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A new Shachemydinae (Chelonii, Cryptodira) from the Lower Cretaceous of Laos: preliminary data

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Abstract

The Lower Cretaceous of Laos produced remains of freshwater cryptodiran turtles including some elements of aff. *Xinjiangchelys* and of Trionychoidea: Trionychidae, Carettochelyidae and beautiful specimens of a new species of *Shachemys*. The latter is defined, compared and placed in the family Adocidae. The family is reconsidered and the subfamily Shachemydinae is confirmed; the latter ranges from the Upper Jurassic to the Senonian of Asia. Its good adaptation to aquatic life is asserted. ***To cite this article: F. de Lapparent de Broin, C. R. Palevol 3 (2004)***.

Résumé

Un nouveau Shachemydinae (Chelonii, Cryptodira) du Crétacé inférieur du Laos : résultats préliminaires. Le Crétacé inférieur du Laos a livré des restes de tortues cryptodires d'eau douce comportant quelques fragments d'une forme affine de *Xinjiangchelys* et de Trionychoidea: Trionychidae, Carettochelyidae et une nouvelle espèce de *Shachemy*s. Celle-ci, bien préservée, est définie, comparée et placée dans la famille des Adocidae. La famille est reconsidérée et la sous-famille des Shachemydinae est confirmée, répartie du Jurassique supérieur au Sénonien d'Asie. Sa bonne adaptation à la vie aquatique est montrée. ***Pour citer cet article : F. de Lapparent de Broin, C. R. Palevol 3 (2004)***.

Keywords: aff. *Xinjiangchelys*; Trionychia; *Shachemys*; Adocidae; Cretaceous; Laos

Mots clés : aff. *Xinjiangchelys* ; Trionychia ; *Shachemys* ; Adocidae ; Crétacé ; Laos

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Introduction

La nouvelle faune de tortues cryptodires, d'eau douce [1,2], trouvée par l'équipe Franco-Lao du Pr. P. Taquet entre 1990 et 2001 dans les Grès supérieurs du Crétacé inférieur [1,2,30] de la province de Savannakhet au Laos (Fig. 1, A), comporte: des os de Trionychidae à Tang Vay 1 (Fig. 1, A, 1) ; des restes de petits Carettochelyidae à Tang Vay 4 (Fig. 1, A, 1) et au cimetière de Ban Viengh Hay (Fig. 1, A, 2); un fragment attribué à aff. *Xinjiangchelys* sp. [21,26,27], à Ban Lam Thoy, berge de la rivière Koumkam, site de Tang Vay (Fig. 1, A, 1), distinct du taxon Jurassique de Thaïlande [29]; une nouvelle espèce de *Shachemys*, Adocidae, trouvée avec la précédente à Ban Lam Thoy (Fig. 1, A, 1), ainsi que des écailles de *Lepidotes*. Les Adocidae sont considérés ici comme un groupe monophylétique parmi les Trionychoidea Trionychoidae [15] et non dans les Testudinoidea [17,21] et leurs relations internes sont reconsidérées à partir des caractères du nouveau matériel, comportant le crâne et la carapace complète. Leur position est examinée par rapport aux taxons plus primitifs *Proganochelys* [5], *Kayentachelys* [6] et *« Annemys »* (nomen nudum in [27]). Les Adocinae sont limités ici au groupe *Adocus* [7,8,15,16]. Toutefois, il sera possible d'y inclure de nouveaux taxons de Trionychoidea indéterminés provenant du Néocomien du Japon [10,11] et du Crétacé inférieur (contemporains de ceux du Laos) de Thaïlande [30], lorsque les descriptions complémentaires et les figurations nécessaires seront publiées. Les Adocinae sont séparés ici (Fig. 1, S) des Shachemydinae, comportant *Ferganemys* [23], *« Plesiochelys » tatsuensis* [31] ; voir [20,27] et *Shachemys* [12]. Des diagnoses sont proposées, comportant des homoplasies (voir [4,7,8,14,15,25,27]). Les inter-relations de la superfamille seront examinées par la suite.

Systématique (voir la version anglaise)

Les détails (étymologies, redéfinitions, répartition, matériel) sur les Adocidae Cope, 1870 (Fig. 1, S, noeud A) [3,7–13,15–24,28,27,30], les Shachemydinae Khosatzky in Nessov et Khozatzkii, 1977 [23] (Fig. 1, S, B1) et les Adocinae [23] (Fig. 1, S, C) sont donnés dans la version anglaise.

