

# THE HOMOLOGY OF SUPRAMARGINALS IN TURTLES (REPTILIA: CHELONII)

*[Homología de supramarginales en las tortugas (Reptilia: Chelonii)]*

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**RESUMEN:** En las tortugas, las supramarginales son constantes en su calidad homológica y en su posición. Teniendo esto en cuenta, los escudos supramarginales son usados aquí para su análisis filogenético e interpretación taxonómica. *Priscochelys hegnabrunnensis* n. gen. n. sp., la tortuga hasta ahora más antigua basada en fragmentos del caparazón, fue descubierta en el Muschelkalk superior de Hegnabrunn, cerca de Kulmbach, en Franconia Superior. Está representada por un fragmento de pleural IV izquierda. Se diferencia de la parte similar del caparazón de *Proganochelys quenstedti* Baur, 1887, en el desarrollo de cinco placas supramarginales en vez de cuatro. Es muy probable que el borde periferal del caparazón en *Priscochelys* consista en una parcialmente doble fila de supramarginales.

**Palabras clave:** *Priscochelys hegnabrunnensis* n. gen. n. sp., Muschelkalk superior, Hegnabrunn cerca de Kulmbach, Franconia Superior, criterios de homología, análisis filogenético.

**ABSTRACT:** Supramarginals in turtles are constant in their homologic quality and position. On that base the supramarginal scutes are usefull for phylogenetic analysis and taxonomic interpretations. *Priscochelys hegnabrunnensis* n. gen. n. sp., the hitherto most old turtle founded of body remain was discovered in the Upper Muschelkalk of Hegnabrunn near Kulmbach in Upper Franconia. It is represented by a fragmentary left pleural plate IV from the carapace. This shell fragment differs from the related part from carapace of *Proganochelys quenstedti* Baur, 1887 in the development of five supramarginal plates instead of four. It is

highly probable that the peripheral border of the carapace in *Priscochelys* consists of a partially double row of supramarginal plates.

**Key words:** *Priscochelys hegnabrunnensis* n. gen. n. sp., Upper Muschelkalk, Hegnabrunn near Kulmbach, Upper Franconia, criterias of homology, phylogenetic analysis.

## 1. CRITERIAS OF THE HOMOLOGY OF SUPRAMARGINALS IN TURTLES

The homologous character of the supramarginals with epithelial shell elements of *Dermochelys* was discussed already early (VERSLUYS, 1914). Then it was assumed of the fact that these horn shields served originally as an exterior cover of skin bone plates which were reduced in the course of the evolution. Because these dermal elements would have lain according to the specific position of the supramarginal horny scutes rudimental now about thecal, therefore, these would have been epithelial buildings, comparably to those of the mosaic shell of the leather turtles.

Today is proved that the epithelial shell of the leather turtles is a secondary building which followed the reduction of the thecal sea turtle shell. Actual studies on general turtle shell structure are made by CHEREPANOV (1995), KARL & TICHY (2005) and KORDIKOVA (2002b). Homologous aspects of plastral scales of kinosternid turtles and related taxa describes HUTCHISON & BRAMBLE (1981).

### 1.1. HOMOLOGY OF THE SPECIFIC QUALITY

The specific quality of the supramarginals of turtles is homologous, because they agree in all their characteristics. This is considered to their building zone in the skin just like for their nature as a relic building within the Casichelydia. The reduction of the supramarginals is a derived character which stands in the context with the general reduction of the dermal elements with turtles actually.

### 1.2. HOMOLOGY OF THE POSITION

The position of the supramarginals of turtles is homologous, because they always take the same position in the comparable Bauplan of the turtle shell. As a basic model the structure of *Proganochelys* (figure 1 A) is considered, in this connection. Here the starting constellations of the separate shields are found as position brands for the known relations within the Casichelydia (figure 1 B-E). For example, are considered to *Platycheilus*:

