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EARLY EOCENE TESTUDINOID TURTLES FROM SAINT-PAPOUL, FRANCE, WITH COMMENTS ON THE EARLY EVOLUTION OF MODERN TESTUDINOIDEA.

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Abstract: The description of three Early Eocene fossil turtle species from southern France illustrates the early Eocene radiation of the Testudinoidea, the largest group of living turtles. Two species of the geoemydid *Palaeoemys* Schleich,1994, *P. testudiniformis* (Owen, 1842) and *P. hessiaca* Schleich, 1994, are described on the basis of new shell material from the Ypresian (Early Eocene) locality of Saint Papoul (Aude, France). A new species belonging to the family Testudinidae, *Achilemys cassouleti*, is interpreted as the most primitive taxon of this family. In order to assess their phylogenetic relationships, an evolutionary scenario is proposed mainly on the basis of newly published studies in molecular phylogeny, followed by paleobiogeographical considerations, and by a reappraisal of morphological character evolution.

Keywords: Early Eocene, Southern France, Testudines, Cryptodira, Testudinoidea, *Palaeoemys*, *Achilemys*, Phylogeny.

Les Tortues Testudinoïdes de l'Eocène inférieur de Saint-Papoul : nouvelles données sur l'origine des familles de testudinoïdes modernes.

Résumé : Trois espèces de tortues de l'Eocène inférieur du Sud de la France sont décrites. Ce matériel apporte de nouvelles données sur la radiation des Testudinoïdes modernes, le groupe de tortues actuelles le plus diversifié. Deux espèces du geoemydidé *Palaeoemys* Schleich, 1994, *P. testudiniformis* (Owen, 1842) et *P. hessiaca* Schleich, 1994, sont décrites sur la base d'un matériel nouveau daté de l'Yprésien (Eocène inférieur) de la localité de Saint Papoul (Aude, France). Une nouvelle espèce de Testudinidae, *Achilemys cassouleti,* est interprétée comme le taxon le plus primitif de la famille. Dans le but d'établir les relations de parentés de ces taxons, un scénario évolutif des testudinoïdes est proposé principalement sur la base d'études récentes en phylogénie moléculaire, de considérations paléobiogéographiques, et enfin d'une réinterpretation de l'évolution des caractères morphologiques.

Mot clefs : Eocène inférieur, Sud de la France, Testudines, Crytpodires, Testudinoidea, *Palaeoemys*, *Achilemys*, Phylogénie.

Table 1

Baur, 1893	*Lindholm, 1929*	*Williams, 1950*
Superfamily Testudinoidea	Superfamily Testudinoidea	Superfamily Testudinoidea
Family Emydidae*	Family Chelydridae	Family Dermatemydidae
Family Testudinidae	Family Kinosternidae	Family Chelydridae
	Family Dermatemydidae	Subfamily Chelydrinae
	Family Platysternidae	Subfamily Staurotypinae
	Family Testudinidae	Subfamily Kinosterninae
	Subfamily Emydinae*	Family Testudinidae
	Subfamily Testudininae***	Subfamily Emydinae*
		Subfamily Testudininae***
		Subfamily Platysterninae

Gaffney, 1975	*Mlynarski, 1976*	*Gaffney, 1984*
Superfamily Testudinoidea	Superfamily Testudinoidea	Superfamily Testudinoidea
Family Emydidae*	Family Testudinidae	Family Emydidae
Family Testudinidae	Family Emydidae*	unamed taxa *****
Family Chelydridae	Subfamily Emydinae****	unamed rank / ‘Batagurinae’ **
	Subfamily Batagurinae**	Family Testudinidae

Shaffer et al., 1997	*de-Broin 2000*	*This study*
Super family Testudinoidea	Superfamily Testudinoidea	Superfamily Testudinoidea
Family Lindholemydidae	Family Emydidae	Grade Lindholmemydidae
Family Emydidae	Family Testudinidae *****	Family Emydidae
unamed rank /Testudinoidae	unamed rank/ Geoemydinei **	unamed rank/ Testudinoidae
Family Testudinidae	unamed rank/ Testudininei ***	Family Testudinidae
Family Bataguridae **		Family Geoemydidae

* = Geoemydidae + Emydidae
** = Geoemydidae
*** = Testudinidae
**** = Emydidae
***** = Testudinoidae

1. INTRODUCTION

The Saint Papoul locality is a large clay pit located about 20 km north-west of Carcassonne (Aude, France). It has yielded very abundant turtle remains, including pleurodires (Podocnemidae) (Broin, 1977; Tong, 1999) and several cryptodiran families: Geoemydidae, Testudinidae, Carettochelyidae and Trionychidae. Besides turtles, the Saint Papoul vertebrate fauna includes fishes, crocodiles, birds, and mammals. The fossils come from continental grey clays and sandstones. The mammalian fauna indicates an Ypresian (Early Eocene) age (Sudre *et al.*, 1992). The material studied in this paper has been collected by amateur palaeontologists and by the Musée des Dinosaures (Espéraza, France) during 1992-1998, and is housed in the latter. This paper focusses on the testudinoid turtles discovered in the quarry, and discusses phylogenetic relationships within the Testudinoidea.

Fitzinger first used Testudinoidea as a higher taxon among turtles containing turtles of the genus *Testudo* (Fitzinger, 1826). Later, Baur introduced the Testudinoidea as the superfamily containing the families Emydidae and Testudinidae on the basis of skeletal anatomy (Baur, 1893). Since then, the contents of the Testudinoidea, as well as the classification within the group, as shown in table 1, changed according to different authors. McDowell (1964) attempted a first systematic review of the aquatic turtles of this group and divided the previous Emydinae into Batagurinae and Emydinae. Moreover this author suggested a close relationship between the exclusively terrestrial Testudininae and the Batagurinae. Gaffney & Meylan (1988) raised these subfamilies to separate families (Emydidae, Bataguridae and Testudinidae) of the superfamily Testudinoidea, which is the currently used classification. In a recent phylogenetic analysis of Testudinoidea, McCord and co-workers replaced the family name Bataguridae with Geoemydidae (McCord *et al.*, 2000). We follow McCord *et al.* (2000) since Bataguridae Gray, 1869 is a junior synonym of Geoemydidae Theobald, 1868 (see David (1994), p.83). Previous work has put forward the hypothesis that the Geoemydidae may be a paraphyletic group with respect to the Testudinidae (Hirayama, 1984; Gaffney & Meylan 1988), but very recently, molecular phylogenetic studies have shown that the Testudinidae may be considered as the sister group of the Geoemydidae and that the Geoemydidae are monophyletic (Shaffer *et al.* 1997; Honda *et al.*, 2002; Spinks *et al.*, 2004) (see Yasukawa *et al.*, 2001 for a discussion on morphological features). As a crown group, the Testudinoidea include three extant families: the Geoemydidae (mostly Eurasiatic), the Emydidae (mostly North American), and the Testudinidae *sensu* Gaffney & Meylan (1988). This is the largest group of turtles containing more than half of the extant turtle species. This group has diversified in two main environments (aquatic and terrestrial). Several subsequent authors have included a fourth family in the Testudinoidea: the Lindholmemydidae, known from the Early Cretaceous to the Late Palaeocene of Asia (Shaffer *et al.*, 1997; Gaffney, 1996; Hirayama *et al.*, 2000; Sukhanov, 2000). The Lindholmemydidae is a primitive group which has both apomorphic features of modern Testudinoidea (i.e. well developed axillary and inguinal buttresses contacting costal bones, cervical vertebra pattern (biconvex eighth cervical with a double articulation for the seventh cervical): Gaffney, 1996; Hirayama *et al.*, 2000) and plesiomorphic features (persistence of inframarginal scutes), but its monophyly remains an open question (Hirayama *et al.*, 2000; Sukhanov, 2000).

In summary, the classification of the Testudinoidea used here is as follows:

Superfamily Testudinoidea, Batsch, 1788
Family Lindholmemydidae, Chkhikvadze, 1970
Family Emydidae, Rafinesque, 1815
Family Testudinidae, Batsch, 1788
Family Geoemydidae, Theobald 1868
(Bataguridae Gray, 1869 of some authors)

Few studies have addressed the early evolution and the origin of the families of Testudinoidea; fewer have attempted to interpret their fossil record from a phylogenetic point of view. Only Hirayama (1984) included the Eocene taxon *Echmatemys* in his phylogenetic analysis of the Bataguridae (= Geoemydidae in the present paper) and Shaffer *et al.* (1997) discussed the higher relationships in turtles incorporating the Lindholmemydidae (*Mongolemys* and *Lindholmemys*).

The oldest geoemydid and testudinid turtles are recorded from the Early Eocene of North America, Europe, and Asia (Hutchison, 1998; Holroyd *et al.*, 2001; Lapparent de Broin, 2001). The first emydids (*sensu stricto*) are reported from the Late Eocene of North America (Clark, 1937). However, Holroyd *et al.* (2001) have referred an undescribed taxon from the Early Eocene of North America to the Emydidae. Presumed Emydidae are also reported from the Early Eocene of Ellesmere Island (Canada) by Estes and Hutchison (1980). Emydids are considered to be the sister group of the Testudinidae plus Geoemydidae (Hirayama, 1984; Gaffney & Meylan, 1988; Shaffer *et al.*, 1997; Honda *et al.*, 2002; Spinks *et al.*, 2004), consequently the radiation of the modern families of the Testudinoidea occurred no later than the Early Eocene. Testudinoids from Saint Papoul described in the present paper include both geoemydid and testudinid turtles. Because of its stratigraphical position, the turtle fauna of Saint Papoul is of particular interest for our understanding of the early radiation of the modern families of the Testudinoidea. After a systematic paleontological description, we provide a phylogenetic scenario of the Testudinoidea based on the results of recent molecular phylogenetic studies, followed by paleobiogeographical considerations, and by a reappraisal of character evolution.

2. SYSTEMATIC PALAEONTOLOGY

Order Testudines Linnaeus, 1758
Suborder Cryptodira Cope, 1868
Superfamily Testudinoidea Batsch, 1788 (fide Baur, 1893)
Family Geoemydidae Theobald, 1868
Genus *Palaeoemys* Schleich, 1994

Synonymy:
Emys Owen, 1842: 161-163
Emys Owen & Bell, 1849: 67-70, 73-74
Chrysemys Lydekker, 1889: 118-119
Chrysemys Woodward et Sherborn, 1890: p.217-218
Emys Woodward et Sherborn, 1890: 228
Ocadia Staesche, 1928: p.8-16
Testudo Bergounioux, 1933: 508-520
Palaeochelys Broin, 1977: 236
Chrysemys Moody, 1980: 24
Chrysemys Benton & Spencer, 1995: 276-279
Palaeoemys Schleich, 1994: 82-87.
Palaeoemys Hervet, 2003a: 620-622
Juvemys Hervet, 2003a: 622-623
Francellia Hervet, 2004a: 19-21, 23
Owenemys Hervet, 2004a: 24-26
Euroemys Hervet, 2004a: 26-29

Emended Diagnosis: Relatively low carapace about 20-40 cm long in the adult. Second to seventh neural plates hexagonal with shortest sides anterolateral; narrow vertebral scutes; anterior part of the first vertebral included in the nuchal plate; second pleural scute in contact with the fifth, sixth, and seventh marginal scutes. Carapace attached to plastron by suture, with very strong buttresses. Axillary buttress inserting on the lateral half of the first costal plate, and linked to the first and second rib heads by a strong ridge; inguinal buttress inserting on the lateral half of both fifth and sixth costal plates. Thick plastron with the anterior margin straight and a swelling on the visceral side of the hypoplastron linking the two inguinal buttresses; short gulars just or not reaching the epi-entoplastral suture on the ventral side, and forming a very short anterolateral lip on the visceral side of the epiplastron; humero-pectoral sulcus placed far behind the entoplastron; humero-pectoral and pectoro-abdominal sulci convex posterior and parallel to each other. Pygal small, wider than long, only slightly or not intersected by the posterior sulcus of the fifth vertebral scute.

Type species: *Palaeoemys hessiaca* Schleich, 1994
Included species : *Ocadia messeliana* Staesche, 1928; *Emys testudiniformis* Owen, 1842; *Testudo corroyi* Bergounioux, 1933.
Distribution: Ypresian (Early Eocene) to Lutetian (Middle Eocene), Europe.
Discussion: *Palaeoemys* is a testudinoid because of the presence of well developed axillary and inguinal buttresses reaching costal plates and a deep anal notch (Hirayama, 1984; Gaffney & Meylan, 1988; Hirayama *et al.*, 2000). It should be excluded from Lindholmemydidae, because of the absence of inframarginal scutes (only inguinal and axillary scutes are present). It is a member of the Geoemydidae because of the musk ducts enclosed within the peripheral plates and the small pygal plate (McDowell, 1964; Hirayama, 1984; Gaffney & Meylan 1988). Moreover it exhibits lateral keels on the carapace (at least in juvenile specimens), a feature only observed in certain Geoemydidae (e.g. *Ocadia*, *Chinemys*, *Malayemys*, *Melanochelys*, *Geoemyda*, *Cuora)* among the Testudinoidea. Pa*laeoemys* retains some plesiomorphic features: humero-pectoral sulcus excluded from entoplastron, a feature found in Lindholmemydidae, in Testudinidae, in some Geoemydidae (*Batagur* complex, *Orlitia*, *Malayemys*, *Geoclemys*, and some *Geoemyda*), and in some Emydidae (Deirochelyinae); narrow vertebral scutes, a feature observed in several Lindholmemydidae (*Elkemys*, *Lindholmemys*, *Gravemys*, some *Mongolemys*), some *Echmatemys* species, and some primitive Testudinidae (see below); very short epiplastral lip, a feature found in the Lindholmemydidae and some Geoemydidae (i.e. *Batagur* complex, *Orlitia*, *Malayemys*, *Geoclemys*, *Paleochelys*); short gular scutes, a feature present in lindholmemydids and some Geoemydidae (*Batagur* complex, *Orlitia*, *Malayemys*, *Geoclemys*, and some *Geoemyda*). Among geoemydids, *Palaeoemys* differs from previously defined members of the Geoemydinae (Hirayama, 1984) in the neural plates with short antero-lateral sides, and it differs from *Batagur, Callagur*, *Kachuga*, *Hardella*, and *Morenia* in the fourth marginal scute not reaching the second pleural scute (thus *Palaeoemys* is more primitive for this character). We consider *Palaeoemys* to be a relative of *Geoclemys* and *Malayemys* since the lateral keels are located near the medial margin of the pleural scutes, (for the species of *Palaeoemys* which do not exhibit lateral keels in adult, a keel configuration similar to *Geoclemys* and *Malayemys* can be found in small and juvenile specimens (when avaible)). In all other three-keeled geoemydids, the lateral keels are situated more laterally. Moreover, as in *Geoclemys*, *Malayemys*, and *Orlitia*, the plates of *Palaeoemys* are very thick, corroborating our phylogenetic interpretation. *Palaeoemys* differs from *Orlitia*, *Geoclemys* and *Malayemys* by its humero-pectoral sulcus positioned far behind the entoplastron, and by the posterior sulcus of the 5th vertebral plate placed near or crossing the pygal plate.

The newly defined genera, *Juvemys* (Hervet, 2003a), *Euroemys*, *Francellia*, *Owenemys* (Hervet, 2004a) show insignificant differences with *Palaeomys* and we consider them as junior synonyms of the latter. Indeed, the diagnoses of these genera are based mostly on characters that are variable at the intraspecific level and highly related to growth and ontogeny (slight differences in development of the buttresses, wider versus narrower vertebral scute patterns, relative width of the plastron, or slight difference in the development of gular lips). They are irrelevant to define turtle species or genera.

We consider *Borkenia* Schleich, 1994, from the Lutetian of Germany, to be closely related to *Palaeoemys* because they share the following characters: posterior position of the humero-pectoral sulcus, small epiplastral lips, straight border of the anterior plastral lobe, thick plates. *Borkenia* differs from *Palaeoemys* by its wider vertebral scutes, its emarginate nuchal plate, the more developed epiplastral lips, its gular scute never reaching the entoplastron (although this feature may be variable in some living geoemydids (see Nakamura, 1934)), and the weaker axillary and inguinal buttresses. *Borkenia* (containing the species *B. oschkinisi* and *B. germanica*) might be a synonym of *Palaeoemys*, since the above cited features are variable at the generic level. Further studies on the variability in the two genera are needed. In addition, the newly described specimen of *Hummelemys ambigua* Hervet 2004b (from the same locality as *B. germanica*) is most likely a junior synonym of *B. germanica*, and then should belong to either *Borkenia* or *Palaeoemys*, pending a further revision of these two genera.

The genera *Palaeochelys* and "*Ocadia*", known from the Eocene to the Miocene in Europe, are known to be polyphyletic (Schleich, 1985, 1993; Jimenez-Fuentes *et al.*, 1990; Schleich, 1993; Broin *et al.*, 1993; Lapparent de Broin, 2001). The type species of *Palaeochelys*, *P. busseliensis* Meyer, 1847 (Meyer, 1847; Hervet & Lapparent de Broin, 2000) is defined from a single carapace from the Late Oligocene of Germany and differs from *Palaeoemys* in having the first vertebral scute wider than the nuchal plate and wide vertebral scutes. *Bergounioux-chelys*, *Cucullemys*, *Provencemys* described recently by Hervet (2004a), are considered here as junior synonyms of *Palaeochelys* since they are not significantly different from the latter. *Cuvierichelys parisensis* from the upper Eocene of France (Gray, 1831; revised in Hervet, 2004a) differs from *Palaeoemys* in having the first vertebral scute wider than the nuchal bone, wide vertebral scutes, a rather rounded anterior plastral lobe, and the humero-pectoral sulcus crossing or located near the entoplastron.

Palaeoemys differs from *Grayemys*, an Eocene geoemydid from Asia (Ckhikvadze, 1970; Flerov *et al.*, 1974) by a narrower vertebrals, a straight anterior margin of the anterior plastral lobe, and straight xiphiplastral lateral margins. *Palaeoemys* differs from *Echmatemys*, a North American geoemydid (Hay, 1908) by the shape of gulars, the presence of lateral keels, and its weak epiplastral lip. Some Asiatic geoemydids have been attributed to the genus *Echmatemys*: *E. orlovi* Ckhikvadze, 1970; *E. zaisanensis* Ckhikvadze, 1970; *E. chingaliensis* Kusnetzov and Ckhikvadze, 1974; *E. borisovi*, Ckhikvadze, 1990 (Flerov *et al.*, 1974). However, such inferences should be considered with caution because of the numerous putative cases of convergence during the Eocene. Moreover all of these species are based on so poor material that their validity is doubtful. In any case, further material will be necessary to support, or refute this attribution.