Les Adocidae sont des Trionychoidae à conjonction unique de caractères dérivés, homoplasiques, dont : un allongement des éléments antérieurs et postérieurs de la carapace étrécie, notamment les périphériques postérieures allongées et étrécies; les marginales chevauchant la suprapygale suivant un arrondi antérieur; la tendance à la réduction de la série neurale postérieure et de la suprapygale 1 ; la cervicale étroite et tendant à disparaître, le crâne allongé dans la région otico-cérébrale. **Les Shachemydinae** se distinguent principalement des Adocinae par la tendance à la réalisation d'une charnière épi / hyo-entoplastrale, avec réduction de la partie antérieure de l'entoplastron et racourcissement des intergulaires, et un abaissement et un allongement avec étrécissement des éléments du crâne (notamment à l'arrière ventral du crâne, mieux ossifié, et dans la région otico-cérébrale, avec la trochlée saillant seulement latéralement) et des éléments post-crâniens. Tous les caractères ne sont pas connus dans chaque genre. **Les Adocinae** ont une ornementation de minuscules cupules plus ou moins alignées et, dans le groupe *Adocus*, un important chevauchement (autapomorphie) par les marginales de la suprapygale à la pleurale 2 ou 1 [16]; le crâne a des caractères adaptatifs, éventuellement réversifs par rapport à « *Annemys levensis* » (noeud x [29]) et aux Shachemydinae. ***Shachemys*** Kuznetsov, 1976 [9,12,13,23,24] (Fig. 1, S, noeud B3) est principalement caractérisé par la charnière complète, avec coïncidence de la suture épi / hyo-entoplastrale et du sillon gularo-intergulaire / humérales, l'absence presque totale de neurales, l'absence de suprapygale 1 et de cervicale, le prootique très étroit et le processus trochléaire le plus proche du postorbitaire échancré. En cela, *Ferganemys* (Fig. 1, B1 avant B2) est plésiomorphe; son lobe antérieur trapézoïdal-arrondi [23] (trapézoïdal chez *Adocus* [7,8] et le Trionychoidea indet. de Thaïlande [30] est primitif ou homoplasique; *Ferganemys* est dérivé par la décoration de la carapace, faite de fines crêtes séparant des fins sillons et petites cupules [18,21]), le lobe postérieur plus pointu [23] et plus que chez *A. amtgai* [16], et par quelques autres détails (crâne, inframarginales). Avec quelques caractères encore primitifs pour la famille, *« Plesiochelys » tatsuensis* (dans la mesure où il est connu) partage avec *Shachemys* (Fig. 1, S, node B2) la présence effective de la charnière avec angle antérieur entoplastral devenu, respectivement, presque plat à totalement plat.

***Shachemys laosiana* n. sp.**, du nom du peuple Lao; site de Tang Vay, Ban Lam Thoy, berge de la rivière Koumkam, S de Muong Phalan, province de Savannakhet, R.D. Lao, Fig. 1, A, 1; Grès supérieurs, Aptien-Albien, Crétacé inférieur [1,2,28]. *Musée des Dinosaures* of Savannakhet. BLT 1 à 4; holotype, BLT 1, Fig. 1 B-G et paratypes BLT 2 et BLT 3 (Fig. 1, H-R), BLT 4.

Diagnose : il diffère de *S. b. baibolitica* Kuznetsov, 1976 [12,13] et *S. b. ancestralis* Nessov, 1984 in [24] (dans la mesure où ce dernier est connu), par le bord antérieur arrondi de la carapace, ovoïde par allongement des périphériques et de la nuchale sans encoche antérieure, les plus larges vertébrales, les marginales chevauchant seulement une partie médiale de la suprapygale, le lobe antérieur élargi et arrondi d'où des encoches axillaires étroites, la très faible encoche anale xiphiplastrale. Caractères additifs : décoration lisse, avec très petits sillons dichotomiques et granulations par places (pont, plastron, Fig. 1, J) et grosses punctuations séparées visibles au MEB. La forme de la carapace est ovoïde, le plastron atteignant ou non le bord antérieur nuchal. Les longueurs et largeurs (en millimètres) sont : carapace, ca 190 × 143 (BLT1 : mâle?), ca 165 × 145 (BLT2 : femelle?) et ca 210 × 155 (BLT3) ; une vertèbre cervicale (allongée et étroite comme les ceintures et membres, Fig. 1, B, C), BLT 1 : 15 × 4; fémur, BLT1 : 33 × 6 distalement, plus long que l'humérus, BLT1 : 28 × 6, sans palette natatoire. Ces élongations peuvent être génériques ou subfamiliales, mais *S. laosiana* n. sp. est la forme qui protège le mieux les membres, cou et tête.