1. Supramarginal plate 1 at the intersection of central 1, lateral 2, marginal 1, 2 and 3;

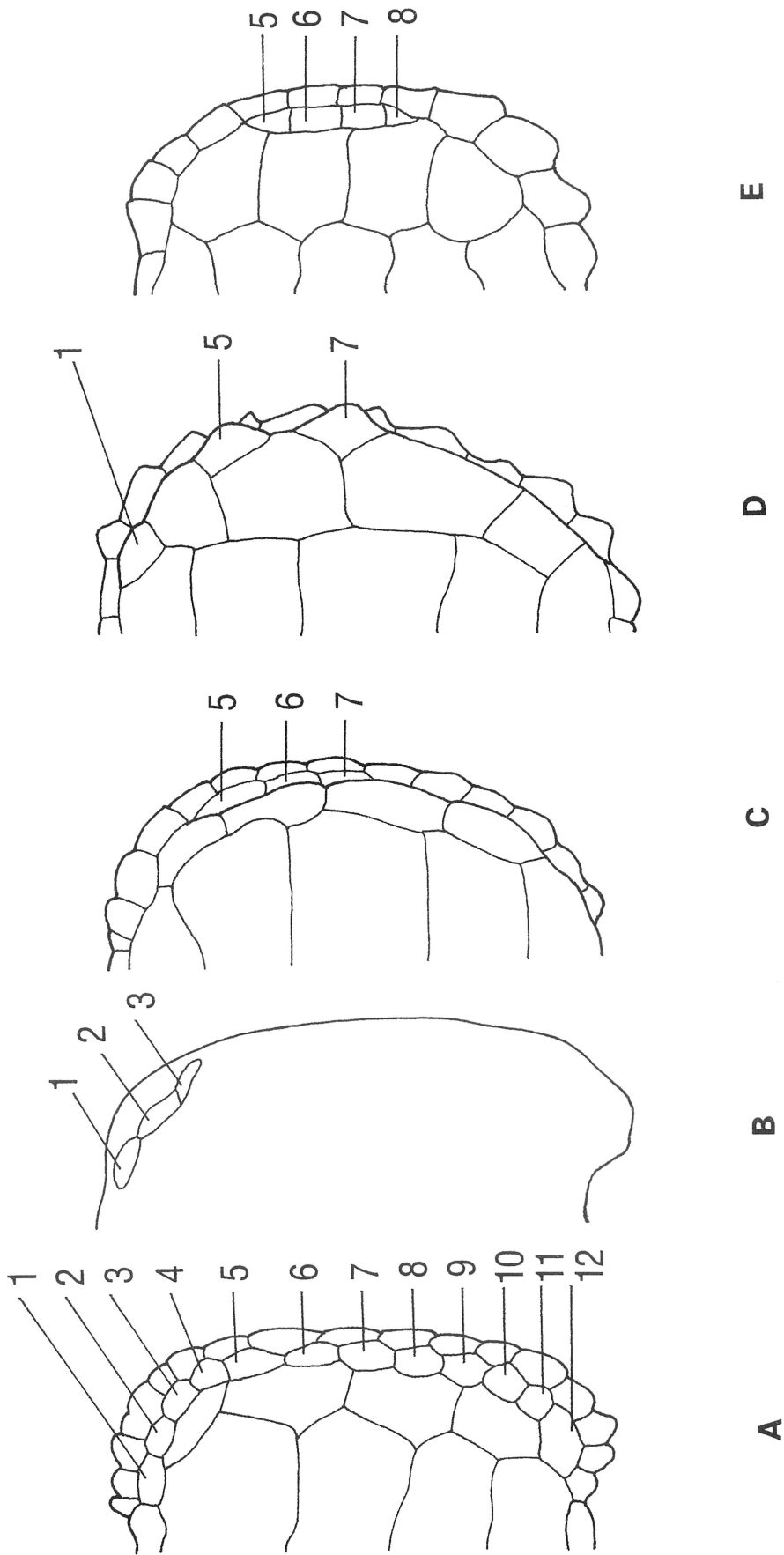


Figure 1. Homology of position of supramarginals in Chelonii.  
 A = Proganocheilus; B=Palaeochersis; C = Murrhardtia; D = Platycheilus; E = Macroclemys.  
 The figures 1-12 state the numbers of the separate supramarginals. Without scale.

2. Supramarginal plate 5 at the intersection of laterals 1 and 2 as well as marginals 4 and 5;

3. Supramarginal plate 7 at the intersection of laterals 2 and 3 as well as marginals 6 and 7.

*Proganochelys* hitherto was so far the only Taxon with continuous supramarginal row of the marginal 1 up to the marginal 16, i.e. supramarginals corresponds with every laterals from 1 to 4 by which latter conclude no contact with the marginals. With all other Taxa out the Proganochelydia known till present with supraneurals no propagation of these shields after the lateral 3 is known.

## 2. CHARACTER ANALYSES

The character analyses and tree constructions are made with the programmes PAUP (Madison & Madison), PHYLIP (Josef Felsenstein), NEXUS and TreeView (both Roderic Page).