Some undescribed skulls from the Eocene of Germany (Messel and Geiseltal) are known (Keller & Schaal, 1988; Gassner *et al.*, 2001) and might be referred to *Palaeoemys* or *Borkenia* (because they are associated with shells similar to *Ocadia messeliana* or *Ocadia germanica*). Those skulls are reminiscent of geoemydids such as *Geoclemys* or *Siebenrockiella*, and the triturating surface seems to be similar to *Siebenrockiella*. The foramen orbito-nasale is relatively developed and is similar in shape to that of *Geoclemys* or *Orlitia*.

Palaeoemys testudiniformis (Owen, 1842)
(Plate 1, Figure 1)

Synonymy:
Emys testudiniformis Owen, 1842
Emys testudiniformis Owen & Bell, 1849
Emys bicarinata Bell, 1849
Chrysemys testudiniformis Lydekker, 1889
Chrysemys bicarinata Lydekker, 1889
Chrysemys sculptata de Stefano, 1902
Owenemys testudiniformis, Hervet, 2004a
Francellia salouagmirae, Hervet, 2004a
Juvemys labarrerei, Hervet, 2003a

Referred material: two partial carapaces (MDE-sp51 and MDE-sp 95), anterior plastral lobe (MDE-sp132), partial plastron (MDE-sp53), right costal plate (MDE-sp250), nuchal plates (MDE-sp40 and MDE-sp96), and more than one hundred shell fragments from the Ypresian of Saint Papoul, southern France (collection of the Musée des Dinosaures, Espéraza).

Measurements: See table 2. The estimated carapace length from MDE-sp51 is 210 mm., and the estimated shell width is 176 mm.

Distribution: Ypresian (Lower Eocene: MP-8 to MP-10) of France and England.

Diagnosis: A species of *Palaeoemys* with one central keel and two lateral continuous keels, persisting in most mature individuals. The shell is trapezoidal in cross section. The anterior part of the second vertebral is wider than the posterior part. The pygal bone is not crossed by the posterior sulcus of the fifth vertebral scute.

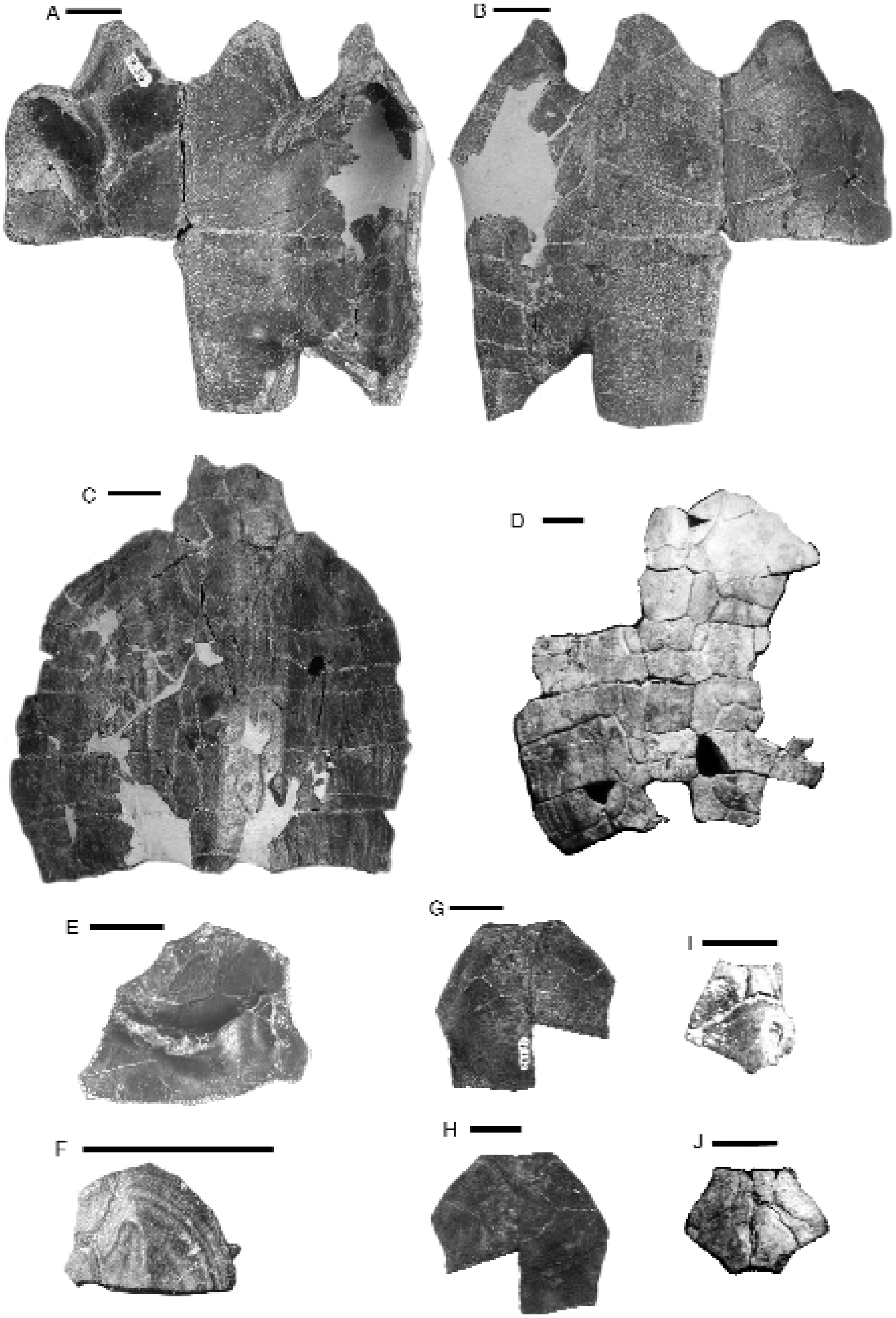


Plate 1: *Palaeoemys testudiniformis,* Saint Papoul (Early Eocene of Southern France) (scale bars = 2 cm)
A: visceral view of the partial plastron MDE-sp53
B: ventral view of the partial plastron MDE-sp53
C: dorsal view of the partial carapace MDE-sp51
D: dorsal view of the partial carapace MDE-sp95
E: visceral view of the first right costal plate MDE-sp250 showing the well developed axillary process
G: visceral view of the anterior plastral lobe MDE-sp132
H: ventral view of the anterior plastral lobe MDE-sp132
I: dorsal view of the nuchal plate MDE-sp40
J: dorsal view of the nuchal plate MDE-sp96
Palaeoemys sp., Saint Papoul
(Southern France, Early Eocene) (scale bar = 2 cm)
F: dorsal view of a right small costal plate (MDE-sp252), showing the well developed lateral keel of a juvenile individual

Table 2: Main Measurements (mm.) for the material referred to *Palaeoemys testudiniformis*

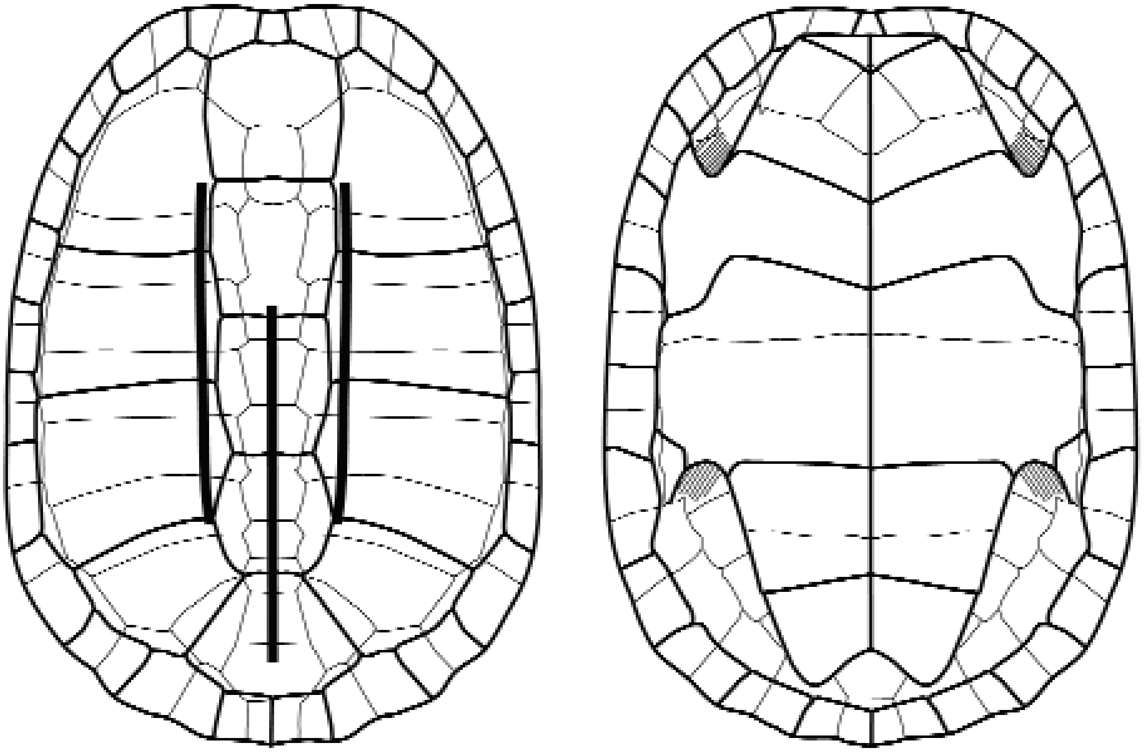
specimen number	Maximal length	Maximal width
MDE-sp51	144*	150
MDE-sp95	155	148
MDE-sp53	146	86**
MDE-sp250	61	44
MDE-sp96	45	34
MDE-sp40	34	-

* Length from the nuchal plate to the fifth neural plate
** width between the midline suture of hypoplastron and peripheral plate

Description:

The carapace is oval with three distinct keels. The shell has a trapezoidal shape in cross section. The keels are weak, as in *Annamemys*, but continuous, and placed more medially as in *Geoclemys* or *Malayemys*. In mature specimens, the median keel appears from the second or third neural plate or even farther posteriorly. The lateral keels are present from the posterior part of the first costal to the sixth costal plate, they are rather blunt and tend to form a slight knob on each pleural in juveniles. In most specimens, the ornamentation on the carapace surface consists of growth annuli, especially under the vertebral and pleural scutes. The nuchal plate is hexagonal and relatively small. Neural plates are wide and thick, the neural formula is 4,6A,6A,6A,6A,6A,6A,6 but may have some variation (e.g. the neural formula for MDE-sp95 is 4,6A,6A,6A,7A,5A,?,?). There are neither suprapygal nor pygal plates preserved in our specimens, but they are known from other specimens referred formerly to *Juvemys labarerrei* (Hervet, 2003a). The first costal plate is nearly as long as the second and third costal plates together. The anterior peripherals are rather short, the posterior ones are longer and can show a slight scalloping pattern as in some *Trachemys*. The peripherals of the bridge are relatively high and form a lateral angle. The third and the seventh peripherals are in contact with the axillary and inguinal buttresses. There is an axillary musk duct enclosed within the third peripheral plate, and an inguinal musk duct within the seventh peripheral plate, both placed near the suture between the peripheral plate and the plastral buttresses.

The first vertebral scute is nearly as long as wide with the lateral margins slightly diverging anteriorly and the anterior margin slightly convex anteriorly. Its anterior part is included in the nuchal plate. The second and third vertebral scutes are narrow, and slightly longer than they are wide. The fifth vertebral is wide posteriorly but does not reach the tenth marginal scutes. The first pleural scute is longer than wide. The second pleural scute is in contact with the fifth, sixth, and seventh marginal scutes. The anterior marginal scutes are short. All marginal scutes are restricted to the peripheral plates except in the pygal region.



Reconstructed shell of *Palaeoemys testudiniformis* from specimens No MDE-sp51, MDEsp-53, MDEsp-132, BMNH R4102, from the holotype of *Emys bicarinata* (Bell, 1849) BMNH 39450, and from the holotype BMNH 39767.
Left: carapace; Right: plastron. (boldest lines represent keels, bold lines are for scute sulci, thin lines for bony sutures)

The plastron is strongly sutured to the carapace. The buttresses are well developed. The axillary buttress inserts on the lateral half of the first costal plate. There is a strong ridge on the visceral side of the first costal plate linking the axillary buttress with the first and second dorsal rib heads. The plastron is thick (maximum thickness = 11 mm. for MDE- sp132 and MDE-sp53). The anterior margin of the plastron is straight and truncated as in *Batagur baska*. The bridge is longer than the posterior lobe. The lateral borders of the anterior and posterior lobes are rounded and thick. The epiplastra are short. The entoplastron is diamond shaped. There is a swelling on the visceral side of the hypoplastron linking the two inguinal buttresses. The hypo-xiphiplastral suture is straight as in most testudinoid species.

The plastron is covered by 12 epidermal scutes. The gular scutes are very short and barely reach the anterior end of the entoplastron. They form a very short antero-lateral lip on the visceral side of the epiplastron. The humeral and pectoral scutes are long. The humero-pectoral sulcus does not cross the entoplastron, but is placed far behind it. The humero-pectoral and pectoro-abdominal sulci are convex backwards and parallel to each other. The femoro-anal sulcus is convex anteriorly.

Comparison and discussion:

The genus *Palaeoemys* was erected by Schleich in 1994 on the basis of a nearly complete shell from the Middle Eocene of Germany (Schleich, 1994). The type-species, *P. hessiaca* Schleich, 1994, has only one midline keel placed on the posterior part of the carapace which is different from the Saint Papoul specimens. However, the specimens described above can be referred to the genus *Palaeoemys* by the following characters: posterior position of the humero-pectoral sulcus, small gular, weak epiplastral lip, narrow vertebrals and developed buttresses.

In 1849 Bell described *Emys bicarinata*, from the London Clay (Early Eocene) of the Isle of Sheppey, which has three keels on the carapace (Owen and Bell, 1849). This species can be referred to *Palaeoemys* since it has narrow vertebral scutes, the first vertebral scute narrower than the nuchal plate, and the humero-pectoral sulcus placed far behind the entoplastron. The Saint Papoul specimens, and *Emys sculptata* de Stefano, a carapace from the Early Eocene of the London Clay (De Stefano, 1902), can be referred to the species *Emys bicarinata* Bell, 1849 because of the presence of three keels on the carapace, the slightly anteriorly divergent lateral sides of the first vertebral scute, and the anterior part of the second vertebral wider than the posterior part. The holotype of *Emys testudiniformis* Owen is based on a partial shell from the Early Eocene of the London Clay and lacks the three keels, however it exhibits exactly the same scute and bone pattern in both plastron and shell as in the holotype of *Emys bicarinata*. The keels on the carapace may vanish or become indistinct in adult or old specimen of some geoemydid species (e.g. *Chinemys reevesi*, *Ocadia sinensis*). We consider *Emys bicarinata* to be a junior synonym of *E. testudiniformis*. Moreover, some material of *Emys testudiniformis* from the Early Eocene of Harwich (England) housed in the Natural History Museum of London provides additional information concerning the posterior part of the carapace. R4102 exhibits three keels and has two suprapygals, the first being trapezoidal and smaller than the second; the second suprapygal is wide and contacts both the pygal and the eleventh peripheral plate with a long suture.

Juvemys labarrerei from St Papoul, defined recently by Hervet (2003a), and *Francellia salouagmirae* (Hervet, 2004a) from the Early Eocene of Rians (Var, France) do not show any significant differences with *Palaeoemys testudiniformis*. They are therefore synonymized with the latter. The slight differences found on the material studied by Hervet (2003a, 2004a) can be fully understood as intraspecific variations (slight differences in the development of the buttresses, the shape of vertebrals) or deformation of the fossil material (e.g. *Francellia salouagmirae*, narrower shell outline). The lyre-shaped first vertebral scute, used by Hervet (2004a) as the diagnostic feature of *Francellia* is in fact a case of intraspecific variation, since similar variation can be found within the living species *Emys orbicularis* (Claude, J., pers. observations).

Palaeoemys hessiaca Schleich, 1994

(Plate 2, Figure 2)

Synonymy: *Palaeoemys occitana* Hervet, 2003a

Referred material: a nearly complete shell (MDE-spT01), a nuchal plate (MDE-sp50), a partial and very crushed carapace (MDE-sp164), and several shell fragments (collection of the Musée des Dinosaures, Espéraza).

Measurements: MDE-spT01: plastral length: 201 mm, plastral width (at the suture between hyoplastron, hypoplastron, and peripherals): 114 mm, maximum shell width: 141 mm, length from nuchal plate to the posterior end of the sixth neural: 158 mm. MDE sp 50: width: 42 mm, length 31 mm. Estimated shell length: 250 mm.

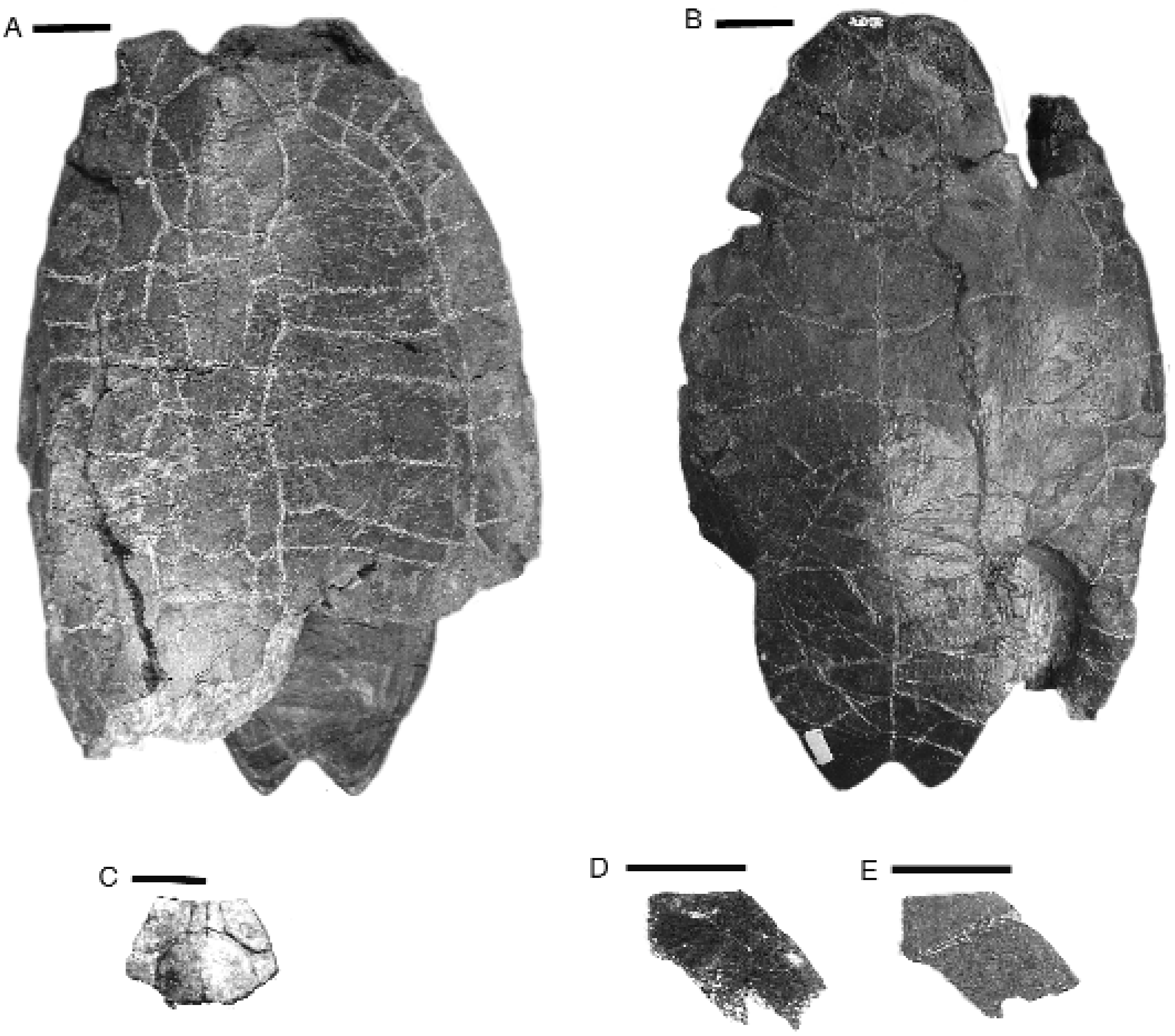


Plate 2: *Palaeoemys hessiaca,* Saint Papoul (Early Eocene of Southern France) (scale bars = 2 cm)
A: dorsal view of the almost complete shell MDE-spT01
B: ventral view of MDE-spT01
C: dorsal view of the nuchal plate MDE-sp 50, *Palaeoemys sp.* Saint Papoul (Southern France, Early Eocene) (scale bars = 2 cm)
D: visceral view of a right epiplastron MDE-sp 251, showing the small epiplastral lip
E: ventral view of MDE-sp 251.