Conclusion

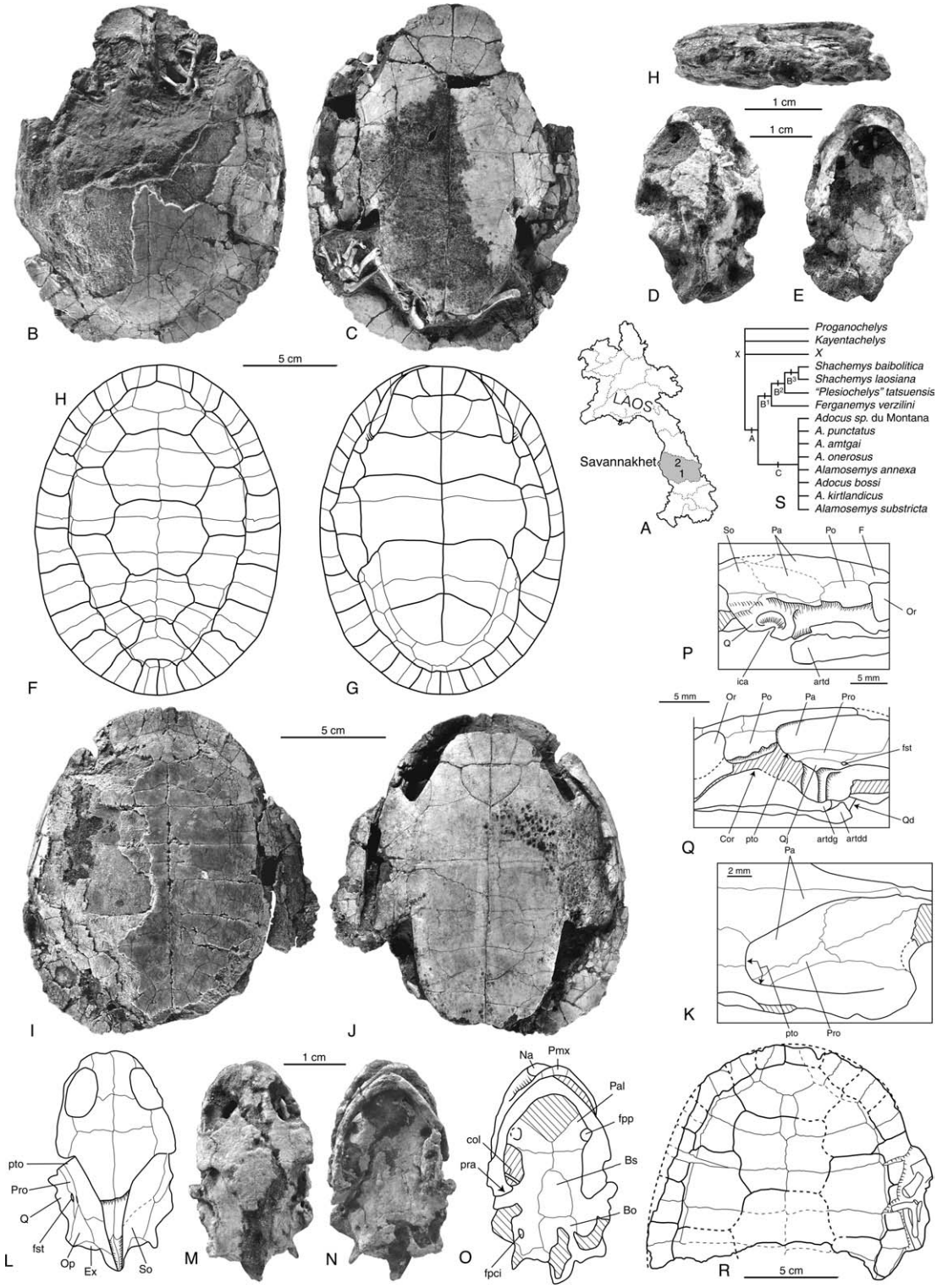
Les Trionychoidea fossiles du Laos ont un haut degré d'évolution (crâne, adaptation à la vie aquatique) pour une époque aussi ancienne, comme cela est connu pour les Trionychia Trionychidae et Carettochelyidae, toujours actuels, à palettes natatoires, les seconds pratiquant le mouvement synchrone des membres antérieurs comme les tortues marines actuelles. Contrairement à celles-ci, le membre antérieur trionychoïde est encore flexible et pas encore plus long que le postérieur. Les Shachemydinae sont bien hydrodynamiques mais dépourvus de palettes natatoires. Ces Trionychoidea sont parmi les plus anciens du monde [10,11,14,19,22,27,30–32], l'Asie étant leur berceau. Les Shachemydinae, restés asiatiques, ont disparu avant le Maastrichtien; les deux précédentes familles, Trionychidae et Carettochelyidae, largement dispersées dans le monde au cours des temps géologiques, sont les plus anciennes de tortues vivant toujours actuellement, dont les Trionychidae au Laos.