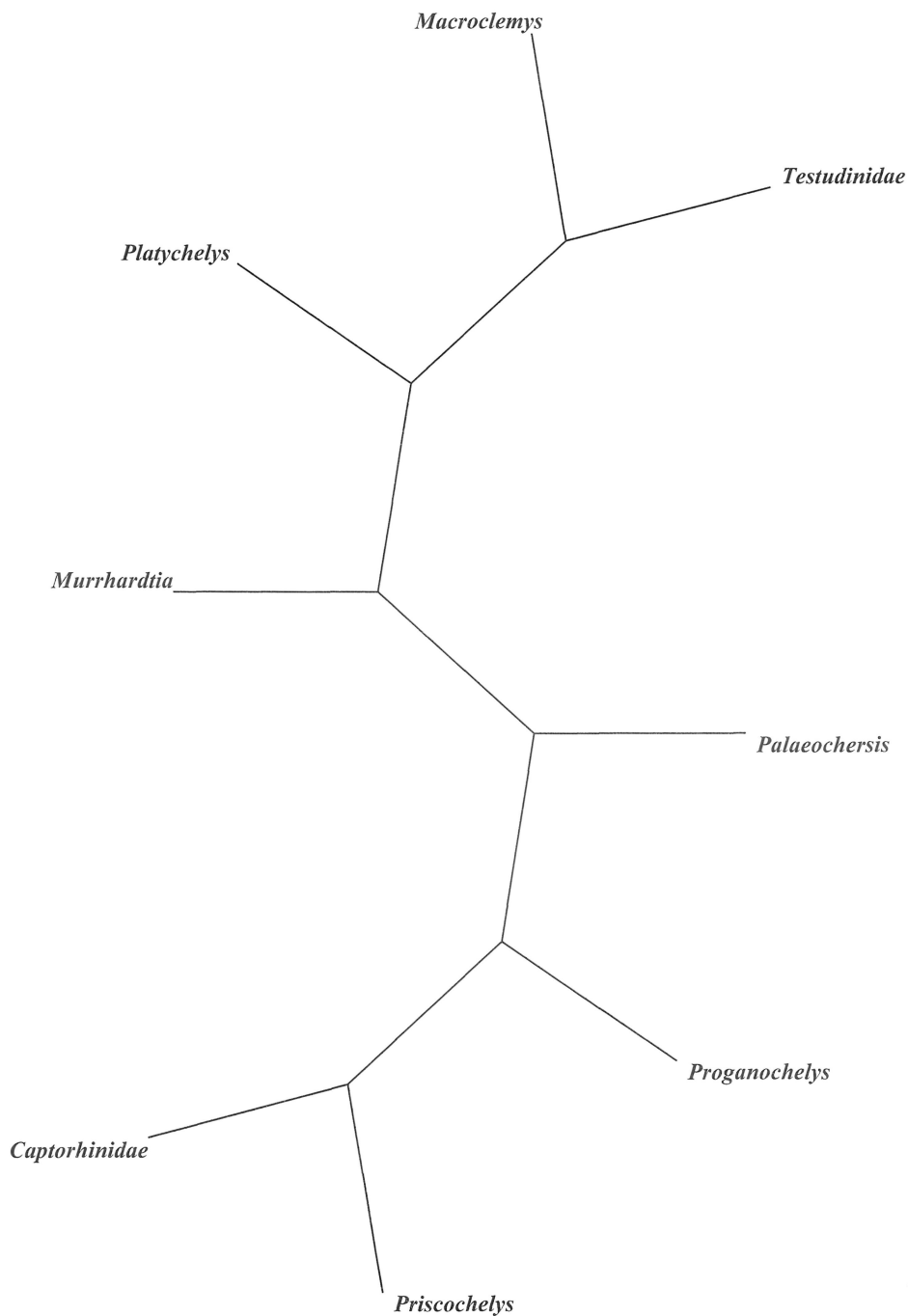
### 2.1. CHARACTER ANALYSIS UNDER INCLUSION OF THE SUPRAMARGINALS (TREE 1)

1. Thecal shell present, yes= 1, no= 0 ;
2. Supramarginal scute 1 present, yes= 1, no= 0;
3. Supramarginal scute 2 present, yes= 1, no= 0;
4. Supramarginal scute 3 present, yes= 1, no= 0;
5. Supramarginal scute 4 present, yes= 1, no= 0;
6. Supramarginal scute 5 present, yes= 1, no= 0;
7. Supramarginal scute 6 present, yes= 1, no= 0;
8. Supramarginal scute 7 present, yes= 1, no= 0;
9. Supramarginal scute 8 present, yes= 1, no= 0;
10. Supramarginal scute 9 present, yes= 1, no= 0;
11. Supramarginal scute 10 present, yes= 1, no= 0;
12. Supramarginal scute 11 present, yes= 1, no= 0;
13. Supramarginal scute 12 present, yes= 1, no= 0;
14. Supramarginal scute 13 present, yes= 1, no= 0;
15. Caudal section with reduction of pygal area present, yes= 1, no= 0.

Outtree:

(Testudinidae, (*Macrochelys*, (*Platycheilus*, (*Murrhardtia*, (*Palaeochersis*, (*Proganochelys*, (*Priscochelys*, (Captorhinidae)))))))).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<b>Captorhinidae</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Priscochelys</i>	1	?	?	?	?	?	?	?	?	1	1	1	1	1	?
<i>Proganochelys</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
<i>Palaeochersis</i>	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Murrhardtia</i>	1	0	0	0	0	1	1	1	0	0	0	0	0	0	1
<i>Platychelys</i>	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0
<i>Macrolemys</i>	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0
<b>Testudinidae</b>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0



**TREE 1**

On the basis of the largely constant qualities in the homologies of the supramarginals of Chelonii as well as their clear differentiation: and consequently their taxonomic usability is indicated.

