

THE CHELONIAN *RHINOCHELYS* SEELEY  
FROM THE UPPER CRETACEOUS OF  
ENGLAND AND FRANCE

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ABSTRACT. The Cretaceous chelonian genus *Rhinochelys* Seeley 1869, which is based on skull material, has been reinvestigated. The foundations for Lydekker's original specific descriptions are shown to be inadequate and new diagnostic features for the genus and species are established. Only three British species are recognized: the type species *R. pulchriceps* (Owen 1851), *R. elegans* Lydekker 1889, and *R. cantabrigiensis* Lydekker 1889. *R. amaberti* Moret 1935 from La Fauge Valley, near Grenoble, France, is compared with the British species. A general description of the skulls and mandibles is given. The taxonomic position of *Rhinochelys* is assessed and the genus is referred to the family Protostegidae, subfamily Chelospharginae. The skulls are compared with those of other Cretaceous turtle genera of the Protostegidae and Cheloniidae and a relationship is suggested. It is suggested that carapace and plastral material originally described as *Chelone (Cimochelys) benstedii* (Mantell 1841) probably belongs to *Rhinochelys*.

THE chelonian genus *Rhinochelys* was erected by Seeley (1869) for the type skull of *Chelone pulchriceps* Owen 1851, from the Lower Cenomanian Cambridge Greensand. Lydekker (1889) amended the description of the type species and described five new species of *Rhinochelys* (*R. macrorhina*, *R. elegans*, *R. cantabrigiensis*, *R. jessoni*, and *R. brachyrhina*) on skull material from British strata, ranging in age from Albian to Upper Cenomanian. In addition to these properly described and named species, an additional fifteen species were named but not described by Seeley (1869); they are therefore *nomina nuda*, so that the correct taxonomic positions of these specimens is not established. The type material of all these British species is housed in the British Museum (Natural History) and the Sedgwick Museum, University of Cambridge. The only other species known, *R. amaberti*, was described by Moret (1935) from the Vraconien of La Fauge Valley, near Grenoble, France.

The taxonomic position of *Rhinochelys* is at present uncertain. Seeley (1869) thought it showed emydian affinities; Lydekker (1889) considered that it resembled the pleurodires. Williston (1898) thought that it was probably related to his genus *Desmatochelys* and family Desmatochelyidae, from the Cretaceous of Kansas, and Romer (1956) also placed *Rhinochelys* in this family. However, Zangerl and Sloan (1960) suppressed the Desmatochelyidae when they showed, on the evidence of post-cranial material, that *Desmatochelys* has close affinities to the Cheloniidae.

As a result of the availability of new material, it is now possible to provide a more thorough description of *Rhinochelys*. Examination and detailed comparison of the British type specimens and of the other skulls of *Rhinochelys* has also permitted a new assessment of the validities and synonymies of the species and of the taxonomic position of the genus. This in turn has suggested that post-cranial material, known from the same deposits as the skull material, may in fact also belong to the genus *Rhinochelys*, the carapace of which is otherwise unknown.

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TAXONOMY OF THE GENUS *RHINOCHELYS*

*Generic diagnosis.* Skull has slight posterior emargination and no ventral emargination. Squamosal not in contact with parietal; blunt ant-orbital beak; nasal and prefrontal bones distinct; prefrontals excluded from narial margin and from meeting medially; epidermal sulci cross frontal and maxilla. No secondary palate; posterior margin of internal nares formed by maxillae and palatines; vomer divides internal nares as sharp ridge and extends only short way between palatines; palatines meet medially; grinding (tritulating) surface of maxillae and premaxillae has broad lingual ridge and deep groove in midline; pterygoids very narrow, emarginate and meet along their length, palatal surface slightly ridged; basisphenoid narrowly triangular and not ridged on palate.

*Type species.* *Chelone pulchriceps* Owen 1851, p. 8, pl. vii, figs. 1-3. Lower Cenomanian Cambridge Greensand, Barnwell, near Cambridge.

*Holotype.* B55775, Sedgwick Museum, Cambridge.

*Remarks.* As noted, twenty-two species have been ascribed to *Rhinochelys* by Owen, Seeley, Lydekker, and Moret, but only seven have been described. When Lydekker (1889) described his five new species and redescribed *R. pulchriceps* he used the following diagnostic features:

1. Size and shape of the external nares.
2. Size and shape of the nasal.
3. Inclusion of the prefrontal in the narial margin.
4. Depth of the premaxillae.
5. Swelling on the prefrontal.
6. The angle that the premaxillae make with the palate edge in profile.
7. Presence of a hook on the tip of the upper jaw.
8. The ratio of the height to the overall length of the skull.

The size and shape of the nares and nasal bones are variable features and too individual to be of use in distinguishing species.

The inclusion of the prefrontal in the narial margin was considered to be a feature of *R. brachyrhina* and *R. jessoni*. Close examination of the type of *R. brachyrhina* (text-fig. 4) reveals that the specimen is very worn and that the nares are enlarged until most of the nasals have been lost. The suture between the nasal and maxilla practically borders the nares, but it is clear that the prefrontal is definitely excluded from contributing to the narial margin. The suture lines on the very well-preserved type of *R. jessoni* (text-fig. 3) are not very distinct, but it can be seen with a lens that the maxilla and nasal meet and exclude the prefrontal from the narial margin, as in all the other specimens examined.

The depth of the premaxillae was used to distinguish *R. macrorrhina* from *R. elegans*. The type of *R. macrorrhina* (text-fig. 5d) is a poorly preserved snout with an eroded jaw edge. The bone is eroded for about half the depth of the premaxillae, which is evident from the structure of the tritulating surface of the palate. The relative depth of the premaxillae is, in any case, subject to individual variation.

A peculiar lateral swelling on the prefrontal was thought to be present in *R. elegans* alone. This area does not, however, appear to be more swollen on this specimen than on any other.

Although the first five characters used by Lydekker are not reliable, the remaining three (i.e. the height/length ratio, the angle that the premaxillae make with the palate edge, and the presence or absence of a hooked tip to the upper jaw), divide the British types into three groups, as can be seen from Table 1. Although these features can therefore be used as specific characters, Lydekker's descriptions are not comprehensive enough for practical purposes. The position becomes clear, however, when these features are defined as follows:

1. The height  $Y$  (height measured just anterior to the orbits) relative to the length  $Z$  (length between the frontal/parietal suture and the jaw tip).  
Relative height =  $(Y/Z) \times 100$ .
2. The angle between the anterior surface of the premaxillae and the edge of the palate, as seen in profile. (This is referred to as the premaxillary angle.)
3. The presence or absence of a hooked tip to the upper jaw.  
The measurements used are shown in text-figs. 1, 2.

Nevertheless these characters alone are not considered sufficient to assign all the specimens to valid species, and other distinctions were therefore sought. The following features are thought to be sufficiently distinct and constant to be of value:

4. The width  $X$  (width just posterior to the orbits) relative to the length  $Z$ .  
Relative posterior width =  $(X/Z) \times 100$ .
5. The angle between the two maxillae. (This is referred to as the 'jaw angle'.)
6. The presence or absence of a ridge over the maxillary sulcus.
7. The convexity or straightness of the premaxillae in profile.

Table 1 shows all these features as they appear on the type species, Lydekker's types, Seeley's named skulls, and on *R. amaberti* taken from Moret's plates and figures (1935, pl. 27, figs. 1-4). (Names in square brackets are the *nomina nuda* of Seeley.)

From Table 1 it can be seen that the British specimens fall into three groups and that none is referable to *R. amaberti*.

In the first group, *R. pulchriceps*, the relative width is over 100 but this is measurable on one specimen only; the relative height (47-51), is the lowest in the groups; the jaw angle is broad (72-80°); the premaxillary angle is acute (70-74°); there is no ridge over the maxillary sulcus; the premaxillae are straight in profile; and there is no hooked tip to the upper jaw.

In the second group, *R. elegans*, [*R. mastocephalus*], [*R. stenicephalus*], *R. brachyrhina*, *R. macrorhina*, the relative width (91-96), is the narrowest in the three groups, as it does not exceed 100; the relative height (51-61) is greater than that of the first group; the jaw angle (50-60°) is narrower than that of the first group; the premaxillary angle (80-90°) is not quite a right-angle; there is no ridge over the maxillary sulcus; the premaxillae are straight in profile; and there is no hook to the tip of the upper jaw. *R. brachyrhina* and *R. macrorhina* are poorly preserved snouts; however, they do not show any features of the other groups, and are therefore doubtfully included here.

In the third group, *R. cantabrigiensis*, *R. jessoni*, [*R. cardiocephalus*], [*R. dayi*], [*R. eurycephalus*], [*R. platyrhinus*], [*R. rhexorhinus*], [*R. sphenicephalus*], the relative width is the broadest of the three (87-108); the relative height (59-63) is the greatest of the three; the jaw angle (42-56°) is slightly narrower than that of the second group; the

premaxillary angle equals or exceeds a right angle; it is the only group with a ridge over the maxillary sulcus, a convex profile to the premaxillae, and a hooked tip to the upper jaw.

