia* is best preserved on the left side and seems to be formed entirely by the pterygoid. It occupies the space between the *rostrum basisphenoidale* and the *crista pterygoidea* and lies in the floor of the *sulcus cavernosus*. Only a thin plate of the pterygoid separates the *foramen* from the *rostrum basisphenoidale*. The position of the *foramen caroticum laterale* in *Solnhofia* is similar to the position of this structure in other cryptodires and does not suggest relationships with any particular group.

In *Solnhofia* the *canalis caroticus lateralis* extends posteriorly, probably within the pterygoid as in many other cryptodires. Near its posterior end the *canalis caroticus lateralis* communicates with the *canalis caroticus internus*. This situation also seems similar to other cryptodires. In most cryptodires the *canalis caroticus lateralis* ends at its junction with the *canalis caroticus internus*. In *Solnhofia*, however, as opposed to all other turtles that I am familiar with, the *canalis caroticus lateralis* continues posteriorly and emerges on the ventral surface of the skull. This opening is visible in both specimens but has been probed with bristles only in the Teyler Museum skull.

There are a number of possible arterial interpretations regarding this ventral opening of the *canalis caroticus lateralis*, but I have chosen two as being most likely. Figure 19 is a diagrammatic restoration of these two possible arterial patterns that are compatible with the canals and foramina

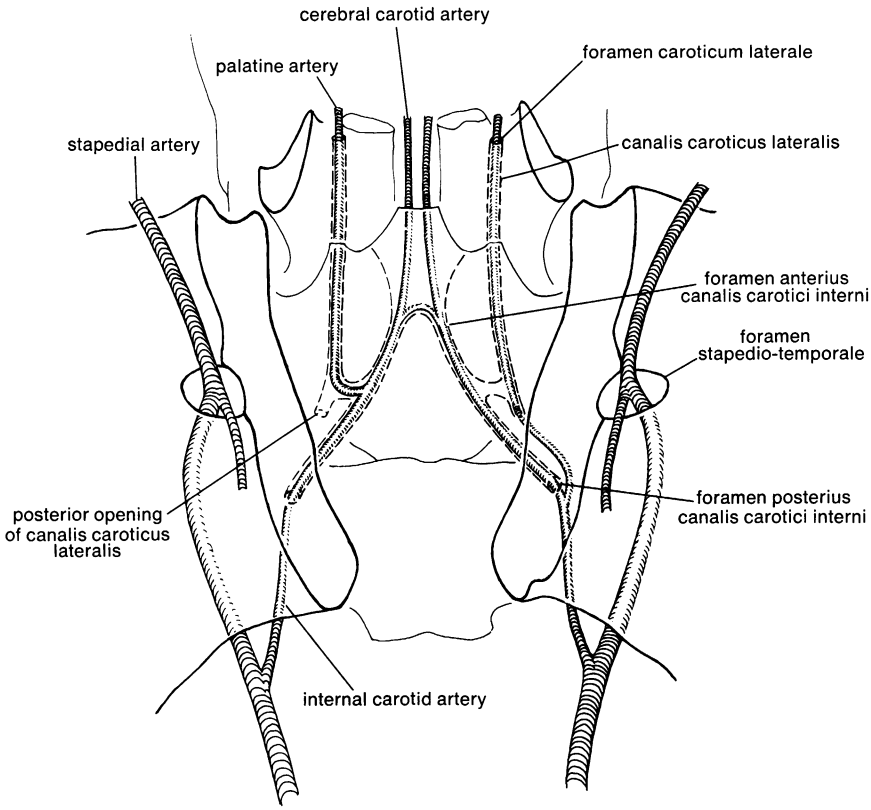


FIG. 19. *Solnhofia parsonsi*, new genus and new species. Semi-diagrammatic view of basicranial canals with arteries restored. The right side portrays one possible arterial restoration and the left side an alternative restoration. (See fig. 17 for complete basicranium. See text for discussion.)

