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A REDESCRIPTION OF *ELKEMYS AUSTRALIS* (YEH, 1974), A POORLY KNOWN BASAL TESTUDINOID TURTLE FROM THE PALEOCENE OF CHINA

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ABSTRACT

In this study we provide a redescription of the type series of *Elkemys australis*, a poorly known basal testudinoid turtle ('Lindholmemydidae') from the Paleocene of China. Based on new observations we report on some previously overlooked shell characters of *Elkemys australis*, and also provide a new diagnosis and a new reconstruction for this species. Among 'lindholmemydids', *Elkemys australis* is most similar to *Gravemys barsboldi* from the Late Cretaceous of Mongolia. *Elkemys australis*, *Gravemys* spp. and *Hokouchelys chenshuensis* from the Paleocene of China differ from other 'lindholmemydids' and testudinoids in general in an unique inframarginal pattern (four or five pairs of wide inframarginal scutes which strongly extend on to peripherals), and may form a natural group (either a clade or a grade) of basal testudinoids. Some other characters shared by *E. australis*, *G. barsboldi* and *H. chenshuensis* (large anal notch and relatively narrow vertebrals 2 and 3) are characteristic of some geoemydids and testudinids, that may indicate closer relations of the three mentioned genera to these groups.

Key words: China, *Elkemys*, 'Lindholmemydidae', Paleocene, Testudinoidea, Turtles

ПЕРЕОПИСАНИЕ *ELKEMYS AUSTRALIS* (YEH, 1974), ПЛОХО ИЗВЕСТНОЙ БАЗАЛЬНОЙ ТЕСТУДИНОИДНОЙ ЧЕРЕПАХИ ИЗ ПАЛЕОЦЕНА КИТАЯ

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РЕЗЮМЕ

В этой работе мы даем переописание типовой серии *Elkemys australis*, плохо известной базальной тестудиноидной черепахи ('Lindholmemydidae') из палеоцена Китая. На основе новых наблюдений мы сообщаем о некоторых ранее незамеченных панцирных признаках этого вида, а также даем его новый диагноз и новую реконструкцию. Среди 'линдхольмемидид' *E. australis* наиболее сходен с *Gravemys barsboldi* из позднего мела

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Монголии. *Elkemys australis, Gravemys* spp. и *Hokouchelys chenshuensis* из палеоцена Китая отличаются от других 'линдхольмемидид' и тестудиноидей в целом уникальным инфрамаргинальным паттерном (четыре или пять широких инфрамаргинальных щитков, которые сильно заходят на периферальные пластинки) и могут представлять естественную группу (кладу или граду) базальных тестудиноидей. Некоторые другие признаки общие для *E. australis, G. barsboldi* и *H. chenshuensis* (крупная анальная вырезка и относительно узкие вертебральные щитки 2 и 3), характерны также для некоторых геоэмидид и тестудинид, что может говорить о близости упомянутых родов к этим группам.

INTRODUCTION

'Lindholmemydidae' Chkhikvadze, in Shuvalov et Chkhikvadze, 1975 is a paraphyletic assemblage of basal testudinoid taxa known from the Cretaceous and Paleocene of Asia (see Hirayama 2000; Hirayama et al 2000; Danilov 2001; Claude and Tong 2004). In this paper we use the term 'lindholmemydids' or basal testudinoids for these Late Cretaceous and Paleocene testudinoids, while modern (= crown) testudinoids will be used for the four living testudinoid families: Testudinidae Batsch, 1788, Emydidae Rafinesque, 1815, Geoemydidae Theobald, 1868 and Platysternidae Gray, 1869. Platysternidae for a while considered as part of Chelydridae Swainson, 1839, have been recently shown to belong to the testudinoid clade (Parham et al. 2006). Platysternidae probably branched early in the testudinoid tree as suggested by molecular data (Lourenco et al. 2012).