TABLE 1. Skull measurements of *Rhinochelys* (a—absent, p—present, s—straight, c—curved)

Types	$\frac{X}{Z} \times 100$	$\frac{Y}{Z} \times 100$	Jaw angle (in degrees)	Premaxillary angle (in degrees)	Ridge over sulcus	Premaxillary profile	Hooked tip
<i>R. pulchriceps</i>	107	51	72	74	a	—	a
<i>R. pulchriceps</i>	—	47	80	70	a	s	a
<i>R. elegans</i>	96	57	57	85	a	s	a
<i>R. elegans</i>	—	56	60	80	a	s	a
[ <i>R. mastocephalus</i> ]	95	61	54	88	a	s	a
[ <i>R. stenicephalus</i> ]	91	55	50	86	a	s	a
<i>R. brachyrhina</i>	—	61	—	—	a	—	—
<i>R. macrorhina</i>	—	51	—	90	a	s	—
<i>R. cantabrigiensis</i>	107	62	50	90	p	c	p
<i>R. jessoni</i>	99	63	55	97	p	c	p
[ <i>R. cardiocephalus</i> ]	87	61	45	94	p	c	p
[ <i>R. dayi</i> ]	93	59	52	98	p	c	p
[ <i>R. eurycephalus</i> ]	105	58	50	101	p	c	p
[ <i>R. platyrhinus</i> ]	108	60	42	92	p	c	p
[ <i>R. rhexorhinus</i> ]	—	—	56	95	p	—	—
[ <i>R. sphenicephalus</i> ]	100	60	44	93	p	c	—
<i>R. amaberti</i>	135	65	?105	93	a	s	a

In *R. amaberti* the relative width (135) is very broad; the relative height (65) is greater than that of the British types; the jaw angle is obtuse (?105°) and very much broader than that of the others; the premaxillary angle agrees with the third group but there is no ridge over the maxillary sulcus; the profile of the premaxillae is straight, and there is no hooked tip to the upper jaw.

Thus we have three distinct British species, *R. pulchriceps*, *R. elegans*, and *R. cantabrigiensis*. The names used are the senior taxa in the groups.

*Abbreviations.* The following abbreviations are used: British Museum (Natural History)—BMNH; Sedgwick Museum, University of Cambridge, SM; Institute of Geological Sciences, GSM. The material used in the charts includes the following specimens in addition to those mentioned:

*R. pulchriceps.* BMNH 2224, R1806, 2236, R2232: Isolated lower jaws: 46373, R2238, 35184, R35185, 47211, 49920, R793. SM B55771, B55772, B55779, B55811.

*R. elegans.* BMNH 35193, R2225, 41796, 46371, 46371a, 35194, 35197, R27, R2228, R2229, R2230, R2231, R2237, 35195. SM B55773, B55776, B55780, B55784, B55792, B55798, B55800.

*R. cantabrigiensis.* BMNH R1558, R2227, R2233, R2234, 35196. SM B55774, B55781, B55782, B55783, B55785, B55786, B55787, B55788, B55791, B55793, B55795, B55799, B56572, B56573, B56574, B56576, B56580.

### *Rhinochelys pulchriceps* (Owen 1851)

Plate 67, figs. 1–8; Plate 68, figs. 1–2

- 1851 *Chelone pulchriceps* Owen, p. 8, pl. 7, figs. 1–3.  
 1869 *R. pulchriceps* (Owen); Seeley, p. xviii.  
 1869 *R. dacognathus* Seeley, p. xviii.  
 1889 *R. pulchriceps* (Owen); Lydekker, p. 230, pl. 8, fig. 1.

*Holotype.* Skull lacking lower jaw, SM B55775.

*Measurements.* Holotype, over-all length 58.5 mm., width 40 mm.

*Horizon and locality.* Lower Cenomanian Cambridge Greensand, Barnwell, near Cambridge.

*Diagnosis.* Skull shallow, height *Y* less than half length *Z*; jaw angle broadly acute; premaxillary angle acute; profile of premaxillae straight; area over maxillary sulcus smooth; no hooked tip to upper jaw.

*Rhinocelys elegans* Lydekker 1889

Plate 68, figs. 3-7

- 1889 *R. elegans* Lydekker, p. 230, pl. 8, fig. 4.
- 1869 *R. mastocephalus* Seeley, p. xviii.
- 1869 *R. stenicephalus* Seeley, p. xviii.
- 1889 *R. brachyrhina* Lydekker, p. 231, pl. 8, figs. 3, 3a.
- 1889 *R. macrorhina* Lydekker, p. 230, pl. 8, fig. 7.

*Holotype.* Skull lacking lower jaw, BMNH 2226.

*Measurements.* Holotype, over-all length 64 mm., width 39.8 mm.

*Horizon and locality.* Lower Cenomanian Cambridge Greensand, near Cambridge.

*Diagnosis.* Skull high and narrow, height *Y* about three-fifths length *Z*; width *X* less than length *Z*; jaw angle narrow; premaxillary angle just less than right-angle; profile of premaxillae straight; no ridge over maxillary sulcus; no hooked tip to upper jaw.

*Rhinocelys cantabrigiensis* Lydekker 1889

Plate 68, figs. 8-16

- 1889 *R. cantabrigiensis* Lydekker, p. 230, pl. 8, figs. 2, 2a, 2b.
- 1889 *R. jessoni* Lydekker, p. 231, pl. 8, figs. 6a, 6b.
- 1869 *R. cardiocephalus* Seeley, p. xviii.
- 1869 *R. dayi* Seeley, p. xviii.
- 1869 *R. eurycephalus* Seeley, p. xviii.
- 1869 *R. platyrhinus* Seeley, p. xviii.
- 1869 *R. rheporhinus* Seeley, p. xviii.
- 1869 *R. sphenicephalus* Seeley, p. xviii.

*Holotype.* Skull lacking lower jaw, BMNH 43980.

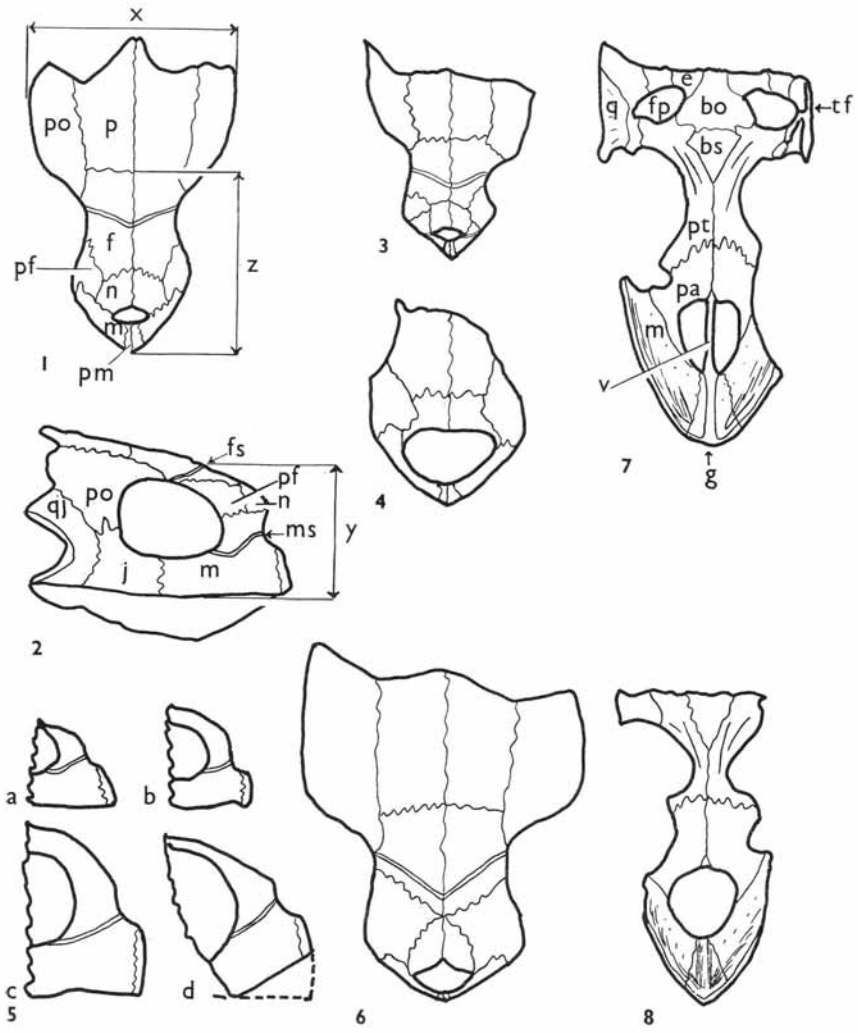
*Measurements.* Holotype, over-all length 42.5 mm., width 32.5 mm.

*Horizon and locality.* Lower Cenomanian Cambridge Greensand, near Cambridge.

*Diagnosis.* Skull high, broad, domed, height *Y* about three-fifths length *Z*; jaw angle narrow; premaxillary angle is right-angle or greater; profile of premaxillae convex; heavy ridge over maxillary sulcus; tip of upper jaw slightly hooked.

It must now be considered whether these diagnoses are supported by any other material.

In the collections examined, there are a further forty skulls which can be assigned to *Rhinocelys*. The specific features of these are carefully tabulated on text-fig. 9.



*Synopsis of text-fig. 9.*

*Fig. A.* The jaw angle is broader in *R. pulchriiceps* (66–80°) than in *R. elegans* (49–80°) and *R. cantabrigiensis* (40–63°). The figure for *R. amaberti* may be distorted as the measurement has been taken from a photograph, but the jaw-angle appears to be obtuse and very much broader than the other species at ?105°.