Type locality: Lutetian (Middle Eocene) of Stolzenbach/ Borken (Hesse), Germany
Distribution: Early Eocene (Ypresian, MP-10) to middle Eocene (Lutetian, MP-13) of France and Germany.
Emended Diagnosis: A species of *Palaeoemys*, differing from *P. testudiniformis* in having only a central keel on the carapace, extending from the sixth neural plate to the second suprapygal in the adult; in the first vertebral scute elongated antero-posteriorly with strongly convex anterior margin and convex lateral margins.
Description:

MDE-spT01 consists of an almost complete shell lacking the right seventh to eighth, and left sixth to eighth costal plates, seventh to eighth neural plates, posterior peripherals, pygal, and suprapygal plates. There is no pygal or suprapygal plate in the referred material, however the suprapygal pattern is known from the holotype (Schleich, 1994).

This species is similar to *P. testudiniformis*. The shell surface is smooth, although growth annuli are present in some specimens. The carapace is oval as in *P. testudiniformis* but lacks lateral keels. A neural keel is present on the sixth neural plate of MDE-spT01 and is supposed to extend on to the suprapygal as in the holotype (Schleich, 1994), although this part is missing in the specimens from St-Papoul. The nuchal emargination is small and shallow as in *P. testudiniformis*. The neural formula is 4,6A,6A,6A,6A,6A,6A,6 as in emydids and some geoemydids. The first costal plate is long as in *Lindholmemys* and in some geoemydids (*Kachuga*, *Hardella*, *Malayemys*, or *Batagur*). The peripheral plates of the bridge region form a rim on the lateral border of the carapace, but not rounded as in *Orlitia* or *Geoclemys***,** they seem to be lower than in *P. testudiniformis*.

The scute sulci are deeply impressed. The vertebral scutes are narrow (narrower than in *Palaeoemys testudiniformis*). The first vertebral scute is oval in shape and its anterior part is included in the nuchal plate, which contacts the first marginal scute by an oblique sulcus. The second and third vertebrals are much longer than wide, the second being wider anteriorly as in *Palaeoemys testudiniformis*. The marginal scutes are restricted to the peripheral bones, and may reach slightly the second suprapygal. The cervical scute is square in shape and small.

The plastron is thick. It is elongated and strongly sutured to the carapace. The axillary and inguinal buttresses are well developed. The axillary buttress inserts on the lateral half of the first costal plate, and is linked to the first and second dorsal rib heads by a strong ridge. The inguinal buttress inserts on the lateral half of both fifth and sixth costal plates, as in *P. testudiniformis*. The anterior lobe is truncated, and the posterior lobe has a semi-circular anal notch. The lateral margins of the anterior lobe are straight. The lateral borders of the anterior and posterior lobes in *P. hessiaca* are flattened laterally as compared to *P. testudiniformis*. The midline suture between the epiplastra is short (similar to *Batagur baska* and *Geoemyda spengleri*). The hypo-xiphiplastral suture is straight.

The gular scutes are short and reach only the anterior end of the entoplastron. On the visceral side, the epiplastral lip is weak, only marked laterally. The humero-pectoral sulcus is placed far behind the entoplastron as in *Batagur, Callagur, Kachuga* and *Lindholmemys*. The femoro-anal sulcus is convex anteriorly. The xiphiplastral lip is weakly developed on the visceral side of the xiphiplastron.

Comparisons and discussion:

This species is similar to *P. testudiniformis* for most plate and scute features. The lateral keels are probably present in juvenile specimens of *P. hessiaca*, since all small geoemydid from Saint Papoul have three keels, as in many other geoemydid turtles (see discussion). *P. hessiaca* differs from *P. testudiniformis* mainly by lacking the lateral keels in adults and the shape of the first vertebral scute. *P. testudiniformis* has a wider first vertebral scute with a slightly convex anterior margin, whereas *P. hessiaca* has a more elongated and oval first vertebral scute. Moreover it differs from *P. testudiniformis* by more flattened free plastral margins.

In 1849, Bell described *Emys crassus* on the basis of isolated plastral fragments from the upper Eocene of Hordwell (England), which are very similar to some *Borkenia*, *Palaeoemys* or *Cuvierichelys*, in the position of the humero-pectoral sulcus and in the swelling which links the two inguinal buttresses on the inner side of the hypoplastron. However, it is not possible to refer these specimens to any definite genus or species because the material is too poor.

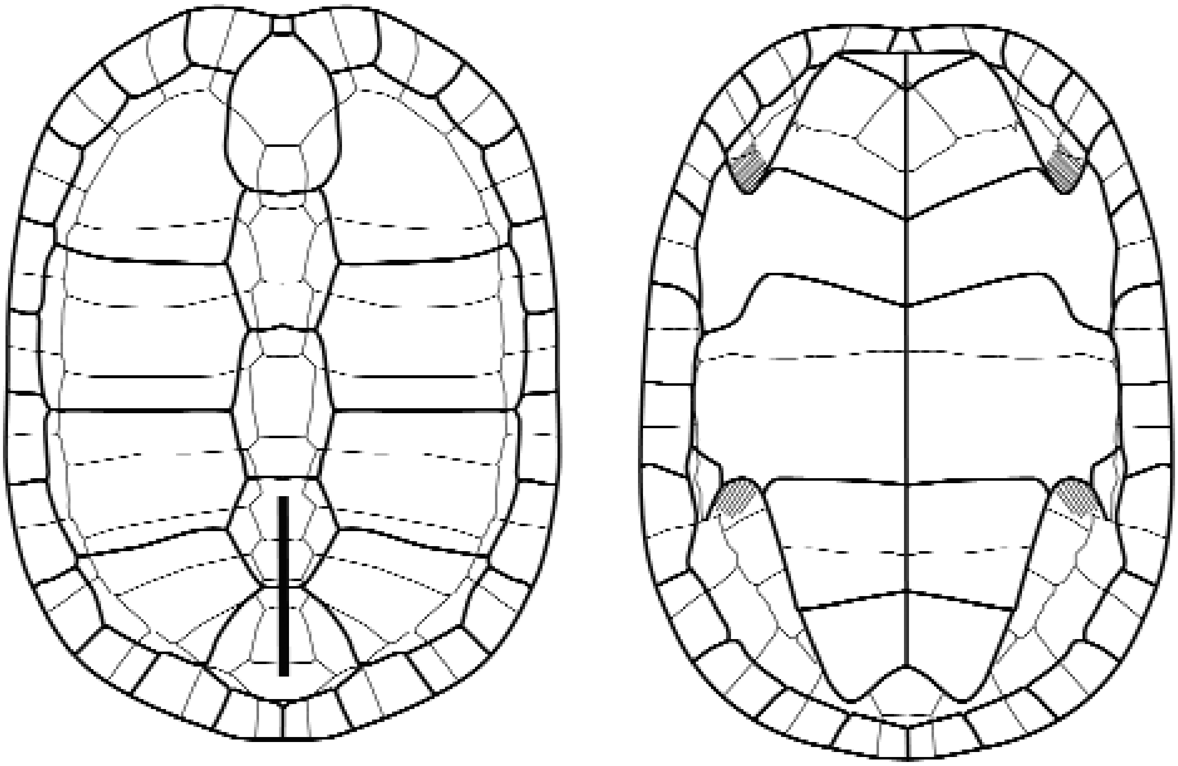


Figure 2: Reconstruction of *Palaeoemys hessiaca* from specimens no MDE-spT01 and from the holotype (Schleich, 1994). Left: carapace; Right: plastron. (Bold lines are for scute sulci, thin lines for bony sutures)

These specimens should be considered as Geoemydidae indet. and *Emys crassus* should be considered as *nomen dubium*. From the same locality, Seeley (1876) described the species *Emys hordwellensis* and Lyddeker described *Ocadia oweni* (1889). *Ocadia oweni* may be considered as a younger synonym of *Emys hordwellensis*. Indeed the only differences found by Hervet (2004a) between these two species is the relative development of the epiplastron, which we consider to be variable at the intraspecific level. Then the combinations *Landreatochelys oweni* (Hervet, 2004a) (for anteriority reasons) and *Cuvierochelys crassa* (Hervet, 2004a) (because the type material of this taxon is not diagnostic) should be avoided. The combination *Cuvierochelys hordwellensis* may solve reasonably this problem, since the specimens from Hordwell fit rather well in the diagnosis of *Cuvierochelys*.

The species "*Ocadia" messeliana* and "*O." kehreri* from the Lutetian of Messel (Staesche 1928) are referred here to *Palaeoemys* because they exhibit all the characters of the diagnosis of the genus. "*O." kehreri* may be considered as the synonym of "*O." messeliana*. The slight differences in shape and size between them can be interpreted as differences between younger ("*Ocadia" messeliana)* and older individuals ("*O*". *kehreri*). "*Ocadia" messeliana* exhibits a medial keel as *Palaeoemys hessiaca* but differs by the width of vertebral scutes, the shape of the first vertebral (rounded in *P. hessiaca*), and margin of the plastral lobe (straight in *P. hessiaca*). Moreover in *"O." messeliana*, the pygal pattern is known and the posterior vertebral sulcus does not cross the small pygal plate, and the gulars are usually shorter.

"*Testudo corroyi*" Bergounioux, 1933 from the Early Ypresian of Palette (France) consists of an almost complete shell. Hervet (2004a) reported new material from the same locality and erected a new genus, *Owenemys*. "*Testudo corroyi*" exhibits the diagnostic characters of *Palaeoemys.* It differs from the other species of *Palaeoemys* in having a narrower straight part of the anterior lobe, posterior lateral keels, and a more quadrangular vertebral scute. These differences are not significant enough to erect a new genus, we consider *Owenemys* as a junior synonym of *Palaeoemys*.

? Palaeochelys sp. described and figured in Groessens Van Dyck, 1978 (photo 1), from the Lutetian of Messel, may be referred to *Palaeoemys hessiaca* or *Palaeoemys messeliensa* because of the morphology of its neural keel and its short pygal, as in Geoemydidae. The holotype of *Palaeoemys hessiaca* (Schleich, 1994, fig. 1) has been interpreted as lacking the cervical scutes. However this part of the shell is broken, and this interpretation may be considered as doubtful.

Palaeoemys occitana defined by Hervet (2003a) from Saint Papoul, is synomimized with *P. hessiaca* here, since it shows few differences with the latter. Differences such as weaker buttresses, narrower vertebral scutes can be interpreted as allometric changes during growth. Indeed, the holotype of *P. hessiaca* is bigger than the Saint Papoul specimens. Size differences can be understood as interspecific or interregional variation within a species.

Testudinidae Batsch, 1788

Achilemys Hay, 1908

Emended diagnose: A primitive testudinid with a small pygal plate not intersected by the posterior sulcus of the fifth vertebral scute, an upturned posterior margin of the carapace, and a short epiplastral lip without posterior thickening.

Type species: *Achilemys allabiata* (Cope, 1872)

Distribution: Early Eocene (Ypresian) of France, and Early Middle Eocene (Bridgerian B) of Wyomming, USA.

Achilemys cassouleti nov. sp.

(Plate 3, figure 3)

Derivatio nominis: from ‘cassoulet’, a traditional dish of southwestern France cooked in a pan made of the clay from the Saint Papoul area.

Holotype: an associated partial carapace, plastron, right humerus, and left femur (MDE-sp37, collection of the Musée des Dinosaures, Espéraza).

Referred material: a femur (MDE-sp90), and some unnumbered shell fragments.

Type locality: Saint Papoul (Aude, France)

Horizon: Early Eocene (Ypresian, MP-10)

Diagnosis: a species of *Achilemys*, with elongated second and third vertebral scutes (the third being longer than the second); last pair of marginal scutes not fused; slightly undulated posterior margin; cervical scute as long as wide. It differs from *A. allabiata* by its less truncated anterior plastral lobe, by the undulating posterior margin and by the gular excluded from the entoplastron.

Description:

MDE-sp37 consists of an associated right humerus, left femur, plastron and carapace lacking the first to ninth left peripherals, the second to fifth right peripherals, the fourth to sixth neural plates, the sixth and seventh right costal plates, and the fourth to sixth left costal plates.

The estimated length of the carapace of MDE-sp37 is 370 mm, its estimated width is 260 mm. The plastral length is 357 mm, and the plastral width (at the suture of hyo-hypoplastral suture and peripherals) is 228 mm, the length of the bridge is 171 mm. The total length of the femur from the head to the tibia articulation is 86 mm. The total length of the humerus from the head to the radius articulation is 91 mm.

“The total length of the femur (MDE-sp90) from the head to the tibia articulation is 81 mm.”

The carapace is disarticulated and has been restored. It is dome-shaped and has an oval outline in dorsal view. The plates are relatively thick with a smooth surface. The nuchal emargination as restored is very shallow and wide. Its posterior margin is undulated and upturned.

The nuchal plate is relatively wide. Although the neural series is not complete, the shape of the missing ones can be made out from the shape of surrounding plates. The neural formula is 6P,4,8,4,6A,6A,6A,6. The first neural is long, having a very short suture with the second costal plate. The costal plates are typically testudinid in shape (Auffenberg, 1974), with the odd costals wider medially, and the even ones wider laterally. The first peripheral is quadrangular in shape. The eleventh peripheral is roughly triangular in shape and is sutured with the eighth costal, the suprapygal, and the pygal plates.

The cervical scute is square in shape. The first vertebral scute has a rounded outline, as in the lindholmemydid *Gravemys barsboldi* from the Late Cretaceous of Mongolia (Sukhanov & Narmandakh, 1983), and contacts the first marginal, the second vertebral and the first pleural scutes.

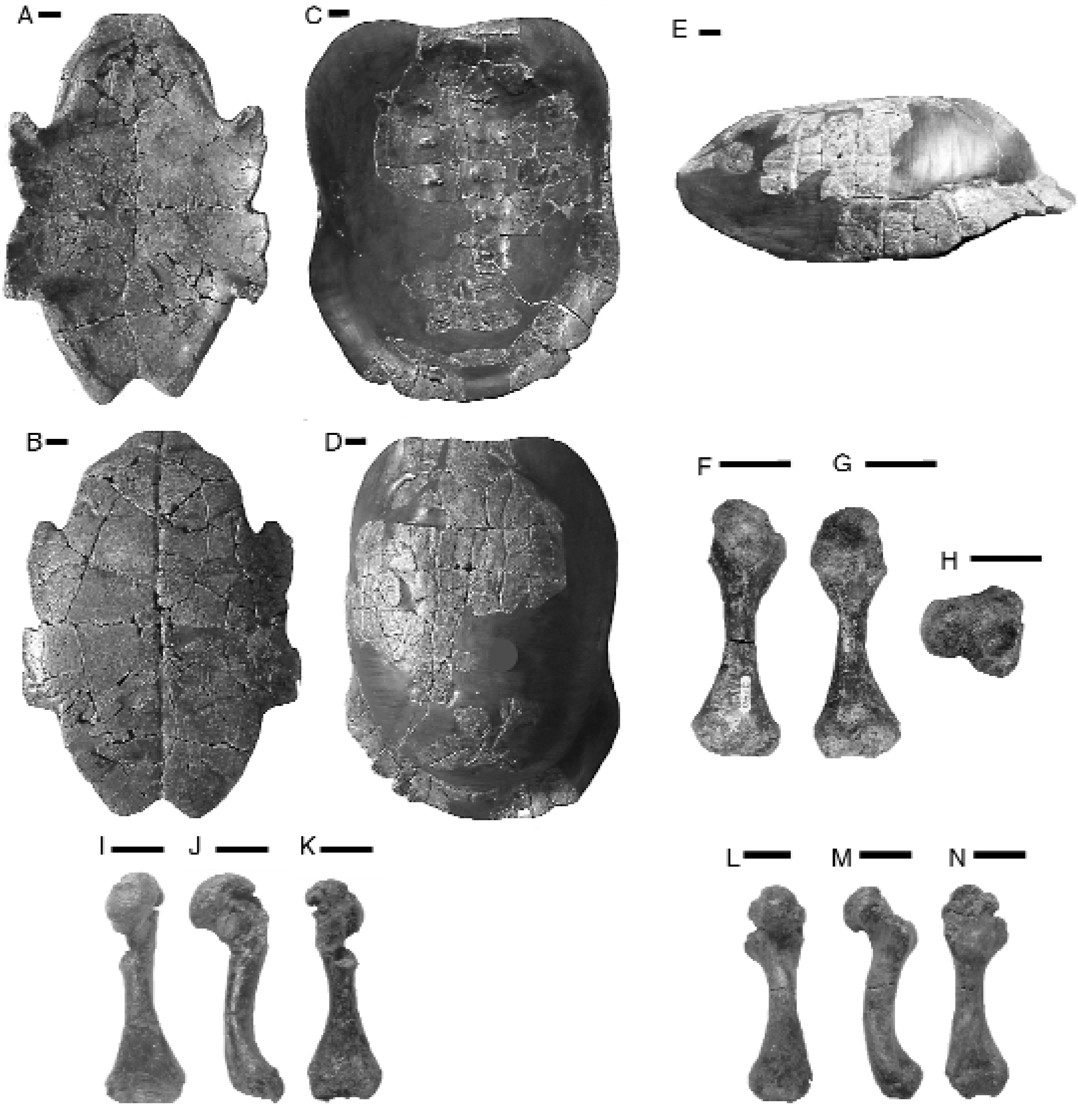


Plate 3: *Achilemys cassouleti nov. sp*., Saint Papoul (Early Eocene of Southern France) (scale bars = 2 cm).
A-E: MDE-sp37 (holotype: shell); A: Visceral view of the plastron, B: Ventral view of the plastron,
C: Visceral view of the carapace, D: Dorsal view of the carapace, E: Left lateral view of the carapace.
F-H: right femur (MDE-sp90); F: anterior view, G: posterior view, H: proximal view.
I-N: MDE-sp37 (holotype: femur and humerus); I: left femur, anterior view, J: left femur, lateral view,
K: left femur, posterior view, L: right humerus, anterior view, M: right humerus, lateral view,
N: right humerus, posterior view.

