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DISTRIBUTION AND BIOGEOGRAPHY OF NON-MARINE CRETACEOUS TURTLES

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During the Cretaceous, non-marine turtles show strong patterns of provincialism, mirroring the pattern of land masses resulting from the breakup of Pangea since the Jurassic. These patterns are a result of several factors, of which vicariancy and ecological controls on the distribution of groups of turtles are considered the most significant. The large scale patterns, such as the dominance of pleurodires in the southern land masses, including Africa, South America, and India, and the dominance of Cryptodires in the northern land masses cannot be strictly attributed to vicariancy because exceptions to both distributional patterns are present. The pleurodires in Europe and North America during the Late Cretaceous may reflect the removal of the barriers that prevented the terrestrial faunal interchange between the northern and southern continents. Two groups of cryptodires that occurred in the southern continents during the Cretaceous, the Meiolaniidae and *Otwayemys*, seem to reflect a widespread distribution of the very primitive cryptodires which were diverse prior to the breakup of Pangea in the Early or possibly Middle Jurassic. In Laurasia, three regions of turtle diversity can be identified, the North American region, the European region, and the Asian region. In the Early Cretaceous, North American region is dominated by members of the Paracryptodira, and the Asian region is dominated by members of the Eucryptodira. Europe includes taxa from both groups. In the Late Cretaceous, Eucryptodires become increasingly more abundant and diverse in North America. The Baenidae which are not found outside North America appears to be truly endemic to this region. Two groups of "modern," non-marine cryptodires or Chelomacryptodira, the Testudinoidea and the Trionychoidea, appear to have an Asian origin. Both have their earliest record in the Neocomian of Japan.

Key words: Non-marine turtles, Cretaceous, Phylogeny, Distribution, Gondwana, Laurasia.

INTRODUCTION

A general concordance between the Mesozoic fragmentation of Pangea, particularly during the Cretaceous, and the distribution of terrestrial vertebrates such as dinosaurs, mammals, and birds has been reiterated over the past few years (Russell, 1995; Hedges et al., 1996; Krause et al., 1997; Le Loeuff, 1997). Non-marine turtles offer another important candidate for understanding the biogeography at this age. Turtles become abundant and diverse during the Mesozoic. In the Cretaceous, the remains of turtles are among the most abundant fossils in most terrestrial vertebrate assemblages (Figs. 1, 2; Table 1; Hutchison and Archibald, 1986). Further, largely as a result of work by Gaffney and Meylan (l988), Gaffney (l996), and Shaffer et al. (1997), the interrelationships of fossil and extant turtles are well understood.

Two major groups of turtles are present in the Cretaceous, cryptodires and pleurodires. de Broin (l988) provides an extensive discussion of the distribution of Mesozoic and Paleocene pleurodires. However, a review of the distribution of Mesozoic cryptodires based on a definition of groups from cladistic analysis has never been done. Here, we present the preliminary results of a comprehensive cladistic analysis of cryptodires and describe the distributional patterns in the Cretaceous of the clades that emerge, and offer hypotheses explaining the origin of these differences.

A concordance between turtle distribution and paleogeographic patterns of land masses suggests that vicariant evolution is an underlying cause for that distribution. According to this explanation, the turtle assemblages of particular land masses are distinctive because they contain groups that originated and diversified on that land mass and were prevented

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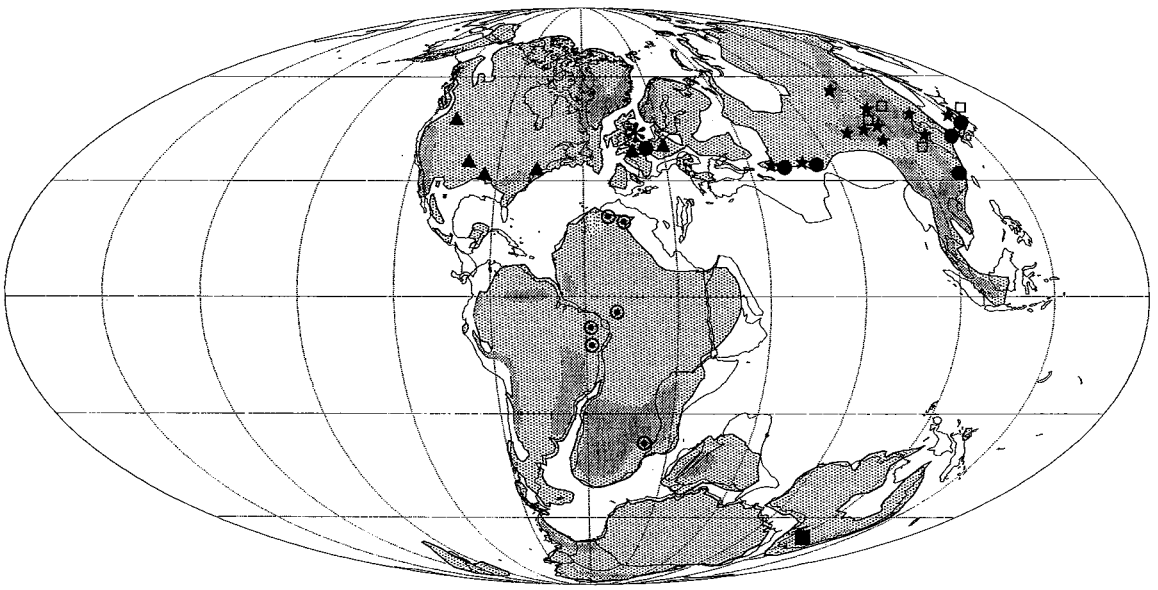

Fig. 1. Distribution of land turtles of the Early Cretaceous. ●) Chelomacryptodira (Trionychoidea and Testudinoidea); ⊙) Pleurodira, ★) Sinemydidae; ▲) primitive cryptodires with mesoplastra retained; □) Sinochelyidae; ■) *Otwayemys*; ∗) *Brodiechelys* and *Chitracephalus*. Paleogeographical map after Smith et al. (1994: Map 18, Barremian-Hauterivian).

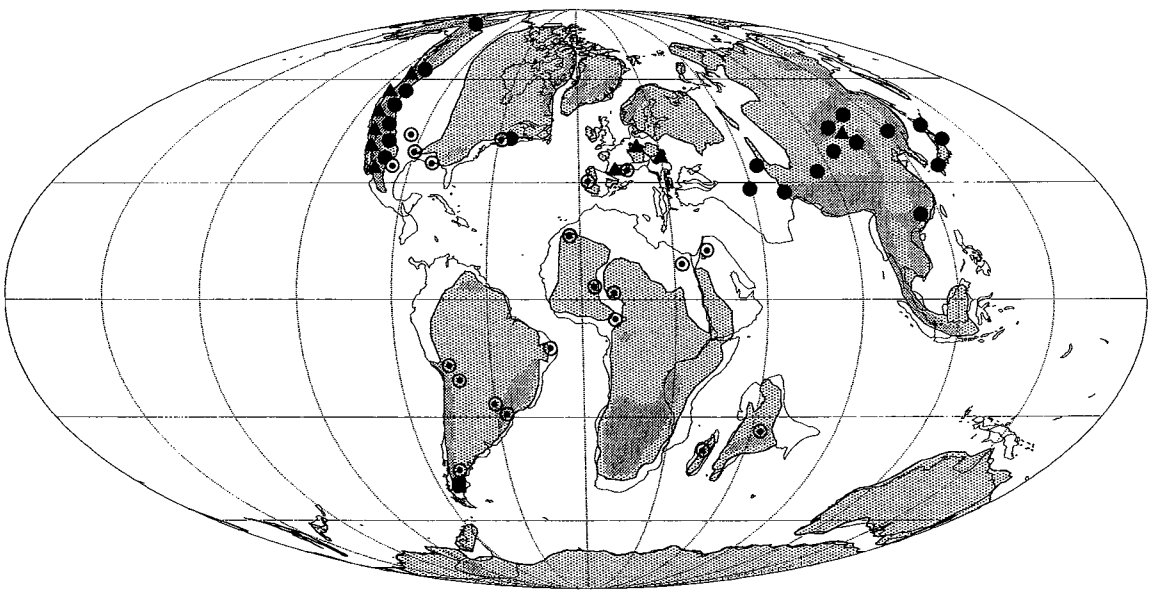

Fig. 2. Distribution of land turtles of the Late Cretaceous. ●) Chelomacryptodira (Trionychoidea and Testudinoidea); ⊙) Pleurodira; ▲) primitive cryptodires with mesoplastra retained; ■) Meiolaniidae. Paleogeographical map after Smith et al. (1994: Map 11, Campanian).

from dispersing further because of physical barriers. Paleoecological hypotheses are an alternative to the vicariance model in explaining differences in turtle assemblages in different geographic regions. This explanation suggests that differences in the turtle assemblages of different areas are a result of the diver-