as known in *Solnhofia*. The internal carotid and stapedial arteries are the same in both interpretations; the primary difference is the position of branching of the palatine artery. On the left side of the figure the palatine artery is restored as coming off the internal carotid within the skull via the short canal between the *canalis caroticus lateralis* and the *canalis caroticus internus*. This interpretation is most consistent with living turtles and requires no fundamental change in arterial pattern. However, the posterior opening of the *canalis caroticus lateralis* is not accounted for. The right side of the diagram interprets the posterior opening as the point of entry of the palatine artery after it branches off the internal carotid outside of the skull. To my knowledge, the palatine artery of living turtles never branches off before entering the skull; however, there is also no opening to the outside of the skull of the canal housing the palatine artery (the *canalis caroticus lateralis*) in living turtles. In this second interpretation the communication between the *canalis caroticus lateralis* and the *canalis caroticus internus* is unaccounted for. It is likely that knowledge of the path of the vidian nerve would enable us to make a choice between these interpretations because in *Chrysemys* (Albrecht, 1967, fig. 1) the posterior part of the *canalis caroticus lateralis* communicates with the *canalis nervi vidiani*. The latter, however, has not been determined in *Solnhofia* and, although I assume that it was present, its relation to the *canalis caroticus lateralis* is unknown.

Canals in the Orbital Floor

The *foramen palatinum posterius* is a prominent opening between the *fossa orbitalis* and the

palate in most cryptodires. The *foramen* transmits an artery (inframaxillary of Albrecht, 1967) and a nerve (inframaxillaris of Bojanus, 1819) to the palate. It is possible that a small vein accompanies these structures but I have not been able to substantiate this. In most turtles with a primary palate that lack any expansions of the triturating surfaces (such as *Chelydra*) the *foramen palatinum posterius* is relatively large. But in many turtles the triturating surfaces are modified and expanded medially restricting the size of the *foramen*. The extreme condition is reached in the living cheloniids in which this structure is absent. The condition in *Solnhofia* is similar to that in many testudinids and emydids (*sensu* Wermuth and Mertens, 1961) in which the *foramen palatinum posterius* is considerably restricted in diameter but not absent. In both specimens of *Solnhofia* the *foramen* is single on the left side but double on the right, similar to a specimen of *Geochelone* (AMNH 87330).

The *canalis alveolaris superior* lies within the lateral edge of the maxilla and transmits nutrient vessels from the main head arteries into the horny tissue making up the rhamphotheca. In most turtles this canal is fed via two foramina: an anterior one, the *foramen alveolare superius* (described by Parsons and Williams, 1961, p. 54), and a posterior one, the *foramen supramaxillare*. The *foramen supramaxillare* enters the *canalis infraorbitalis* which connects with the *canalis alveolaris superior*. Because of the highly modified nature of the palate, a number of structures in the orbital floor are seen to be in different positions relative to one another, when compared with a more generalized condition, such as occurs in *Chelydra* (see Gaffney, 1972b, figs. 11, 12). The dorsal exposure of the maxilla is considerably reduced in comparison to turtles having a primary palate and the *foramen supramaxillare* is formed by the palatine and jugal rather than by the maxilla and jugal (*Chelydra*) or maxilla alone (*Chrysemys*).

THE RELATIONSHIPS OF *SOLNHOFIA*

The method used here to develop a theory of relationships concerning *Solnhofia* is based on the distribution of shared derived characters. This method has been expounded by Hennig (1966) and Brundin (1966, 1968) and aspects of it have recently been discussed by Eldredge (1972), Schaeffer, Hecht, and Eldredge (1972), and Gaffney (1972a).

A phylogenetic study of *Solnhofia* is difficult because the animal is relatively isolated morphologically from other turtles. In the words of Kluge (1971, pp. 21-22): "A relatively discontinuous morphocline is difficult to recognize as the product of a single evolutionary trend because too few of the intermediate character states persist." This is a common problem and results in phylogenies of lower probability than those determined with a greater number of intermediate character states.

Parsons and Williams (1961, p. 43) identified *Solnhofia* as an amphichelydian. Elsewhere (Gaffney, In press), I have suggested that this higher taxon is polyphyletic in the strict sense and should be abandoned. *Solnhofia* agrees in all determinable characters with the taxon Cryptodira as diagnosed by me (Gaffney, 1972a, p. 249[1]). In particular the following characters of *Solnhofia* are diagnostic of the Cryptodira.