The second vertebral scute is slightly longer than wide and the third vertebral is more elongated. The fifth vertebral is wider than long, it contacts the eleventh and twelfth marginal scutes. The sulcus between the pleural and marginal scutes matches the suture between peripheral and costal plates as in other testudinids.

The carapace is sutured to the plastron. The axillary and inguinal buttresses are moderately developed. The axillary buttress contacts the third peripherals and reaches the first costal plate, the inguinal buttress contacts the seventh peripheral and probably the distal end of the fifth costal plate.

The plastron consists of nine plates. The epiplastra are relatively short compared to most of the other Testudinidae (e.g. *Hadrianus*, *Kinixys*, *Gopherus*…). The anterior border of the epiplastron is nearly straight, reminiscent of the morphology of *Pseudemys* or *Malaclemys*. On the visceral side, the epiplastral lip is weak, it extends no more than half the length of the epiplastron, without posterior thickening. There are no "epiplastral projections" as in some species of the genera *Hadrianus*, *Geochelone*, and *Gopherus*. The entoplastron is diamond shaped and large. The anal notch is large and wide.

The plastron is covered by twelve scutes. The gulars are relatively small, wider than long and do not reach the entoplastron. The humero-pectoral sulcus is placed posterior to the entoplastron. The pectoral scute is short on the midline and the abdominal is long as in most Testudinidae. The femoro-anal sulcus does not reach the hypo-xiphiplastral suture. On the visceral side of the xiphiplastra, the anal scute forms a well developed lip. There is a small axillary scute and an inguinal scute, the latter does not contact the femoral scute.

The trochanters of the femur are coalesced. The humeral trochanters seem not to extend beyond the humeral head as in *Manouria or Gopherus*, and the humerus is strongly curved backward. The ectepicondylar foramen is present as a deep groove in the distal humeral condyle.

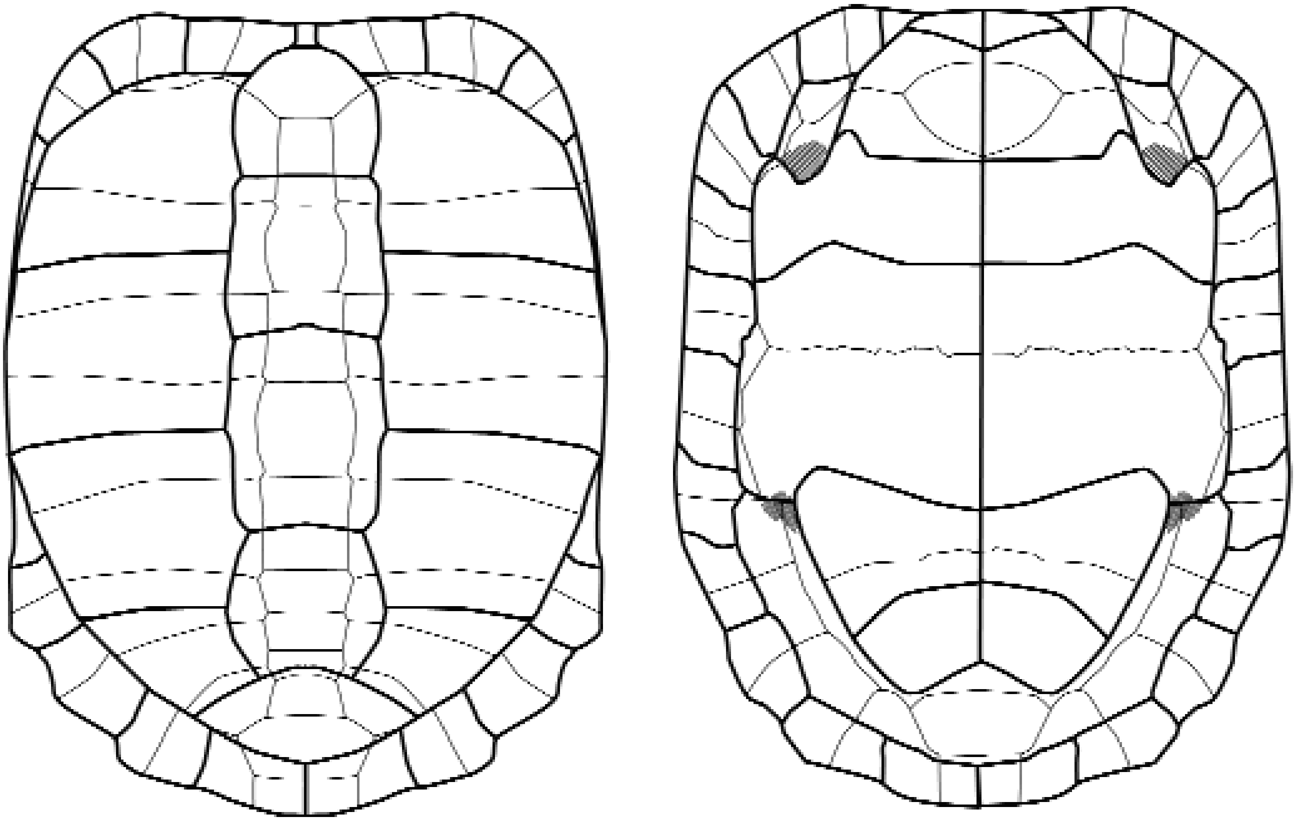


Figure 3: reconstruction of *Achilemys cassouleti* from observations of MDE-sp37
Left: carapace; Right: plastron. (Bold lines are for scute sulci, thin lines for bony sutures)

Comparisons and discussion

The alternating costal plate pattern of the carapace with odd costals wider medially and even ones wider laterally, and the plastron with a long abdominal scute and a rather short pectoral scute seen in MDE-sp37 are characteristic of the Testudinidae, although the last character is also observed, to a lesser extent, in some lindholmemydid species, and in some geoemydids. Moreover the coalesced femoral trochanters are another synapomorphic character of the Testudinidae (Auffenberg, 1974).

The epiplastral structure (weak epiplastral lip, absence of anterior epiplastral projection, and absence of posterior thickening of the epiplastron), and the pygal wider than long, differentiate the Saint Papoul specimen from the other putative primitive forms of testudinids: *Hadrianus* (Eocene of Asia, North America, and Europe (Lapparent de Broin, 2001)), *Ergilemys* (Upper Eocene and Oligocene of Europe and Asia (Lapparent de Broin, 2001)), and *Manouria* (extant Asiatic genus). This primitive epiplastral structure is reminiscent of some geoemydids. *Cheirogaster* from the Upper Eocene of Europe (Lapparent de Broin, 2001) differs from the Saint Papoul testudinid in having the more apomorphic features of Testudininae: fusion of the twelfth pair of marginals, epiplastral excavation present, absence of the cervical scute (Broin, 1977; Lapparent de Broin, 2001). *Dithysternon* Pictet & Humbert, 1855, an enigmatic member of the Testudinoidea and possibly a member of the Testudinidae (Lapparent de Broin, 2001) from the Upper Eocene of Switzerland differs from *Achilemys* in having a double hinged plastron.

The genus *Achilemys* is known only by the type specimen, from the Middle Eocene of Wyoming (Hay, 1908). The material is very fragmentary, consisting of a half anterior plastral lobe, two anterior and three posterior peripherals, and a portion of last suprapygal and pygal (Hay, 1908). Few characters can be pointed out on the basis of such fragmentary material. However, MDE-sp37 can be attributed to the genus *Achilemys* because of the small pygal plate which is not intersected by the posterior sulcus of the fifth vertebral scute, the upturned posterior margin of the carapace, and the short epiplastral lip without backward thickening and epiplastral excavation. It differs from the type species, *A. allabiata*, in the slightly undulated posterior margin of the carapace, the position of the gulo-humeral sulcus, and in the longer anterior plastral lobe with a more rounded anterior margin.

The comparison between the Saint Papoul specimen and both fossil and extant testudinid species reveals that *Achilemys* presents a large set of plesiomorphic characters for Testudinidae: narrow vertebrals (as in some lindhomemydids, some geoemydids, and *Palaeoemys*), pygal plate not crossed by the fifth vertebral scute (as in geoemydids and some lindholmemydids), no fusion of the twelfth pair of marginal scutes in one caudal scute (as in some primitive Testudinidae, such as *Manouria* and *Hadrianus*), and no epiplastral excavation (this character occurring in *Ergilemys*, and in *Malacochersus*, in small The Testudinidae (*Testudo hermannii*, *Homopus*), and in some island forms such as the *Dipsochelys* and *Chelonoidis nigra* complexes). The plesiomorphic epiplastral and pygal features are shared with the geoemydids. This leads us to consider *Achilemys* as the most primitive taxon of Testudinidae.

3. A PHYLOGENETIC SCENARIO FOR THE TESTUDINOIDEA

We provide here a possible phylogenetic scenario for testudinoids (fig. 4) with special emphasis on skeletal anatomy, particularly that of the shell since most Eocene and earlier testudinoids species are known only from shell material.

Our knowledge of early testudinoids is increasing since a large number of fossils have been described, but no phylogenetic hypotheses incorporating more than one fossil genus from the key period, the Eocene, have been proposed. The apomorphic and plesiomorphic conditions for morphological characters are given below for each group, allowing testudinoid fossils to be considered in a phylogenetic context.

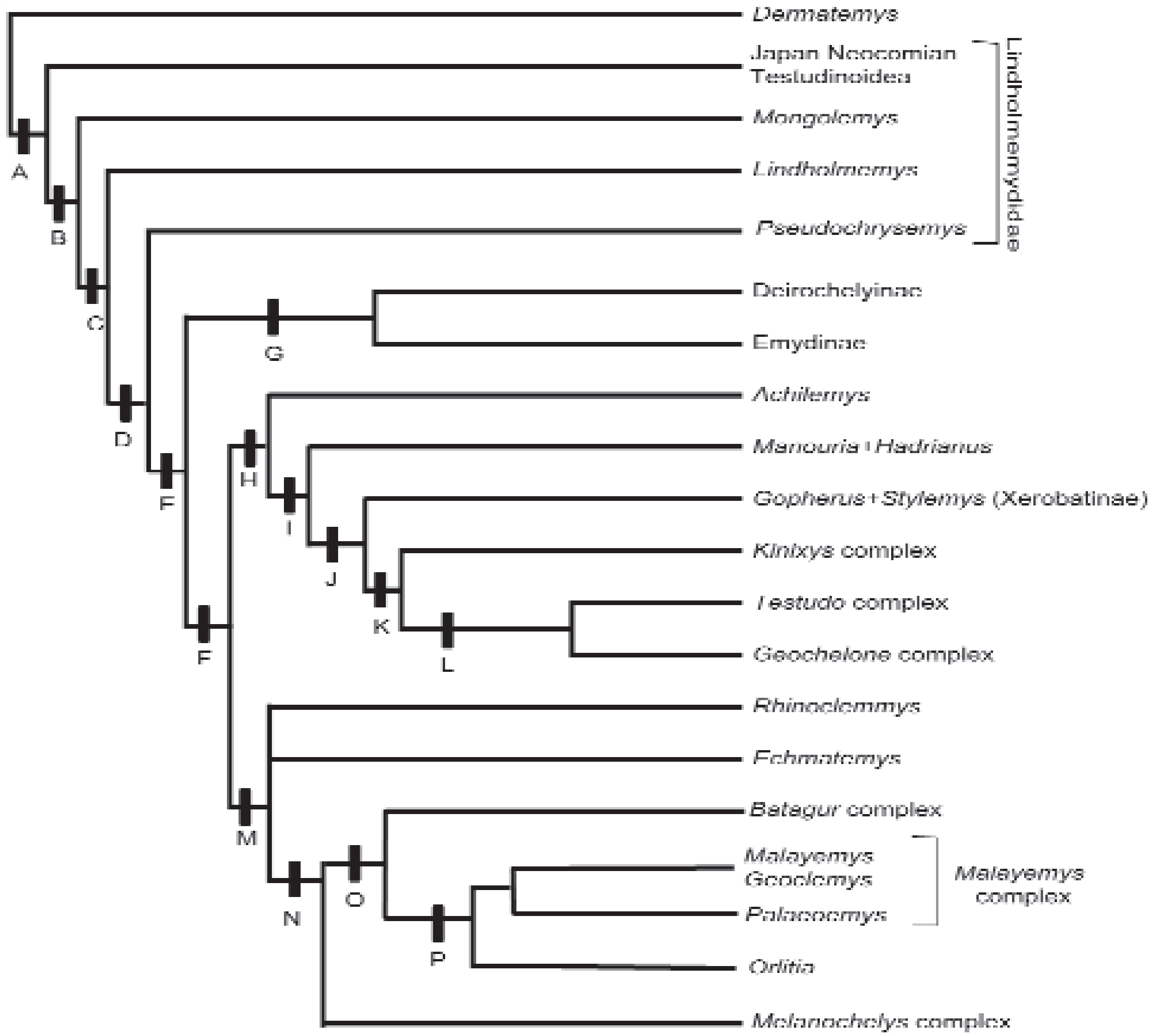


Figure 4: Hypothesised phylogenetic relationships among Testudinoidea (letters refer to nodal clades in the text).

3.1. Previous work and biogeographical considerations

Our phylogenetic scenario is based mostly on a reinterpretation of morphological characters in regard to recent molecular phylogenies (Lamb & Lydeard, 1994; Bickham *et al.*, 1996; Caccone *et al.*, 1999, Shaffer *et al.*, 1997, Wu *et al.*, 1999b; McCord *et al.*, 2000; Feldman & Parham, 2002; Honda *et al.*, 2002; Van der Kuyl, 2002; Fujita *et al.*, 2004, Spinks *et al.*, 2004). These new data provide some consensus which is in disagreement with the studies based only on morphology (compare for example with Hirayama, 1984, and Yakusawa, 2001). In their review of phylogenetical relationships among turtles, Gaffney and Meylan (1988) noted that “the systematics within Bataguridae is a current problem area”. It appears still to be true, since up to now, few clades are well supported morphologically, not only for Geoemydidae but also for the whole superfamilly. Moreover, Claude *et al.* (2003a; in press), noted the importance of convergent evolution in the general shape of skull and shell between Emydidae and Testudinoidae. Thus we are not confident in the use of a parcimony analysis to resolve the phylogenetic relationships of Testudinoidea, using only morphology. With the assistance of the results of molecular sequence studies and palaebiogeographical data, we propose a new scenario for the morphological evolution of Testutinoidea, in order to reinterpret the evolution of morphological characters and to discuss the position of fossil species. This allows some characters to be redefined and other to be identified. We are aware that our approach is unorthodox, and we are not defending molecular data against morphology. We moreover do not assert that this scenario is the true evolution of Testudinoidea, but we use it as a working hypothesis. It will be infirmed or confirmed by more data in palaeontology, morphology, and DNA-RNA analysis in the future or by combination of several information data-sets as it was recently done for the Emydidae (Stephens and Wiens, 2003). Such combinations of data are interesting but are out of the scope of this paper, since most living Testudinidae have not been sequenced yet.

From a palaeobiogeographical point of view, it seems that the modern Testudinoidea radiated from the stem group Lindholmemydidae. From the Cretaceous to the Palaeocene, all described testudinoids are Asiatic. There is no certain record of testudinoids from the Cretaceous and Palaeocene of North America. *Gyremys spectabilis* from the Late Cretaceous of North America, previously referred to the Testudinoidea (Hay, 1908; Ernst *et al.*, 1994), has no diagnostic features of the group. The absence of anal notch, the very wide vertebral scutes and the short abdominal scute allow to exclude this taxon from the Testudinoidea. In addition, its very peculiar shell shape (wider posteriorly) is reminiscent of some bothremydids or baenids. The species *Clemmys backmanni* from the Palaeocene of North America is not a Testudinoidae and was later referred to the Macrobaenidae (Gaffney, 1992; Parham & Hutchison, 2003). Hutchison and co-workers mentioned "Emydidae" from the Cretaceous and Palaeocene of North America (Hutchison & Archibald, 1986; Hutchison, 1998) and Testudinidae from the late Palaeocene (Hutchison, 1998), but this material is not yet described. We therefore prefer to consider such occurrences with caution. The possible occurrence of testudinoids at the same period in Europe should not be excluded. Indeed, some shell fragments from the Palaeocene of Belgium (Groessens Van Dyck, 1982, 1983, 1984) and France (Broin, 1977) which have been tentatively referred to the Platysternidae or the Baenidae are strongly reminiscent of the Lindholememydidae. But on the basis of such incomplete material, it seems that a distinction between these families may be difficult. Thus, the existence of the Lindholemydidae in the Palaeocene of Europe is possible but not confirmed. It seems that the Lindholmemydidae originated in Asia, where several taxa have been described on the basis of important material (Sukhanov, 2000).

No Lindholmemydidae has been reported after the Palaeocene-Eocene boundary. It is interesting to note that all described testudinoids from the Cretaceous to the Palaeocene have inframarginal scutes and that similarly all testudinoids known from the Eocene lack them. The only Palaeocene genus referred to the Testudinoidea which lacks inframarginal scutes is *Anhuichelys* Yeh, 1974, from China (see also Yeh, 1983). *Anhuichelys* exhibits a wider nuchal plate that is reminiscent of Platysternidae or Chelydridae. On the general shape of the plastron and the shell, this genus might be referred to the Platysternidae (small peripheral plates, emarginated and relatively wide nuchal plate), and there is no reason a priori to consider it as testudinoid since its buttress morphology is unknown. *Lindholmemys*, from the Cretaceous of Asia (Sukhanov, 1983) and *Pseudochrysemys gobiensis* from the Paleocene of Asia (Sukhanov and Narmandakh, 1976) are morphologically closest to modern Testudinoidea since their inframarginal scutes are reduced and their abdominal scutes contact marginal scutes.