1. Introduction

The Franco-Lao team led by Pr. P. Taquet from 1991 to 2001) [1,2] found a new freshwater fossil fauna of cryptodire turtles in the continental Lower Cretaceous beds of the Savannakhet province of Laos (Fig. 1, A). Based on several works, summarized in [1,2], these beds belong to the Grès supérieurs Formation of the Indosinias Group. They are attributed to the continental Aptian-Albian, principally on the presence of freshwater Trigonioidacea bivalvia. The turtle fauna includes:

- Trionychidae indet. (of two sizes): limb bones, Tang Vay area (Fig. 1, A, 1), locality Tang Vay 1;
- Carettochelyidae indet. (small size): isolated plates, locality Tang Vay 4 (Fig. 1, A, 1) and locality of the Ban Viengh Hay cemetery (Fig. 1, A, 2);
- Aff. *Xinjiangchelys* sp. (Xinjiangchelyidae): a part of a large dorsal shell, locality Ban Lam Thoy, bank of the Koumkam river, Tang Vay area (Fig. 1, A, 1); it is approximated to this taxon, because it compares more favourably with the specimens of this form from the Late Jurassic of China [26,27,31] than with the taxon from the Middle Jurassic of Thailand [27]; and lastly
- the new species of *Shachemys*, Adocidae, Ban Lam Thoy (Fig. 1, A, 1), found at the same place as the Xinjiangchelyid, in sediments which also provided *Lepidotes* scales, indicating the presence of a stream.

The Adocidae are considered as a monophyletic group in the Trionychoidea Trionychoidae, according to Meylan and Gaffney [15], and their interrelationships are reconsidered with the help of additional characteristics provided by the new material. A preliminary study, performed with the Hennig 86 program, has firstly examined their position (Fig. 1, S) with respect to the very primitive *Proganochelys* [5] and to *Kayentachelys* Gaffney et al. 1987 [6]. Since this study, a new publication has produced new possible outgroups, i.e.


B
C
H
1 cm
1 cm
D
E
5 cm
H
F
G
LAOS
Savannakhet
2
1
A
Proganochelys
Kayentachelys
X
Shachemys baibolitica
Shachemys laosiana
"Plesiochelys" tatsuensis
Ferganemys verzilini
Adocus sp. du Montana
A. punctatus
A. amtgai
A. onerosus
Alamosemys annexa
Adocus bossi
A. kirtlandicus
Alamosemys substricta
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Pal
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O
R
5 cm

the two "species"of the taxon X of the cladogram, "genus *Annemys*" (nomen nudum in [27] with *"A. latiens"*, a shell, and *"A levensis"*, a skull) from the Upper Jurassic of Mongolia, not photographed and not yet sufficiently described and measured. Both of these are relatively primitive but with some derived characteristics that occur in Adocidae. Nessov already situated *Shachemys* as *Ferganemys* in the Adocidae [24], considered as members of the Testudinoidea [17,21]. Meylan and Gaffney [15] interpreted the Adocidae, containing *Adocus* and possibly *Ferganemys*, to be within the Trionychoidea, while *Shachemys* was provisionally considered to be *incertae sedis*. I include *"Plesiochelys" tatsuensis* Yeh, 1963 [31] in the Adocidae, as in [20,27], although a new observation would be necessary. Separation is made here between Adocinae, preliminary limited here to the *Adocus* group, and Shachemydinae. New possible members of the ingroup are a new Trionychoidae indet. from the Neocomian of the Kuwajima Formation of Central Japan [10,11] and a new adocid-like trionychoid indet. from the Early Cretaceous of the Sao-Khua Formation of Thailand [30]. They are not yet accurately measured, with contradictions between the photographs and the reconstruction of the skull (possibly too narrow and long snout in [10,11]; isolated skull and shell elements), or not at all measured (in [28]; shells only). However, based on the short preliminary descriptions, they are members of the Adocidae, notably because of the reduction of the posterior neural series and suprapygal 1 and the punctate ornamention of the plates; the form from Japan has the marginals 11 and 12 on the suprapygal 2 as in Adocidae, (unknown in the Thailand form) and several skull characteristics of Adocinae (see below). The Adocinae of the node C (Fig. 1, S) are the best figured [7,8,15,16] (other species are mentioned in the following references [3,9,18,19–24,27] which also provide necessary supplementary references). The characteristics of the diagnoses are either homoplastic (same evolutionary process leading to the same result) or only analog (different processes and not exactly similar results) in Mesozoic Asiatic cryptodires [27], in some Testudinidae [4,14] and in Trionychia [4,7,8,15] and in the European Cretaceous *Pleurosternon* Owen, 1853 [25]). A further study of all the Laos turtle fauna will give the complete detailed cladistic analysis and better examine the interrelationships of the superfamily.