TABLE 1. Distribution of the Cretaceous Land Turtles

	Australia	South America	India	Africa	North America	Europe	Western and Central Asia	Mongolia and China	Japan
Maastrichtian		1	1	1	1, 4*, 4, 8, 10c1, 10d1, 10f, 10g, 10h	1, 3			
Campanian		1, 2?		1	1, 3*, 4, 10d1, 10f	1, 3*		2a, 9, 10d1, 10d2, 10d3, 10f	10f
Santonian					1		7, 9, 10c1, 10c3, 10f		
Coniacian					1		7, 9, 10c1, 10c3, 10f	9, 10c1, 10d2, 10e, 10f	10d?
Turonian		1			4, 10f		7*, 9, 10c1, 10d, 10e, 10f		10d2
Cenomanian				1	10f	3*	7*, 9, 10c2, 10d, 10e, 10f		7*, 10c1, 10c3, 10d1, 10d2, 10e, 10f
Albian		1		1	3*, 4	3*	7, 9, 10c2, 10d?, 10e, 10f	2c, 7, 9?	
Aptian	2b			1		3*, 4*?, 6, 10a			
Barremian								2c, 7	7?, 9, 10c1, 10d1, 10f
Hauterivian						3*, 4*, 5			7?, 9, 10c2, 10e?
Valanginian									2c, 7, 9, 10b
Berriasian						3*, 4*, 5			

Note. 1) Pleurodira; 2) Meiolaniidae; 2a) *Mongolochelys*; 2b) *Otwayemys*; 2c) Sinochelyidae; 3) *Kallokibotion*; 3*) *Tretosternon*; 4) Baenidae; 4*) Pleurosternidae; 5) *Hylaeochelys*; 6) *Brodiechelys*; 7) Sinemydidae; 7*) Tienfucheloides (Sinemydidae); 8) Chelydridae; 9) Lindholmemydidae (Testudinoidea); 10) Trionychoidea; 10a) *Peltochelys*; 10b) undescribed new Trionychoidae; 10c) Adocidae; 10c1) *Adocus*; 10c2) *Ferganemys*; 10c3) Shachemys; 10d) Nanhsiungchelyidae; 10d) *Basilemys*; 10d2) Nanhsiungchelys; 10d3) *Zangerlia*; 10e) Carettochelyidae; 10f) Trionychidae; 10g) Emarginachelys; 10h) Kinosternidae. Data from Benton and Spencer (1995), Brinkman and Peng (1993a, 1993b, 1996), Chkhikvadze (1987), Danilov (1998), de Broin (1988), de Broin and de la Fuente, (1993), Lapparent de Broin and Murelaga (1996), Lapparent de Broin and Werner (1998), Gaffney (1972), Gaffney et al. (1998), Hay (1908), Hirayama (1996a, 1998a, in press), Hirayama and Chitoku (1994), Hutchison and Archibald (1986), Jerzykiewicz and Russell (1991), Khosatzky (1997), Kito et al. (1998), Langston (1956), Nessov (1985, 1995), Parrish et al. (1987), Tong and Bufetaut (1996), Wiman (1930), Wolfe et al. (1997), and Yeh (1994).

sification of different groups in different paleoecological settings. For example, many differences between the assemblages of the Late Cretaceous of China and Mongolia and western North America could be a result of the different paleoenvironmental settings that are represented. The Asian beds were deposited in semiarid to arid conditions while the Late Cretaceous beds of western North America were generally deposited in wet coastal environments. To resolve the degree to which a vicariance or a paleoecological model accounts for observed patterns of turtle distribution, exceptions to the typical patterns assume importance, since these exceptions falsify a strict vicariance model. Where no exceptions are present, the vicariance model is most strongly supported, especially when there are assemblages from separate

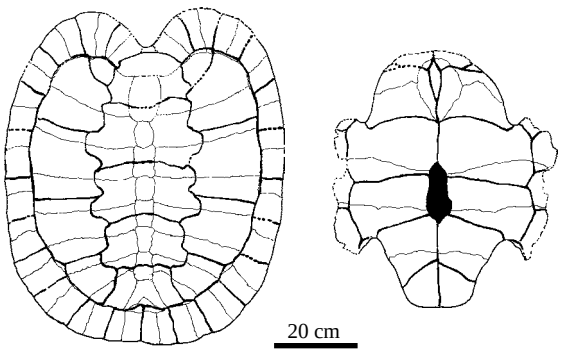

Fig. 3. Shell of *Tretosternon* (= *Naomichelys*) *speciosa* (Hay, 1908; FMNH PR273). Trinity Sandstone Formation, Early Cretaceous (Albian), Montague County, Texas, USA. Carapace in dorsal view, plastron in ventral view.

land masses that are preserved in comparable paleoenvironmental settings. The historical biogeographic hypotheses presented here will be continually tested by new information on the diversity, distribution and interrelationships of the taxa involved, and on the paleoecology of the beds in which they are found.

MATERIAL AND METHODS

Phylogenetic analysis of 76 characters for 21 turtle taxa, including 17 cryptodires, was conducted using PAUP program (version 3.0) of Swofford (1989). A list of the 76 osteological characters utilized in the analysis, and their character states, is provided in *Appendix I* and *II*. The data on turtles discussed below are largely based on Gaffney (1996), Hirayama and Chitoku (1996), and Hirayama (1998b). In those instances where the characters are drawn from sources other than this literature, a reference is provided in *Appendix II*. All characters were coded as reversible, and multistate characters were coded as unordered to avoid a priori assumptions of transformation vectors.

Outgroup polarity for Rhaptochelydia (turtles exclusive of *Proganochelys*; Gaffney and Kitching, 1994, 1995) was determined using characters of *Proganochelys*. Information on turtles is derived from the following references: *Proganochelys* (Gaffney, 1990); Australochelyidae (Gaffney and Kitching, 1995; Rougier et al., 1995); *Proterochersis* (de Broin, 1984; Gaffney, 1990); *Notoemys* and Eupleurodira (Meylan, 1996); *Kayentachelys* (Gaffney et al., 1987); Meiolaniidae (Hirayama and Chitoku, 1996; Gaffney, 1996); Sinochelyidae (= Peishanemydidae) (Bohlin, 1953; Ckhikvadze, 1985; Chow, 1954; Nessov and Verzilin, 1981; Wiman, 1930); *Mongolochelys* (Khosatzky, 1997; Hirayama, personal observation); *Otwayemys* (Gaffney et al., 1998); *Kallokibotion* (von Nopcsa, 1923; Gaffney and Meylan, 1992); Paracryptodira (Pelurosternidae and Baenidae) (Brinkman and Nicholls, 1991, 1993; Evans and Kemp, 1975; Gaffney, 1972, 1979a, 1996; Owen, 1853); Plesiochelyidae, Chelydroidea, Chelonioidea, Trionychoidea, and Testudinoidea (Hirayama and Chitoku, 1996; Hirayama, 1998b); Xinjiangchelyidae (Kaznyshkin et al., 1991; Peng and Brinkman, 1993; Sukhanov, in press); Sinemydidae (Brinkman and Peng, 1993a, 1993b; Brinkman and Wu, 1999; Sukhanov and Narmandach, 1974). See below for *Tretosternon*, *Hylaeochelys*, and *Brodiechelys*.

Character state changes have been optimized on the resulting trees using PAUP's DELTRAN option. This optimization was selected because we feel it to be slightly more conservative in terms of assigning synapomorphies to clades in a data matrix with a substantial amount of missing data.

Institutional Abbreviations

BMNH: Natural History Museum, London, UK. **DCM**: Dorset County Museum, Dorchester, UK. **FMNH**: Field Museum of Natural History, Chicago, USA. **IBEF**: Izumi Board of Education Fukui, Izumi, Japan. **SBEI**: Shiramine Board of Education Ishikawa, Shiramine, Japan. **THU**: Teikyo Heisei University, Ichihara, Japan. **TMP**: Royal Tyrrell Museum of Paleontology, Drumheller, Canada.

NOTES ON SOME CRETACEOUS LAND CRYPTODIRES

Although representatives of many extinct groups of turtles have been redefined and redescribed in recent years, several taxa with potentially significant implications for interpreting patterns of interchange between turtle assemblages have been only poorly described and diagnosed. In order to incorporate these turtles into the discussion of turtle biogeography during the Cretaceous, we provide comments on the basic characters of these turtles and discuss their phylogenetic position.