*Fig. B.* The relative height of *R. pulchriiceps* (43–51) is less than that of the other three species, *R. elegans* (51–76), *R. cantabrigiensis* (50–66), and *R. amaberti* (65).

*Fig. C.* The premaxillary angle in *R. pulchriiceps* is acute (63–77°). It is generally just less than a right-angle in *R. elegans* (80–100°), but in *R. cantabrigiensis* (89–105°) and *R. amaberti* (93°) it is slightly obtuse.

*Fig. D.* Only two specimens of *R. pulchriiceps* are sufficiently well preserved to allow the relative width to be used, but these differ widely. The relative width in *R. elegans* (74–97) does not exceed 100; however in *R. cantabrigiensis* this relative width is 87–109, i.e. the width *X* is generally in excess of the length *Z*, although there is a slight overlap. *R. amaberti* at 135 is very much broader.

In the few specimens with concurrent measurements, the other specific features are present and well defined. It is inevitable that there is a degree of variation within a biological group, but the majority in each species can be clearly differentiated using proportional measurements and angles alone. For a list of the other material used see p. 358.

The evidence presented here shows that these skulls can also be placed in three groups which agree with the specific diagnoses, and that all are distinct from *R. amaberti*. Analysis of these specimens also shows additional differences between the palate and mandible of *R. pulchriiceps* and those of *R. elegans* and *R. cantabrigiensis*. In the formation of the ridges and grooves there are differences between the palate of the type of *R. pulchriiceps* (Pl. 67, fig. 3, text-fig. 7) and those of two other specimens, one referable to *R. elegans* (SM B55792) (text-fig. 8) and the other to *R. cantabrigiensis* (SM B56574).

In *R. pulchriiceps* the lingual ridge runs alongside the median groove and appears to join the cutting edge anteriorly. The anterior tip of the premaxillae is notched. The mandibles which fit the broad-angled jaw, and can be referred to *R. pulchriiceps*, have a sharp median crest which extends right across the symphysis.

## TEXT-FIGS. 1–8.

Figs. 1, 2. *R. elegans* SM B55776. 1, Dorsal view,  $\times 1$ ; 2, Lateral view,  $\times 1$ . *Z*, length from the frontal-parietal suture to the jaw tip; *X*, width just behind the orbits; *Y*, depth just anterior to the orbits

Fig. 3. Type of *R. jessoni* showing the prefrontals are excluded from meeting medially,  $\times 1$ .

Fig. 4. Type of *R. brachyrhina* showing the prefrontals are excluded from the narial edge.

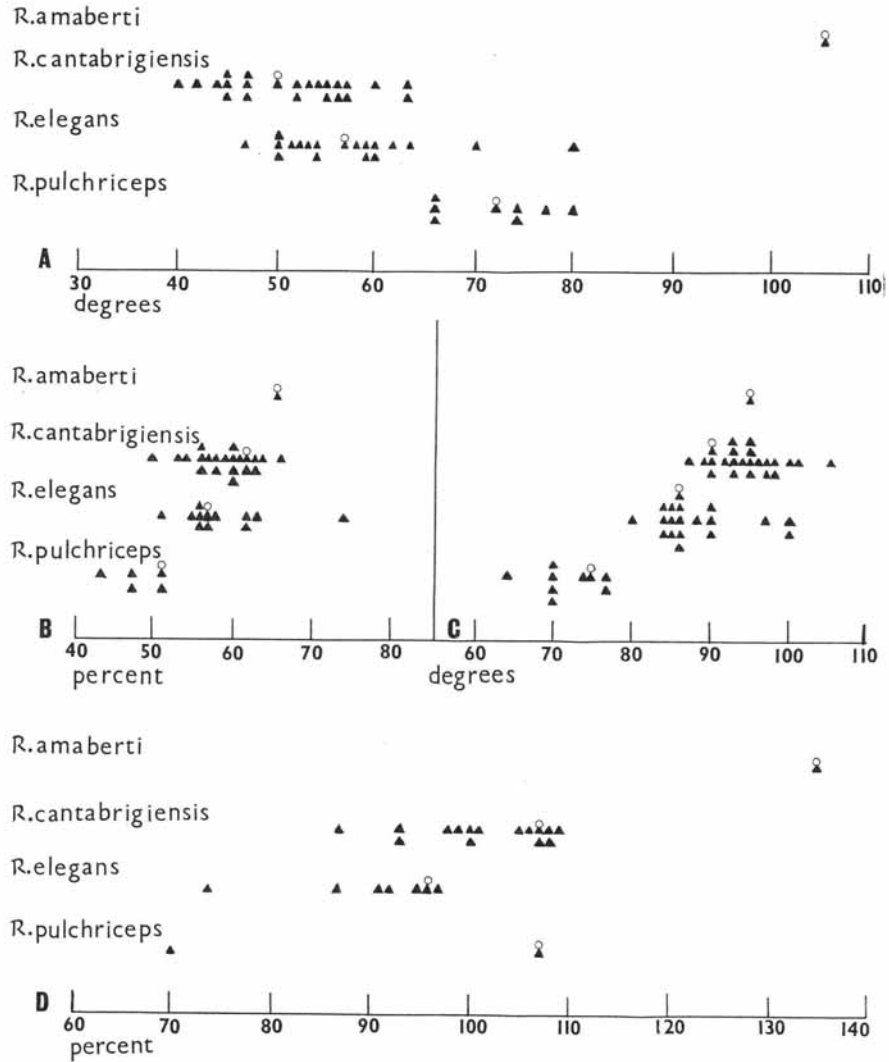
Fig. 5. Profile of the beaks. *a*, *R. pulchriiceps*; *b*, *R. cantabrigiensis*; *c*, *R. elegans*; *d*, Reconstructed beak of *R. macrorhina*.

Fig. 6. *R. amaberti* (after Moret 1935, pl. xxvii, fig. 1).

Fig. 7. *R. pulchriiceps*, palatal view,  $\times 1$ .

Fig. 8. *R. elegans*, palatal view,  $\times 1$ .

Explanation of abbreviations: *bo*, basioccipital; *bs*, basisphenoid; *f*, frontal; *fs*, frontal sulcus; *fp*, fenestra postotica; *g*, premaxillary groove; *j*, jugal; *m*, maxilla; *ms*, maxillary sulcus; *n*, nasal; *p*, parietal; *pa*, palatine; *pm*, premaxilla; *po*, postorbital; *pf*, prefrontal; *pt*, pterygoid; *qj*, quadratojugal; *q*, quadrate; *tf*, tympanic fossa; *v*, vomer.



TEXT-FIG. 9. Each triangle represents an individual measurement. All those belonging to the same species are placed along a single horizontal line; where more than one individual has the same measurements, further triangles are added above or below this horizontal line. Measurements derived from the type-specimens of valid species are distinguished by a circle above the triangle.

A, angle between the maxillae: the jaw angle.

B, proportion of height  $Y$  to length  $Z$ :  $(Y/Z) \times 100$ .

C, angle between the premaxillae and the palate edge: the premaxillary angle.

D, proportion of width  $X$  to length  $Z$ :  $(X/Z) \times 100$ .



On the other two palates, the lingual ridge does not join the cutting edge but is separated by the confluent grooves. The premaxillae are not grooved at the tip. The narrower mandibles, which can be referred to either of these species, have median crests which extend only part of the way across the symphysis, leaving the tip smooth.

One other of Seeley's types, *R. dacognathus* (SM B55809, B55810) can be referred to *Rhinochelys*. The 'type' consists of two mandible tips each with a broad symphysis, smooth ventral surface and a sharp median crest on the grinding surface which extends across the symphysis to the tip. The angle between the rami is broad. These specimens are here referred to *R. pulchriceps*.

*R. grptocephalus* Seeley is a poorly preserved posterior region of a skull and is indeterminate. The other *nomina nuda*, *R. colognathus*, *R. dimerognathus*, *R. grypus*, *R. leptognathus*, and *R. platycephalus*, are all mandibles of various sorts, but none of these is referable to *Rhinochelys*.

Using the new basis for distinguishing the species, it is evident that *R. amaberti* is a separate species although known by only one specimen. The following features are mentioned by Moret (1935) in his description: the skull is flat on top, not domed, and has a greater relative posterior width than *R. elegans*; the premaxillae form a right-angle with the palate edge and are straight in profile, not convex. To this can be added the following observations taken from his plate (op. cit., pl. 27): the jaw angle is obtuse, about 105°, and there appears to be no ridge over the maxillary sulcus.

#### CRANIAL MORPHOLOGY OF RHINOCHELYS

In the preceding taxonomic study, the different specimens which in the past have been placed in the genus *Rhinochelys* have been either rejected from, or accepted into, the genus, and the species composition of the genus has been established. It is therefore now possible to use those specimens which belong in the genus to make a detailed study of the cranial morphology of *Rhinochelys*.