2. Systematics

Order Chelonii Brongniart (Latreille), 1800
Infra-order Cryptodira Cope, 1868

A, Map of Laos with the location of the Savannakhet province; 1, area of Tang Vay; 2, Ban Viengh Hay cemetery. B-R, *Shachemys laosiana* n. sp., Tang Vay, Ban Lam Thoy, bank of the Koumkam river. B-G, BLT1, holotype; B, C, carapace, dorsal and ventral views; D, E, skull, dorsal and ventral views; F, G, carapace reconstruction, dorsal and ventral views. H-K, BLT2, paratype; H, skull, left lateral view; I, J, carapace, dorsal and ventral views; K, skull detail, left lateral view, showing the very elongated otic area with the trochlear process up to the postorbitary, much notched, and the narrow and elongated prootic; L-R, BLT3, paratype; L-O, skull, dorsal and ventral views; P, skull detail, right lateral view; Q, skull detail, left lateral view, showing the ascending coronoid process in the lateral skull emargination and, as in L, the otic trochlear process only laterally salient, and the elongated and narrow prootic with the stapediotemporal foramen, small and posterolaterally situated; R, dorsal carapace drawing. S, hypothetical relationships of the examined taxa.

Artd, d, g, dentary articular area, right, left/ région articulaire dentaire, droite, gauche; Bo, basioccipital; Bs, basisphenoid/ basisphénoïde; col, *columella auris*, (shift/ déplacée); Cor, coronoid/ coronoïde; Ex, exoccipital; F, Frontal; fpci, *foramen posterius canalis carotici interni*; fpp, *foramen palatinum posterius*; fst, *foramen stapedio-temporale*; ica, *incisura columellae auris*; Na, external nare/ narine externe; Op, opisthotic/ opisthotique; Or, orbit/ orbite; Pa, parietal/ pariétal; Pal, palatine/ palatin; Pmx, premaxillary/ prémaxillaire; Po, postorbitary/ postorbitaire; pra, dentary articular process/ région articulaire dentaire; Pro, pootic/ prootique; pto, *processus trochlearis oticus*; Q, quadrate/ carré; Qd, right quadrate/ carré droit; Qj, quadratojugal; So, supraoccipital.

A, Carte du Laos avec l'emplacement de la province de Savannakhet; 1, sites de Tang Vay; 2, site du cimetière de Ban Viengh Hay. B-R, *Shachemys laosiana* n. sp., Tang Vay, Ban Lam Thoy, berge de la rivière Koumkam. B-G, BLT1, holotype; B, C, dossière et plastron, faces dorsale et ventrale; D, E, crâne, faces dorsale et ventrale; F, G, reconstitution de la carapace, faces dorsale et ventrale. H-K, BLT2, paratype; H, crâne, face latérale gauche; I, J, carapace, faces dorsale et ventrale; K, détail du crâne en vue latérale gauche montrant la région otique très allongée avec le processus trochléaire jusqu'au postorbitaire, très encoché, et le prootique étroit et long; L-R, BLT3, paratype; L-O, crâne, faces dorsale et ventrale; P, détail du crâne, vue latérale droite; Q, détail du crâne, vue latérale gauche, montrant la montée du coronoïde dans l'encoche latérale du crâne, le processus trochléaire otique saillant seulement latéralement, comme en L, et le prootique étroit et allongé avec le *foramen stapedio-temporale* petit et en position latéropostérieure; R, dessin de la carapace dorsale. S, Schéma hypothétique des relations de parenté des taxons examinés.

Superfamily Trionychoidea Fitzinger, 1826
Epifamily Trionychoidae Fitzinger, 1826

2.1. Family Adocidae Cope, 1870

Etymology: from the type-genus *Adocus* Cope, 1868, type-species *Emys beatus* Leidy, 1865, Greensands of Mullica Hill, senior synonym of *A. punctatus* Marsh, 1890, Hornerstown Formation, both from the Upper Cretaceous of New Jersey, USA [8].

Distribution: Upper Jurassic-Eocene of Asia, Upper Cretaceous-Paleocene of North America.

Emended diagnosis (Fig. 1, S, node A). Combination of homoplastic features: - elongated and narrowed shell elements, in particular elongated and narrowed nuchal and posterior peripherals; - reduction of the posterior neurals-suprapygal 1 series; - posterior marginals overlaping the suprapygal along a rounded line; - tendency to a strong reduction up to absence of the cervical; - vertebrals 2d to 5th narrowed; - thoracic rib 1 reduced to its medial part, thinned and diverging from the 2d one; - skull elongated in the otico-cerebral area; - prootic narrowed through its whole length, including anteriorly.

Additive characteristics: The posterior dorsal emargination of the skull is strong. The neck formula may be that of *Adocus* sp. from Montana, with opisthocoelous vertebrae, i.e. that of the Trionychoidae [15]. The flexion of the bridge and plastral buttresses, which elevates the dorsal shell with respect to the plastron, may be acquired either at the Adocidae node or before.