Tretosternon (Fig. 3): *Tretosternon* Owen, 1842 was originally described on the basis of fragmentary shells from the Early Cretaceous of England of which the type species is *T. backwelli* (Mantell, 1827) from the Wealden Formation (Lydekker, 1889a). Various similar forms sharing the uniquely pustulated sculpture on the shell surface have been described from

throughout the Cretaceous of Western Europe. These include *Helochelys*, *Trachydermochelys*, *Helochelydra*, and *Solemys* (Andrews, 1920; Lapparent de Broin and Murelaga, 1996, 1999; Lydekker, 1889b; von Meyer, 1855; von Nopcsa, 1928). Naomichelys from the Early Cretaceous of North America is also characterized by a similarly pustulated sculpture on the shell surface. We consider all these forms could be junior synonyms of *Tretosternon* because they share the same distinctive sculpture pattern on the shell and, where known, several unique features of the scute pattern and the shell structure. These shell features include an entoplastral scute of entoplastron and the emarginated nuchal bone. These features are present in FMNH PR273, an undescribed nearly complete skeleton from the Early Cretaceous of North America (Ostrom, 1970), the shell of which is figured for the first time here (Fig. 3). Shell fragments with the distinctive sculpture pattern from the basal Judith River Group of Alberta (e.g., TMP 90.60.7) document the presence of *Tretosternon* in the Mid Campanian of North America (Brinkman, personal observation).

Pleurosternidae (Fig. 4): The Pleurosternidae is best represented by *Pleurosternon* (Fig. 4*a*) from the Early Cretaceous of England and *Glyptops* from the Jurassic of North America (Owen, 1853; Lydekker, 1889b; Gaffney, 1979a). The skull of *Pleurosternon* associated with fragments of postcranial skeleton was originally described as *Mesochelys* (Evans and Kemp, 1975; Gaffney and Meylan, 1988). The long basisphenoid reaching palatines is a prominent synapomorphy of this group (Gaffney, 1979a). "*Glyptops" ruetimeyeri* from the Early Cretaceous of England (Fig. 4*b*; Lydekker, 1889b; Watson, 1910) seems an another pleurosternid closely related with *Pleurosternon* based on shell features such as the finely pitted sculptures and a median notch of xiphiplastra. Holotype (BMNH 48357) of *Platychelys*? *anglica* Lydekker presumed as a pleurodire (Lydekker, 1889b; Benton and Spencer, 1995), is actually considered as a junior synonym of "*Glyptops*" *ruetimeyeri,* especially because of its finely pitted sculptures on shell surface (Hirayama, personal observation). *Compsemys* from the Late Cretaceous and Paleocene of North America might be also a member of the Pleurosternidae (Hutchison, 1987). This turtle shares with *Pleurosternon* a median notch of xiphiplastra, lack of a cervical scute, a sinuous mid-line sulcus of plastral scutes, and a relatively large entoplastron (Gaffney, 1972).

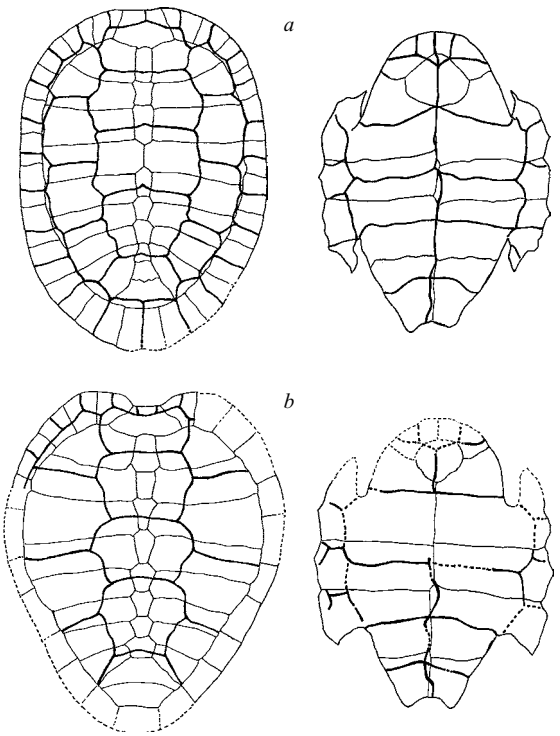

Fig. 4. Shell of Pleurosternidae from the Purbeck Limestone Formation (Early Cretaceous) of Durlstone Bay, Dorset County, UK. Carapace in dorsal views, plastron in ventral views. *a*) *Pleurosternon bullocki* (Owen, 1842); carapace based on BMNH 28618 (holotype of *Pleurosternum ovatum* Owen, 1853; carapace 500 mm long as preserved), plastron based on BMNH R3413 (carapace 441 mm long as preserved). *b*) "*Glyptops*" *ruetimeyeri* (Lydekker, 1889); carapace largely based on BMNH 40676 (holotype; carapace 260 mm long as estimated) with additions from BMNH R6888 and Watson (1910), plastron largely based on Watson (1910) with additions from BMNH R6888.

Hylaeochelys (Fig. 5): This genus was described from the Early Cretaceous of southern England and characterized by a shell with broad vertebral scutes and strong plastral buttresses reaching costals, as in Jurassic Plesiochelyidae (Lydekker, 1889b; von Nopcsa, 1928). Mesoplastra are lost in this turtle. *H. belli* (Mantell, 1844), a type species, seems an only valid taxon of this genus, although several species has been proposed (Lydekker, 1889b; von Nopcsa, 1928). The skull described as *Dorsetochelys* also from the Early Cretaceous of southern England (Evans and Kemp, 1976) might belong to this taxon because *Dorsetochelys* shows some characters suggesting its plesiochelyid affinities. These include an incompletely floored canalis caroticus internus between pterygoid and basisphenoid and the medial meeting of pala-

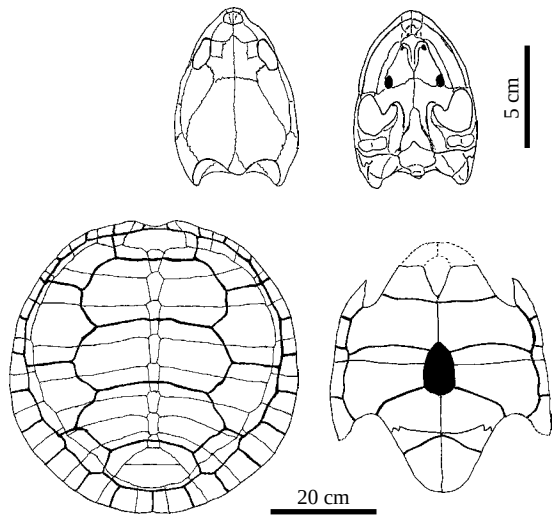

Fig. 5. Skull and shell of *Hylaeochelys belli* (Mantell, 1844). Purbeck Limestone Formation, Early Cretaceous (Berriasian), Durlstone Bay near Swanage, Dorset County, UK. Skull based on DCM G23 (holotype of *Dorsetochelys delairi* Evans and Kemp), modified from Evans and Kemp (1976). Carapace (dorsal view) largely based on DCM G20 (holotype of *Pleurosternum latiscutatum* Owen, 1853) with additions from DCM G16 (holotype of *Pleurosternum emarginatum* Owen, 1853) and von Nopcsa (1928). Plastron (ventral view) based on BMNH R6882 and R5937.

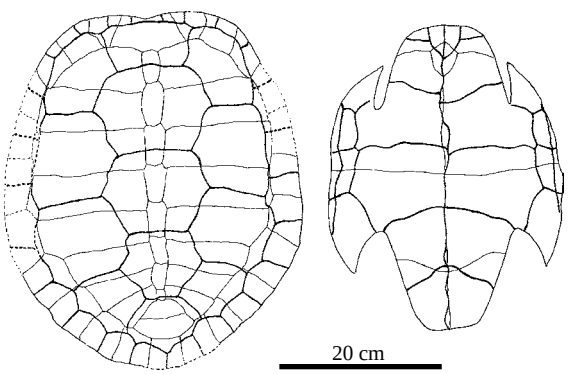

Fig. 6. Shell of *Brodiechelys brodiei* (Lydekker, 1889). Vectis Formation, Early Cretaceous (Barremian), near Atherfield Point, Brighstone Bay, Isle of Wight, UK. Carapace (dorsal view) largely based on BMNH R11146 with additions from BMNH R11147. Plastron largely based on BMNH R11146 with additions from BMNH R11147 and R11174.

tines, characters not reported in the original description (Hirayama, personal observation).