##### *Generic description*

The skulls are small to medium size (30–60 mm. long) with width about two-thirds of the length. The posterior edge is emarginate to a depth of about a third of the length of the parietal. The temporal fossa is well roofed over by the parietal, postorbital and squamosal. The squamosal does not meet the parietal. The frontal extends to form part of the rim of the orbit and meets the nasal and prefrontal anteriorly. The prefrontal and nasal are distinct. The prefrontals are moderate in size, do not meet medially and do not form part of the narial margin. The nasal is moderately large; it meets the frontal posteriorly, the prefrontal postero-laterally, the maxilla antero-laterally, and forms the posterior margin of the external nares. The external nares are oval in shape, with the long axis running horizontally. The antorbital beak is blunt and not produced. The premaxillae meet in a sharp angle. The maxilla extends from the nares to meet the jugal in the posterior part of the lower orbital rim to form a jugo-maxillary bar. The jugal forms the postero-ventral and posterior rim of the orbit. It extends dorsally to meet the postorbital and posteriorly to meet the quadratojugal. The quadratojugal bounds the tympanic fossa anteriorly and antero-dorsally. The tympanic fossa is notched postero-ventrally for the passage of the columella from the incisura columella auris.

*Palate*

The palate is flat and there is no secondary palate. The maxillae and premaxillae form a broad grinding surface which borders the internal nares. This surface is grooved internally from the cutting edge, and passes into a broad ridge on the lingual margin. There is a deep groove at the midline which would oppose the crest on the mandible. The posterior margin of the internal nares is formed by the palatines and maxillae. The vomer divides the internal nares, forming a sharp ridge, and extends only a short way between the palatines. The palatines meet medially and meet the maxillae laterally; there is a dorsal extension which meets the ventral projections of the nasal and prefrontal to form the anterior orbital wall. The orbito-palatal edge of the palatine is deeply notched; this area is not well preserved on any specimen but it does not appear that this notch was surrounded by bone to make a posterior palatine foramen, although the notch would serve the same function (Pl. 67, figs. 3, 8). The pterygoid does not join the maxilla. The two pterygoids meet medially and are narrow, emarginate and slightly ridged. The basisphenoid is exposed as an antero-posteriorly elongate triangle and is flat. The basioccipital is broad anteriorly, narrow posteriorly, and level with the palate.

*Epidermal sulci*

Two pairs of sulci are evident on all the skulls. One crosses the maxillae from the orbits to the nares, running posteriorly and slightly ventrally. The other crosses the frontal, near to the frontal-nasal suture, as a sinuous curve from the orbits, anteriorly to the midline.

On a small skull of *R. cantabrigiensis* (SM B55791) the dorsal surface is further subdivided into a larger number of scutes by well-marked epidermal sulci. The prefrontal scute is divided into two by a straight sulcus and in addition there are a frontal, parietal, and two postorbital scutes clearly marked (Pl. 68, fig. 16).

*Mandible*

The mandibles are preserved on two skulls, one referable to *R. elegans* (SM B55776, text-fig. 2) and the other to *R. cantabrigiensis* (SM B55791, Pl. 68, figs. 14, 15). The

## EXPLANATION OF PLATE 67

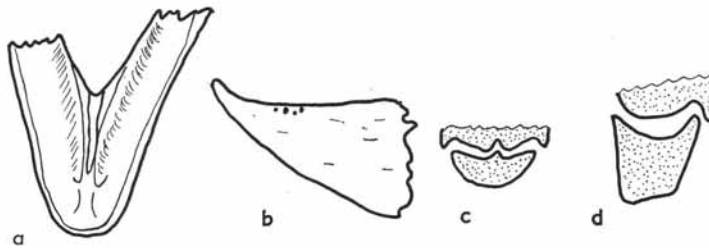
- Figs. 1-5. *Rhinochelys pulchriiceps*. Skull of type species, SM B55775. Dorsal, palatal, anterior, and lateral views,  $\times 1$ . Fig. 2 is an enlarged view of the tympanic fossa.  
 Fig. 6. *R. pulchriiceps*. BMNH 2224, lateral view,  $\times 1$ .  
 Figs. 7, 8. *R. pulchriiceps*. BMNH R1806, dorsal and lateral views,  $\times 2$ .

## EXPLANATION OF PLATE 68

- Figs. 1, 2. *R. pulchriiceps*. BMNH R1806, lateral and anterior views,  $\times 2$ .  
 Fig. 3. Type skull of *R. macrorhina* (*R. elegans*). BMNH 35193, lateral view,  $\times 1$ .  
 Fig. 4. Type skull of *R. brachyrhina* (*R. elegans*). BMNH R2225, anterior view,  $\times 1$ .  
 Figs. 5-7. *R. elegans*. Holotype skull, BMNH 2226; dorsal, lateral, and anterior views,  $\times 1$ .  
 Figs. 8-10. *R. cantabrigiensis*. Holotype skull, BMNH 43980; dorsal, lateral, and anterior views,  $\times 1$ .  
 Figs. 11-13. Type skull of *R. jessoni* (*R. cantabrigiensis*). BMNH R2227; dorsal, lateral, and anterior views,  $\times 1$ .  
 Figs. 14-16. *R. cantabrigiensis*. SM B55791; lateral, ventral showing the lower jaw, and dorsal views,  $\times 1$ .

angle between the mandibular rami is about  $5^\circ$  less than the jaw angle. The symphysis is well fused and long, about a third of the length of the rami. The ventral surface of the symphysis is smooth and tapers in an even curve at an angle of about  $40^\circ$  from the grinding surface. The posterior depth at the symphysis is about half the symphyseal length. The lateral medial surfaces of the rami meet ventrally to form a very sharp ridge. The sutures between the bones are indistinct due to poor preservation.

Pieces of mandible, showing the grinding surface at the symphysis but otherwise similar to the articulated mandibles, are fairly commonly recorded. Text-fig. 10 shows a mandible (BMNH R401) from the Chalk of Weymouth, Dorset. The grinding surface is concave with a sharp median crest at the symphysis, and deeply grooved with sharp marginal ridges along the rami.



TEXT-FIG. 10. Mandible BMNH R401. *a*, dorsal view of symphysis; *b*, lateral view of anterior part; *c*, transverse section of mandibular symphysis and maxillae; *d*, cross-section of jaw rami and maxilla.

#### Braincase

The posterior part of a large skull (SM B94606) (text-figs. 11, 12; Pl. 69, figs. 1–4) with part of a maxilla, premaxilla, and vomer of *Rhinochelys* is recorded from the Upper Senonian, Quadrata zone of Shawford, Hampshire (loc. 1086; Brydone 1912, p. 100).

All external features preserved agree with the generic characters of *Rhinochelys* as defined above, but there is not enough evidence to allocate it to a species. Most of the brain cavity and otic capsule are well preserved and show structures which have not as yet been described in *Rhinochelys*. A natural mould in chalk of the upper brain cavity is also preserved (Pl. 69, fig. 4).

*Description.* A heavy ridge runs across the inner surface of the roofing bones of the temporal fossa, from the anterior part of the brain cavity to the posterior rim of the orbit. The area is thus divided into lachrymal and temporal surfaces. A faint ridge is discernible in the recent *Chelonia*. The ventral extension of the parietal meets the pterygoid ventrally, and the prootic and supraoccipital posteriorly. It forms the anterior side wall of the brain cavity. The suture between the pterygoid and parietal is indistinct and it is uncertain whether an epipterygoid is present or not.

The trigeminal nerve foramen is kidney-shaped and does not extend above the level of the otic capsule. Posteriorly it is bordered by the prootic dorsally and by the quadrate ventrally.

The prootic forms a small part of the wall of the brain case. It projects laterally with a heavy anterior ridge to form the anterior roof of the otic capsule. The stapedia (temporal) canal passes through it near the posterior margin.

The supraoccipital is partially preserved, but the crest is broken. It forms the roof of the posterior part of the brain cavity. The opisthotic is an irregularly shaped bone, extending between the prootic anteriorly, the squamosal laterally, the exoccipital postero-ventrally, and the supraoccipital dorsally. It forms the posterior roof of the otic capsule and part of the dorsal edge of the fenestra postotica.

The exoccipital forms the edge of the foramen magnum medially and of the fenestra postotica laterally. It meets the supraoccipital dorsally, the opisthotic dorso-laterally and the basioccipital ventrally. It does not appear to meet the pterygoid laterally, nor does it extend over the basioccipital to form the posterior floor of the brain cavity.

The quadrate forms the lateral part of the otic capsule. The tympanic fossa is concave with a deep notch and groove, the incisura columella auris, on the posterior margin. Ventrally the bone meets the lateral extension of the pterygoid. The articular condyle is eroded. A fragment of squamosal lies over the quadrate and forms the roof of the stapedia canal.

*Brain cavity.* The basioccipital forms the floor of the posterior part of the brain cavity. It is concave and broad, with a median anterior ridge which terminates abruptly in a knob, the basi-tuberculi basalis, at the basisphenoid suture. Deep grooves flank this knob, and the area posterior to it is rough. Hypoglossal nerve foramina open into the postero-lateral part of this surface.

The basisphenoid is in two parts and forms the anterior floor of the brain cavity. Posteriorly the bone is broad and concave, the surface is rough with a small median crest which tapers out midway. The clinoid processes are two small peaks on the anterior rim of the main part of the bone and flank the dorsum sellae. The dorsum sellae is vertical and forms a beak which protrudes into the fossa hypophysialis. The basisphenoidal rostrum is long, narrow, and grooved; it terminates abruptly in a vertical oval face. It lies over the suture between the pterygoids and is flanked on either side by the sulcus cavernosus. The abducens nerve foramen lies in the dorsum sellae just below the clinoid process.