Although the fossil record of the Testudinoidea is poor during the Palaeocene and Cretaceous, a large number of species of "modern testudinoids" are reported as early as the Early Eocene (Hay, 1908; Hutchison, 1998; Lapparent de Broin, 2001; Hervet, 2004a). McDowell was the first to recognise that the modern Testudinoidea was an assemblage of two well defined geographical groups: the Emydinae (Emydidae in this paper) and Batagurinae (Geoemydidae in this paper), and that there is a close relationship between testudinids and geoemydids (McDowell, 1964). The further phylogenetic studies of Hirayama (1984), Shaffer *et al.* (1997), Honda *et al.* (2002), and Spinks *et al.* (2003) strengthen this hypothesis. Two of the three families of modern testudinoids have been reported from the early Eocene of Europe: the Geoemydidae and Testudinidae (Lapparent de Broin, 2001; this study). All three families (Testudinidae, Geoemydidae, Emydidae) are known from the Early Eocene of North America: (Hutchison, *et al.* 1998; Holroyd, *et al.* 2001).

Extant Emydidae *(s.s.)* are represented by exclusively American species except *Emys*, which is thought to have migrated to Europe in the Late Miocene (Lapparent de Broin, 2001). Most references to Asiatic emydids are doubtful and several have been assigned after reexamination to the Geoemydidae. For example, *Terrapene cultularia* Yeh (1961) is a synonym of *Cuora flavomarginata* (Sun *et al.*, 1992). Emydids from the Eocene of North America have been reported since the 1930s (Clark, 1937). Recently, Hutchison (1998) and Holroyd *et al.* (2001) have reported a taxon named « Emydidae P » from the Early Eocene. Estes and Hutchison (1980) also reported an Emydidae from the Early Eocene of Ellesmere Island, but whether it belongs to Emydidae is unclear since its inguinal buttresses contact both the 5th and 6th costal plate, a feature never observed in other Emydidae. The Emydidae became more diversified during the Miocene in North America with the appearance of several genera: *Emydoidea*, *Glyptemys*, *Terrapene*, *Emys* (Hutchison, 1981; Holman, 1987; Holman & Fritz, 2001; Lapparent de Broin, 2001).

The Geoemydidae are known both in the early Eocene of Europe, with the appearance of *Palaeoemys* (this study), and an undescribed new species referred to *Palaeochelys* (Nel *et al.*, 1999; Hervet, 2003b), and North America with the appearance of *Echmatemys* (Hutchison, 1998). The Geoemydidae persisted until after the Eocene in Europe and Asia (Lapparent de Broin, 2001) but disappeared from the fossil record in North America (Hutchison, 1998). However, geoemydids are known in central America as early as the Miocene with the occurrence of *Rhinoclemmys* (Webb & Perrigo, 1984), and this may represent a relic of North American Eocene taxa. It could be expected that Central America acted as a refuge for the Geoemydidae when climatic changes occurred at the Eocene-Oligocene boundary. The hypothesis of a close relationship between *Rhinoclemmys* and Eocene North American geoemydids (McDowell, 1964; Ernst, 1978; West & Hutchison, 1981) is more parsimonious than alternative ones (e.g. Hirayama, 1984) since it does not require that Geoemydidae migrate twice from Eurasia to North America. This opinion is strengthened now by the molecular data which propose *Rhinoclemmy*s as the sister group of all recent Asiatic genera (McCord *et al.*, 2000; Spinks *et al.*, 2004). It seems then that only one clade or a primitive grade of geoemydids evolved in North America. Except for *Rhinoclemmys* and *Echmatemys*, all other Geoemydidae are represented by Eurasiatic taxa, and may represent a monophyletic group. Indeed, *Rhinoclemmys* and *Echmatemys* share at least one plesiomorphic feature compared to all geoemydids: the absence of lateral keels even in juvenile individuals. Most members of living Geoemydidae exhibit three keels, at least in juveniles. This feature is never observed in emydids, testudinids or lindholmemydids, *Echmatemys*, and *Rhinoclemmys*. *Palaeoemys* is the oldest described Geoemydidae with three keels. It may be concluded from this feature, that Eurasiatic geoemydids and *Palaeoemys* constitute a monophyletic clade, that evolved only in Eurasia.

The situation for the Testudinidae is more complicated since they appear in the early Eocene in both Eurasia and North America, and later in Africa and in South America. The Testudinidae should share a unique common ancestor with geoemydids, as attested by skull features (no contact between postorbital and squamosal bones (a character which may have a broader distribution), angular not reaching the sulcus cartilaginis meckelii) (McDowell, 1964), chromosomic data (52 chromosomes) (Bickham and Carr, 1983), and genetic sequence data (Shaffer *et al.*, 1997; Spinks *et al.*, 2004).

3.2. Characters examined and distribution of their states

3.2.1. Skull

1: Basioccipital-basisphenoid contact

Morphology: The morphology and contacts of these bones are discussed in detail in Gaffney (1979). In cryptodiran turtles, in palatal view, the basioccipital contacts the basisphenoid along its entire width. However, this contact is narrower in the Emydidae (absence of batagurine process of McDowell (1964)).

Primitive condition: A wide anterior margin of the basioccipital (wider than the posterior margin of basisphenoid) is observed in most cryptodiran turtles (with the exception of *Kayentachelys*, Emydidae, and some Pleurosternidae).

The primitive condition for Testudinoidea is a wide anterior margin of basioccipital, reaching the pterygoid bones.

Derived condition: Emydidae have a reduced contact between the basioccipital and basisphenoid (McDowell, 1964).

Homoplasy: Among Testudinoidea, the distribution of this character does not show homoplasy.

2: Pterygoid-basioccipital contact

Morphology: The pterygoid is described in detail in Gaffney (1979). The morphology of the posterior process of the pterygoid is discussed in McDowell (1964) for aquatic Testudinoidea.

Primitive condition: The pterygoid does not reach the basioccipital in *Proganochelys*, *Kayentachelys*, and some Pleurosternidae.

However, in closer relatives of Testudinoidea such as Chelydridae, Baenidae, Chelonioidea, and Trionychoidea, the pterygoid reaches the basioccipital, which may define the primitive condition for Testudinoidea.

Derived condition: A reduced or absent contact of basioccipital with pterygoid is considered as a derived condition among Testudinoidea. This character occurs in most Emydidae with the exceptions of molluscivorous species (*Graptemys* and *Malaclemys*).

Homoplasy: A reduced or absent contact between pterygoid and basioccipital occurred only once among Testudinoidea. A wider contact between basioccipital and pterygoid in emydid molluscivorous species (*Graptemys*, *Malaclemys*) may be considered as the result of a secondary adaptation to a durophagous diet.

Discussion: This character is correlated with character 2. However its distribution is different because of the condition found in molluscivorous species of the Emydidae and it is thus not completely redundant. We were unable to score the batagurine process of McDowell (1964).

3: Epipterygoid

Morphology: The morphology and contacts of the epipterygoid are discussed in Gaffney (1979). McDowell (1964) has given the morphological condition for epipterygoid shape among Testudinoidea.

Primitive condition: The epipterygoid lies rectilinearly above the pterygoid, between the processus inferior parietalis of the parietal and the dorsal suture of the pterygoid. The extension of this bone is limited to the braincase surface. This condition is found in Chelonioidea, Trionychoidea, Cretaceous Testudinoidea (*Mongolemys*), Geoemydidae and Testudinidae.

Derived condition: The epipterygoid extends antero-laterally and may reach ultimately the jugal in emydids and chelydrids.

Homoplasy: Among Testudinoidea, the anterior edge of the epipterygoid is variably developed in emydids and can be developed in some molluscivorous geoemydids such as *Malayemys*, *Geoclemys*, and some *Chinemys*. Although this character can show important variation, we think it may be informative if the derived state is considered as the the anterolateral development of this bone but not its contact with the jugal.

4: Foramen carotico-pharyngeale

Morphology: The foramen carotico-pharyngeale is a ventral opening in the pterygoid, connecting with the canalis caroticus lateralis (Gaffney, 1979).

Primitive condition: Members of the Lindholmemydidae (Sukhanov, 2000) and the Emydinae have a relatively large foramen carotico-pharyngeale, which may be considered as the primitive condition for all the Testudinoidea.

Derived condition: The derived condition is a reduction or an absence of the foramen carotico-pharyngeale. This is observed in most modern Testudinoidea. The *Testudo* complex (*Testudo* + *Indotestudo*), some geoemydids (*Batagur* complex, *Rhinoclemmys*), and most deirochelyines usually have small foramina carotico pharyngeale, whereas most testudinids and most geoemydids lack them. The derived condition occurred in the Early Eocene as attested by *Echmatemys* (Hay, 1908).

Homoplasy: The reduction of the foramen carotico-pharyngeale occurred at least twice, in Geoemydidae + Testudinidae and in Deirochelyinae.

5: Foramen orbito-nasale

Morphology: The foramen orbito-nasale is described and figured in Gaffney (1979).

Primitive condition: A medium-sized to large foramen orbito-nasale is known in most cryptodiran turtles including the Baenidae, Plesiochelyidae, Trionychoidea, and Chelydridae. This condition is known also in an undescribed specimen of Lindholmemydidae from the Paleocene of Mongolia (J. Claude, personal observation). The Cretaceous lindholmemydid *Mongolemys* exhibits a rather small foramen orbito-nasale, but it is more developed than in some modern testudinoids, which can exhibit a very small foramen orbito-nasale. The primitive condition for the Testudinoidea is therefore a medium-sized to large foramen orbito-nasale.

Derived condition:

1. The foramen orbito-nasale is minute. This character state occurs in certain Testudinoidea.

2. The foramen orbito-nasale is huge (as defined in Hirayama, 1984).

Homoplasy: The foramen orbito-nasale was reduced once in the Emydidae (Emydinae), and several times in the Geoemydidae (e.g. *Rhinoclemmys* and *Melanochelys* complex) and in the Testudinidae. A huge foramen orbito-nasale is present only in the *Batagur* complex, this state was then acquired just once in Testudinoidea. A medium-sized foramen orbito-nasale is present in *Ocadia*, and we interpret it as a reversal. *Pyxidea mouhoti* exhibits a relatively large orbito-nasal foramen, which is considered as a reversion. Discussion: Because this character shows some important variation in Testudinoidea and shows an important homoplasy within the group, we consider the first derived condition as a latent feature for the entire group of modern testudinoids.

6: Angular extension

Morphology: The angular is described in Gaffney (1979). Variations in its shape and relations to other bones of the mandible in testudinoids are reviewed in McDowell (1964).

Primitive condition: In the Trionychoidea, Emydidae, and Chelonioidea, the angular has a long anterior extension and reaches the sulcus cartilaginis meckelii because of the intervention of the prearticular (see Gaffney, 1979: Fig 235G).

Derived condition: The angular is reduced and does not reach the sulcus cartilaginis meckelii in lingual view in both Testudinidae and Geoemydidae.

Homoplasy: Not known in Testudinoidea.

7: Contact between squamosal and postorbital

Morphology: The squamosal and postorbital are described in Gaffney (1979). The shape and contacts of these bones are figured and described for Testudinoidea in McDowell (1964).

Primitive condition: In primitive cryptodiran turtles, the squamosal reaches the postorbital, the same condition is reported in *Mongolemys* (Sukhanov, 2000) and in Emydidae. This condition is considered as plesiomorphic for Testudinoidea.

Derived condition: In Testudinidae and Geoemydidae, the contact between the squamosal and the postorbital is absent.

Homoplasy: The distribution of this character is consistent among Testudinoidea. Only *Ocadia* and some *Mauremys* species have the postorbital developed posteriorly, reaching the squamosal, which may be considered as a reversal (which corroborates the molecular phylogeny of McCord *et al.*, 2000). The condition of *Ocadia* and *Mauremys* looks somewhat different from emydids, since in emydids the postorbital is mostly developed posteriorly in its ventro-lateral part, in contrast to *Mauremys* and *Ocadia* where this bone is developed on its whole height. It should be considered as non homologous.

Discussion: We use this character as a synapomorphy for Testudinidae and Geoemydidae, although Gaffney and Meylan (1988) use it as a synapomorphy of Chelomacryptodira. Considering recent results of molecular phylogenies (Shaffer *et al.*, 1997; Fujita *et al.*, 2004), the monophyly of Chelomacryptodira is questionable, and this condition may have evolved in separate lineages (as it evolved independently in Cryptodira and Pleurodira), such as Kinosternidae + Dermatemydidae and Trionychia.

8: Incisura columellae auris

Morphology: the quadrate is described in Gaffney (1979). This bone usually encloses the stapes in Reptilia.

Primitive condition: The incisura columellae auris is open in *Proganochelys*, in the Emydidae, Geoemydidae, and *Mongolemys*. This state is considered primitive for Testudinoidea.

Derived condition: The incisura columellae auris is closed in Testudinidae.

Homoplasy: Not known in Testudinoidea. However this feature occurs by convergence in other turtle clades (e.g. Meiolanidae, Chelydridae, and Trionychia.)**.**

9: Fissura ethmoidalis

Morphology: The descending processes of the prefrontals form the fissura ethmoidalis. Gaffney described and reviewed this structure (Gaffney, 1979).

Primitive condition: Primitively, the fissura ethmoidalis is narrow, oval or keyhole- shaped in Chelonioidea, Chelydridae, Dermatemydidae, Emydidae, Geoemydidae and *Mongolemys*.

Derived condition: All testudinids have a wide fissura ethmoidalis.

Homoplasy: This character does not show homoplasy within Testudinoidea. However the shape of the fissura ethmoidalis varies to a certain degree among geoemydids from keyhole-shaped to oval-shaped (Hirayama, 1984).

10: Foramen palatinum posterius

Morphology: The foramen palatinum posterius is reviewed and described in Gaffney (1979).

Primitive condition: Among the Testudinoidea, the Asiatic Cretaceous genus *Mongolemys* is the only lindholmemydid for which this feature is known. In this genus, the foramen palatinum posterius is medium-sized. The same condition was found in an undescribed Lindhomemydid from the Paleocene of Mongolia (J. Claude, pers. observation) and also found in some other Mesozoic Cryptodira (Sinemydidae, Macrobaenidae, *Toxochelys*), and in Chelydridae and is thus interpreted as the primitive condition for Testudinoidea, although it may be controversial because this condition is not seen in most Trionychoidea.

Derived condition: In several groups of testudinoids, the foramen palatinum posterius is small.

Homoplasy: A small foramen palatinum posterius occurs in all Testudinidae, in some Geoemydidae (*Pyxidea mouhoti*, *Ocadia*, *Chinemys*, *Batagur* complex + *Orlitia* + *Malayemys* complex), and some Emydidae (Deirochelyinae except *Deirochelys*). *Geoemyda* and *Siebenrockiella* exhibit an intermediate condition. *Pyxidea*, *Ocadia* and *Chinemys* exhibit a small foramen which can be interpreted as reversed.

11: Premaxillary-maxillary pointed cusp

Morphology: The premaxilla and the maxilla may form a pointed cusp on the labial ridge at their suture.

Primitive condition: In most turtles (*Proganochelys*, Trionychoidea, Chelonioidea, Baenidae, Pleurosternidae, Plesiochelyidae), this structure is absent.

Derived condition: the Testudinidae evolved a pair of premaxillary-maxillary pointed cusps near or at the suture of premaxilla and maxilla (see Gaffney, 1979, fig. 267, p. 350).

Homoplasy: This character is known to occur only once in Testudinidae. The character condition is considered as reversed for *Kinixys* and *Pyxis*.

12: Posterior maxillary process

Morphology: The maxilla presents a posterior process in the direction of the check emargination.

Primitive condition: In all turtles except Testudinidae, the posterior maxillary process is absent.

Derived condition: A posterior maxillary process occurs in the Testudinidae with the exception of *Manouria* and *Hadrianus*. This character occurs also in *Gopherus*, and to a small extent in *Stylemys* (Hay, 1908) and may be considered as a synapomorphy uniting the Testudininae and Xerobatinae.

Homoplasy: Among testudinids, this character may be reversed. The posterior maxillary process is lost in *Kinixys*, and is considerably reduced in *Malacochersus*, *Homopus* and *Asterochelys*.

13: Labial ridge of the triturating surface

Morphology: The labial ridge borders the triturating surface laterally and is formed by the premaxilla anteriorly and the maxilla posteriorly. The maxillary portion of the labial ridge may be smooth or present denticulations or serrations. The dentary may exhibit analogous structures.

Primitive condition: In most turtles, the maxillary labial ridge is smooth without serrations or denticulations.

Derived conditions:

1. Testudinidae, except *Hadrianus*, and *Manouria*, have a maxillary labial ridge with very small serrations and small irregular denticulations.

2. Among Testudinoidea, some small denticulations may occur in some geoemydids (*Cuora amboinensis*, *Ocadia*, some *Rhinoclemmys* species). However, in these species the denticulate patterns show a considerable regularity, as compared to the Testudinidae, and may be considered as non-homologous.

3. *Batagur*, *Callagur*, *Kachuga*, *Morenia*, and *Hardella* have a maxillary labial ridge with numerous and middle-sized denticulations.

4. *Pseudemys* and *Trachemys* (a few specimens) have a dentary labial ridge with denticulations, but have reduced or absent denticulations on the maxillary ridge.

Homoplasy: Although labial ridge denticulations or serrations are present in several testudinoid lineages, the four different derived conditions are considered as non homologous.

14: Premaxillary midline ridge

Morphology: The premaxillary ridge is an antero-posteriorly directed ridge lying on the triturating surface located at the midline suture between the premaxillary bones.

Primitive condition: The premaxillary ridge is absent in all Testudinoidea except in the Xerobatinae.

Derived condition: The premaxillary ridge is present.

Homoplasy: This character is known only in Xerobatinae (Gaffney & Meylan, 1988) among the Testudinoidea and does not show homoplasy.

15: Central premaxillary cusp

Morphology: The central premaxillary cusp is a small cusp lying at the midline suture of the premaxilla on the middle of the labial ridge.

Primitive condition: Cretaceous and Palaeocene Testudinoidea and Emydidae do not have a central premaxillary cusp.

Derived condition: In the Testudinidae, the central premaxillary cusp is less developed compared to the premaxillary-maxillary pointed cusp in the presumed sister group of Testudininae: e.g. Xerobatinae, *Manouria*. This cusp is more developed in Testudininae.

Homoplasy: The premaxillary central cusp occurs in all Testudinidae and in *Geoemyda*. In *Malacochersus* this cusp is weakly developed.

16. Lingual ridge

Morphology: The triturating surface of the maxilla may present one or two lingual ridges in turtles with or without denticulations. Gaffney (1979) reviewed this structure.

Primitive condition: Many turtle groups do not have lingual ridges. *Mongolemys* from the Late Cretaceous does not present any lingual ridges, but some undescribed skull material from the Paleocene of Mongolia exhibits this character (J. Claude, pers. observation). *Dermatemys*, *Adocus*, and several Chelonioidea (*Chelonia*, *Eretmochelys*) have a well developed lingual ridge. Thus the polarity of this character is controversial. Based on the current assumption, we consider the absence of lingual ridge as the primitive condition for the Testudinoidea.

Derived conditions:

1. *Orlitia*, *Geoclemys*, and *Malayemys* have a triturating surface with a slight and smooth lingual ridge. In *Geoclemys*, the lingual ridge may be very slight or absent.