Brodiechelys (Fig. 6): This genus was originally described as *Plesiochelys brodiei* based on a semi-articulated shell (BMNH R2643) from the Early Cretaceous (Barremian) of the Isle of Wight, southern England (Lydekker, 1889a, b). von Nopcsa (1928) erected *Brodiechelys* for this taxon. *P. valdensis* (Lydekker, 1889b) and *P. vectensis* (Hooley, 1900) based on BMNH 28967 and R6683, respectively, from the same locality and horizon seem junior synonyms of this taxon. The shell features of *Brodiechelys* appear almost identical to those of *Xinjiangchelys* and its allies from the Middle to Late Jurassic of Asia (Peng and Brinkman, 1993; Sukhanov, in press; Hirayama and Danilov, in preparation): 4th to 7th marginals extending onto costals; mid-line sulcus of plastral scutes sinuous; femoral-anal sulcus intersecting hypoplastron. The plastral buttresses of *Brodiechelys* seem restricted within peripherals, not overlying costals, as in *Xinjiangchelys.*

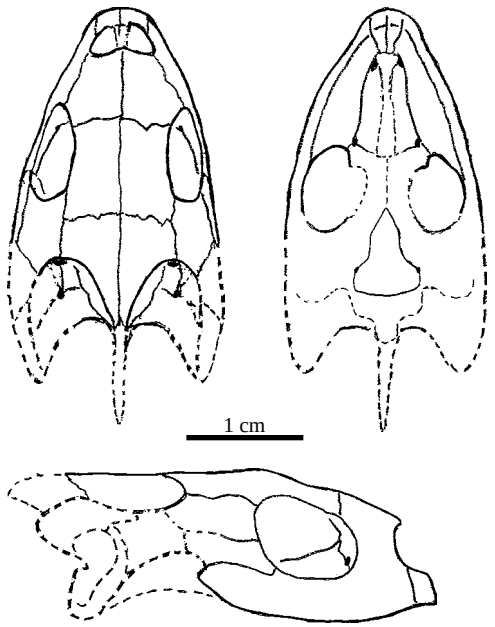

Fig. 7. Skull reconstruction of an undescribed Trionychoidae (SBEI 7) from the Neocomian of Central Japan, in dorsal, ventral, and right lateral views, based on SBEI 7 from the Kuwajima Formation at Shiramine-mura, Ishikawa Prefecture. After Hirayama (in press).

Undescribed Trionychoidea from the Early Cretaceous of Japan (Figs. 7 – 9): Early Cretaceous chelomacryptodires including both trionychoids and testudinoids are represented by almost one thousand specimens from the Early Cretaceous non-marine sediments of the Tetori Group of Central Japan (Gifu, Ishikawa, and Fukui Prefectures) distributed around the Mt. Hakusan, a sacred volcanic mountain (Hirayama, 1996a, 1996b, in press). An undescribed trio-

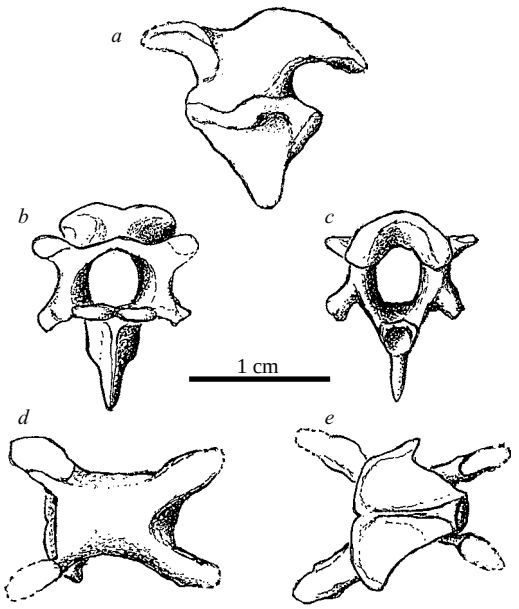

Fig. 8. Eigth cervical vertebra of an undescribed Trionychoidae (IBEF-VP29) from the Neocomian, Okurodani Formation, Shokawa, Japan, Gifu Prefecture, Central Japan. *a*) Left lateral; *b*) anterior; *c*) posterior; *d*) dorsal; *e*) ventral views.

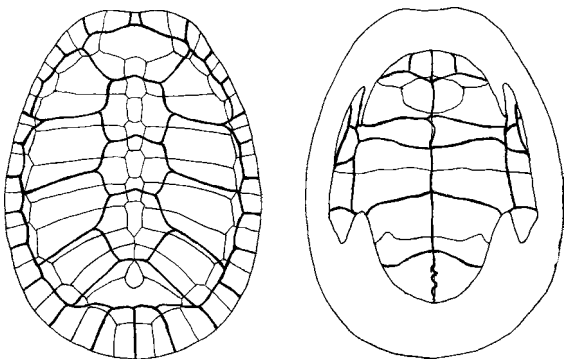

Fig. 9. Composite reconstruction of the shell of an undescribed Trionychoidae from the Neocomian, Kuwajma Formation, Shiramine-mura, Ishikawa Prefecture, Central Japan. Carapqace in dorsal, plastron in ventral views. Largely based on SBEI 585, posterior portion of an articulated shell, with additions from various specimens. Maximum shell length is estimated as about 30 cm. After Hirayama (in press).

nychoid is best known from some hundred specimens, including few articulated shells, good skulls, lower jaws, cervicals and appendicular skeletons preserved from the lower part of the non-marine Tetori Group, the Kuwajima Formation of Ishikawa Prefecture, and the Okurodani Formation, an equivalent horizon of Gifu Prefecture (Hirayama, in press). This taxon is associated with a testudinoid mentioned below and more primitive cryptodires such as an undetermined sinemydid and *Sinochelys* (= *Scutemys*; Sinochelyidae). The Neocomian age of this horizon is supported by both fission-track analysis of the overlying tuff from the Okurodani Formation, yielding an age of 135 ± 7 Ma (Gifu-Ken Dinosaur Research Committee, 1993), and the floral evidence, particularly lack of any angiosperm megafossils (Vakhrameev, 1991). This estimation is also consistent with the occurrence of the "iguanodontid" teeth and dsungaripterid pterosaur from the lower part of the non-marine Tetori Group (Hasegawa et al., 1995; Unwin et al., 1996; Kobayashi and Azuma, 1999). The trionychoid skulls mentioned above lack an anterior medial process of frontals as in Trionychoidae such as *Adocus*, nanhsiungchelyids and carettochelyids (Fig. 7; Gaffney, 1979b). The eight cervical from the Okurodani Formation is completely chelomacryptodiran in the possession of its double central articulation on anterior surface (Fig. 8; Wiiliams, 1950). This is also unique in its possession of opisthocoelous structure as in the other Trionychoidae like *Adocus* and Nanhsiungchelyidae (Meylan and Gaffney, 1989; Brinkman and Peng, 1996; Brinkman, 1998). An isolated elongate (presumed as 5th) cervical vertebra from the Kuwajima Formation is opisthocoelous as well (Hirayama, in press). The shell surface is punctate and its entoplastron is broad as in the other Trionychoidae like *Adocus*. Nonetheless, this Neocomian trionychoid is considered as more primitive than the adocids, including *Adocus* and *Ferganemys*, and the nanhsiungchelyids in having the vertebral scutes broader than long and the 5th vertebral scute overlying the peripheral region (Fig. 9; Hirayama and Danilov, in preparation).

Several dozen disarticulated shells of more advanced trionychoids such as *Adocus* (Adocidae) and *Basilemys* (Nanhsiungchelyidae) are reported as well as a trionychid (known from a costal) from the Kitadani Formation, an uppermost part of the Tetori Group of Fukui Prefecture, Central Japan, which seems to be Barremian to early Aptian in age (Hirayama and Azuma, 1996, in preparation; Isaji, 1993). Thus, the Early Cretaceous trionychoids seem had highly diversified during the age of the Tetori Group (Neocomian to Aptian).

Undescribed Testudinoidea from the Early Cretaceous of Japan (Figs. 10, 11): Primitive Testudinoidea from the Mesozoic, such as *Mongolemys* and *Lindholmemys* from the Late Cretaceous of Asia,

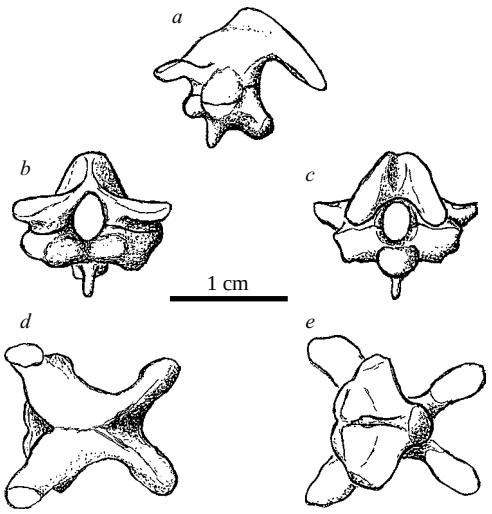

Fig. 10. Eight cervical vertebra of *Mongolemys elegans* (THU 1888) from the Nemegt Formation, Late Cretaceous, Mongolia. *a*) Left lateral; *b*) anterior; *c*) posterior; *d*) dorsal; *e*) ventral views.