*Otic capsule.* The otic capsule is open posteriorly by a wide fenestra postotica, postero-laterally into the tympanic fossa by the incisura columella auris, and anteriorly into the sulcus cavernosus by the carotid canal. The main part of the capsule is divided into three cavities, the cavum labyrinthicum (inner ear cavity) and the medial and lateral parts of the cavum acustico-jugulare (acoustic-jugular cavity).

The inner ear cavity is antero-medial to the other two; it opens into the brain cavity by a large hiatus acusticus, and into the acoustic-jugular cavity by the fenestra ovalis. In the roof lie the three cavities for the semicircular canals: the opisthotic recess posteriorly, the supraoccipital recess medially, and the prootic recess anteriorly. A thin septum of bone separates the inner ear cavity from the medial part of the acoustic-jugular cavity. This septum is pierced by a large oval fenestra perilymphatica.

The medial part of the acoustic-jugular cavity is pear-shaped and lies posterior to the inner ear cavity. It narrows medially and opens into the brain cavity by a small round

anterior jugular foramen and opens into the main part of the acoustic-jugular cavity, laterally, by an oval posterior jugular foramen. This foramen, and the fenestra ovalis beside it, are completely surrounded by bone, and the septum which divides these is fused to the cavity floor. In the Recent cheloniids this bony septum is free of the cavity floor and is completed by cartilage.

The lateral part of the acoustic-jugular cavity is the largest of the three. There is a lateral groove over the floor which passes anteriorly into the carotid canal between the pterygoid, quadrate, and prootic. This canal joins the sulcus cavernosus medial to the trigeminal nerve foramen, and carries the carotid artery and lateral head vein. The stapedial artery passed dorsally from this cavity, through a canal between the prootic and squamosal bones into the temporal fossa.

*Brain cast.* The chalk formed a natural cast of the upper brain cavity which is partly preserved. The cerebral lobes are faintly discernible and are 11.2 mm. wide, the olfactory lobes lie 12 mm. anteriorly and are 5 mm. wide. The hind region of the brain is flexed ventrally at an angle of 30° from the anterior part.

*Measurements.* Posterior width 60 mm., height 37 mm.

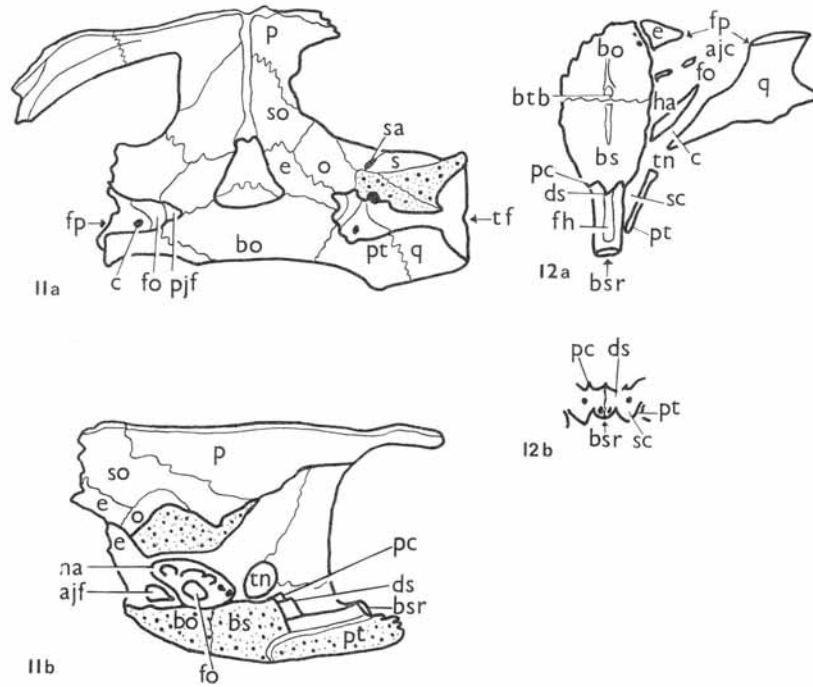
#### Discussion

The internal structure of this skull is of chelonioid type and can be compared with skulls of other marine turtle families, the Toxochelyidae, the Cheloniidae, both described from the Cretaceous of North America, and the Recent Dermochelyidae. (The internal cranial morphology of the Protostegidae is not well enough known for comparison to be possible.) There are morphological differences which need emphasizing although the precise significance of these is uncertain.

The passage of the carotid artery and lateral head vein through the acoustic-jugular cavity is essentially simple. In the cheloniids and toxochelyids, the blood vessels are enclosed in the pterygoid and enter the skull close to the occipital condyle. In the Recent cheloniids the basisphenoid, anterior part of the basioccipital, and the pterygoid are thickened, dropping the posterior part of the palate. The ventral surface of the basioccipital, instead of being horizontal as in *Rhinochelys*, is inclined at an angle of 30°. The pterygoid has incorporated the blood vessels within itself and these pass into the sulcus cavernosus much as in that of *Rhinochelys*, but in a toxochelyid skull described by Zangerl (1953b, p. 152) the internal carotid passes directly into the basisphenoidal rostrum and does not enter the sulcus cavernosus. The projection of the dorsum sellae into the fossa hypophysis is found also in the Recent *Eretmochelys*, but in other cheloniids and toxochelyids the dorsum sellae is sloped and concave. The basisphenoid and exoccipital are both extended laterally in the cheloniids and the exoccipitals fuse together across the dorsal surface of the basioccipital.

It seems possible that the more complex and sturdier cheloniid skulls could have evolved from a simple condition such as that of *Rhinochelys*. On investigating the skull of a Leathery Turtle, it became clear that this too could have evolved from a skull like *Rhinochelys* but not through the cheloniids or toxochelyids. Apart from specialized features which can only be related to the group, the *Dermochelys* skull is more like the skulls of the Chelonioidea than any other Cryptodire. The basic pattern of the skull is

very similar in the two groups but *Dermochelys* shows a remarkable simplicity and similarity to *Rhinochelys* in the features that have been discussed. The palate is primary and the posterior part is not thickened but is flat. The carotid artery and lateral head vein pass through the acoustic-jugular cavity and are not enclosed in the pterygoid. The



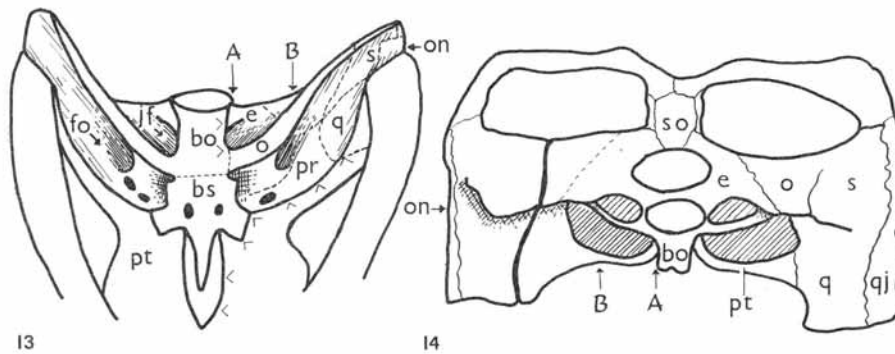
TEXT-FIGS. 11, 12. *Rhinochelys* sp. Upper Chalk skull, SM B94606. 11a, posterior view,  $\times 1$ ; 11b, lateral view with otic capsule removed,  $\times 1$ ; 12a, dorsal view of the floor of the brain cavity and plan of the otic capsule; 12b, anterior view of the dorsum sellae looking along the basisphenoidal rostrum. Explanation of abbreviations: *ajc*, acoustic-jugular cavity; *ajf*, anterior jugular foramen; *bsr*, basisphenoidal rostrum; *btb*, basituberculi basalis; *c*, carotid canal; *ds*, dorsum sellae; *fh*, fossa hypophysialis; *fo*, fenestra ovalis; *fp*, fenestra postotica; *ha*, hiatus acusticus; *o*, opisthotic; *pc*, clinoid process; *pjf*, posterior jugular foramen; *s*, squamosal; *sa*, stapedia arterial canal; *sc*, sulcus cavernosus; *so*, supra-occipital.

structure of the basioccipital (except in the floor of the brain cavity), pterygoid, and exoccipital are similar to *Rhinochelys*. Zangerl (1953a) suggested that the Leathery Turtles could have descended from the Protostegidae; such a relationship might explain this similarity, but it could alternatively be a general, primitive, condition retained by both genera.

So far I have briefly discussed the differences within the superfamily, which are not very extensive. It is far more interesting to demonstrate the developing pattern of

structural changes. The *Rhinochelys* skull, as the first record of the Chelonioida (Cox *et al.* 1967), is conveniently placed for such a study. Although 'modernized' in type, this skull is uncomplicated by extra bone growth as is seen in the later cheloniids, and is still close enough to the primitive stock to retain a simplicity of structure.

The chelonian skull is specialized in the formation of an acoustic-jugular cavity and a tympanic fossa. All known chelonians possess these features in one form or another, except the primitive Triassic *Proganochelys*.



TEXT-FIGS. 13, 14. *Proganochelys quenstedti*. 13, posterior part of the palate. 14, occiput. Reconstructed from Parsons and Williams (1961, pl. 5, 6). Magnification not stated. Explanation of abbreviations: *if*, jugular foramen; *on*, otic notch; *pr*, prootic.