1. Skull with trochlear surface for *cartilago transiliens* developed on *processus trochlearis oticum*.
2. Pterygoid extending posteriorly between quadrate and braincase.
3. Epipterygoid present, as well as *fossa cartilaginis epipterygoidei*.
4. No development of hemispherical articulation on lower jaw.
5. *Foramen palatinum posterius* in floor of *fossa orbitalis*.
6. *Foramen supramaxillare* present.
7. Descending process of prefrontal meeting vomer ventromedially.

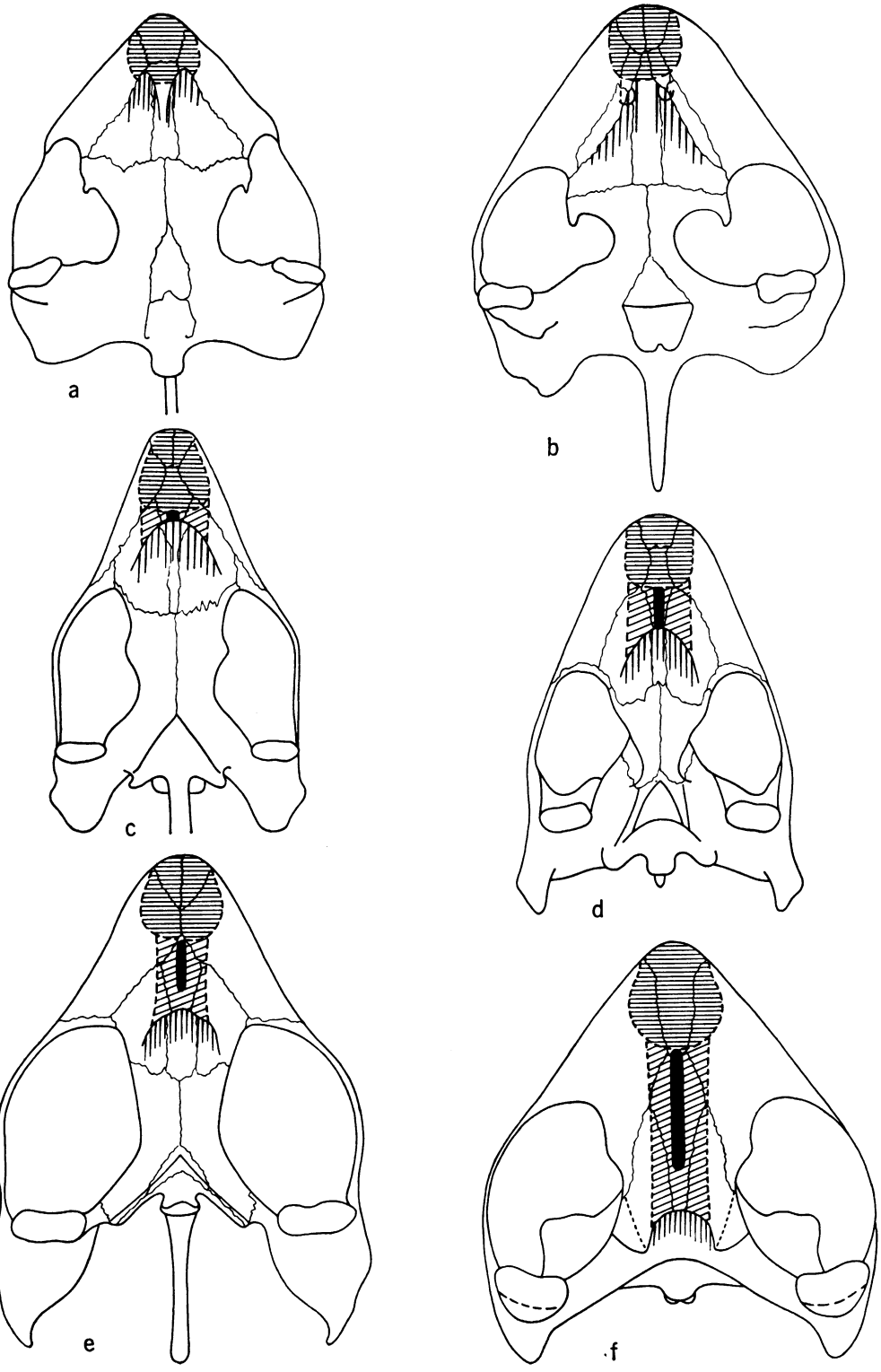
Within the Cryptodira I have recognized four superfamilies:

Baenoidea—extinct forms described by me (Gaffney, 1972a).