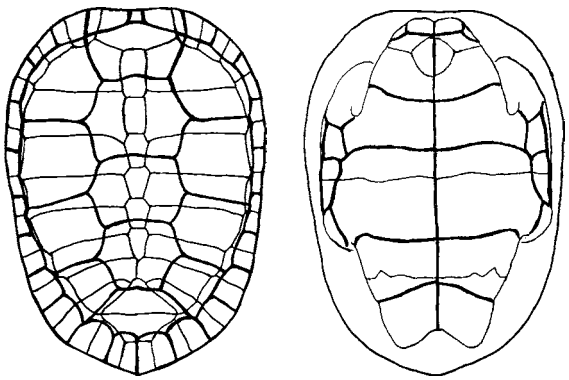

Fig. 11. Composite reconstruction of the shell of an undescribed Testudinoidea (Lindholmemydidae) from the Neocomian of Central Japan, based on various specimens (e.g., SBEI-V205, partial shell including 1st and 2nd suprapygals, right 4th to 7th costals, hypoplastron, and left xiphiplastron) from the Kuwajima Formation, Shiramine-mura, Ishikawa Prefecture. Carapace in dorsal, plastron in ventral views. Maximum shell length is estimated as 20 cm. After Hirayama (in press).

were originally classified as the Dermatemydidae, formerly a wastebasket of the primitive eucryptodires of the Cretaceous and Paleogene with complete inframarginals retained (Khosatzky and Mlynarski, 1971). Meylan and Gaffney (1989) first noted possible testudinoid affinities primarily on the basis of the strong plastral buttresses reaching the costals, an unique feature among eucryptodires other than plesiochelyids and their allies. The Lindholmemydidae has been proposed for these primitive testudinoids (Ckhikvadze, 1987; Danilov, 1998; Sukhanov et al., 1999), although this seem to be a paraphyletic group, lacking any its own synapomorphy (Shaffer et al., 1997; Hirayama, in press). Testudinoid affinities of *Mongolemys* are more clearly shown in its uniquely biconvex and doubly articulated eight cervical vertebra as in the Cenozoic testudinoids (Fig. 10; Williams, 1950). An undescribed complete skull of *Mongolemys* seems a generalized testudinoid in its structure, being quite similar to living *Emys orbicularis*, an emydid (E. S. Gaffney, personal communication; Hirayama, personal observation; Danilov, in preparation).

A Neocomian testudinoid from the lower part of the non-marine Tetori Group of Central Japan associated with primitive trionychoids is represented by several hundred disarticulated shells and a skeleton including several shell elements and procoelous caudals (Fig. 11; Hirayama, 1996a, 1996b, in press). This small turtle (complete carapace is estimated as less than 20 cm long) is characterized by the rather strong plastral buttresses reaching costal plates (first and fifth costals), an anal notch formed by xiphiplastra and a complete series (four pairs) of inframarginals as in the other lindholmemydids. The possession of vertebral scutes broader than long and two pairs of gular scutes in this Neocomian taxon, however, are considered as plesiomorphic condition not seen in the other lindholmemydids (Hirayama, in press).

PHYLOGENETIC ANALYSIS (Fig. 12)

The results of our phylogenetic analysis is generally in agreement with the analysis of Gaffney (l996) exclusive of the position of the meiolaniids and their allies. Although meiolaniids share several derived features with eucryptodires, particularly the morphology of the foramen posterius canalis caoticus internus and the presence of well formed central articulations, the lack of a series of derived features shared by many other cryptodires results in its position as a very basal cryptodire in this analysis. These features are a distinct lower cheek emargination with lateral exposure of the processus pterygoideus externus (absent in Meionaliidae), well developed cervical ribs (present in the Meiolaniidae), an anterior position of the transverse processes (positioned mid-way along the centrum in the Meiolaniidae), and the absence of dorsal processes of the epiplastra (present in the Meiolaniidae). The placement of the Meiolaniidae with *Mongolochelys*, a primitive cryptodira with meso-

plastra retained, which was recently described by Khosatzky (1997) from the Late Cretaceous of Mongolia, is based on the shared presence of the enlarged squamosals reaching supraoccipital and the prominent lingual ridge of maxilla. The placement of the meiolaniids and *Mongolochelys* with the Sinochelyidae from the Early Cretaceous of Asia is supported by a ventral knob on the nuchal. *Otwayemys*, a newly described turtle from the Early Cretaceous of Australia, was originally presumed to be a member of the Centrocryptodira, possibly closely related with the Sinemydidae of Asia on the basis of the opisthocoelous cervicals (Gaffney et al., 1998). Both anterior and posterior caudals of this turtle, however, are opisthocoelous as in *Meiolania*, *Mongolochelys*, and baenids, and its vertebral scutes are unusually broad for centrocryptodires including sinemydids. *Otwayemys* seems to be closely related to the sinochelyids among the meiolaniids and their possible allies on the basis of the loss of mesoplastron (Fig. 12). Thus, formed central articulation on the cervical and caudal vertebrae, and the loss of mesoplastron are presumed as independently acquired in this group and the centrocryptodires in our analysis. Nonetheless, both sinochelyids and *Otwayemys* are very poorly known, and additional information, particularly from the cranial, cervical and caudal series, is likely to modify this result.

A relationship between *Kallokibotion* and *Tretosternon* has not previously been suggested. It is supported in this analysis by the shared presence of a first suprapygal larger than the second. This clade is advanced relative to meiolaniids and their allies in the presence of a ventral keel on the cervical vertebrae (known only in *Kallokibotion*), the reduction in size of the cervical ribs (apparently lost in *Kallokibotion*, not known in *Tretosternon*) and the loss of dorsal process of the epiplastron.

The Paracryptodira (Baenidae and Pleurosternidae) are advanced relative to *Kallokibotion* in the presence of ventral cheek emargination, although this is only weakly developed in the primitive members of the group. The remaining cryptodires, the Eucryptodira, are derived relative to the pleurosternids and other more primitive cryptodires in the loss of the eustachian tube enclosed within an elongate incisura columellae auris and in the anterior position of the cervical transverse processes. The position of the eustachian tube was initially considered a derived feature of Baenids by Gaffney (l972), but is also present in meiolaniids, *Mongolochelys*, *Kallokibotion*, and in

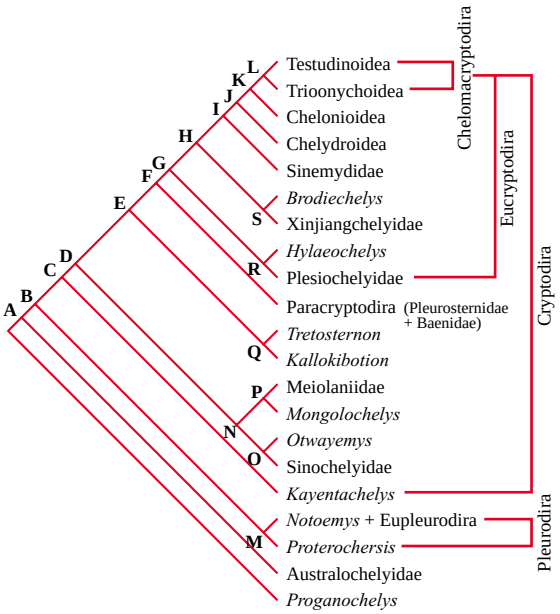

Fig. 12. Shortest cladogram showing relationships among turtles produced by PAUP ver. 4.0b3a for Macintosh (Swofford, 1989), tree length 130, CI = 0.639, RI = 0.754. Distribution of apomorphies at each Node is shown by numbers which correspond to characters in *Appendix II* and scored in *Appendix I* as follows. Homoplasies are marked with (*). Node **A**: Rhaptochelydia (14, 19, 23, 28); **B**: Casichelydia (2*, 6, 7*, 12, 15, 24, 26, 27*, 51, 52, 55, 56*); **C**: Cryptodira (5, 18, 21, 25, 57*, 65*, 73*); **D**: unnamed taxon (16, 20, 22, 71*); **E**: Selmacryptodira (34*, 38, 60*, 66*, 69*); **F**: Diacryptodira (11, 35*); **G**: Eucryptodira (27*, 30*, 36, 74*); **H**: unnamed taxon (3, 8, 9, 49*, 50*, 59*, 66*, 68*); **I**: Centrocryptodira (39*, 41*, 67, 70*, 72*, 75*); **J**: Polycryptodira (1, 31*, 33, 37, 38, 40, 42, 44); **K**: Procoelocryptodira (45, 48*, 50*); **L**: Chelomacryptodira (43*, 68*, 72*); **M**: Pleurodira (53, 60*, 66*, 76*); **N**: unnamed taxon (39*, 49*, 50*, 58*, 63*); **O**: unnamed taxon (74*); **P**: unnamed taxon (4*, 10, 13, 41*); **Q**: Kallokibotionidae (61); **R**: unnamed taxon (17, 31*, 32); **S**: Xinjiangchelyidae including *Brodiechelys* (62*, 64*).

pleurodires, suggesting it is pleiomorphic character-state among casichelydidians.