Photographs of a well-preserved skull of *Proganochelys quenstedti* Baur, housed in the Museum of Natural History at Stuttgart, were published by Parsons and Williams (1961). While a full description of the skull has yet to be published, the photographs are clear and show that the acoustic-jugular cavity is not floored, but is a simple concavity in the back of the skull, very similar to that found in other primitive reptiles. Parsons and Williams (p. 91) briefly discuss this and say:

a cultriform process is plainly visible between the separated pterygoids. Posteriorly also the situation is primitive; the quadrate ramus of the pterygoid does not send any flange inward to floor the cranioquadrate passage as on all other known turtles, and the foramina for the *vena capitis lateralis*, the internal carotid, and the stapedia artery, as well as the *fenestra ovalis* are all exposed in ventral view.

In text-figs. 13 and 14 I have interpreted this region of the skull of *Proganochelys*, using the photographs shown in Parsons and Williams (1961, pl. 5, 6) but showing only features which are well defined. The arrows indicate the areas and direction of growth of the bones which would be required to produce the morphology of this region as found in *Rhinochelys*. In *Proganochelys* there are two large fenestrae opening laterally. One, close to the condyle, is the jugular foramen; the other, antero-lateral to this, is the fenestra ovalis. Anteriorly there are two foramina on one side but only one is apparent on the other. One of these is for the stapedia artery and the other possibly for the lateral head vein. The pair of foramina on the basisphenoid could possibly be the internal carotid foramina; however these are placed in a different position from normal. In the



modern chelonians the internal carotid artery enters the basisphenoid through the dorsum sellae; it is possible that the change of position of these foramina is caused by the medial and posterior growth of the pterygoid.

The basisphenoid is slightly proud of the floor of the inner ear cavity as there is a distinct shadow laterally. The basipterygoid processes are sutured anteriorly and laterally to the pterygoids. The pterygoid sends only a thin bar posteriorly and laterally to the quadrate. The articular condyle is level with the occipital condyle.

The otic notch is simply curved and open. It seems to be bordered by the quadratojugal anteriorly and the squamosal dorsally and is lined by the quadrate. The quadrate appears to be in a primitive vertical plane.

The bar of bone which separates the jugular foramen from the fenestra ovalis is probably part of the opisthotic and this bone probably also extends anteriorly to the prootic, flooring the inner ear cavity. These conditions would then be similar to those in *Rhinochelys* where the opisthotic forms the bony septum between the medial acoustic cavity and the inner ear cavity, and floors the latter.

As far as I can see, to reach the condition seen in *Rhinochelys*, the following developments have taken place:

The basioccipital has grown at point *A* laterally to point *B*. It lies ventral to the other bones and has grown alongside the opisthotic bar forming the floor to an extended 'jugular canal' (medial acoustic-jugular cavity), and joins the opisthotic level with the floor of the inner ear cavity, and the pterygoid at point *B*. This 'jugular canal' is completed by the exoccipital which has extended from point *A*, laterally, to form a posterior wall. This canal opens into the brain cavity by the anterior jugular foramen and into the main part of the acoustic-jugular cavity by the posterior jugular foramen.

The pterygoid has grown along its entire posterior margin. It has extended backwards to floor the lateral concavity and so forms the acoustic-jugular cavity. Posteriorly it meets the basioccipital, underlies the floor of the inner ear cavity, completely surrounds the basisphenoid (except posteriorly), and encloses the internal carotid and the lateral head vein between itself, the prootic, and the quadrate. Medially the pterygoids have grown under the basipterygoid processes and the cultriform process, and the internal carotid enters the basisphenoid through the cultriform process, dorsal to the pterygoids.

The quadrate fills the otic notch and forms the tympanic fossa. The articular condyle is pushed anteriorly. In *Rhinochelys*, the original position of the otic notch is suggested by the curved quadratojugal.

#### TAXONOMIC POSITION OF *RHINOCHELYS*

Having described the cranial morphology of *Rhinochelys*, it is now possible to use this information in attempting to establish to which family the genus belongs. Seeley (1869) said quite simply that the genus had emydian affinities, but gave no reason for this remark. The modern concept of the Testudinidae (Romer 1956, Loveridge and Williams 1957) emphasizes the following features: the presence of a squamosal antrum, the fenestra postotica is almost closed, the pterygoid meets the maxilla, and the nasal bones are absent. Since none of these features is present in *Rhinochelys*, there seems to be no reason for further considering this relationship.



Lydekker (1889) considered that the genus was probably pleurodiran and gave the following reasons: distinct nasals are present only in the Chelydidae, the palatines unite in the midline only in the Pelomedusidae, and there is the same relationship of bones around the internal nares as in *Pelomedusa*. He said also that the narrow palatines and pterygoids and complete roofing of the temporal fossa was more like the Cryptodires than the Pleurodires. However, since Lydekker's time, there has been a major revision of the taxonomy of the Chelonia, and there are diagnostic features of the Pleurodires in the present concept (Romer 1956) which are not present in *Rhinochelys*. These are: the absence of a descending process of the prefrontal, the broad pterygoid with a rolled up lateral expansion, and the meeting between the quadrate and the basisphenoid. On this basis there seems to be little evidence of relationships between *Rhinochelys* and this group of families.

In his description of *Desmatochelys* Williston (1898) compared it with *Rhinochelys* and referred them both to his new family, the Desmatochelyidae. This was followed by Romer (1956). Zangerl and Sloan (1960) suppressed the Desmatochelyidae when they demonstrated the affinities of *Desmatochelys* to the Cheloniidae, on post-cranial material. The relationship between the two genera is discussed below.

Thus *Rhinochelys* has not been satisfactorily assigned to any family, and this will now be considered using modern taxonomy.

Firstly, there can be little doubt that *Rhinochelys* belongs to the superfamily Cheloniioidea, which is in the suborder Metachelydia of Zangerl (1969). The characteristics of this superfamily as given by Romer (1956) are as follows: temporal region well roofed; premaxillae unfused; vomer meets premaxilla, separates internal nares and separates the palatines; parietal with descending process; epipterygoid present; pterygoids constricted at mid-length, broadly in contact with one another and separate the basisphenoid from the palatine; pterygoid not in contact with the maxilla. *Rhinochelys* shows all these features except that the vomer does not separate the palatines.

The three families in the Cheloniioidea (the Cheloniidae, the Toxochelyidae, and the Protostegidae) are all recorded from the Cretaceous. The position of *Rhinochelys* is shown most clearly by tabulating the condition in respect of a number of cranial features in *Rhinochelys* and in each of these three families. The features of the Toxochelyidae and the Protostegidae are taken from Zangerl (1953 *a, b*), and Wieland (1900), and of the Cheloniidae from Loveridge and Williams (1957).

As can be seen from Table 2, *Rhinochelys* has the salient features of the Protostegidae, especially the structure of the mandible and palate, and is best referred to this family. The Protostegidae contains two subfamilies, the Protosteginae (large, highly specialized genera) and the Chelospharginae (two small and primitive genera, *Chelosphargis* and *Calcarichelys*). *Rhinochelys* is obviously neither large nor specialized; in fact it is distinctive in its lack of specialization, which fits in with the subfamily Chelospharginae as diagnosed by Zangerl (1953*a*, p. 128):

Small blunt straight premaxillary beak. Frontal bones large and with lateral processes towards orbital rims. Prefrontal bones excluded from sagittal contact by nasal bones. Otic and exoccipital area very similar to the condition in cheloniid turtles. Symphysis mandibuli long, with rami fused even in juvenile individuals. Slight, but sharp, sagittal crest on the triturating surface of lower jaw.

The skull of *Calcarichelys* is not known. The skull of *Chelosphargis* has been described by Zangerl (1953*a*, pp. 81-4, figs. 21*a-d*, 22). Comparing this with *Rhinochelys*, the close

relationship between the two genera is unmistakable. The shape of the temporal roofing bones, the ant-orbital beak, the primary palate, the structure of the lower jaw and the epidermal sulci crossing the maxilla and the dorsal bones, are closely comparable in the two genera. Unfortunately the palate and otic region on the specimens of *Chelosphargis* are not preserved in any detail. The occipital region on one specimen, however, is described by Zangerl (op. cit., p. 82), who states that this region resembles *Chelonia* rather than *Dermochelys*, although in his figures 22a, b, the exoccipital does not appear to contribute to the occipital condyle as it does in *Chelonia*.