## 2.2. CHARACTER ANALYSIS OF THE KNOWN TRIASSIC AND SOME JURASSIC TURTLE TAXA (TREE 2)

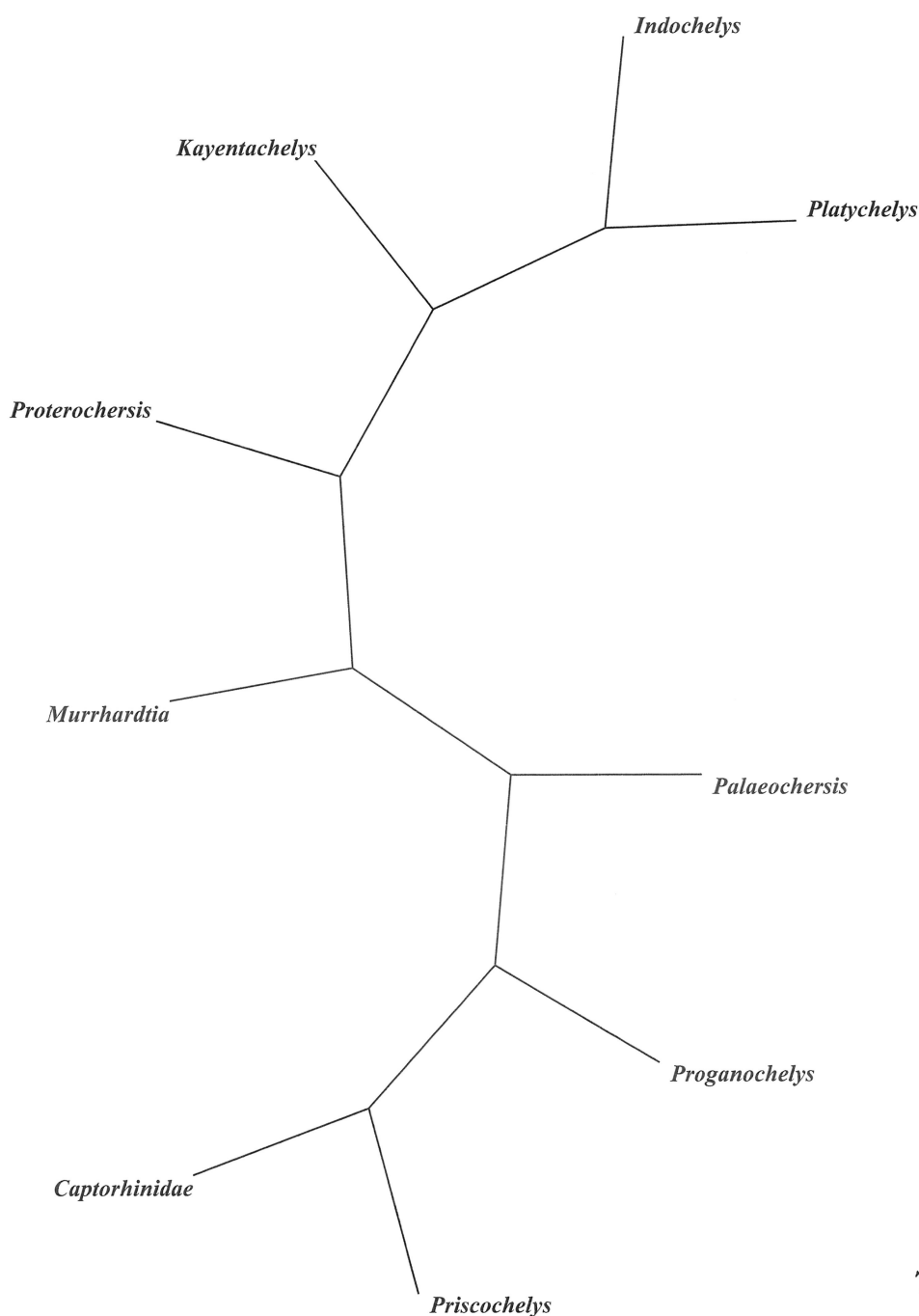
1. Supramarginals at lateral 4, yes= 1, no= 0;
2. One intergular divide gulars, yes= 1, no= 0;
3. One pair mesoplastrons present, yes= 1, no= 0;
4. Entoplastron divides epiplastra complete, yes= 1, no= 0;
5. Clearly caudal section present, yes= 1, no= 0;
6. Anal section strong developed, yes= 1, no= 0;
7. Interanal present, yes= 1, no= 0;
8. Two pairs mesoplastrons present, yes= 1, no= 0;
9. Submarginals present, yes= 1, no= 0;
10. Infraplastrals present, yes= 1, no= 0;
11. Two intergulars divides gulars, yes= 1, no= 0;
12. Nuchal "zack" may developed, yes= 1, no= 0;
13. Only one single gular present, yes= 1, no= 0;
14. Nuchal not broader than peripherals, yes= 1, no= 0;
15. Bridge fontanelles present, yes= 1, no= 0;
16. Axillars and inguinals present, yes= 1, no= 0.