2.2. Subfamily Shachemydinae Khosatzky in Nessov and Khozatzkii, 1977

Etymology: from the type-genus *Shachemys* Kuznetsov, 1976 (see below).

Distribution: Asia s.s., Upper Jurassic of China - Santonian of Kazakhstan. *Ferganemys verzilini* Nessov and Khozatskii 1977 [23], Kirghistan, Albian; *F. itemirensis* Nessov, 1981 [18], Albian?-Cenomanian of Itemir, Kyzyl Kum, Uzbekistan; *"Plesiochelys" tatsuensis* Yeh, 1963 [31], Upper Jurassic of Szechuan, China; *Shachemys laosiana* n. sp, Lower Cretaceous, Aptian-Albian, Laos; *Shachemys* sp., Cenomanian?, Mifune group, Occidental Japan [9]; *S. baibolitica ancestralis* Nessov, 1984 in [24], Upper Turonian-Coniacian, Uzbekistan; *S. b. baibolitica*, Kuznetsov, 1976 [12,13], Santonian, Kazakhstan. Other references above and in [27]. The carapace is preserved as isolated pieces in *Ferganemys* spp. and most of *Shachemys* spp.; the pleural disc of *"P." tatsuensis* is incomplete; skulls known only in *S. laosiana* n. sp. and *F. verzilini*.

Emended diagnosis (Fig. 1, S, node B1): The Shachemydinae differ from the species of the node C, Adocinae, in: - the more flattened shell; - the ventral border of the marginals progressively more narrowed toward the nuchal; - the posterior border of the intergulars truncated just in front of the entoplastron which is anteriorly shortened.

Characteristics of the skull: *S. laosiana* n. sp. and *F. verzilini* differ from *Adocus* sp. from the Montana [15] (only Adocine known skull; Fig.1, S, C) in: - the greater lateral emargination with the rounded posterolateral maxillary border; - the whole skull more elongated, more depressed, the narrower interorbitary space and the more dorsal orbits (four characteristics already acquired at node x in "*A. levensis*", either homoplastic with Shachemydinae or reversed in *Adocus* and the trionychoid from Central Japan [10,11]); - the still more elongated otico-cerebral area and the trochlear process projected only laterally (as in Trionychidae); - the still more narrowed prootic (homoplastic with some Testudinidae); - the completely closed carotid canal which is posteriorly open, in an elongated pterygoid covering the postotic fenestra (as in Trionychidae), by a posterior carotid foramen which is posterior to the basisphenoid-basioccipipal suture.

Characteristics partly homoplastic with the Adocinae: - the tendency to the reduction of the suprapygal 1 (partial reduction of the suprapygal 1 in some *Adocus* [7,8] and in the new Trionychoidae from Japan [10,11]), as in *Ferganemys*; complete reduction in *Shachemys*); - the axillary processes drawn back up to the posterior limit of the peripheral 2 (as in *Adocus* sp. from Montana [15]) or beginning of the 3d; - vertebrals progressively narrowed as one proceeds from the 2d to the fourth in *Ferganemys, S. laosiana* n. sp. and the *Adocus* group; - anterior lobe either rounded or trapezoidal.

Additive characteristics: The incisure of the columella is still open, V-shaped, short and rather narrow (narrower in *Adocus* but still not closed as it is in Trionychia) and the triturating surfaces are narrow (as in *"A. levensis"*) (both primitive characteristics). The Shachemydinae have a more hydrodynamic shape than

the Adocinae, all their elements being elongated, low and slender (carapace, skull, vertebrae, girdles and limbs) with a ligamentous plastron-carapace junction (pedomorphosic and primitive), the limit of which still basically coinciding with the inframarginals-marginals sulcus, this not sinuous and not more or less (specifically) overlaping the peripherals as in *Adocus*. Besides, the Adocinae (Fig. 1, S, C) (Lower Cretaceous-Upper Eocene of Asia, Upper Cretaceous-Paleocene of North-America (Fig. A, C) have a characteristic carapace ornamentation of minute pits, more or less in line [7,8,21] and, in the *Adocus* group, a very important overlap of marginals (autapomorphy), from the 12th and 11th on the suprapygal to the detriment of the vertebral 5 and then forward on the pleurals, to the detriment of the costals, up to the pleurals 2 and even 1 in *A. amtgai* |16], from the Turonian-Lower Santonian of Mongolia (*"Adocoides"* Sukhanov and Narmandakh in press, nomen nudum in [3,27]) (analogy in *Pleurosternon*); the skull of *Adocus* sp. from Montana has a very marked otic trochlea, salient on each side, which seems in relation with a durophageous diet according to the strong coronoid process, the wide upper triturating surfaces (wide also in the Trionychoidae of Central Japan [10,11]), wide lower triturating surfaces and crested upper ones, the more robust skull shape with a wider and shortened snout, with a wider interorbitary space and a salient inferoposterior maxillary angle (both characteristics also present in the latter [10,11]). The lack of skulls and the mosaic distribution of the shell characteristics do not allow one to clearly define the relationships between the *Adocus* species.