TABLE 2. Comparison of cranial features of *Rhinochelys*, Protostegidae, Toxochelyidae and Cheloniidae (a—absent, p—present)

	<i>Rhinochelys</i>	<i>Protostegidae</i>		<i>Toxochelyidae</i>	<i>Cheloniidae</i>
		<i>Chelospharginae</i>	<i>Protosteginae</i>		
Postorbital extends back to squamosal tip	a	unknown	a	p	a
Prefrontals meet dorsally	a	a	p	p	p
Vomer separates the palatines	a	unknown	a	p	p
Palatine fenestra	a	unknown	a	p	a
Pterygoids joined to maxillae or jugals	a	unknown	a	maxillae	jugals
Secondary palate	a	a	a	a and p	p
Mandibular symphysis very wide, about one-third length of the rami	p	p	p	a	a
Sharp symphyseal ridge	p	p	p	a	a and p

#### RELATIONSHIP OF *RHINOCHELYS* TO OTHER CRETACEOUS TURTLES

In establishing the family position of *Rhinochelys*, the skull structure of the Recent Cheloniidae is used. All the criteria of this family are based upon the structure of the limbs, girdles, and plastron. The cheloniid method of locomotion apparently underwent little change after its development (Zangerl 1953b), but the structure of other parts of the skeleton, including the skull, seems to have been subjected to evolutionary experiment over the long period of time involved. From North America there are two other genera of Cretaceous turtles, *Corsochelys* Zangerl (1960) and *Desmatochelys* Williston (1894), which have been placed in the Cheloniidae on the evidence of the postcranial skeleton. The skulls in these genera show features which are not present in later cheloniids. Table 3 demonstrates the similarities and differences between these two genera, *Rhinochelys*, *Chelosphargis*, and the Recent cheloniids and advanced protostegids.

*Corsochelys* and *Desmatochelys* closely resemble *Rhinochelys* and *Chelosphargis* but do not display the distinctive protostegid mandible and palate (where preserved), and show cheloniid features. Thus there are four unspecialized genera in the Cretaceous showing distinct features of two families (the Cheloniidae and the Protostegidae) but also possessing many common features which are not shared by the more advanced members of these families. It seems logical to surmise that they have inherited these features from a common ancestry.

TABLE 3. Comparison of cranial features of *Rhinochelys*, *Chelosphargis*, *Desmatochelys*, *Corsochelys*, *Corsochelys*, Recent Cheloniidae and advanced Protostegidae (a—absent, p—present)

	<i>Rhinochelys</i>	<i>Chelosphargis</i>	<i>Desmatochelys</i>	<i>Corsochelys</i>	Recent Cheloniidae	Advanced Protostegidae
<b>Similarities</b>						
Nasal bones present	p	p	p	p	a	a
Squamosal separated from the parietal	p	—	p	p	a	a
Prefrontals excluded from meeting medially	p	p	p	—	a	a
Primary palate	p	p	p	—	a	p
Vomer does not separate the palatines	p	—	p	—	a	p
Frontal extends to the rim of the orbit	p	p	p	p	a	a
Exoccipital does not meet the pterygoid nor extend over the basioccipital	p	—	—	p	(except in <i>Chelonia</i> )	—
<b>Differences</b>						
Quadratojugal extends to orbital rim	a	—	p	—	a	a
Epidermal sulci	p	p	a	—	a	a
Flat palate	p	—	concave	—	secondary	p
Wide mandibular symphysis	p	p	a	—	a	p

CARAPACE AND PLASTRAL MATERIAL POSSIBLY  
BELONGING TO *RHINOCHELYS*

A number of remains of carapaces and plastra is known from the Albian to Turonian of south-east England. Unfortunately skull material is not associated with any of these. However, these carapaces and plastra appear (as will be shown) to be of chelospharginid type and, now that *Rhinochelys*, from the same area and deposits, is known to be a chelospharginid, it seems worth investigating the possibility that this material belongs to *Rhinochelys*. The first specimen to be described was a small, probably juvenile, carapace which Mantell (1841) named *Emys benstedii*. Owen (1841) transferred it to the genus *Chelone* and also considered that it was sufficiently distinct to merit subgeneric status, naming it *Cimochelys*. This has been used as a generic name by Zangerl (1960).

*Description.* The type-specimen of *Emys benstedii* is BMNH 28706. This has been broken and part of the carapace is lost. Other material which appears to be related includes BMNH 39112 (text-fig. 15), R1350, 47210 (text-fig. 16); GSM442; SM B20607.

The type material has unfortunately been partly lost since it was described, and therefore the following description is taken from Owen's figured specimen BMNH 39112 (1851, pp. 7-8, pl. 3) which in all points resembles what remains of the type, the original description, and the figures.

The carapace is heart-shaped with moderate fontanelles and a sharp neural keel which is flattened anteriorly. The sides slope more or less straight from the neurals to the peripherals. The neurals are rectangular, very narrow, long, and of even size, except the eighth, which is triangular and half the length of the seventh. The sutures between the costals and between the neurals correspond, instead of being offset as in the Cheloniidae. The costals are straight, slope at a steep angle and, about halfway along their length, taper into broad striated ribs which continue to taper until they articulate in deep pits in the inner surface of the peripherals. The 2nd peripheral is thin and flat and lies across the front of the carapace. The 3rd is flat anteriorly but broadens posteriorly to become deeply triangular in cross-section; it is crescent-shaped and forms the broad curved angle of the carapace. The 4th-6th peripherals are deeply triangular in cross-section with a convex dorsal and a concave ventral surface. Each peripheral has a deep medial pit in the inner surface for the rib articulation. The 7th-11th peripherals have shallower cross-sections. The medial border of these bones is smooth. The 8th neural, suprapygal, pygal, 11th peripheral, 8th costal and rib, together form a solid bony posterior to the carapace.

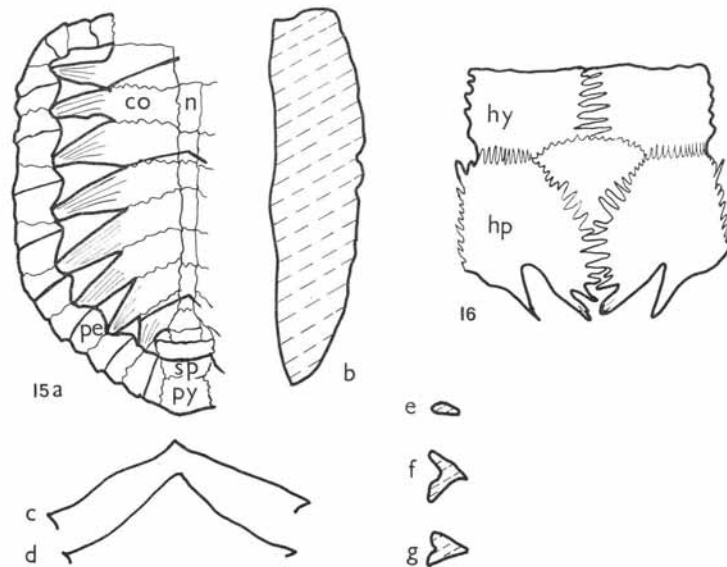
Epidermal shield sulci cross the 1st, 3rd, 5th, and 7th costal and neural bones (the 1st neural is not preserved but was presumably the same). These sulci form three small peaks across the neural keel. Each peripheral is notched on the outer margin by a sulcus which gives a serrated appearance to the carapace edge, especially posteriorly.

*Plastron.* The description of the plastron is taken from the type-specimen. The hyo- and hypoplastra only are preserved and are subrectangular in outline with a moderate

EXPLANATION OF PLATE 69

Figs. 1-4. *Rhinochelys* sp. SM B94606. 1, Occiput,  $\times 1$ . 2, Lateral view of the brain cavity with the otic capsule removed,  $\times 1$ . 3, Enlarged view of the hiatus acusticus, inner ear cavity, and the anterior jugular foramen. 4, Dorsal view of a natural cast of the upper brain cavity,  $\times 1$ .

fontanelle in the centre. The hypoplastra are the smaller and meet medially with long digitations, and laterally and posteriorly with short fine digitations. The digitations bordering the fontanelle are fine anteriorly and become larger posteriorly, forming twelve or so large fingers between the hypoplastra. The posterior margin of these plates has two long fingers of bone curving backwards and inwards. In BMNH 47210, from the Gault of Folkestone, Kent (text-fig. 16), the posterior part of the plastron is concave, dipping steeply in from the sides to a depth of 10 mm. Comparison with the Recent turtles suggests that this is probably a male sexual character.



TEXT-FIGS. 15, 16. *Cimocheilus benstedii*. 15, BMNH 39112; *a*, reconstructed carapace,  $\times 0.5$ ; *b*, longitudinal section; *c*, anterior transverse section; *d*, posterior transverse section; *e*, cross-section through the second peripheral; *f*, cross-section through the fourth peripheral; *g*, cross-section through the ninth peripheral. 16, Plastron, BMNH 47210, reconstructed ventral view,  $\times 0.5$ . Explanations of abbreviations: *co*, costal; *n*, neural; *hy*, hyoplastron; *hp*, hypoplastron; *pe*, peripheral; *py*, pygal; *sp*, suprapygal.

*Discussion.* The material was originally described by Mantell (1841) as *Emys benstedii*, although the plastron resembled that of the marine turtles. Mantell considered that the carapace was like that of the juvenile *Emys* because the ribs diminish in width towards the circumference, which might indicate a gradual growth and tendency towards complete infilling of the interspaces. He also pointed out that in marine turtles the broad part of the rib is sharply demarcated from the linear part. However, the carapace in the Testudinidae is usually solid even in juveniles and is very different from *Emys benstedii*. The neurals are hexagonal and generally broader than long; the peripherals are solid and double wedge-shaped with a thin dorsal plate under which lies the tip of the rib;

they are not triangular in cross-section nor open medially. The plastron is not reduced and forms a solid bony plate which is well fused to the carapace.