Xinjiangchelys from the Middle to Late Jurassic of Asia seems more advanced than the plesiochelyids (and *Hylaeochelys*) in the possession of the extensive posterior temporal emargination, the procoelous and opisthocoelous caudals, and narrower vertebral scutes.

The Sinemydidae is a group that flourished in the Cretaceous of Asia (Hirayama, 1996c). It is more advanced than *Xinjiangchelys* in the possession of completely formed central articulation on the cervical vertebrae.

The Polycryptodira, including chelydroids, chelonioids, testudinoids and trionychoids, are primarily characterized by the structure associated with the development of neck retraction system that includes such features as the posterior cervical centra much wider than high, the thin ventral keel of the posterior cervical centra, the 8th cervical centrum shorter than the 7th, the double cervical articulation between 7th and 8th cervicals, and the 1st thoracic vertebra with its anterior articulation facing ventrally or anteroventrally.

The Procoelocryptodira, consisting of chelonioids, testudinoids and trionychoids, are characterized by the loss of isolated chevron and the presence of procoelous caudal centra at the base of the tail.

Both Testudinoidea and Trionychoidea are unique among cryptodires in the possession of the ability to completely withdraw the skull within the shell and united as the Chelomacryptodira, a crown-group clade of the cryptodires, or "modern" cryptodire, characterized by the possession of the double cervical articulation between 6th and 7th cervicals (Williams, 1950).

DISTRIBUTION

The distribution of pleurodires and non-marine cryptodires during the Cretaceous is summarized in Table 1 and Figs. 1 – 2. One of the major patterns is the north-south separation of turtle assemblages into a southern, pleurodire-dominated assemblage in the Gondwana continents and a northern, cryptodire-dominated assemblage on the Laurasian continents. Pleurodires are absent from non-marine sediments in the northern continents during the Early Cretaceous. In the Late Cretaceous they are present in both Europe and North America. Their occurrence in the northern continents during the Late Cretaceous may mark the removal of barriers preventing their introduction into the continent earlier as also documented by the hadrosaurian dinosaurs of South America and Antarctica (Novas, 1997; Case et al., 1998).

Two groups of cryptodires are present in Australia. One of these is the Meiolaniidae, remains of which from Argentina have been reviewed by de Broin and de la Fuente (1993) and Gaffney (1996). A second is *Otwayemys* from the Early Cretaceous of Australia (Gaffney et al., 1998). Since, according to the analysis presented above, both meiolaniids and *Otwayemys* are the most primitive basal cryptodires during the Cretaceous, their presence in the southern continents and presumed affinities with *Mongolochelys* and the Sinochelyidae of Asia could reflect a widespread distribution prior to the breakup of Pangea in the Early or possibly Middle Jurassic.

The cryptodire-dominated assemblage of the northern continents can be subdivided into distinct Asian, North American, and European assemblages. The North American assemblage is distinctive in the abundance of baenids, which are not known outside North America. The Aptian-Albian record includes *Trinitichelys*, the oldest known member of the Baenidae, and *Tretosternon*, which, as discussed above, is here considered the senior synonym of *Naomichelys.* Two undescribed specimens may document the occurrence of eucryptodires in the Aptian-Albian age of North America. One of these is a shell from the Cedar Mountain Formation of Utah which is without a mesoplastron (Brinkman, personal observation, Brigham Young University specimen BYU 9440), a feature that is typically of eucryptodires. The second is a series of carapace fragments of the Blairmore Formation of Alberta that are similar to members of the Sinemydidae of Asia in the presence of an upturned antero-lateral edge and sculpturing of the shell (Brinkman, personal observation on the Tyrrell Museum specimen).

The turtle assemblage of Cenomanian to Santonian times of North America is only beginning to emerge (Wolf, 1997). The first record of chelomacryptodires in North America is a specimen of the Trionychidae from the Cenomanian Dunvegan Formation of Alberta, Canada (Brinkman, personal observation, Tyrrell Museum specimen TMP 94.384.1).

The Campanian-Maastrichtian record is best known from formations deposited in the North-central portion of the central plains, particularly Alberta, Montana, and Wyoming.

Paracryptodires remain a dominant element of this assemblage with two major groups being represented, the Baenidae and the Pleurostenindae. *Tretosternon* extends into the Middle Campanian. A diverse assemblage of chelomacryptodires is also present. Notable in this group are the trionychoids, including the primitive representatives *Adocus* and *Basilemys*, as well as members of the Trionychidae. Chelydrids are present in the Campanian, and kinosternoids first appear in the late Maastrichtian in this area. In addition, undescribed material (Tyrrell Museum specimen TMP 87.2.1) documents the presence in this area of primitive, aquatic, non-marine cryptodires tentatively assigned to the Macrobaenidae (Brinkman, personal observation).

In Europe, the Early Cretaceous record of non-marine cryptodires is best documented from the Early Cretaceous Durlston and Wealdan Formations of western Europe. Pleurosternids, represented by *Pleurosternon*, "*Glyptops*" *rudemeyeri*, and *Tretosternon* are the most abundant taxa in these beds. Several eucryptodires are also known. *Hylaeochelys* appears to be a plesiochelyid, and *Brodiechelys*, as discussed above, appears to be a member of the Xinjiangchelyidae. *Peltochelys* from Belgium, known only from a single shell, is currently placed in the Trionychoidae (Meylan, 1988). *Chitracephalus* from the Early Cretaceous of Belgium (Dollo, 1884) may also be a eucryptodire, although poor preservation prevents its relationships from being established. An assemblage of eucryptodires from the Early Cretaceous of Spain is less well known, but appears to be dominated by eucryptodires such as *Brodiechelys* (Sanz et al., 1988; Perez-Moreno, personal communication).

Non-marine cryptodiran turtles from the Late Cretaceous of Europe are known from France, Spain, and Romania. *Kallokibotion* is the sole turtle from Romania. Pleurodires become rather common in the Late Cretaceous of France (Buffetaut et al., 1996; de Broin, 1988; Lapparent de Broin and Murelaga, 1996, 1999).

The Asian turtle assemblage is dominated by eucryptodires, particularly diverse chelomacryptodires, but also includes a number of primitive cryptodires. Non-marine turtles are known from three principal areas, the paleogeographically inland area (northern China, Mongolia, and the Lake Baikal region of Russia), the paleogeographically western coastal region (Uzbekistan, Kyrgyzstan, and Kazakhstan), and the paleogeographically eastern costal area (western part of Japan). Primitive cryptodires are represented by the Sinochelyidae from the Early Cretaceous of China and Mongolia, and *Mongolochelys* from the Late Cretaceous of Mongolia. In the paleogeographically western coastal region, a succession of assemblages has been documented extending from the Early Cretaceous through the Late Cretaceous. The Early Cretaceous beds are thought to be Albian in age, and preserve a diverse assemblage of Chelomacryptodira, or 'modern' cryptodires, including members of the Trionychidae, Adocidae, Nanhsiungchelyidae, and Testudinoidea (Lindholmemydidae; Nessov, 1985, 1995; Danilov, 1998). A series of Early Cretaceous assemblages from inland basins in Northern China include primitive cryptodires placed in the Sinemydidae. These Sinemydidae-dominated assemblages are thought to be earlier in age than the Kazakhstan-Uzbekistan assemblage, although correlation is difficult. Two members of the Chelomacryptodira from the Early Cretaceous of this region have been described. One is *Tsaotanemys*, a primitive testudinoid (Lindholmemydidae) from Gansu described by Bohlin (l953). Unfortunately, the relative age of the locality that yielded this taxon is unknown. The second is the trionychid "*Aspideretes*" *maortuensis* from the Alashan basin, described by Yeh (l965). Based on the dinosaur assemblage, however, the formation yielding this taxon is thought to be early Late Cretaceous (Yeh, 1994).

The Japanese assemblage, as described above, is significant in documenting the chelomacryptodires in the Neocomian, the first occurrence of this group, as well as the more diverse trionychoids from the Barremian to the early Aptian.

Late Cretaceous assemblages across Asia are dominated by members of the Trionychoidea and Testudinoidea. Within the Trionychoidea, the Adocidae are particularly diverse in Central Asia (Sukhanov, in press; Hirayama and Danilov, in preparation). Primitive cryptodires such as *Mongolochelys* and primitive aquatic eucryptodires generally placed in the Macrobaenidae are also characteristic members of this assemblage.

DISCUSSION

As with dinosaurs and mammals, the distribution of non-marine cryptodiran turtles during the Early Cretaceous shows a strong concordance with the Mesozoic fragmentation of Pangea. Asian assemblages are distinct in the abundance of eucryptodires including diverse chelomacryptodiran turtles, North American assemblages are distinct in the abundance of paracryptodires, and European assemblages, at least during the Early Cretaceous, have a mixture of both groups of which chelomacryptodires are rare or absent.