2.3. Genus *Shachemys* Kuznetsov, 1976

Etymology: from Shach-Shash, locality of the type-species.

Type-species: *Shachemys baibolitica*, Kuznetsov, 1976 [12], Santonian, Kizyl-Orda District, east to Aral Sea, Kazakhstan.

Distribution: Lower Cretaceous in Laos (*S. laosiana* n. sp.), ?Cenomanian in Japan (*S.* sp., [9], Upper Turonian-Coniacian in Uzbekistan (*S. baibolitica ancestralis* Nessov in [24]), and Santonian in Kazakhstan (*S. b. baibolitica* [12]).

Emended diagnosis (Fig. 1, S, node B3): Narrowed axillary notches; the epi / hyoentoplastral hinge coincides exactly with the gularointergular / humeral sulcus; most narrowed nuchal for the family, anteriorly and posteriorly; absence of neurals except the first one, pentagonal, sometimes present in each species; absence of the first suprapygal; robust and small thoracic rib 1 [see in 13], reduced to its more medial part, short but rather wide and abruptly diverging from the rib 2. Based on *S. laosiana* n. sp., with respect to *Ferganemys verzilini* [17,21]: small foramen stapediotemporale; more narrowed prootic; smaller orbits; otic trochlear process closer to the postorbitary; less sinuous transversal prefrontofrontal suture.

Homoplastic characteristics: humeropectoral sulcus medially extended on the posterior part of the entoplastron (as in some *Adocus* [8,16], Testudinidae and others); complete absence of cervical (as in some *Adocus* [8] and some Testudinidae).

Some of the above characteristics, lacking in *"Plesiochelys" tatsuensis* (skull, pleural disc, [31]) and *S. baibolitica* (skull, parts of the shell, [12,13,20]), may be either subfamilial or specific.

Additive comparative characteristics: Besides the skull characteristics, *Ferganemys* (Fig. 1, B1 before B2, known by isolated pieces) differs from *Shachemys* by the: - shell ornamentation of fine ridges and sulci or minute pits [18,21]); - modified inframarginals (limits not completely known) [18,23,24]; - more narrowed vertebral 1; - anterior limit of the marginals 12 and 11 on the suprapygal (homoplastic with *S. b. ancestralis* [20,24]); - posterior lobe strongly narrowed toward the back, narrower and less rounded than in *Shachemys,"P". tatsuensis* and the *Adocus* from the North American Upper Cretaceous-Paleocene [7,8]: it is even sharper [23] than in *Adocus amtgai* [16]. The posterior gular limit is slightly distant from the epi / hyoentoplastral suture, owing to the not straight anterior angle of the entoplastron (although much obtuse), a hinge being not present, and the suprapygal is not completely reduced: both characteristics are plesiomorphic with respect to the node B2 (*Shachemys* and *"P". tatsuensis*); the anterior border of the anterior lobe, semi-trapezoidal [23], is less rounded than in *Shachemys* and *"P". tatsuensis* (a well trapezoidal lobe is acquired in *Adocus* but not in the form from Central Japan). "*A. latiens*" is much more primitive than the Adocidae, particularly by its wide carapace, wide and short nuchal and long and narrow entoplastron; its femoroanal sulcus medially overlaps the hyoplastra, an ambiguous character present in vari-

ous Mesozoic taxa, often by intraspecific variation (when several specimens are known); "*A. latiens*" has, as the Trionychia and Adocidae, a tendency to the reduction of the posterior neurals (linked pleurals 8) (also as in other Mesozoic taxa [27]) and a tendency of marginals to overlap the pleurals as in various cryptodire taxa including the Adocidae: in some specimens, marginals laterally overlap the pleurals 2 (*S. laosiana*) or 8 (*S. b. baibolitica*) or 2 and 5 (*F. verzilini*), besides the very strong overlap of the pleurals 1-2 up to the suprapygal by the marginals in the *Adocus* group (autapomorphy).