Owen (1841, 1851) placed the species in *Chelone* on the following points: the carapace is pointed posteriorly with moderate fontanelles, narrow neurals and peripherals which do not join to the plastron; the central fontanelle of the plastron is more like that of the marine turtles than that of *Emys*. He considered, at this time, that most marine turtles belonged to the genus *Chelone*. However, he suggested a subgeneric name, *Cimochelys*, as he believed that these specimens had particularly close affinities to the Emydidae.

Since Owen's time, marine turtles of three families have been described from the Cretaceous: the Protostegidae, Toxochelyidae, and Cheloniidae. The characteristics of *Cimochelys* may therefore now be compared with those of the members of these three families.

At family level, *Cimochelys* has the following features in common with the Protostegidae: narrow, long, rectangular neurals; sharp neural keel; neural and costal sutures coincide; gradual demarcation between the costal plates and the ribs; and sub-rectangular (rather than saddle-shaped) hyo- and hypoplastra. In none of these features is it like the Toxochelyidae or the Cheloniidae. Next, comparing *Cimochelys* with the two subfamilies in the Protostegidae, it may be noted that it is like the Chelospharginae, and unlike the Protosteginae, in the lack of reduction of its carapace and plastron, and in the absence of digitations along the medial border of the peripherals (Zangerl 1953a, p. 128). The differences in the other two genera in the Chelospharginae (*Chelosphargis* and *Calcarichelys*) and *Cimochelys* appear to lie mainly in the degree of formation of the peaks on the neural keel and serrations around the posterior edge of the carapace. In *Calcarichelys* these appear to be accentuated, but *Chelosphargis* is relatively smooth.

Thus the carapace material is characteristic of the Protostegidae, subfamily Chelospharginae, and closely related to *Chelosphargis* and *Calcarichelys*. Since the *Rhinochelys* skulls from similar deposits are also related to these genera, it is suggested that *Cimochelys benstedii* could be the missing post-cranial material of *Rhinochelys*.

*Synonymy.*

- 1841 *Emys benstedii* Mantell, pp. 153-8, pl. 11, 12.
- 1841 *Chelone (Cimochelys) benstedii* (Mantell); Owen, pp. 176-7.
- 1851 *Chelone benstedii* (Mantell); Owen, pp. 1-11, pl. 6-8.

SUMMARY

A critical examination of all available British material of the Cretaceous turtle *Rhinochelys* reveals the inadequacy of Lydekker's descriptions and generic diagnosis. Three species only are truly distinguishable; of these, two species (typified by the types of *R. elegans* and *R. cantabrigiensis*) comprise the bulk of the collections, while *R. pulchriceps* is the least common. *R. jessoni* is considered to be a junior synonym of *R. cantabrigiensis*, and *R. macrorrhina* and *R. brachyrhina* are considered to be junior synonyms of *R. elegans*. The cranial distinctions between these species are restated and they are compared with the French species *R. amaberti*. Charts of angles taken about the skull and proportional measurements reveal characteristic differences between the three species. These are definable even if superficial features have been eroded. The charts are also of value when handling skulls of different growth stages as there appears to be little

ontogenetic variation. A very finely preserved brain case and otic capsule of *Rhinochelys* is described from the Chalk of Hampshire.

The posterior part of the palate and occiput of a skull of *Proganochelys quenstedti* Baur has been reconstructed from the photographs in Parsons and Williams (1961, pl. 5, 6). The obvious features are discussed and a possible mode of development of the skull into that described in *Rhinochelys* is suggested.

*Rhinochelys* is referred to the family Protostegidae, subfamily Chelospharginae, mainly on the evidence of the mandible and palate structure. It is compared with the skulls of other Cretaceous turtles and a close relationship in the cranial morphology between the primitive protostegids and the primitive cheloniids is clearly shown.

Since no associated post-cranial material is recorded, all generic and specific descriptions are based on skulls. Carapace and plastral remains have been described from the Upper Cretaceous of south-east England as *Chelone (Cimochelys) benstedti* (Mantell 1841). These are referable to the same subfamily as *Rhinochelys* and are provisionally referred to the same genus.

The Protostegidae, hitherto restricted to the Late Cretaceous of North America, is extended in range to the Albian–Turonian of Europe.

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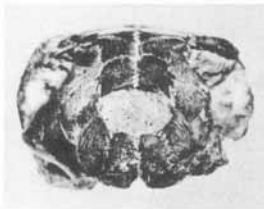
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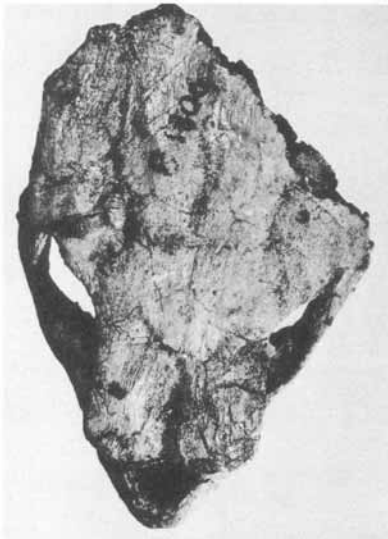
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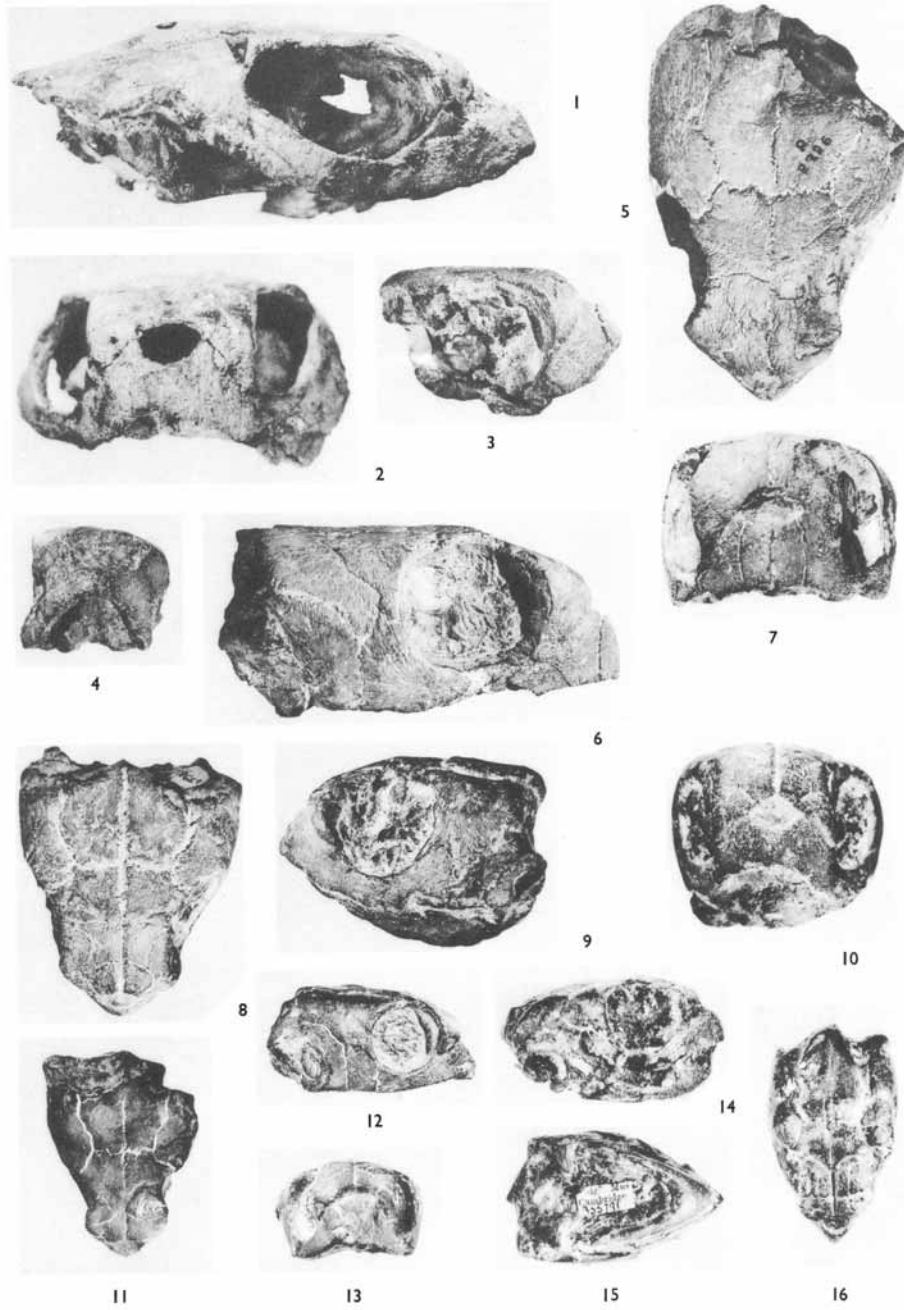


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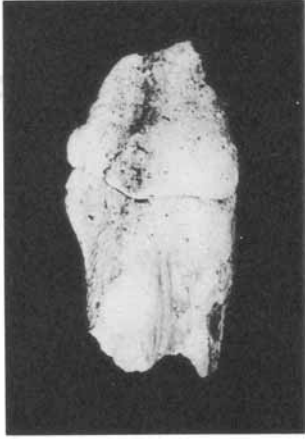


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COLLINS, *Rhynchonella*



COLLINS, *Rhinocelys*



4



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COLLINS, *Rhinochelys*