Trionychoidea—including the recent families (*sensu* Wermuth and Mertens, 1961) Trionychidae, Kinosternidae, Carettochelyidae, and Dermatemydidae.

Chelonioidea—including Cheloniidae, Toxo-

[1] There is an important error beginning in line 6 of the diagnosis. The clause "hyomandibular nerve in its own canal traversing cranio-quadrate space" should read: "hyomandibular nerve traverses cranio-quadrate space in *canalis cavernosus*."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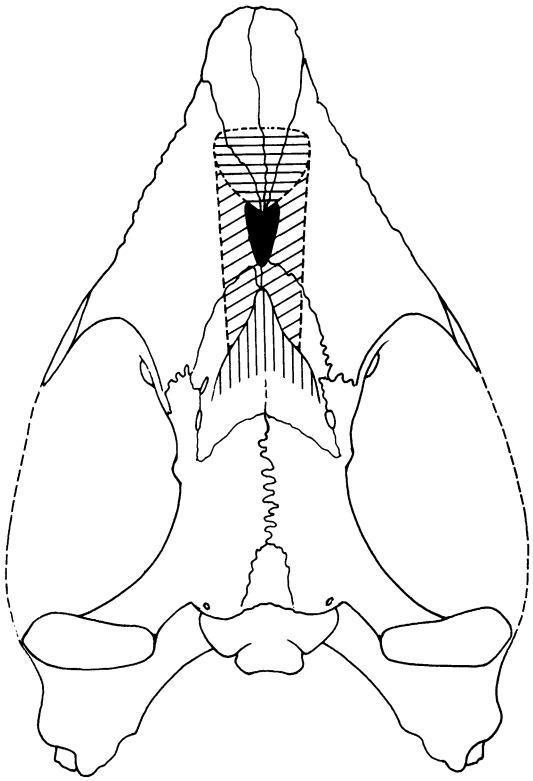

FIG. 21. *Solnhofia parsonsi*, new genus and new species. Ventral view drawn using conventions in figure 20 for comparison with palatal structures.

chelyidae, Protostegidae, and Dermochelyidae.

Testudinoidea—including Testudinidae, Emydidae, and Chelydridae.

The last three of these superfamilies are hypothesized to be a monophyletic unit, the Eucryptodira, that is the sister group of the Baenoidea (Paracryptodira). The basis for this relationship is the position of the internal carotid entry into the skull (discussed in detail in Gaffney, In press). The derived character for baenoids is that the *foramen posterius canalis carotici interni* lies midway along the length of the basisphenoid-pterygoid suture, whereas in eucryptodires the *foramen* lies at or near the posterior end of the pterygoid and is largely formed by that bone. I have argued (In press) that both conditions are derived with respect to the Cryptodira as a group and this brings us to the significance of *Solnhofia*.

Parsons and Williams (1961, p. 60) mentioned a foramen in the ventral surface of the pterygoid anterior to the *foramen posterius canalis carotici interni*. As I am suggesting that the position of the carotid artery is diagnostic of large groups of turtles, any "extra" foramina or structures apparently intermediate between the baenoid and eucryptodiran condition would be of some interest as a possible negative test of my hypothesis. As can be seen from the previous basicranial description, however, Parsons and Williams were correct in their identification of the position of the *foramen posterius canalis carotici interni*, and the "extra" foramen is apparently not part of the *canalis caroticus internus* but seems to be related to the *canalis caroticus lateralis.*

Solnhofia, then, is clearly a eucryptodire. The relationship of *Solnhofia* within the Eucryptodira, however, is much more difficult. Table 2 compares diagnostic features of the eucryptodiran superfamilies with *Solnhofia*, and it can be seen that *Solnhofia* lacks the derived characters of the Trionychoidea and Chelonioidea. The Testudinoidea, however, lack shared derived characters and, at present, there is no reason to think that it is a monophyletic group. Therefore, the present state of work on shared derived characters within the Eucryptodira really allows only three choices until more characters are proposed:

1. *Solnhofia* is most closely related to trionychoids.
2. *Solnhofia* is most closely related to chelonioids.
3. *Solnhofia* is closely related to neither of the above groups as presently construed.