These regionally distinctive assemblages are not strictly a result of geographic barriers preventing interchange between these land masses during the Cretaceous, since most higher taxa, and a few genera, are present on more than one land mass. A distinctly Asian component in the turtle assemblage from the Early Cretaceous of Europe is provided by *Brodiechelys*, a member of the more typically Asian family Xinjiangchelyidae. The presence of members of the Trionychoidea in the Early Cretaceous of both Europe and Asia is another similarity in these assemblages, if *Peltochelys* is accepted as a trionychoid.

The trionychoids first occur in the Neocomian of Japan and are present in the Aptian (or Barremian) bed of Europe. Thus, although their first occurrence in Asia is significantly older than their first occurrence elsewhere on the continent, their presence in the Early Cretaceous of Europe suggests that their distribution during the early stages of their history might be largely controlled by paleoenvironmental factors.

Nonetheless, it should be significantly noted that chelomacryptodiran turtles, if present, seem never become dominant in Europe during the Cretaceous. Rather, Europe seems have functioned primarily as a biogeographical "Jurassic Park" or protected area for primitive cryptodires such as pleurosternids, *Tretosternon*, *Kallokibotion*, plesiochelyids, and xinjiangchelyids during the Cretaceous.

A close connection between Europe and North America during the Early Cretaceous is indicated by the presence of *Tretosternon* in both areas.

There are few non-marine cryptodiran turtle taxa present in both Asia and North America during the Early Cretaceous, although shell fragments from the Early Cretaceous of Western Canada may be evidence for the presence of the Sinemydidae in North America. In the Late Cretaceous, the similarities between the turtle assemblages of the Asian and North American continents become much more evident and stronger. During this time, the Asian and North American assemblages are similar in the presence of a diverse assemblage of Trionychoidea, including the families Adocidae, Nanhsiungchelyidae, and Trionychidae, and a members of a group of primitive aquatic non-marine eucryptodires generally placed in the Macrobaenidae. Two genera, *Adocus* and *Basilemys*, occurs in both areas.

Despite this evidence for interchange between Asia, North America, and Europe during the Cretaceous, three examples of higher taxa that are endemic to one of the land masses can be identified. These are the Testudinoidea which only occur in Asia at this time, and the Baenidae and Chelydridae, which only occur in North America. Vicariant evolution is a the most probable hypothesis in accounting for these distributional patterns for each of these groups.

The Baenidae first occur in the Early Cretaceous and are one of the most diverse groups of turtles in the Late Cretaceous of North America. Paleoenvironments containing baenids in North America are matched by comparable paleoenvironments in Asia. In North America, baenids are found in fluvial-lacustrine and estuarine sediments deposited in a semiarid to humid paleoenvironment. The estuarine paleoenvironment of North America is environmentally similar to the estuarine beds of Kazakhstan, Kyrgyzstan, and Uzbekistan and contains other faunal elements that are similar, such as the horned ceratopsians (Brinkman et al., 1998). The fluvial-lacustrine beds of Japan document the fauna present in the eastern margin of Asia in a humid fluvial-dominated paleoenvironment.

Chelydrids first occur in the Campanian of North America. They are not known outside North America during the Cretaceous. However, the evidence that they are truly endemic to North America during this time is weaker than the evidence that the baenids are endemic to North America since Campanian and Maastrichtian assemblages from fluvial and estuarine beds in Asia are not well documented.

The Testudinoidea, first represented in Asia in the Neocomian of Japan and abundant in the Late Cretaceous across Asia, appear to be a strictly Asian group throughout the Cretaceous. They occur in paleoenvironments in Asia that are matched by turtle-bearing paleoenvironment in North America, so their absence in North America is not likely to be a result of inadequate sampling in appropriate paleoecological contexts.

It seems most significant in the early history of the chelomacryptodiran turtles that both western and eastern coastal regions of Asia had been dominated by Trionychoidea and Testudinoidea since the Neocomian. This suggests a scenario that this crown-group of cryptodires originated at the coastal region of Asia at the beginning of Cretaceous and then extended their distribution into its inland area and also North America (probably through the Beringia) in the Late Cretaceous.

CONCLUSION

1. During the Cretaceous, non-marine turtles show strong patterns of provincialism, mirroring the pattern of land masses resulting from the breakup of Pangea during the Jurassic. These patterns are a result of several factors, of which vicariance and ecological controls on the distribution of groups of turtles are considered the most significant.

2. The large scale patterns, such as the dominance of pleurodires in the southern land masses and the dominance of cryptodires in the northern land masses cannot be strictly attributed to vicariance because exceptions to both distributional patterns are present. The occurrence of pleurodires in Europe and North America during the Late Cretaceous may re-

flect the removal of barriers that previously prevented the terrestrial faunal interchange between the northern and southern continents. Two groups of cryptodires occurred in the southern continents during the Cretaceous. The Meiolaniidae from South America and *Otwayemys* from Australia, seem to reflect a widespread distribution of primitive cryptodires that may have diversified prior to the breakup of Pangea in the Early or possibly Middle Jurassic.

3. In Laurasia, three regions can be identified, a North American region, a European region, and a Asian region. In the Early Cretaceous, the North American region is dominated by members of the Paracryptodira. The Asian region is dominated by members of the Eucryptodira, particularly diverse chelomacryptodires of the coastal region, since the Neocomian. Europe includes taxa from both groups, but chelomacryptodiran turtles appears to be rare or absent. In the Late Cretaceous, Eucryptodires, including various trionychoids, become increasingly more abundant and diverse in North America. Such distribution suggests that coastal region of Asia might be an important place for origin and early diversification of the chelomacryptodiran turtles.

4. Within the North American and Asian region, clades that appear to be truly endemic can be identified. One of these is the Baenidae, which are not found outside North America. In Asia, two groups of "modern" cryptodires or Chelomacryptodira, appear to have an Asian origin. One of these is the Testudinoidea, which first appears in the Neocomian of Japan and is restricted to Asia throughout the Cretaceous. The second is the Trionychoidea, although the record for that group is less complete, so the vicariance hypothesis is less strongly supported.

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APPENDIX I. DATA MATRIX

The symbol "?" represents missing or equivocal data. The following symbols are used to represent character states in polymorphic taxa: a = (0, 1), b = (1, 2), c = (0, 2), d = (0, 1, 2), e = (0, 1, 2, 3).

	10	20	30	40	50	60	70	76
Proganochelys	0000000000	0000000000	0000000000	0000000000	0000000000	0000010001	?000200000	000000
Australochelyidae	000000?000	0001000010	0010000100	0000000000	000???0000	000000100??	??00?0??00	000?00
Proterochersis	??????????	??????????	??????????	??????????	??????????	??1???0?00	??00010010	000001
Pleurodira	a1a0011ad0	a1a1b?a01?	001101110c	00a1100010	ba00a0112b	11101010d0	c0a0210000	101001
Kayentachelys	0100111000	0101100110	101111?100	000000000??	?????00000	1?00101001	1000000000	001000
Meiolaniidae	0a01111001	0111110111	1111111103	0000000000	10000?0011	110011111?	?11??00?00	101?00
Sinochelyidae	??0a???000	01??1?????	??11?1?1??	??????????	???????0???	110?1?1110	00a1000000	101100
Mongolochelys	0101111001	0111110111	1111111100	0000000010	10000??011	1100101101	1010000000	101000
Otwayemys	?????????0	??0???????	1?11?1?1??	????000?1?	20?00??011	??0???1?0?	?010000?0	10?100
Kallokibotion	0000111000	0101110?11	1111111100	00?1?00100	0000000?00	?1001?1000	3000010010	101000
Tretosternon	??????1000	01??????11	1111111?0	?????????0	0000??0???	11001?1000	31100?0010	101000
Paracryptodira	010a111ad0	1101110111	1111111111	1aa11001aa	d0000000da	11001010b0	ce00010a10	101000
Plesiochelyidae	01a0111aa0	1101111111	1111110103	1101110100	0000000000	11001010a0	00a0010010	101100
Hylaeochelys	0100111000	?101111111	1111110?3	11????????	???????0???	??0???1000	001001?0??	??1100
Xinjiangchelyidae	0010?11120	1101110111	1111110103	0??1110100	0000000021	1100101010	0201000110	101100
Brodiechelys	??????????	??????????	??????????	??????????	??????????	??0???1?10	0201000110	101100
Sinemydidae	a1a01111b0	1101110111	1111110103	00010a0110	b000010021	1100101ab0	aaa0001111	111110
Chelydroidea	11111111c0	a101110111	1111110103	1011111211	b111aa0021	1100101010	0000d01a11	111110
Chelonioidea	a1aa110ad0	a1a111ab11	1111110103	101111abaa	1a0a100122	11001011ba	c0a0001111	111110
Trionychoidea	111a111120	a1a111a111	1111110103	1a11111211	f111110122	11011a1ab0	eaaaa0a01a	1011a0
Testudinoidea	111a111120	11a1110111	1111a10103	1aa1111211	2111a0012b	11001a10b0	e000a11010	101101