2. The acquisition of a well defined lingual ridge occurs in the Emydidae (Deirochelyinae with the exception of *Deirochelys*), in the Geoemydidae (independently in the *Batagur* complex, *Ocadia* and *Hieremys*), and in the Testudinidae.

3. An additional lingual ridge is present in the geoemydid *Batagur*, and in some members of the Testudinidae (some species of the *Geochelone* complex)

Homoplasy: Acquisition of a lingual ridge occurs independently in several clades of Testudinoidea. Some Testudininae and *Batagur* have independently evolved an additional lingual ridge (Boulenger, 1889; Hirayama, 1984). Secondary loss of the lingual ridge occurred in Testudinidae (*Kinixys* complex) and in molluscivorous Deirochelyinae.

Discussion: If we consider the absence of lingual ridge as a derived character for testudinoids, we obtain an important homoplasy: independent loss in Testudinidae, in *Melanochelys* complex, in Emydinae, and in Deirochelyinae.

17: Premaxillary crenated notch

Morphology: The premaxilla may be situated in a crenated notch seen in palatine view in some testudinids (see Gaffney, 1979; p. 342, fig. 258, bottom right).

Primitive condition: The premaxillary labial ridge is in continuity with the maxillary labial ridge in most turtles. There is no premaxillary notch in the primitive condition.

Derived condition: The premaxillary notch occurs only in Testudininae with the exception of *Kinixys*, *Chersina*, *Malacochersus*, *Homopus*, and *Psammobates*. This character supports a clade consisting of the *Testudo* complex and the *Geochelone* complex.

Homoplasy: This character is supposed to be not homoplastic.

18: Commisural ridge

Morphology: The commisural ridge is a lingual ridge of the triturating surface situated at or near the premaxillary-maxillary suture.

Primitive condition: In most turtles, the commissural ridge is absent. It is absent in Lindholmemydidae, Geoemydidae, Emydidae, Xerobatinae, the *Testudo* complex, and the *Kinixys* complex.

Derived condition: The derived condition is the presence of a commisural ridge.

Homoplasy: This character occurs only once in the *Geochelone* + *Pyxis* complex. It is supposed to be non homoplastic.

19: Contribution of the palatine to the bony wall of the braincase.

Morphology: The contacts and structures of the palatine are described and figured in Gaffney (1979).

Primitive condition: In most turtles, the contacts of the palatine are restricted to the maxilla and pterygoid. The palatine contributes to the bony wall of the braincase in the Trionychoidea. The palatine contributes to a limited extent to the braincase bony wall, contacting the parietal, in most members of the Testudinoidea. Since at least some of the Trionychoidea are considered as the sister group of Testudinoidea (Gaffney, 1996; Hirayama *et al.*, 2000), a contribution of the palatine to the bony wall of the braincase and contact to the parietal is interpreted as the primitive condition for Testudinoidea.

Derived condition: The palatine does not contact the parietal and does not contribute to the lateral wall of the braincase in some testudinids and some geoemydids.

Homoplasy: The palatine contact is restricted to the pterygoid and maxilla in members of the *Testudo* complex (*Indotestudo* + *Testudo*), in *Kinixys*, and in some geoemydids.

3.2.2. Axial skeleton

20: Eighth cervical vertebrae central articulations

Morphology: The cervical central articulations of living turtles are reviewed and figured in Williams (1950), and Hoffsteter and Gasc (1969). These vertebrae may be opisthocoelous, amphicoelous, procoelous or biconvex. The eighth cervical vertebra may be amphicoelous, procoelous or biconvex. The articulation of this vertebra with the seventh cervical may be simple or double.

Primitive condition: The primitive condition for turtles, as seen in *Proganochelys*, *Kayentachelys*, and *Kallokibotion*, is an amphicoelous eighth vertebral centrum and a simple articulation between the eighth and seventh vertebrae. The eihgth cervical is biconvex in Testudinoidea, *Sinemys*, *Dracochelys*, *Ordosemys*, *Baptemys*, *Platysternon* and *Carettochelys*. The articulation with the seventh vertebra is single in most cryptodiran turtles and is double in the Testudinoidea, Trionychoidea, Cheloniidae, and *Platysternon* (Gaffney, 1996; Brinkman & Wu, 1999).

Derived condition: All testudinoids have a biconvex eighth vertebra with a double articulation for the seventh vertebra. The association of these two character states is supposed to be one of the synapomorphies of the Testudinoidea (Hirayama *et al.*, 2000). However *Platysternon*, *Carettochelys*, *Baptemys*, and *Zangerlia* have acquired this derived pattern too (Williams, 1950; Brinkman & Wu, 1999).

3.2.3. Appendicular skeleton

21: Iliac bone

Morphology: Pelvic girdles of recent turtles are figured and described in Zug (1971), Walker (1973) and Yasukawa *et al.* (2001).

Primitive condition: The iliac blade is straight with a single origin for the ilio-tibialis muscle in most cryptodiran turtles except testudinoids.

Derived condition: Testudinoidea have an iliac blade with a double attachment for the ilio-tibialis. This condition is present in fossil genera such as *Mongolemys* and *Stylemys* (Hirayama, pers. communication).

Homoplasy: Modern testudinoids are the only known crytpodiran taxon to exhibit this character state. It is considered as a synapomorphic feature of Testudinoidea (Gaffney & Meylan, 1988).

Discussion: Gaffney & Meylan (1988) discussed the validity of this character.

22: Antero-laterally flared iliac blade (Yasukawa *et al.*, 2001)

Morphology: see character 22.

Primitive condition: In most turtles the iliac blade is not flared anterolaterally

Derived condition: This character state was supposed to be an exclusive apomorphic condition for Geoemydidae (Yasukawa *et al.*, 2001), but a similar condition appears in at least some species of *Terrapene* (eg. *T. carolina*). In most Emydidae and Testudinidae, the iliac blade is curved laterally but does not show an anterolateral flaring.

Homoplasy: This character appears independently in Geoemydidae and in some *Terrapene*.

23: Trochanters of the femur (Auffenberg, 1974)

Morphology: The morphology of femur and posterior limb muscle attachments are discussed in Walker (1973). Auffenberg (1974) gives a description of the shape of trochanters of the femur in the Testudinidae.

Primitive condition: The femoral trochanters are not coalesced in most turtles and other Reptilia, which is the primitive condition

Derived condition: The trochanters of the femur are coalesced.

Homoplasy: Among the Testudinoidea, the trochanters of the femur are coalesced in all Testudinidae. This character occurs also in two species of *Terrapene*. A similar pattern is found in *Peishanemys*. This character is known also in sea turtles (Chelonioidea).

Discussion: Coalesced trochanters of the femur occurred three times in terrestrial turtles and also in marine turtles. Whether this fusion of trochanters may be adaptive to both marine or terrestrial life, the origin of this fusion seems to have a different development and functional causes in terrestrial species as compared to marine species. Contrary to marine turtles, the two trochanters are of about the same size and the trochanter major does not extend beyond or proximally to the end of the head of the femur in terrestrial species (Walker, 1973).

3.2.4. Shell

24: Fusion of the 12th Marginal scutes (caudal scute)

Morphology: Most Turtles have 12 pairs of marginal scutes.

Primitive condition: The presence of twelve pairs of marginal scutes is the primitive condition for Testudinoidea.

Derived condition: The fusion of the twelfth marginal scute, forming the single caudal scute, is considered as the derived condition.

Homoplasy: In all testudinids, except *Achilemys*, *Hadrianus*, *Manouria*, *Stylemys*, and *Pyxis*, the twelfth pair of marginal scutes is at least partially fused. The condition of *Pyxis* is regarded as reversed.

25: Contact between the third pleural and the sixth marginal scutes (Hirayama, 1984)

Morphology: Among turtles, the third pleural scute usually reaches the seventh, eighth and sometimes the ninth marginal scutes.

Primitive condition: In Trionychoidea, and Palaeocene and Cretaceous Testudinoidea (lindholmemydids), the sixth marginal scute contacts only the second pleural scute.

Derived condition: In some Testudinoidea, the sixth marginal scute reaches the third pleural scute to a relatively large extent.

Homoplasy: The contact between the sixth marginal scute and the third pleural scute occurs by convergence in the *Batagur* complex, and in all testudinids with the exceptions of *Achilemys*, *Manouria*, *Hadrianus*, *Testudo*, *Indotestudo*, and *Kinixys*. For these three latter genera, the condition is apparently reversed.

26: Contact between the second pleural and fourth marginal scutes (Hirayama, 1984)

Morphology: The second pleural in turtles usually contacts the fifth and sixth marginal scutes, and sometimes the seventh or the fourth.

Primitive condition: In most Testudinoidea, Dermatemydidae, and Kinosternidae, the fourth marginal scute contact is restricted to the first pleural scute.

Derived condition: The fourth marginal scute has a relatively important contact with the second pleural scute in three groups: the *Batagur* complex among Geoemydidae and Xerobatinae and *Geochelone elegans* among the Testudinidae.

Homoplasy: This character is considered to have occurred at least three times among the Testudinoidea.

27: Neural series

Morphology: Neural plates are above the thoracic vertebrae in turtles. The number of neural plates is variable among turtle families (Pritchard, 1988).

Primitive condition: A complete neural serie is usually interpreted as the primitive condition for turtles. However, in *Dermatemys*, some Chelonioidea, some Kinosternidae, some Xinjiangchelyidae, and an Early Cretaceous testudinoid and trionychoid from Japan (Hirayama *et al.*, 2000) the neural series is incomplete with the seventh and eighth costals having a midline contact.

Derived condition: Most Testudinoidea have a complete neural series formed by eight neural bones, reaching the suprapygal bones. As both the presumed sister group of Testudinoidea (Kinosternidae and Dermatemydidae) and the first occurrences of Testudinoidea exhibit incomplete neural series, the complete neural series of most Testudinoidea is interpreted as a derived condition.

Homoplasy: Some advanced Testudinoidea (*Morenia*, some hinged forms (*Terrapene*, *Cuora*)) exhibit an incomplete neural series, which may be interpreted as a reversion.

Discussion: Our assumption about the polarity of this character may appear not obvious since a complete neural series is generally considered as the primitive state for turtles. However, numerous possible outgroups and the Cretaceous testudinoid from Japan exhibit an incomplete neural series which can support our assumption. An alternative scenario would be that the configuration observed in the specimen from Japan is autapomorphic.

28: Neural patterns

Morphology: Neural patterns and variations among living turtles have been reviewed in Pritchard (1988).

Primitive condition: Most turtles have neural plates with short antero-lateral sides. This condition is found in Emydidae and in all the Cretaceous and Palaeocene Testudinoidea.

Derived conditions: Several neural morphologies evolved from the primitive pattern: alternating octagonal and quadrangular neurals, or neurals with short postero-lateral sides.

1. Neurals with short postero-lateral sides appeared first in the Early to Middle Eocene in both Geoemydidae (*Geoemyda saxonica* and *Geoemyda ptychogasteroides*; Hummel, 1935) and Testudinidae (*Hadrianus, Achilemys*).
2. A clearly alternating pattern of octogonal and quadrangular neurals occurred in a clade of Testudinidae composed of *Testudo*, *Indotestudo* and *Geochelone* (*s.l.*).

   Alternating octagonal and quadrangular neurals are reported from the Late Eocene (e.g. *Cheirogaster maurini* from Europe (Broin, 1977) and *Geochelone ammon* from Africa (Andrews, 1906)

Homoplasy: Among testudinoids only geoemydids and testudinids evolved distinct neural patterns from the primitive condition. However, in both groups, the neural shape presents an important variability across species (Pritchard, 1988). The phylogenetic analyses of McCord *et al.* (2000) and Spinks *et al.* (2004) support the hypothesis that short postero-lateral side neurals evolved several times in geoemydids. We interpret the important interspecific variability of neural shape as a shared evolutionary process of both Testudinidae and Geoemydidae (presumably some kind of relaxation of a developmental constraint).

29: Costal pattern (Auffenberg, 1974)

Morphology: Eight costal bones form the carapace in most turtle species. They fuse with thoracic ribs and have an origin in the carapacial ridge (Burke, 1989).

Primitive condition: Most turtles have rectangular costal plates with the length of the lateral end equal to that of the medial end. This condition is found in emydids, Cretaceous and Palaeocene testudinoids, and in geoemydids.

Derived condition: Testudinids evolved a distinct alternative costal pattern consisting of odd costals with short distal end and long medial end, and even costals with long distal end and short medial end. In the Testudinoidea, the derived condition occurs for the first time during the Early Eocene in *Achilemys* and *Hadrianus*.

Homoplasy: This character is supposed to be unique among Testudinoidea. However in *Peishanemys*, *Anhuichelys*, and Nanhsiungchelyidae a similar alternative pattern is reached by convergent evolution. In nanhsiungchelyids this pattern is clearly different, since odd costals have a long distal end and a short medial end.

30: Width of vertebral scutes

Morphology: The shape and position of vertebral scutes have been discussed in Zangerl (1969).

Primitive condition: Early turtles, *Proganochelys*, Pleurosternidae, Baenidae, *Kallokiboton*, Plesiochelyidae, have wide vertebral scutes. However the sister group of Testudinoidea (Trionychoidea) has longer than wide vertebral scutes. All Cretaceous to Early Eocene Testudinoidea (except the undescribed specimen from the early Cretaceous of Japan ; Hirayama *et al.*, 2000) have longer than wide vertebral scutes, which we consider as the primitive condition for Testudinoidea.

Derived condition: The derived condition for Testudinoidea is wide vertebral scutes. Wide vertebral scutes among Testudinoidea appear in the Early Eocene (e.g. *Echmatemys pusilla*).

Homoplasy: Among Testudinoidea, vertebral scutes that are wider than long are present in the three modern families. This acquisition is supposed to be independent occurrences since most Lindholmemydidae, early Testudinidae(e.g. *Achi-lemys)*, and early Geoemydidae (*e.g. Palaeoemys*) exhibited longer than wide vertebral scutes.

Discussion: Among Geoemydidae, several living taxa have elongated vertebral scutes: *Kachuga*, *Callagur*, *Hardella*, *Malayemys*, *Palaeoemys*, *Orlitia*, *Morenia*, and *Siebenrockiella*. The width of vertebral scutes shows a considerable variation during ontogeny, juvenile turtles exhibiting wider vertebral horny shields.

31: Shape of the pygal bone

Morphology: The pygal is the most posterior peripheral bone.

Primitive condition: A long and relatively wide pygal plate crossed completely by the posterior sulcus of the fifth vertebral scute, as seen in most primitive testudinoids from the Cretaceous to the Palaeocene and also in the Emydidae. This is considered as the primitive condition for the Testudinoidea.

Derived condition: The pygal plate is small and wider than long in the Geoemydidae and *Achilemys*. A short pygal is found as early as the early Eocene in *Echmatemys* (North America) and *Palaeoemys* (Europe).

Homoplasy: A short, and wider than long pygal is observed in *Achilemys* supporting the common ancestry of Geoemydidae and Testudinidae. Testudinids other than *Achilemys* exhibit a pygal plate that is as long as wide, which may be considered as a reversion. However the Testudinidae are distinct from the Lindholmemydidae and the Emydidae in having a pygal plate not intersected by the posterior sulcus of the fifth vertebral scute.

The character state of Testudinidae is considered as non homologous to the plesiomorphic condition.

32: Lateral keels

Morphology: The turtle shell may present no keel, one medial keel or one medial keel plus two lateral keels. The shape, position, and extent of keels is variable among species.

Primitive condition: Within the Testudinoidea, the Lindholemydidae, Emydidae, and Geoemydidae have one central keel at least in juveniles. Only certain geoemydids have a three-keeled carapace, at least in juveniles. The primitive condition is considered to be the presence of a central keel, at least in juveniles.

Derived conditions:

1. Testudinidae have no medial or lateral keels, even in juveniles.

2. Most geoemydids, except the two American genera *Rhinoclemmys* and *Echmatemys,* have three keels at least in juveniles.

2bis. *Palaeoemys*, *Geoclemys*, *Malayemys* have three distinct keels on the carapace with lateral keels situated near the vertebral scutes. This case is a special case of character 2, that is why we refer it to 2bis.

Homoplasy: Lateral keels are absent in *Orlitia*, in the *Batagur* complex, in *Sacalia*, *Cuora galbinifrons*, which might be interpreted as a reversal, but we have not seen very young individuals for these species.

Discussion: The presence of keels is strongly related to ontogeny. Old individuals tend to have weaker keels or to loose them. Then the presence or absence of this character is mostly based on the observation of juvenile and small individuals, when observations on adults are not obvious. In the Testudinoidea, carapaces with three keels are known since the Early Eocene of Europe (*Palaeoemys*) and unpublished material of a new taxon from the early Eocene of France (Hervet, 2003b).

33: Cervical scute

Morphology: The cervical scute is a small unpaired scute lying on the midline of the anterior edge of the nuchal plate.

Primitive condition: The cervical scute is present in most cryptodiran turtles. It is square in Trionychoidea with dermal scutes, and Chelydridae; and wider than long or square in Chelonioidea. The primitive condition is the presence of a square cervical scute.

Derived conditions:

1. The cervical scute may be absent in some Testudinidae.

2. The cervical scute may be antero-posteriorly elongated and narrow in some Emydidae, Testudinidae, and Geoemydidae.

Homoplasy:

The cervical scute is absent in two independent clades among Testudinidae: some *Kinixys*, and in *Chelonoidis* + *Geochelone*.

The cervical is much longer than wide in several extant taxa of modern Testudinoidea : Deirochelyinae (but not *Graptemys* and *Malaclemys*), some *Terrapene* (Emydinae), *Cuora*, *Cistoclemmys* (Geoemydidae), and most Testudininae.

34: Inguinal buttress

Morphology: Inguinal buttress is formed by the hypoplastron and sutures the plastron to the carapace. The inguinal buttress is developed dorsally and reaches the costal plates in Testudinoidea. We separate the inguinal buttress and the axillary one, since the distribution of character states is different for the posterior and anterior buttresses.

Primitive condition: The inguinal buttress does not reach the costal plate in *Proganochelys* and most cryptodiran turtles.

Derived condition: All testudinoids, except hinged forms, have a dorsally developed inguinal buttresses meeting the costal plates.

Homoplasy: The inguinal buttress is developed dorsally and reaches the costal plates several times in turtle evolution: in Testudinoidea, in Pleurosternidae, in Plesiochelyidae, in Bothremydidae, and in Baenidae (Gaffney & Meylan, 1988; Gaffney, 1996; Hirayama *et al.*, 2000). In Testudinoidea, the inguinal buttress is reduced in the species with hinged plastron, which is considered as a reversed condition.

35: Contact between inguinal buttress and costal plates

Morphology: See character 34. When present, the contact of the inguinal buttress with costal plates may concern both fifth and sixth costal plates or be restricted to the fifth one.