Outtree:

(*Platycheilus*, (*Indochelys*, (*Kayentachelys*, (*Proterochersis*, (*Murrhardtia*, (*Palaeochersis*, (*Proganochelys*, (*Priscochelys*, Captorhinidae)))))))).

The homology of supramarginals in turtles (Reptilia: Chelonii)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<b>Captorhinidae</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>Priscochelys</b>	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<b>Proganochelys</b>	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
<b>Palaeochersis</b>	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
<b>Murrhardtia</b>	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0
<b>Proterochersis</b>	0	0	0	0	0	1	1	1	0	0	0	1	1	1	0	0
<b>Kayentachelys</b>	0	1	1	1	0	0	0	0	1	0	0	0	0	0	1	1
<b>Indochelys</b>	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1
<b>Platychelys</b>	0	1	1	1	0	0	?	0	0	0	0	0	0	0	1	0



**TREE 2**

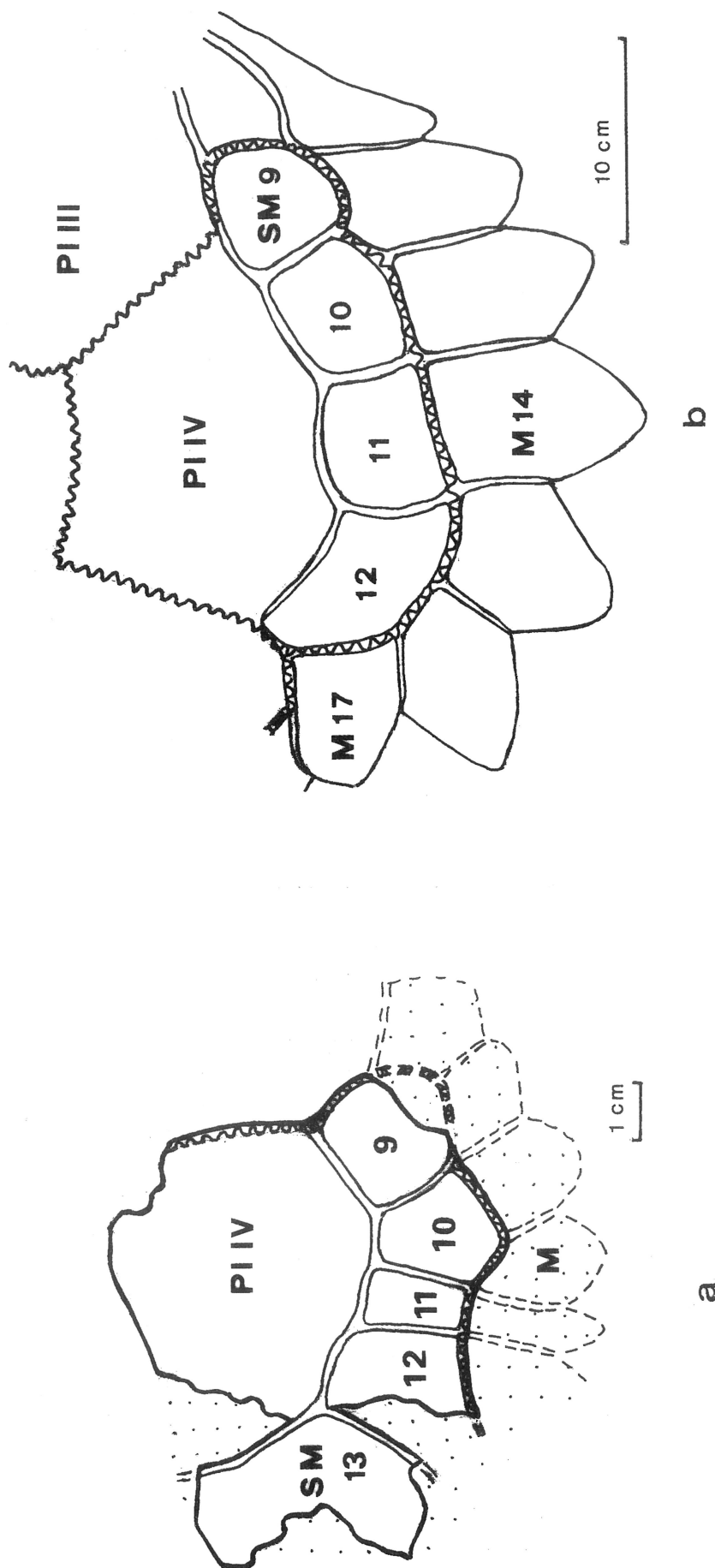


Figure 2. Homologous position of supramarginals on the pleural IV of the *Proganochelydia*. a = *Priscochelys hegnabrunnensis* n. gen. n. sp., SMNS 80141 (holotype), Upper Muschelkalk, Hegnabrunn near Kulmbach, Franconia; original; b = *Proganochelys quenstedti* Baur 1887; Combinated sketch of SMNS 16980 from the Knollenmergel of Trossingen and SMNS 15759 from the Middle Stubensandstein of Aixheim near Rottweil. Abbreviations: PIV = pleural plate IV, SM 9-13 = supramarginals, double line = horny scute board, single zig-zag line = sutures, dashed line = possible board, wave line = breaking line, points = reconstruction areas. Sketches by H.-V. Karl & R. Wild. Scales: a = 1 cm, b = 10 cm.