APPENDIX II.
CHARACTERS AND CHARACTER STATES

Skull and Lower Jaw

1. Nasal: (0) = present, (1) = absent.
2. Apertura narium externa: (0) = subdivided, (1) = confluent (Gaffney, 1990).
3. Medial meeting of prefrontals: (0) = absent, (1) = present.
4. Prefrontal-postorbital contact: (0) = absent, (1) = present (Gaffney, 1979b).
5. Prefrontal-vomer contact: (0) = absent, (1) = present.
6. Lachrymal bone and duct: (0) = present, (1) = absent (Gaffney, 1990; Gaffney et al., 1987).
7. Processus inferior parietalis: (0) = reduced or absent, (1) = prominent (Gaffney, 1979b; Hirayama, in press).
8. Parietal-squamosal contact: (0) = present, (1) = absent.
9. Posterior temporal emargination: (0) = foramen stapedio temporale concealed from dorsal, (1) = foramen stapedio temporale exposed from dorsal, (2) = entire of processus trochlearis oticum exposed.
10. Prominent enlargement of squamosal: (0) = absent, (1) = present, reaching supraoccipital (Gaffney, 1983, 1996; Chkhikvadze, 1987).
11. Lower cheek emargination: (0) = absent or shallow with processus pterygoideus externus concealed from lateral, (1) = moderate to deep with processus pterygoideus externus exposed from lateral (Gaffney, 1979b).
12. Supratemporal: (0) = present, (1) = absent (Gaffney, 1990).
13. Prominent lingual ridge of maxilla: (0) = absent, (1) = present (Gaffney, 1983; Khosatzky, 1997).
14. Vomerine teeth: (0) = present, (1) = absent (Gaffney, 1990).
15. Vomer: (0) = paired, (1) = single, (2) = absent (Gaffney, 1990; Gaffney et al., 1987).
16. Palatal teeth: (0) = present, (1) = absent (Gaffney, 1990; Gaffney et al., 1987).
17. Palatines medially meeting: (0) = no, (1) = yes.
18. Processus pterygoideus externus: (0) = no flange, (1) = with vertical flange, (2) = absent.
19. Basipterygoid articulation: (0) = open, (1) = fused (Gaffney, 1990; Gaffney et al., 1987).
20. Interpterygoid vacuity: (0) = open, (1) = closed.
21. Processus trochlearis oticum formed by prootic and quadrate: (0) = absent, (1) = present.
22. Ventral exposure of prootic concealed by a posteromedial process of pterygoid: (0) = absent, (1) = present (Gaffney et al., 1987).
23. Processus paroocipitalis of opisthotic: (0) = loosely articulated, (1) = tightly sutured.
24. Lateral wall to middle ear region: (0) = absent, (1) = present.
25. Pterygoid-basioccipital contact: () = absent, (1) = present (Gaffney, 1979b).
26. Incisura columellae auris: (0) = absent, (1) = present (Gaffney, 1990).
27. Eustachian tube enclosed within elongate incisura columellae auris: (0) = no, (1) = yes (Gaffney, 1979b).
28. Quadrate pocket: (0) = present, (1) = absent (Gaffney, 1990).
29. Fenestra perilymphatica: (0) = large, (1) = small.
30. Foramen posterius canalis caroticus internus: (0) = limited within basisphenoid, (1) = formed by both basisphenoid and pterygoid, (2) = entirely formed by prootic, (3) = entirely formed by pterygoid.
31. Split palatine artery and internal carotid artery: (0) = outside skull, (1) = enclosed in bone.
32. High coronoid process: (0) = absent, (1) = present (Meylan and Gaffney, 1989).
33. Splenial: (0) = present, (1) = lost (Gaffney, 1979b).

Axial Skeleton

34. Cervical ribs of large size: (0) = present, (1) = lost.
35. Transverse process of cervicals: (0) = double, (1) = single.
36. Transverse process of cervicals: (0) = on middle of centrum, (1) = on anterior of centrum.
37. Proportion of cervical central articulation: (0) = as high as wide throughout cervicals, (1) = much wider than high at posterior cervicals.
38. Ventral keel of cervical centra: (0) = absent, (1) = present, (2) = present with thin keel at posterior cervicals.
39. Cervical central articulation: (0) = amphicoelous and not formed, (1) = more or less formed.
40. 8th cervical centrum shorter than 7th: (0) = no, (1) = yes.
41. 8th cervical centrum: (0) = amphicoelous, (1) = procoelous, (2) = biconvex, (3) = opisthocoelous (Williams, 1950).
42. Double cervical articulation between 7th and 8th cervicals: (0) = absent, (1) = present.
43. Double cervical articulation between 6th and 7th cervicals: (0) = absent, (1) = present (Williams, 1950).
44. 1st thoracic vertebra: (0) = with its anterior articulation facing anteriorly, (1) = facing ventrally or anteroventrally.
45. 1st thoracic rib: (0) = distal ends extending laterally beyond nuchal, (1) = distal ends limited within nuchal width.
46. 10th thoracic rib: (0) = reaching 8th pleural, (1) = free from costal (Meylan and Gaffney, 1989).
47. 10th thoracic vertebra: (0) = free from sacrum, (1) = incorporated in sacrum.
48. Chevron: (0) = present, (1) = absent.
49. Anterior portion of caudals: (0) = amphicoelous, (1) = opisthocoelous, (2) = procoelous.
50. Posterior portion of caudal: (0) = amphicoelous, (1) = opisthocoelous, (2) = procoelous.

Appendicular Skeleton

51. Coracoid foramen: (0) = present, (1) = absent (Gaffney, 1990; Rougier et al., 1995).
52. Acromial process: (0) = triangular plate, (1) = rod-like (Gaffney, 1990).
53. Pelvis shell attachment, (0) = pelvis attached to shell by ligaments, (1) = all three bones of pelvis tightly sutured to shell (Gaffney and Meylan, 1988).
54. Therial process of ilium: (0) = absent, (1) = present (Meylan and Gaffney, 1989).
55. Hypoischium: (0) = present, (1) = absent (Gaffney, 1990; Rougier et al., 1995).
56. Short digits toward terrestrial habit (0) = absent, (1) = present (Gaffney, 1990; Rougier et al., 1995).

Shell

57. Supramarginal scales: (0) = present, (1) = absent.
58. Ventral knob or keel articulated with 8th cervical: (0) = absent, (1) = present.
59. Vertebral scutes: (0) = much broader than costal scutes, (1) = as broad as costals and broader than long, (2) = 2nd to 4th vertebrals longer than broad (Gaffney, 1990).
60. 9th costal plate: (0) = absent, (1) = present (Gaffney et al., 1987; Gaffney, 1990; Khosatzky, 1997).
61. Suprapygal: (0) = nearly equally subdivided into two, (1) = first suprapygal much smaller than second, (2) = first suprapygal absent, (3) = second suprapygal absent or much smaller than first.
62. Marginals reaching pleurals: (0) = absent, (1) = partially present, (2) = 4th to 7th marginals yes (Meylan and Gaffney, 1989; Peng and Brinkman, 1993).
63. Plastral fontanelles surrounded by hyo-hypoplastra: (0) = absent, (1) = retained in adult.

APPENDIX II (continued).

64. Midline plastral scute sulcus sinuous: (0) = no, (1) = yes (Meylan and Gaffney, 1989; Peng and Brinkman, 1993).
65. Inframarginals: (0) = four or three pairs present, (1) = two pairs (axillary and inguinal) present, (2) = absent (Meylan and Gaffney, 1989).
66. Plastral buttresses: (0) = reaching only peripherals, (1) = reaching costals.
67. Gular scutes: (0) = two pairs, (1) = one pairs.
68. Femoral-anal sulcus reaching hypoplastron: (0) = no, (1) = yes (Peng and Brinkman, 1993).
69. Dorsal process of epiplastra: (0) = present, (1) = absent.
70. Epiplastron: (0) = moderately broad, (1) = narrow.
71. Epiplastra subdivided by entoplastron: (0) = yes, (1) = no (Rougier et al., 1995).
72. Entoplastron: (0) = moderately broad, (1) = narrow.
73. Elongate dorsomedial keel of entoplastron: (0) = present, (1) = absent (Rougier et al., 1995).
74. Mesoplastron: (0) = present, (1) = absent.
75. Xiphiplastron: (0) = moderately broad, (1) = narrow.
76. Anal median notch of xiphiplastra: (0) = absent, (1) = present (Meylan and Gaffney, 1989).

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