"P." tatsuensis and *Shachemys* (Fig. 1, S, node B2) share an epi / hyoentoplastral hinge, the anterior entoplastral angle being nearly and completely straight, respectively. The former differs from *Shachemys* by characteristics much more evolved than in *Proganochelys* and *Kayentachelys* but less than in the other Adocidae, which implies several homoplasies in the adocid genera: the longer anterior lobe (medial length with respect to the epiplastral width at the epihyoplastral suture = ca 80% versus < 77% in other Adocidae), the more elongated epiplastra posterolaterally, even more than in *"Annemys latiens"*, and, correlatively, the lateral border of the gulars not fused with the epihyoplastral suture despite the presence of a hinge; it is however more derived than in *"A. latiens"* particularly in: the more anterior humeropectoral sulcus, the wider entoplastron and the narrowed posterior lobe extremity. Its ornamentation is finely pitted to granuloid.

2.4. *Shachemys laosiana n. sp*

Etymology: from the name of the Lao people.

Type locality and horizon: Area of Tang Vay, Ban Lam Thoy, bank of the river Koumkam, 16° 24' 16″ N, 105° 40' 49″ E, south of Muong Phalan, Savannakhet province, R.D. Lao, Fig. 1, A, 1; Grès supérieurs Formation, Aptian-Albian, Lower Cretaceous [1,2,30].

Material: *Musée des Dinosaures* of Savannakhet. BLT 1 to 4, all elements found associated: **holotype**, BLT 1, Fig. 1, B-G, carapace (anteriorly incomplete dorsal shell, plastron), posterior cervical vertebrae with eroded condyles, remains of the girdles, anterior and posterior limbs, skull. Paratypes: BLT 2, Fig. 1, H-K, carapace (dorsal shell posteriorly incomplete, plastron), skull; BLT 3, Fig. 1, L-R, incomplete carapace (dorsal shell up to pleurals 5, plastron without the posterior lobe), scapula and partial humerus, skull; BLT 4, part of a carapace only dorsally prepared (pleurals 2 to posterior extremity).

Diagnosis: differs from *S. baibolitica* in the: - anterior border of the dorsal carapace rounded, ovoid by progressive elongation toward the mid-line of the anterior peripherals and all the nuchal, not notched; - narrower axillary notches because of the more rounded and wider border of the anterior lobe; - very weak medial depression on the rounded posterior lobe border; - the anterior limit with the vertebral 5 of the marginals 12 only medially on the suprapygal (up to the pleural 8 in *S. b. ancestralis*). More primitive in the wider vertebrals.

Additive characteristics: There are four inframarginals. The ornamentation is smooth with minute dichotomic sulci, to finely granulous by places (bridges, plastron, Fig. 1, J) and spaced punctuations are visible by SEM. The shell shape is ovoid, the plastron reaching (BLT3) or not (BLT2) the anterior border of the nuchal. The shell length and width are (in mm): 180 preserved of ca 190 × 143 (BLT1: male?), 159 of ca 165 × 145 (BLT2: female?) and 142 of ca 210 × 155 (BLT3). The cervical vertebrae are elongated and slender (a posterior of BLT1: 15 x 4 mm) as are the girdles and limbs (Fig. 1, B, C). The posterior limb (femur, BLT1: 33 x 6 mm distally) is longer than the anterior one (humerus, BLT1: 28 × 6 mm), seemingly not paddle-shaped. These elongations and slenderness are probably generic and even subfamilial but *S. laosiana* n. sp. is the form which better protects its limbs, neck and skull.

3. Conclusions

The freshwater trionychoids from the Lower Cretaceous of Laos are remarkable by the high evolutionary degree for such an early time, in the skull construction as well as in the aquatic adaptation. This is well known for the still extant Trionychia Trionychidae and Carettochelyidae (with paddles and the latter even possessing the synchroneous movement of the anterior limbs, as the extant marine turtles) and this is visible in the Shachemydinae, although they are less adapted to swimming (without paddles). The trionychoid anterior limb is still flexible and shorter than the posterior one, contrary to the marine extant forms. The trionychoids

from the Lower Cretaceous from Laos (Trionychia, Shachemydinae) are among the oldest in the World [14,27]. The geological age is close to that of the new forms from the Early Cretaceous (Neocomian) of Japan [10,11], which are possibly slightly older, and as old as the new form from the Early Cretaceous of Thailand [30]. Trionychids are also present in the Early Cretaceous of Japan [11] and in the Lower-Middle Albian from Kirghistan [19]. Before, Trionychoid forms are known in China from the Upper Jurassic [31] (Carettochelyidae and Shachemydinae) and Early Cretaceous [32] (Trionychidae) showing that Asia is the birthplace of the whole group. The age of separation between the Adocinae and Shachemydinae and between the Adocidae and the Trionychia is Jurassic. The Shachemydinae, which remained Asiatic s.s., disappeared before the Maastrichtian, while the Adocids are known up to the Eocene of Asia. On the other hand, the two former families of Trionychia, Trionychidae and Carettochelyidae, spread widely in the world, where they are the oldest still living family of turtles, among which is the Trionychidae in Laos.

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