'Lindholmemydids' differ from modern testudinoids, except Platysternidae, by the primitive persistance of three to four inframarginal scutes , whereas in most modern testudinoids inframarginals, if present, are represented only by two pairs, known as axillary and inguinal scutes, which are separated by a long contact of plastral (pectoral and abdominal) and marginal scutes (Claude and Tong 2004). At least one taxon (*Pseudochrysemys gobiensis* Sukhanov et Narmandakh, 1976 from the late Paleocene of Mongolia, primarily described as a member of Emydidae sensu McDowell 1964; see Sukhanov and Narmandakh 1976), displays an intermediate morphology with one inframarginal scute remaining on the bridge in addition to axillary and inguinal scute but with a contact between marginal and plastral scute, and will be considered as a basal testudinoid in this study too. Morphology (even shell) of most 'lindholmemydids' remains poorly known either due to incomplete materials and/or inaccurate descriptions and therefore systematics of basal testudinoids is particularly dif-

ficult to understand. Some taxa need a redescription and reexamination. Our paper is devoted to one of such taxa, *Elkemys* (orig. *Mongolemys*) *australis* (Yeh, 1974) from the Paleocene of China.

Mongolemys australis was based on a series of nine specimens represented by shells and shell fragments. Yeh (1974) referred this new species to the genus *Mongolemys* Khosatzky et Młynarski, 1971 (type species – *M. elegans* Khosatzky et Młynarski, 1971 from the Late Cretaceous of Mongolia). At that time, the genus *Mongolemys* was assigned to the family Dermatemydidae Gray, 1870 based on a general similarity in the morphology of the shell (Yeh 1974). Later, Chkhikvadze (1976) placed *M. australis* in a separate genus, *Elkemys,* and removed it from the waste-basket of Asiatic Dermatemydidae to the basal testudinoid family Lindholmemydidae. According to Chkhikvadze (1976), *Elkemys* differs from *Mongolemys* by the sulcus dermo-scuti (= skin-scute sulcus) that is displaced from the free margin of the visceral sides of the plastral lobes, and by a well-developed anal notch. Later, Chkhikvadze (1987) published a new reconstruction of the plastron of *Elkemys* and assigned it to the subfamily Geoemydinae Theobald, 1868 (sensu Chkhikvadze 1984), which corresponds to part of the current Geoemydidae (see Danilov 2005). The view that *Elkemys* might be related to the geoemydids is shared by Lapparent de Broin (2001).

Since its original description and until now, the few proposed phylogenetic scenarios for *E. australis* are based entirely on morphological data taken from the short original inception of *Elkemys* (Yeh 1974). Our paper presents a redescription of most specimens of the type series of *E. australis* and highlights previously unknown and misunderstood aspects of its morphology. Besides that, we compare *Elkemys* with some other basal testudinoid taxa and speculate about its affinities.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA;

CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; ZIN PH, Zoological Institute of the Russian Academy of Sciences, Paleoherpetological Collection, Saint Petersburg, Russia.

MATERIAL

We reexamined seven specimens from the type series of *Mongolemys australis* (Figs 1–3): IVPP V3107.1 and V3107.2, almost complete but depressed shells; IVPP V3107.3, a partial compressed shell missing the posterolateral parts of the carapace, most of the posterior plastral lobe and right posterior part of the plastron; IVPP V3107.4, a posterior part of the plastron; IVPP V3107.5, a posterior portion of the shell, including posterior part of the carapace and posterior plastral lobe; IVPP V3107.6, a partial shell missing its anterior third; IVPP V3107.7, an almost complete plastron with right bridge peripherals. Two specimens of the type series, IVPP V3107 (the holotype, consisting of the posterior two thirds of the shell [Yeh 1974, pl. I: 1, 4]), and IVPP V3107.8, "other fragments" (Yeh 1974, p. 35), were not examined. Measurements of the examined specimens are presented in Table 1.