Primitive condition: Within cryptodiran turtles, only the Testudinoidea, Baenidae, some Plesiochelyidae, and Pleurosternidae have strong plastral buttresses contacting the costal plates. In the Pleurosternidae, Baenidae, and Cretaceous to Palaeocene Testudinoidea, the inguinal buttress contacts the fifth and sixth costal plates, which is considered as the primitive condition.

Derived condition: The costal-inguinal buttress contact, when present, is restricted to the fifth costal plate.

Homoplasy: The restriction of the inguinal buttress to the fifth costal plate occurred several times in the Testudinoidea: in the Emydidae and in several clades of the Geoemydidae (e.g. *Rhinoclemmys*, *Geoemyda*, *Heosemys*, *Mauremys*).

Discussion: The condition of *Ocadia* and some *Mauremys* (e.g. *Mauremys mutica*), is primitive, however, following a recent molecular phylogeny (McCord *et al.*, 2000), this group evolved from a group with a contact limited to the fifth costal plate. We interpreted the condition of *Ocadia* and some *Mauremys* as a reversal.

36: Musk duct foramina (Hirayama, 1984; Yasukawa *et al.*, 2001)

Morphology: the morphology of musk duct foramina in geoemydids is reviewed in detail in Yasukawa *et al.* (2001).

Primitive condition: Discrete and well defined musk duct foramina penetrating in the thoracic cavity (behind axillary buttress and beside inguinal buttress) are absent in Trionychoidea, Chelydridae, in Cretaceous and Palaeocene Testudinoidea (except maybe *Tsaotemys* (Ckhikvadze, 1987)), in Emydidae, and in Testudinidae.

Derived condition: Axillary and inguinal musk duct foramina penetrating the thoracic chamber are present only in Geoemydidae with the exception of *Morenia* (Yasukawa *et al.*, 2001). This character occurred at least first in the Early Eocene (*Palaeoemys* and *Echmatemys*).

Homoplasy: The condition of *Morenia* is interpreted as a reversion. In geoemydid box turtles, the foramina are absent, but a canal is visible on the visceral side of peripheral plates, which is interpreted as homologous to the musk duct foramina structure of Geoemydidae. Musk duct foramina are also present in other turtle families (Gaffney and Meylan, 1988), but they are quite different from the condition found in geoemydids in their position and definition (see Yakusawa *et al.*, 2001).

37: Loss of extragular scutes (Hutchison & Bramble, 1981)

Morphology: Hutchison & Bramble (1981) discussed the shape and the homology of plastral scutes. They propose seven pairs of plastral scutes for ancestral types. This pattern is found in *Kayentachelys*, Pleurosternidae, Adocidae, Plesiochelyidae, Baenidae and Meiolaniidae. All Testudinoidea, except the Early Cretaceous testudinoid from Japan (Hirayama *et al.*, 2000), exhibit six pairs of plastral scutes (gulars, humerals, pectorals, abdominals, femorals, anals) and have lost the extragular scutes (the “second scute” in the nomenclature of Hutchison & Bramble (1981).

Primitive condition: The primitive condition for Testudinoidea is seven pairs of plastral scutes, as seen in the undescribed Testudinoidea (Lindholmemydidae) from the Early Cretaceous of Japan (Hirayama *et al.*, 2000).

Derived condition: The derived condition is the loss of the extragular scutes.

Homoplasy: This character is supposed to be not homoplastic among Testudinoidea. However, some Chelydridae (*Platysternon*) and some Macrobaenidae (e.g. *Hangaiemys*) present the same plastral scute composition as Testudinoidea, which may be considered as a convergence.

38: Inframarginal scutes and development of contacts between plastral scutes and marginal scutes (Gaffney & Meylan, 1988)

Morphology: Inframarginal scutes occurred in most cryptodiran turtles and are located at or near the suture between the plastron and the carapace. They prevent the plastral scutes from contacting the marginal scutes of the bridge. Their number is variable among cryptodiran families.

Primitive condition: The primitive condition is the presence of a well developed row of inframarginal scutes preventing plastral scutes from contacting marginal scutes.

Derived conditions:

1. The inframarginal scutes are reduced, and short contacts between plastral scutes and marginal scutes may occur. The Late Cretaceous taxa *Lindholmemys* has three inframarginal scutes and a contact between marginal and plastral scutes, which is considered as an intermediate condition between most Cretaceous and Palaeocene Lindholmemydidae and modern families of Testudinoidea.
2. The inframarginal scutes are much more reduced and the contact between plastral and marginal scutes is longer than in *Lindholmemys*. The Paleocene taxa *Pseudochrysemys* has three inframarginal scutes and rather long contacts between marginal and plastral scutes, which is considered as an intermediate condition between *Lindholmemys* and modern families of Testudinoidea.
3. All known post-Palaeocene Testudinoidea lack inframarginal scutes, and have a broad contact between plastral scutes and marginal scutes which is considered as the more derived condition.

Homoplasy: This character is considered as not homoplastic among Testudinoidea.

39: Elongated gular scute

Morphology: The gular scute corresponds to the plastral scute 1 of Hutchison & Bramble (1981).

Primitive condition: With few exceptions (*Pseudochrysemys* and *Gravemys barsboldi)*, most Cretaceous and Palaeocene Testudinoidea have a short gular scute, reaching barely or not at all the entoplastron. The gulo-humeral sulcus is parallel to the humero-pectoral sulcus.

Derived condition: The midline sulcus of gular scutes is long and clearly overlaps the entoplastron, and the humero-pectoral sulcus and the gulo-humeral sulcus are no longer parallel.

Homoplasy: In several groups of modern testudinoids, the gulo-humeral sulcus becomes oblique and is no longer parallel to the humero-pectoral sulcus. The Emydidae, Testudinidae, and some Geoemydidae may have independently evolved this pattern (*Geoclemys*, *Echmatemys* + *Rhinoclemmys*, *Melanochelys* complex).

40: Epiplastral lip

Morphology: The gular scutes may extend backward on the visceral surface of the epiplastron and produce an epiplastral lip. Below this horny shield the epiplastra may be swollen or even produce a posterior excavation (epiplastral excavation).

Primitive condition: The epiplastral lip is weak or reduced in most cryptodiran turtles, and in Cretaceous Testudinoidea.

Derived conditions:

1. Among crytpodirans, an elongated epiplastral lip is a unique feature observed in many Testudinoidea, especially in modern families. It appears first in species which may belong to Lindholmemydidae: *Pseudochrysemys gobiensis* and probably *Elkemys* from the Palaeocene of Asia (Chkhikvadze, 1987).
2. An epiplastral excavation occurs only in some Testudinidae. The first appearance of this feature is attested from the Late Eocene (*Cheirogaster* (Broin, 1977), *Geochelone ammon* (Andrews, 1906)). This character state is thought to have evolved from an elongated epiplastral lip which allows a swelling in this region. Epiplastral excavation, therefore, should be considered as a more derived condition.

Homoplasy:

1. A long epiplastral lip may have evolved twice or thrice in each of the three families: Testudinidae, Geoemydidae, and Emydidae.
2. The epiplastral excavation is absent in some small Testudinidae (*Homopus*, *Testudo hermannii*) and in insular giant species (*Chelonoidis nigra* and *Aldabrachelys elephantopus*), which is considered as a reversal (Gaffney & Meylan, 1988).

Discussion: Among the Geoemydidae, only the *Batagur* complex + the *Malayemys* complex + *Palaeoemys* and *Orlitia*, have a small or absent epiplastral lip which may be considered as primitive. *Achilemys* is interpreted as the most primitive Testudinidae for this feature since it exhibits a long epiplastral lip without either swelling or excavation. This character can show some intraspecific variation, but we consider that our categories are far above the level of intraspecific variability.

41: Position of the humero-pectoral sulcus relative to entoplastron

Morphology: The humero-pectoral sulcus corresponds to the contact of the pectoral and humeral scutes.

Primitive condition: The humero-pectoral sulcus does not cross the entoplastron in some Dermatemydidae, Plesiochelyidae, Baenidae, Pleurosternidae, Chelonioidea, and Cretaceous to Palaeocene Testudinoidea. This is considered as the primitive condition for Testudinoidea.

Derived condition: The humero-pectoral sulcus crosses the entoplastron. Among the Testudinoidea, this character appears first in the Geoemydidae *Echmatemys* from the Early Eocene of North America (Hay, 1908).

Homoplasy: The derived condition appears independently in some Geoemydidae, in some Emydidae, and in one Lindholmemydidae (*Elkemys*) (Ckhikvadze, 1987). *Geoemyda sylvatica* is variable for this character. In *Malayemys*, *Orlitia* and *Geoclemys*, the humero-pectoral sulcus is just behind the entoplastron, and can reach it barely in some specimens.

42: Shape of the anterior plastral lobe

Morphology: The anterior plastral lobe, formed by epiplastron, entoplastron and the anterior part of the hyoplastrons is variable in shape among cryptodiran turtles. Its anterior margin may be straight (and then have a truncated appearance) or rounded.

Primitive condition: Most Cretaceous Testudinoidea and some Adocidae have a truncated anterior plastral lobe. This condition is considered to be the primitive condition for Testudinoidea.

Derived condition: the anterior plastral lobe is relatively rounded in shape. The first appearance of this condition is attested with the genus *Elkemys* from the Palaeocene of Asia (Ckhikvadze, 1987).

Homoplasy: The anterior plastral lobe became rounded independently in Emydidae, Geoemydidae, Lindholmemydidae, and Testudinidae.

43: Epiplastral projections

Morphology: The anterior lobe of the plastron may present one or two forward projections produced by the epiplastron in some Testudinidae.

Primitive condition: Most turtles lack the epiplastral forward projection, which is considered as the primitive condition.

Derived condition: Epiplastral forward projections appear in some Testudinidae. This character is especially evident in large Testudinidae.

Homoplasy: Among Testudinoidea, Testudinidae are the only group having evolved epiplastral projections. Epiplastral projections are relatively short in small species but more developed in large species such as *Geochelone sulcata* or *Astrochelys*. These projections were acquired independently in the trionychoid genus *Basilemys*.

Discussion: The development of epiplastral projections is related to size and is subject to sexual dimorphism (male with longer epiplastral projections).

3.2.5. Chromosome data

44: Number of chromosomes (Bickham, 1981; Bickham and Carr, 1983).

Morphology: Bickham (1981) and Bickham and Carr (1983) have commented the morphology and number of chromosomes among cryptodiran turtles. The number of chromosomes of Testudinoidea is the lowest among cryptodirans and is constant within each clade. Among Testudinoidea, Emydidae have 50 chromosomes, and Geoemydidae + Testudinidae have 52 chromosomes (with the exception of some *Rhinoclemmys* species having 56 chromosomes).

Primitive condition: Other cryptodiran turtles have more chromosomes. Thus, the primitive condition is likely at least 54 or 56 chromosomes, the karyotypic formula found in Kinosternidae.

Derived conditions: The number of chromosomes decreased to 52 chromosomes in Testudinoidea as seen in Testudinidae and Geoemydidae and to 50 chromosomes in Emydidae.

Homoplasy: Chelydridae (*Chelydra* and *Macroclemmys*) have 52 chromosomes but this arrangement is obviously convergent, since the numbers of macrochromosomes and microchromosomes is different from Testudinoidea.

Discussion: The 56 chromosomes of *Rhinoclemmys punctularia* and the chromosomic arrangement of *Rhinoclemmys funerea* may be considered as derived conditions from the ancestral condition of the Geoemydidae because of the distribution of macrochromosomes and microchromosomes in these species (see Bickham and Carr, 1983; Hirayama, 1984). Geoemydidae and Testudinidae differ from Emydidae by one less metacentric to submetacentric macrochromosome.

3.3. Phylogenetic Relationships within Testudinoidea

The phylogenetic relationships of Testudinoidea proposed here are based on molecular data, palaeobiogeographical arguments, and morphological features (fig. 4). The morphological apomorphies are given for each clade.

Basic taxa

Unnamed Testudinoidea from the Neocomian of Japan

Hirayama *et al.* (2000) described a testudinoid shell from the Neocomian of Japan, and referred it to Lindholmemydidae. This specimen is the oldest known testudinoid. This is mostly evidenced by the contact between inguinal buttress and costal plates, and the presence of an anal notch. The reconstruction (Hirayama *et al.*, 2000, fig.11) shows extragular scutes, a plesiomorphic feature for the group. It also exhibits an incomplete neural series, that we interpret as primitive for the Testudinoidea. Compared to other lindholmemydids, unusual features such as wide vertebral scutes are present. Hirayama *et al.* (2000) interpret the latter character as plesiomorphic for Lindholmemydidae, but we interpret it as derived for modern testudinoids, since most of their stem groups exhibit narrow vertebral scutes.

Non exclusive autapomorphy within Testudinoidea: character 30.

Lindholmemys (Riabinin, 1935)

Lindholmemys is a Late Cretaceous (Cenomanian-Santonian) Asiatic genus of the Testudinoidea. This genus is characterized by narrow inframarginal scutes and a small contact between plastral scutes and marginal scutes. Several species have been attributed to this genus (*L. elegans*, *L. gravis*, *L. martisoni*). The latter species, *L. martisoni*, has been assigned to a new genus, *Hongilemys* (Sukhanov, 2000). However *Hongilemys* (Sukhanov, 2000), is similar to *Lindholmemys* for the character states analysed in our study (character 24 to 44). We consider that these two genera constitute a monophyletic group.

Mongolemys (Khozatskii and Mlynarski, 1971)

Mongolemys is an Asiatic genus of testudinoids known from the Late Cretaceous to the Palaeocene of Asia. Several species have been attributed to this genus (*M. occidentalis*, *M. elegans*, *M. tatarinovi*, *M. reshetovi*, *M. turfanensis*, *M. barsboldi*, *M. australis*). The two latter ones have been attributed to two distinct genera, *Gravemys* and *Elkemys*, of uncertain affinities (Sukhanov & Narmandakh, 1976; Sukhanov & Narmandakh, 1983, see also Danilov, 2003 for a revision of *Gravemys*). *Mongolemys* is known and figured by a complete skull from the Late Cretaceous (Sukhanov, 2000).

Hokouchelys from the Palaeocene of China (Yeh, 1974; Sun *et al.*, 1992) presents important similarities with *Mongolemys* and probably belongs to the same clade.

Pseudochrysemys gobiensis
(Sukhanov et Narmandakh, 1976)

Pseudochrysemys is a Palaeocene Asiatic genus of the Testudinoidea. It is characterised by narrow inframarginal scutes and a longer contact between plastral and marginal scutes than in *Lindholmemys*. No character allows it to be included in the Emydidae as was suggested by some authors (Sukhanov & Narmandakh, 1976; Chkhikvadze, 1987). It is a Lindholmemydidae, mainly because it retains three inframarginal scutes and a contact between the inguinal buttress and the 5th and 6th costal plates.

However, it shows a rather developed epiplastral lip, a derived and unusual feature among Palaeocene and Mesozoic Testudinoidea (Sukhanov et Narmandakh, 1976).

Subfamily Deirochelyinae (Agassiz, 1857)

Deirochelyinae is a subfamily of Emydidae. Molecular and morphological characters (Gaffney & Meylan, 1988; Bickham *et al.*, 1996 ; Stephens & Wiens, 2003) attest the monophyly of this group. The first Deirochelyinae are reported from the Late Eocene of North America (Clark, 1937).

Non exclusive autapomorphies within Testudinoidea: characters 4, 10, 16(2) (for the latter character *Deirochelys* and molluscivorous species are exceptions, we consider *Deirochelys* as a primitive member of the group and molluscivorous species to have acquired secondary adaptations and the disappearance of the lingual ridge).

Subfamily Emydinae (Rafinesque, 1815)

Emydinae is a subfamily of Emydidae. Molecular and morphological characters attest the monophyly of this group (Gaffney & Meylan, 1988; Bickham *et al.*, 1996; Lenk *et al.*, 1999; Feldman & Parham, 2002 ; Stephens & Wiens, 2003). The first Emydinae are reported from the Miocene of North America (Hutchison, 1981; Holman, 1987; Holman & Fritz, 2001). Non exclusive autapomorphies within Testudinoidea: characters 5 and 16.

Achilemys (Hay, 1908)

Achilemys is a genus represented by two species from the Eocene of Europe and North America (see above).

Manouria (Gray, 1854)

Manouria is an extant genus of testudinids from South Asia consisting of two species. Some authors have referred the fossil genus *Hadrianus* to *Manouria* because of their morphological similarity (Auffenberg, 1974). Although *Manouria* is an extant Asiatic genus, *Hadrianus* is known from the Early Eocene of both Europe and North America (Hutchison, 1998; Lapparent de Broin, 2001).

Subfamily Xerobatinae (Gray, 1873)

The Xerobatinae is a subfamily of Testudinidae containing the genera *Gopherus (s.l.)*, and *Stylemys*. Monophyly of the Xerobatinae is attested by molecular and morphological data (Crumly, 1984; Gaffney & Meylan, 1988; Lamb & Lydeard, 1994; Spinks *et al.*, 2004). However, a molecular study (Lamb & Lydeard, 1994) is in disagreement with others on the monophyly of Xerobatinae + *Manouria* + *Hadrianus*.

Gopherus and *Stylemys* share the presence of a premaxillary ridge, a feature unique among Testudinoidea, which we consider as a good support for the monophyly of Xerobatinae. (see Meylan & Sterrer (2000) for an alternative interpretation of *Stylemys*).

Exclusive autapomorphy: character 14.

Non exclusive autapomorphy: character 26.

Testudo complex: *Testudo*, *Indotestudo*

This complex belongs to the subfamily Testudininae, the monophyly of *Testudo* and *Indotestudo* has recently been attested by molecular phylogenetics (Van der Kuyl *et al.*, 2002).

Morphologically, *Indotestudo* and *Testudo* share at least two apomorphic features: the palatine bone does not contribute to the parietal wall (convergent in *Kinixys*), and small caroticopharyngeal foramina are present on the pterygoid bones (convergent in *Pyxis*).

Non exclusive synapomorphies within Testudinoidea: characters 4 and 19.

Geochelone complex: *Geochelone* (*s.l.*), *Pyxis*

Geochelone and *Pyxis* are considered as a monophyletic group as shown by the molecular study of Caccone *et al.* (1999).

This interpretation is new and refutes morphological studies (Crumly, 1984; Gaffney & Meylan, 1988; Meylan & Sterrer, 2000). First fossil occurrence for this group may be Late Eocene with *Cheirogaster* (absence of cervical scute, and presence of an epiplastral excavation) (Broin, 1977).

Exclusive synapomorphy within Testudinoidea: character 18.

Kinixys complex: *Kinixys*, *Chersina*, *Homopus*, *Psammobates*

This clade was never studied by molecular sequence analysis. However, this clade is supported by at least three derived features for Testudininae:

1: premaxillary central cusp developed as compared to lateral cusps situated at the suture between maxilla and premaxilla (convergent in *T. horsfieldi* and *Pyxis*).