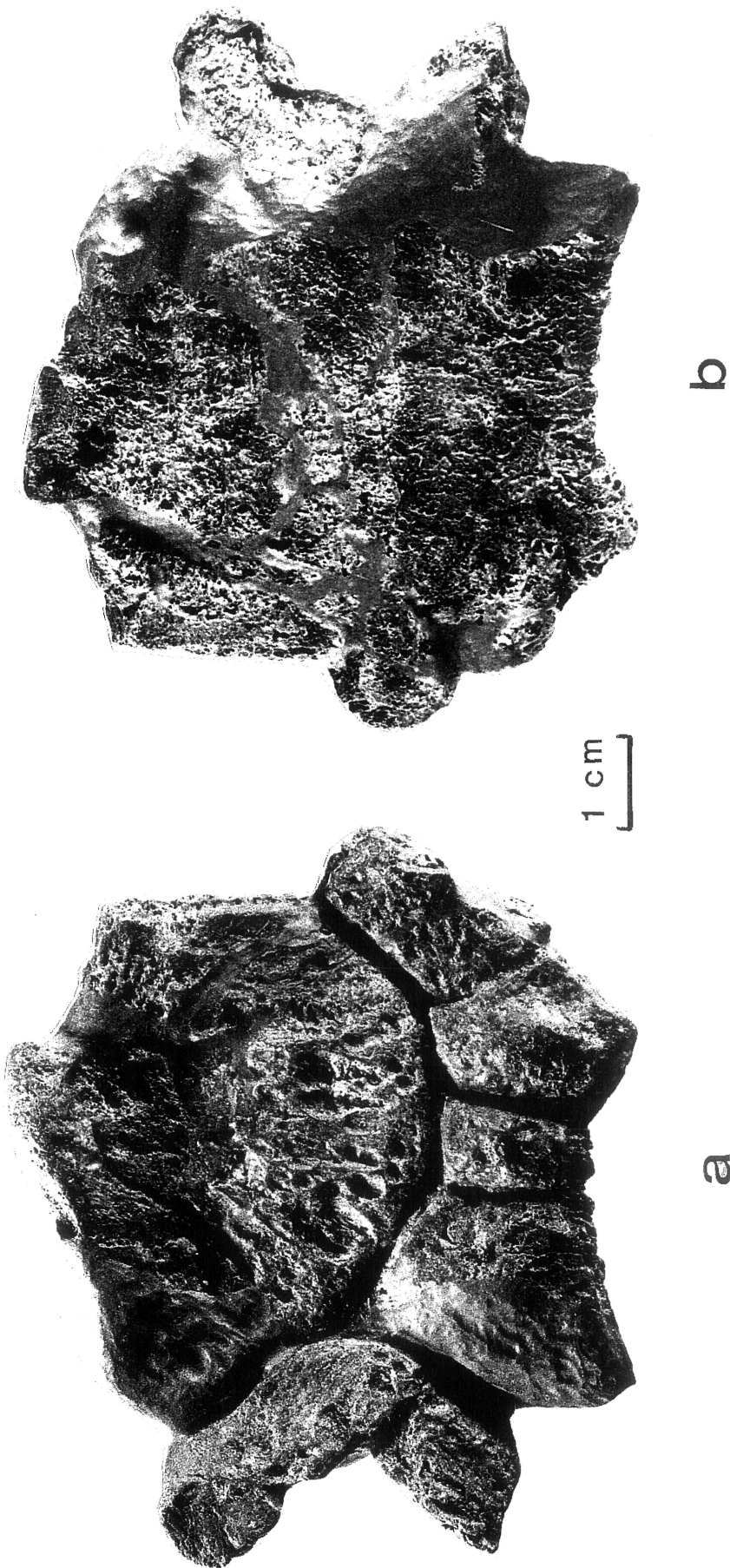


Plate 1. *Priscochelys hegnabrunnensis* n. gen. n. sp., holotype, SMNS 80141, Upper Muschelkalk, Hegnabrunn near Kulmbach, Franconia; figure 1 = fragmentary right pleural plate IV of carapace from dorsal; figure 2 = same as figure 1, from visceral, scale 1 cm. Photos: R. Harling, SMNS. Original.

### 3. DESCRIPTION OF A NEW PROGANOCHELYID TAXON

*Priscochelys hegnabrunnensis* n. gen. n. sp.