FIG. 20. Comparison of palatal structures in a series of turtles: a, *Chelydra serpentina* (primary palate); b, *Ctenochelys procax* (incipient secondary palate); c, *Eretmochelys imbricata* (secondary palate); d, *Chelonia mydas* (secondary palate); e, *Caretta caretta* (secondary palate); f, *Erquelinnesia gosseleti* (secondary palate). *Symbols*: Horizontal shading, nasal cavity; diagonal shading, nasal passages (*meatus choanae*); vertical shading, choanal openings; black, vomer pillar. From Zangerl, 1971.

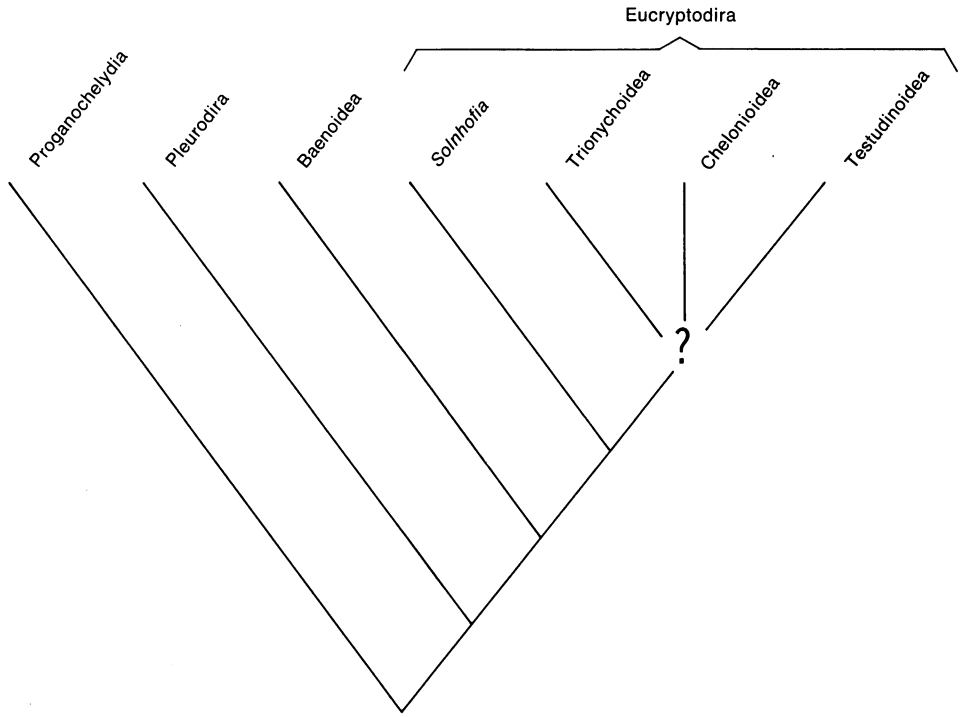

FIG. 22. A cladogram summarizing the hypothesis of relationships developed for *Solnhofia*. Diagram indicates only relative position of common ancestors. Other temporal, morphological, and adaptational parameters are not expressed.

TABLE 1
A Comparison of *Solnhofia* and *Portlandemys*[a]

Character	*Solnhofia*	*Portlandemys*
Snout long, narrow; extending anterior to *apertura narium externa*	Yes	No
Lateral outline of maxilla	Concave	Straight
Secondary palate	Present	Absent
Lingual ridges	Absent	Well developed
Triturating surface	Smooth and broad	Deep channel between lingual and labial ridges
Exposure of vomer on palate	Extremely reduced	Extensive, as in *Chelydra*
Palatines meet medially in ventral view	Yes	No
Processus pterygoideus externus	Reduced to a nubbin	Normally developed
Parietal contacts pterygoid	No	Yes
Processus trochlearis oticum	Extremely developed	Moderately developed
Contribution of prootic to *processus trochlearis oticum*	Forms less than two-thirds	Forms nearly all
Prootic enters margin of *foramen nervi trigemini*	Yes	No
Epipterygoid enters margin of *foramen nervi trigemini*	Yes	No
Foramen nervi trigemini hidden in lateral view by *processus trochlearis oticum*	Yes	No