2: reduction of maxillary process.

3: secondary loss of the lingual ridge on the maxillary triturating surface (reversed in *Chersina* and *Malacochersus*, convergent in *Pyxis*). Although the phylogenetic hypothesis of Meylan & Sterrer (2000) is more parsimonious (in considering *Pyxis* within this clade), we follow the well supported analysis of Caccone *et al.* (1999).

First fossil occurrence for this group is considered to be Early Miocene (Meylan & Auffenberg, 1987; Lapparent de Broin, 2000).

Non exclusive autapomorphies within Testudinoidea: characters 15 and 16.

Rhinoclemmys (Fitzinger, 1835)

Rhinoclemmys is a Geoemydidae from South and Central America. It was supposed to be paraphyletic (Hirayama, 1984; Yasukawa *et al.*, 2001), although McCord *et al.* (2000) and Spinks *et al.* (2004) consider this genus as a monophyletic clade based on molecular data. Some authors include *Echmatemys p*usilla and E. terrestris within the genus Rhinoclemmys (McDowell, 1964; West & Hutchison, 1981), putting forward the idea of a phylogenetic relationship between *Rhinoclemmys* and *Echmatemys*. Moreover *Rhinoclemmys* and *Echmatemys* are the only known New World Geoemydidae. *Rhinoclemmys* is recorded from the Eocene of North America and the Miocene of Central America (Webb & Perrigo, 1984). It could constitute either a clade or a grade with *Echmatemys* but these two genera are not united by any synapomorphy. They are considered as a basal multichotomy with three keeled Geoemydidae in our phylogenetic scenario.

Non exclusive autapomorphies within Testudinoidea: characters 28(1), 30, 35, and 39.

Echmatemys (Hay, 1906)

Echmatemys is represented by at least 20 species in the Eocene of North America, the status of the genus *Echmatemys* and referred species merits a systematic revision in the future. Following Hirayama (1984), we consider that *Echmatemys* might be a polyphyletic plesion, including both *Echmatemys pussilla* and *Echmatemys terrestris*. *Echmatemys* is known since the Early Eocene (Huchison, 1998).

Batagur complex: *Batagur*, *Callagur*, *Kachuga*, *Morenia*, *Hardella*

The monophyly of this group has been shown by both molecular and morphological studies (Hirayama, 1984; Gaffney & Meylan, 1988; McCord *et al.*, 2000; Spinks *et al.*, 2004). The earliest members of this group are described from the Siwalik Hills of Asia (Miocene to Pliocene) (West *et al.*, 1991). This group has the following synapomorphies: both labial ridges of maxillary and dentary serrated, foramen praepalatinum concealed by secondary palate (Gaffney & Meylan, 1988), and a huge foramen orbito-nasale.

Exclusive autapomorphies within Testudinoidea: characters 5(2) and 13(3).

Non exclusive autapomorphy for this group: character 25.

Orlitia (Gray, 1873)

Orlitia is known from a unique extant South Asiatic species, *Orlitia borneensis*. Its fossil record is unknown. We do not consider *Orlitia* as a sister taxon of *Siebenrockiella* in our scenario. This clade was principally supported by the narrow vertebral plates which is a primitive character for Geoemydidae. The recent molecular phylogenies of Wu *et al.* (1999b) and Spinks *et al.* (2004) do not support the monophyly of the group. This can be supported by a reinterpretation of the morphologies of *Orlitia* and *Siebenrockiella*. Indeed these two species can be distinguished by the differences in the position of the humero-pectoral sulcus, the morphologies of the triturating surface and the relative development of the foramen orbito-nasale and foramen palatinum posterius. These four morphological features are in agreement with the molecular phylogenies, and thus allow to define morphologically a phylogenetic relationship of *Orlitia* with the *Batagur* + *Malayemys* complexes and a phylogenetic relationship of *Siebenrockiella* with the *Melanochelys* complex.

Malayemys complex: *Palaeoemys, Geoclemys, Malayemys, (Borkenia?)*

These three taxa show many similarities (inguinal buttresses, thick bones, position of the humero-pectoral sulcus, developed triturating surfaces…).

The monophyly of this group is supported by the presence of two lateral keels placed near the vertebro-pleural sulcus. This apomorphic feature is unique among Testudinoidea. This group occurred first in the Early Eocene (see above). *Borkenia* probably belongs to this group, considering its resemblance to *Palaeoemys* (see above).

Exclusive autapomorphy within Testudinoidea: character 32(2bis).

Melanochelys complex: *Mauremys*, *Sacalia*, *Cuora*, *Cistoclemmys*, *Notochelys*, *Heosemys*, *Hieremys*, *Cyclemys*, *Leucocephalon*, *Ocadia*, *Chinemys*, *Palaeochelys, Siebenrockiella?*, *Geoemyda?*.

The monophyly of this group remains unclear according to genetic sequences, principally because of the inclusion of *Siebenrockiella* and *Geoemyda* in this clade. It is supported by some studies (McCord *et al.*, 2000) but not by others (Honda *et al.*, 2002b; Spinks *et al.*, 2004). We follow the hypothesis of McCord *et al.*(2000) for the position of *Geoemyda* since it reduces the number of iterative evolution events in neural morphology, and because *Geoemyda* exhibits small orbito-nasale foramina, a derived character state never found in *Orlitia*, *Malayemys*, or *Batagur* group. For the same reason we consider *Siebenrockiella* to belong to this group (following Wu *et al.*, 1999b and McCord *et al.*, 2000), although its position is variable according to other molecular studies (Spinks *et al.*, 2004).

This unique group of Geoemydidae evolved numerous lineages with hinged plastrons (Yasukawa, 2001; Honda *et al.*, 2002) and is composed of species exhibiting very different skull and shell shapes. Phylogenetic hypotheses within this group vary considerably from one author to another, suggesting that homoplasy is rampant in this group (compare for example Hirayama, 1984, McCord *et al.*, 2000, Yasukawa *et al.*, 2001, Honda *et al.*, 2002, Spinks *et al.*, in press).

The oldest species of this group may be “*Geoemyda*” *ptychogasteroides* from the middle Eocene of Germany (Hummel, 1935) or *“Cuvierochelys” parisiensis* from the middle Eocene of France (Botez, 1921; Hervet, 2004a). An unpublished new genus, formerly referred to *Palaeochelys* (Nel *et al.*, 1999) from the Early Eocene of France may be an older member of this family (Hervet, 2003b).

Non exclusive autapomorphies within Testudinoidea: characters 5, 39, 40(1), and 41.

Nodal Taxa (letters refer to the nodes of fig. 4)

A: Super family Testudinoidea Batsh, 1788 (as a stem group)

This taxon is attested by phylogenetic studies on both morphological and molecular data (Hirayama, 1984; Shaffer *et al.*, 1997).

Synapomorphies: characters 20, 21, and 25.

The first known Testudinoidea occurs in the Early Cretaceous of Asia (Hirayama *et al.*, 2000; Sukhanov, 2000)

B: Unamed taxon

Exclusive synapomorphies within Testudinoidea: characters 27 and 37.

The oldest species belonging to this clade, *Khodzhakulemys occidentalis*, is reported from the lower Cenomanian of Asia (Danilov & Sukhanov, 2000).

C: Unamed taxon

Exclusive synapomorphy within Testudinoidea: character 38(1)

The oldest taxon belonging to this clade is *Lindholmemys martinsoni* from the Late Cretaceous (Turonian-Santonian) of Asia (Danilov, 1999; Danilov & Sukhanov, 2001).

D: Unamed taxon

Exclusive synapomorphy within Testudinoidea: character 38(2)

The oldest taxon belonging to this assumed clade is *Pseuchrysemys gobiensis* from the Paleocene of Asia (Sukhanov and Narmandakh, 1976).

E: Testudinoidea (as a crown group) = modern Testudinoidea

The monophyly of modern Testudinoidea is attested by morphological and molecular analyses (Shaffer *et al.*, 1997; Wu *et al.*, 1999b; Honda *et al.*, 2002).

Exclusive synapomorphy within Testudinoidea: character 38(3).

The oldest modern Testudinoidea are known by several species in the Early Eocene (see introduction).

F: Family Emydidae Rafinesque, 1815

The monophyly of this clade is attested by both molecular and morphological data (McDowell, 1964; Bickham *et al.*, 1996; Shaffer *et al.*, 1997; Wu *et al.*, 1999a; Wu *et al.*, 1999b; Honda *et al.*, 2002)

Exclusive synapomorphies within Testudinoidea: characters 1, 2, 3, and 44.

Non exclusive synapomorphies within Testudinoidea: characters 30, 33(2), 35, 39, 40(1), and 42.

The oldest Emydidae are reported from the Eocene (see introduction).

G: Testudinoidae (fide Shaffer *et al.*, 1997)

The monophyly of this group is attested by morphological and molecular studies (Hirayama, 1984; Shaffer *et al.*, 1997; Wu *et al.*, 1999b; Yasukawa *et al.*, 2001; Honda *et al.*, 2002).

Exclusive synapomorphies within Testudinoidea: characters 6, 7, 31, and 44.

Non exclusive synapomorphy within Testudinoidea: character 4.

The oldest Testudinoidae are known from the Early Eocene of Asia, Europe, and North America (see introduction).

H: Testudinidae (Batsch, 1788)

The monophyly of Testudinidae is attested by morphological and molecular data (Auffenberg, 1974; Crumly,1984; Gaffney & Meylan, 1988; Lamb & Lydeard, 1994; Shaffer *et al.*, 1997; Van der Kuyl *et al.*, 2002).

Exlusive synapomorphies within Testudinoidea: characters 8, 9, 11, and 29

Non exclusive synapomorphies within Testudinoidea: characters 5, 10, 15, 23, 28(1&2), 32(1), and 40(1).

The oldest Testudinidae is known from the Early Eocene (see introduction).

I: Unamed Taxon: Testudinidae without *Achilemys*

Non exclusive synapomorphies within Testudinoidea: characters 30, 31, 39, 40 (intermediate state), 42, and 43.

The oldest species of this clade are known with the occurrence of the genus *Hadrianus* from the Early Eocene of Europe, North America, and Asia (Auffenberg, 1974; Broin, 1977; Hutchison, 1998; Lapparent de Broin, 2001)

J: Unamed Taxon: subfamily Testudininae + subfamily Xerobatinae

The monophyly of this taxon is supported by morphological studies (Crumly, 1984; Gaffney, 1988; Meylan & Sterrer, 2000), but not by some molecular phylogenetic works (Lamb & Lydeard, 1994).

Exclusive synapomorphies within Testudinoidea: characters 12 and 24.

Non exclusive synapomorphies within Testudinoidea: characters 13, 16(2), and 25.

The oldest taxa of this clade occurred in the Late Eocene of Europe and Africa with the genera *Cheirogaster* and *Geochelone* (Andrews, 1906; Lapparent de Broin, 2001).

K: Subfamily Testudininae (Batsch, 1788)

This clade is supported by both molecular and morphological studies (Crumly, 1984; Lamb & Lydeard, 1994; Meylan & Sterrer, 2000, Takahashi *et al.*, 2003).

Exclusive synapomorphies within Testudinoidea: character 15, and 40(2).

Non exclusive synapomorphy within Testudinoidea: character 33.

The first Testudininae occurs in Late Eocene (see node H).

L: Unamed Taxon: *Geochelone* complex + *Testudo* complex

Exclusive synapomorphy within Testudinoidea: character 17.

Non exclusive synapomorphy within Testudinoidea: character 28(2).

The oldest fossil of this group is known from the Late Eocene (see node I).

M: Family Geoemydidae (Theobald, 1868)

The monophyly of Geoemydidae is attested by both morphological and molecular studies (Shaffer *et al.*, 1997; McCord *et al.*, 2000; Yasukawa *et al.*, 2001; Honda *et al.*, 2002).

Exclusive synapomorphy within Testudinoidea: character 22.

Non exclusive synapomorphy: character 36.

The oldest Geoemydidae are known from the Early Eocene with the genera *Palaeoemys* in Europe and *Echmatemys* in North America.

N: Three-keeled Geoemydidae

This group is attested by molecular data (McCord *et al.*, 2000 ; Spinks *et al.*, 2004).

Exclusive synapomorphy within Testudinoidea: character 32 (2).

The oldest three-keeled Geoemydidae are known from the Early Eocene of Europe with the genus *Palaeoemys* (see above).

O: *Malayemys* complex + *Batagur* complex + *Orlitia*

This group is monophyletic owing the study of Spinks *et al.* (2004). McCord and co-workers (2000) do not mention the systematic position of *Malayemys* and *Orlitia*, however the molecular study of Wu *et al.* (1999b) suggests that *Malayemys*, *Orlitia*, and *Morenia* (a species from the *Batagur* complex) may be related. The study by Spinks *et al.* (2004) considers *Orlitia*, *Malayemys* and *Geocle-mys* as forming a basal grade in this group.

Non exclusive synapomorphy within Testudinoidea: character 10.

Palaeoemys from the Early Eocene is the oldest species belonging to this clade.

P: *Malayemys* complex + *Orlitia*

Although *Geoclemys* appears near the *Malayemys-Orlitia* group in a recent molecular phylogeny (Spinks *et al.*, 2004), its inclusion in this group is not yet well supported by these molecular data. We consider that the morphological similarity and possible synapomorphies (see below) are strong enough to support a possible inclusion of *Geoclemys* in this group.

Exclusive synapomorphy within Testudinoidea: character 16(1).

This group shares also very thick bony plates, even if the definition of this character is rather subjective.

The oldest known species from this group is *Palaeoemys*.

4. CONCLUSIONS

As the dominant component of the turtle remains from the Early Eocene Saint Papoul locality, the Testudinoidea include two fresh-water geoemydids and a terrestrial testudinid. *Palaeoemys* is the earliest known tricarinate Geoemydidae and is closely related to the *Malayemys* group, an extant assemblage living in Southeast Asia. *Achilemys* is the most primitive representative of the family Testudinidae. The apomorphic features of Testudinidae observed in *Achilemys*, such as the high domed shell, the pattern of costal plates, and the coalesced femoral trochanters, suggest a terrestrial mode of life for this taxon (see Claude *et al.*, 2003a for an appraisal of shell features adaptive to terrestriality in testudinoid turtles).

The study of the Saint Papoul testudinoids brings new insights for understanding the early radiation of the modern Testudinoidea. In our study, the family Lindholmemydidae is considered as a grade rather than a clade. The grade Lindholmemydidae is hitherto recorded exclusively from Asia. *Pseudochrysemys* is supposed to be the sister taxon of all modern Testudinoidea. Since Lindholmemydidae are only known from Asia, the origin of modern Testudinoidea seems to be Asiatic. Consisting of the families Testudinidae, Geoemydidae, and Emydidae, the monophyletic clade of modern Testudinoidea is the most widespread and diverse group, occurring late in the turtle fossil record, in the Early Eocene or just before. No Palaeocene “modern Testudinoidea” have been described with certainty whereas a large number of species of this group are reported as early as the Early Eocene (Hay, 1908; Hutchison, 1998; Lapparent de Broin, 2001). Thus, it seems that the Early Eocene is a key period for a rapid radiation of modern Testudinoidea, although it must be kept in mind that the turtle fossil record from the Palaeocene is still scanty**.**

During the Early Eocene or earlier, Testudinoidea underwent an important radiation, with the appearance of the three modern families: the Geoemydidae, Emydidae, and Testudinidae. By that time, the migrations of turtle faunas between Eurasia and North America had occurred. After these events, several groups evolved independently in North America (*Echmatemys* + *Rhinoclemmys*, Xerobatiinae, Emydidae) and in Eurasia (three-keeled Geoemydidae and Testudininae) (Hutchison, 1998; Lapparent de Broin, 2001). The Emydidae have evolved from the grade Lindholmemydidae and were restricted to North America from the Eocene to today, except *Emys* which migrated to Europe during the Miocene or earlier (Lapparent de Broin, 2001), and *Trachemys*, which spread to South America during the Pleistocene. Nevertheless, the Emydidae seem to radiate later than the two other families and only in

North America. This radiation probably occurred during the Early Miocene, when both Deirochelyinae and Emydinae are recorded (Holman, 1987; Holman & Fritz, 2001), but a few fossils from the Eocene and Oligocene have been attributed to the Emydidae. On the other hand, the Geoemydidae, known from numerous taxa from the Early Eocene to the Late Eocene of North America (Hutchison, 1998; Holroyd *et al.*, 2001), may have been in competition with emydids. This may explain the late radiation of the Emydidae. As attested by molecular, morphological and chromosome data, Geoemydidae form a monophyletic group, mostly Eurasiatic, with the exception of *Rhinoclemmys* and *Echmatemys*, and some forms present in North Africa (e.g. the extant *Mauremys leprosa*, and other related fossils from the Miocene of Abu Dhabi (Lapparent de Broin & Van Dick, 1999)). *Rhinoclemmys* and *Echmatemys* are considered to constitute an American endemic clade or grade that is the sister group or the stem group of three-keeled Geoemydidae. Most of the broad taxonomic diversity of Geoemydidae was already in existence before the end of the Eocene (Claude *et al.*, 2003b, this study). The Testudinidae share a common ancestor with the Geoemydidae and may have originated in Asia. *Achilemys* exhibits the most plesiomorphic features for the testudinids, and its morphology sheds light on the close relationships of the Testudinidae and Geoemydidae. The Testudinidae expanded rapidly for the first time in North America. Probably later, the Testudininae had a radiation in Africa (*Geochelone* complex, *Kinixys* complex) (at least before the end of the Late Eocene (Andrews, 1906; Lapparent de Broin, 2000)), and in South and Central America at least before the end of the Early Oligocene with the genus *Chelonoidis* (Broin, 1991). The arrival of the Testudinidae in Europe is documented later than that of the aquatic Geoemydidae (MP 9-10 for Testudinidae with *Achilemys* from Saint Papoul (Sudre *et al.*, 1992), and MP-7 for aquatic Geoemydidae with *Palaeoemys corroyi* from Palette (Godinot *et al.*, 1987; Biochro'M, 1997)) and a new unpublished genus from the Early Eocene of France (Nel *et al.*, 1999, Hervet, 2003b). This suggests several migrations of testudinoids from Asia or North America to Europe.

Saint Papoul has yielded other aquatic turtles (Carettochelyids, trionychids and podocnemidids). Most of this fauna is unknown from the Cretaceous or Palaeocene of Europe and it is more diversified than at previous periods. The Late Palaeocene Thermal Maximum (LPTM) and the Early Eocene global warming (CGCO) probably resulted in important northward migrations of turtle faunas (Berggren *et al.*, 1998), thus facilitating the passage between Asia, North America and Europe, and enhancing the rapid radiation of the Testudinoidea. This event is probably also correlated with the global turtle faunal turnover (Hutchison, 1998). The ecological conditions that allowed movements between continents during the Early Eocene seem to have played an important role in the early diversification of Testudinoidea since both aquatic and terrestrial species are now known from the Early Eocene of North America and Eurasia.

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