**Holotype:** Original to plate 1 and figure 2 a, SMNS 80141. Pleural plate IV, dex. Donation Coll. M. Wild, 1988.

**Type locality:** Hegnabrunn near Kulmbach (Quarry Schmidt, 1969), Franconia, Germany.

**Type horizon:** Upper Muschelkalk, high *enodis-laevigatus* Zone to deep *nodosus*-Zone.

**Derivatio nominis:** *Prisco*, *priscus* (lat.) = old, *chelys* (gr.) = turtle, *hegnabrunnensis* = Hegnabrunn as the type locality; advertisement in KARL & TICHY (2002b).

**Diagnosis:** Five supramarginals at the pleural IV present. Anterior supramarginal very much larger as the others at this plate.

**Differential diagnosis:** The limited condition of SMNS 80141 admits only few statements and, however, fundamental characteristic features can be found out which are taxonomic usable. It is, in this connection, particularly about the characteristic building type of the supramarginals. These lie, if existing, between the laterals and marginals on the dorsal side of the Carapax. Rezent have been known them only with a monotypic genus and species: *Macroclermys temminckii* (Harlam, 1835) (figure 1 E, according CARR (1952) shows four and WERMUTH & MERTENS (1961) shows only three supramarginals). Also only three Supramarginalia possess *Palaeochersis* (figure 1 B, according ROUGIER *et al.* in 1995), *Murrhardtia* (figure 1 C, according KARL & TICHY in 2000b), *Platycheles* (figure 1 D, according BRÄM in 1965). With *Platycheles* three supramarginals are present separately. *Proganochelys* (figure 1 A, according GAFFNEY in 1990) possesses on both sides one solid continuous row of twelve supramarginals which are in touch anterior and posterior with the vertebral row. With *Proganochelys* and *Priscochelys* the Supramarginalia are not farther extended as about the Lateralia three after posterior in other turtles. *Proganochelys* (plate 2, figures 1-3 show the so far single Pleurale IV with direct relations with supramarginals; figure 2, figure b) and *Priscochelys* n. gen. (plate 1, figure a-b; figure 2 a) what is seen here as a plesiomorph character of the Proganochelydia.

**Finding circumstances:** Of the tortoises shell remain (SMNS 80141) came with the acquisition of the Muschelkalk collection M. Wild, Kulmbach, in 1988 to the State Museum for Natural History Stuttgart. The fossil was found on 6.3.1969 in the quarry open today "Schmidt" in Hegnabrunn near Kulmbach in Upper Franconia, Bavaria. This quarry lies possibly on half a way with the street between Hegnabrunn and Feuln in the district Kulmbach on ordance survey map No 5935 market choir guest, 1: 25 000. Its coordinates are: R = 4468125 and H = 5550075. The profile opens approximately 16 meters of Upper Muschelkalk from deep *spinosus*-up to high *nodosus*-zone. The fossil was discovered after a spraying in a

Schillkalkbank in the middle area enodis/laevigatus-zone. Therefore, it has a chronostratigraphic age of Lower Ladinian (Fassanian/Longobardian). The tortoise's armour plate broken in several pieces lay in a possibly fist-big Geode filled with soft brown Mulm. This the Schillbank was stored. The Geode was broken open by the spraying. Some small bone parts had fallen out and had got lost in the explosive waste dump. The remaining flat parts were taken from the Mulm, were cleaned with water and were stuck together. Small missing portions were supplemented with synthetic material, so that approximately 8 x 6 cm armoured piece as well as in plate 1 returned presents itself (all informations according a letter by Dr. Rupert Wild).