TABLE 1–(*Continued*)

Character	*Solnhofia*	*Portlandemys*
Basioccipital enters *foramen magnum*	Yes	No
Exoccipital contacts pterygoid	No	Yes
Tuberculum basioccipitale	Well developed	Slightly developed
Precondylar fossa	Deep	Shallow
Precondylar fossa extends to basisphenoid	Yes	No
Trough for attachment of pterygoideus musculature on pterygoid bone	Opens posteriorly	Closed posteriorly by down-turned edge of pterygoid
Basis columellae	Conical	Flat
Posterior opening of *canalis caroticus lateralis*	Present	Absent
Sella turcica	Broad	Narrow
Rostrum basisphenoidale	Short, with trabeculae widely separated	Long, with trabeculae close together
Position of *foramen anterior canalis carotici interni*	Posterior to *sella turcica*, beneath *dorsum sellae*	In floor of *sella turcica*
Shape of *foramen anterior canalis carotici interni*	Large common opening	Two small, paired openings
Dorsum sellae overhangs *sella turcica*	Yes	No
Anterior end of lower jaw upturned to form hook	No	Yes
Prominent lingual ridge on lower jaw	No	Yes
Elongate median trough on dorsal surface of mandibular symphysis	Yes	No
Prominent paired troughs between labial and lingual ridges of lower jaw	No	Yes
Mandibular symphysis length/length of lower jaw	One-half	One-third
Sulcus cartilaginis meckelii	Short	Long
Lateral exposure of coronoid	Extensive	Limited

[a]Gaffney, 1975

TABLE 2
Comparison of *Solnhofia* with the Three Eucryptodire Superfamilies

Character	*Solnhofia*	Trionychoidea	Chelonioidea	Testudinoidea
Foramen stapedio-temporale reduced or absent	No	Often	No	No
Dorsal process on palatine present	No	Yes	No	No
Ossified trabeculae of *rostrum basisphenoidale* lie close together or are fused	No	No	Yes	No
Foramina anterius canalis carotici interni lie close together	Yes	No	Yes	Rarely
Sella turcica reduced or obliterated	No	No	Yes	No
Dorsum sellae high and separated from *sella turcica* by bone surface	No	No	Yes	No
Posterior portion of *sella turcica* concealed by overhanging *dorsum sellae*	Yes	Usually	No	Yes

Choice 3 is clearly indicated and, although it is unsatisfactory because no specific hypothesis of relationships has been advanced, it nonetheless accurately reflects the state of phylogeny development in this group.

LITERATURE CITED

Albrecht, Philip W.
1967. The cranial arteries and cranial arterial foramina of the turtle genera *Chrysemys*, *Sternotherus*, and *Trionyx*: a comparative study with analysis of possible evolutionary implications. Tulane Studies Zool., vol. 14, pp. 81-99.

Andrews, Charles W.
1906. A descriptive catalogue of the Tertiary Vertebrata of the Fayûm, Egypt. London, British Museum (Nat. Hist.), 1906, xxxvii+324 pp.

Bojanus, Ludwig, H.
1819. Anatome Testudinis Europaeae. Reprinted 1970, Soc. Study of Amphibians and Reptiles. Facsimile Reprints in Herpetoly, no. 26, vi+178 pp.

Bräm, Heinrich
1965. Die Schildkröten aus dem oberen Jura (Malm) der Gegend Solothurn. Schweizerische Palaont. Abhandl., vol. 83, pp. 1-190.

Brundin, Lars
1966. Transantarctic relationships and their significance, as evidenced by chironomid midges with a monograph of the subfamilies Pondonominae and Aphroteniinae and the austral Heptagyinae. K. Svenska Vetenskapsakad. Handl., ser. 4, vol. 11, no. 1, 472 pp.
1968. Application of phylogenetic principles in systematics and evolutionary theory. *In* Ørvig, T. (ed.), Current problems of lower vertebrate phylogeny. New York, Intersci. Publ., John Wiley and Sons, Nobel Symp. 4, pp. 473-495.