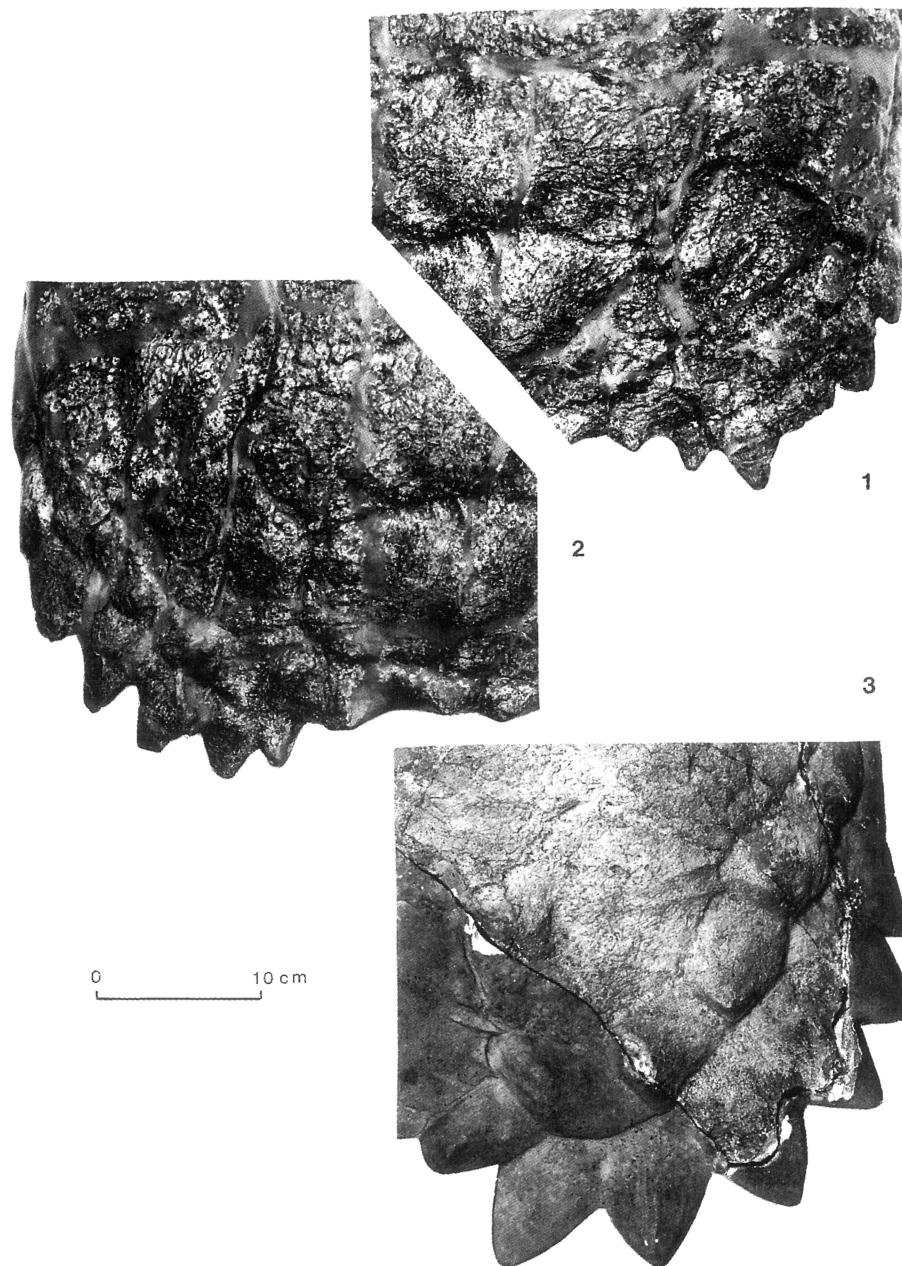


Plate 2. *Proganochelys quenstedti* Baur, 1887; SMNS 16980, posterior peripheral margin; figure 1. dex., figure 2. sin.; SMNS 15759, posterior peripheral margin dex., reconstruction, Photos: Archive SMNS. Scale for all 10 cm.

#### 4. DISCUSSION

The higher number of the present supramarginals with *Priscochelys begnabrunnensis* n. gen. n. sp. from the Muschelkalk takes place on the hypothetical course of development of the turtles shell. This shows continuous evolutional to reduction tendency of different areas, among other things also of the horn sign-posting like the supramarginals. The new and at the same time stratigraphic the oldest body material has from all known turtles the highest number of these horny shields in this body area. This is the development most original so far of this character. It appears, that the cryptodiran *Kayentachelys* (GAFFNEY *et al.*, 1987) also shows very old-fashioned characters distributions. The also Lower Jurassic *Indochelys* is similar (DATTA *et al.*, 2000) however, no submarginal possesses.

The unit structure of the presenting carapace elements of Proganochelyidae is clear different to other Mesozoic reptiles, e. g. Placodontia (see WESTPHAL, 1975; RIEPPEL, 2000), members of the sauropterygians. DE BRAGA & RIEPPEL (1997) discussed these diapsid reptiles in direction to turtles relationships. The reanalysis of skull, roof and palate of *Proganochelys* by KORDIKOVA (2002a) confirms the parareptilian status of ancient turtles. A paedomorphic origin of the ancient turtle palate pattern from that of a basal pareiasaurid lineage is suggested according KORDIKOVA (2002a).

Principally, turtles signs, respectively their tracks named *Chelonipus* (*Chelonipus torquatus* LILIENSTERN, 1939 and *Chelonipus triunguis* KARL & TICHY, 2000a) are known already from the Lower Triassic the Lower Anisian Buntsandstein (Thuringian Chirotherian-Sandstone) from Thuringia in Middle Germany. A further ichnospecies was described as *Chelonipus plieningeri* HAUBOLD, 1971 from Stubensandstein or Schilfsandstein, Middle Keuperian, Upper Triassic of Feuerbacher Heide near Stuttgart in Wurttemberg, South Germany. *Priscochelys* n. gen. to obtain between the oldest signs from the Bunter (Lower Triassic) within the first complete materials of *Proganochelys* from the Keuperian (Upper Triassic). It is a "missing link" in this constellation and a very important fossil remain for voucher and proof of presence the turtles in the Middle Triassic. It is the most old body fossil remain hitherto known of a turtle of the world.

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**Abbreviation:** SMNS= Staatliches Museum of Naturkunde Stuttgart.

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