Cope, Edward D.
1871. On the homologies of some of the cranial bones of the Reptilia, and on the systematics arrangement of this class. Proc. Amer. Assoc. Adv. Sci., 19th meeting, August, 1870, pp. 194-247.

Eldredge, Niles
1972. Systematics and evolution of *Phacops rana* (Green, 1832) and *Phacops iowensis* Delo, 1935 (Trilobita) from the Middle Devonian of North America. Bull. Amer. Mus. Nat. Hist., vol. 147, art. 2, pp. 45-114.

Gaffney, Eugene S.
1972a. The systematics of the North American family Baenidae (Reptilia, Cryptodira). Bull. Amer. Mus. Nat. Hist., vol. 147, art. 5, pp. 241-320.
1972b. An illustrated glossary of turtle skull nomenclature. Amer. Mus. Novitates, no. 2486, pp. 1-33.
[In press.] Phylogeny and classification of the higher categories of turtles.
1975. A Taxonomic Revision of the Jurassic Turtle *Portlandemys* and *Plesiochelys*. Amer. Mus. Novitates, no. 2574, pp. 1-19.

Goodrich, Edwin S.
1916. On the classification of the Reptilia. Proc. Roy. Soc. London, B, vol. 89, pp. 261-276.
1930. Studies on the structure and development of vertebrates. London, Macmillan Co., xxx+837 pp.

Hennig, Willi
1966. Phylogenetic systematics. Urbana, Univ. Illinois Press, 263 pp.

Hunt, Timothy J.
1958. The ordinal name for tortoises, terrapins and turtles. Herpetologica, vol. 14, pt. 3, pp. 148-150.

Kluge, Arnold G.
1971. Concepts and principles of morphologic and functional studies. *In* Waterman, Allyn J., et al., Chordate structure and function. New York, Macmillan Co., pp. 3-41.

Linnaeus, Carolus
1758. Systema naturae. 10th ed. Stockholm, vol. 1, 824 pp.

McDowell, Samuel B.
1961. On the major arterial canals in the ear region of testudinoid turtles and the classification of the Testudinoidea. Bull. Mus. Comp. Zool., vol. 125, no. 2, pp. 23-39.
1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. Proc. Zool. Soc. London, vol. 143, pp. 239-279.

Nelson, Gareth J.
1969. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. Bull. Amer. Mus. Nat. Hist., vol. 141, art. 4, pp. 475-552.

Parsons, Thomas S., and Ernest Williams
1961. Two Jurassic turtle skulls: a morphological study. Bull. Mus. Comp. Zool., vol. 125, pp. 43-107.

Schaeffer, Bobb, Max Hecht, and Niles Eldredge
1972. Paleontology and phylogeny. *In* Dobzhansky, T., et al. (eds). Evolutionary biology. New York, Appleton-Century-Crofts, vol. 6, pp. 31-46.

van Regteren-Altena, C. O.
1967. Note on the history of a Jurassic turtle skull in the Teyler Museum. Geol. Mijnbouw, vol. 46, no. 3, p. 109.

Wermuth, H., and R. Mertens
1961. Schildkröten, Krokodile, Brückenechsen. Jena, Gustav Fischer, xxvi+422 pp.

Wood, Roger C.
1970. A review of the fossil Pelomedusidae (Testudines, Pleurodira) of Asia. Breviora, Mus. Comp. Zool., no. 357, pp. 1-24.

Zangerl, Rainer
1953. The vertebrate fauna of the Selma Formation of Alabama. Part 3. The turtles of the Family Protostegidae. Part 4. The turtles of the Family Toxochelyidae. Fieldiana: Geol. Mem., vol. 3, nos. 3 and 4, pp. 61-277.
1971. Two toxochelyid sea turtles from the Landenian Sands of Erquelinnes (Hain Aut), of Belgium. Inst. Roy. Sci. Nat., Belgique, Mem. no. 169, pp. 1-32.