The following (best known) 'lindholmemydid' and pre-Eocene taxa of basal testudinoids were used for comparison: species of *Gravemys* Sukhanov et Narmandakh, 1983: *G. barsboldi* (Sukhanov et Narmandakh, 1974) from the Late Cretaceous of Mongolia, as described by Sukhanov and Narmandakh (1983), Danilov (2003) (Fig. 4A, B); *G. hutchisoni* Danilov, 2003 from the Late Cretaceous of China, as described by Danilov (2003); *Hokouchelys chenshuensis* Yeh, 1974 from the Paleocene of China, as described by Yeh (1974, 1994); species of *Lindholmemys* Riabinin, 1935: *L. elegans* Riabinin, 1935 from the Late Cretaceous of Uzbekistan, as described by Riabinin (1935) and personal observation (IGD) of CCMGE 34/12898, holotype of *L. elegans*, and collection ZIN PH 7, numerous isolated plates of the shell (Fig. 4 C, D); *L. martinsoni* Chkhikvadze, in Shuvalov et Chkhikvadze, 1975 from the Late Cretaceous of Mongolia, as described by Shuvalov and Chkhikvadze (1975, 1979), Danilov and Sukhanov (2001); *Mongolemys elegans* Khosatzky et Młynarski, 1971 from the Late Cretaceous of Mongolia, as described by Khosatzky and Młynarski (1971), Sukhanov (2000) and person-al observation (IGD) of numerous shells in collection of PIN (Fig. 4E, F); *Pseudochrysemys gobiensis* Sukhanov et Narmandakh, 1976 from the Late Paleocene of Mongolia, as described by Sukhanov and Narmandakh (1976) and personal observation (IGD and VBS) of PIN without number, shell (Fig. 4G, H). Other taxa of 'lindholmemydids', represented by incomplete material (see Danilov 1999; Sukhanov et al., 1999; Danilov et al. 2002), were not considered in this study.

In addition, the following Eocene taxa of modern testudinoids were used for comparison: *Achilemys cassouleti* Claude et Tong, 2004 (Testudinidae) from the early Eocene of France, as described by Claude and Tong (2004); species of *Echmatemys* Hay, 1906 (Geoemydidae): *E. wyomingensis* (Leidy, 1869) from the middle Eocene of USA, as described by Hay (1908) and personal observations (JC) of AMNH 5588; *E. euthneta* (Cope, 1873) from the early Eocene of USA, as described by Hay (1908) and personal observations (JC) of AMNH 6032 and AMNH 6042; species of *Palaeoemys* Schleich, 1994 (Geoemydidae): *P. hessiaca* Schleich, 1994 from the early and middle Eocene of France and Germany, and *P. testudiniformis* (Owen, 1842) from the early Eocene of England and France, as described by Claude and Tong (2004). Data about morphology of modern testudinoids were taken mainly from papers of Claude and Tong (2004) and Joyce and Bell (2004).

SYSTEMATICS

Testudines Batsch, 1788

Cryptodira Cope, 1868

Testudinoidea Batsch, 1788

'Lindholmemydidae' Chkhikvadze, in Shuvalov et Chkhikvadze, 1975

***Elkemys* Chkhikvadze, 1976**

Elkemys: Chkhikvadze 1976, p. 746; 1984, p. 107; 1987, p. 64–65; Claude and Tong 2004, p. 7, 33–35; Danilov 2005a, p. 390; 2005b, p. 23; Brinkman et al. 2008, p. 76.

Type species. *Mongolemys australis* Yeh, 1974, by monotypy.

Diagnosis. A 'lindholmemydid' with a shell length up to 22.5 cm, that is characterized by the following combination of characters: smooth shell surface (1); oval and anteriorly truncated carapace in dorsal view (2); large nuchal emargination (3); relatively large

nuchal, its width being about 35% of the shell width (4); no or very short contact between costals 1 and peripherals 4 (5); wide and trapezoid-shaped cervical scute, covering about 1/4 of the nuchal length (6); vertebral 1 narrowed anteriorly and not contacting marginals 2 (7); vertebrals 2 and 3 longer than wide (8); vertebral 5 reaching or almost reaching marginals 10 (9); marginals 11 not extending on to costals 8 (10); marginals 12 not reaching suprapygal 2 (11); plastral buttresses weakly or moderately developed (12); minimal length of the bridges about 60–70% of the plastron width (13); contributions of the hyoplastra to the minimal length of the bridges greater than those of the hypoplastra (14); anterior plastral lobe length representing about 25% of the plastron length (15); posterior plastral lobe length representing about 30% of the plastron length (16); posterior plastral lobe relatively wide at the base and strongly narrowed posteriorly (17); lateral borders of the posterior plastral lobe convex in the femoral part and straight in the anal part (18); large anal notch (19); relatively large epiplastra (20); hexagonal wider than long entoplastron (21); pectoral scutes extending on to the entoplastron (22); four to five pairs of inframarginals (23); relatively wide inframarginals (24); inframarginals strongly extending on peripherals (25); skin-scute sulcus distant from the free margin of plastral lobes in visceral view (26). *Elkemys* can be differentiated from all other 'lindholmemydids' by characters 4, 9, 16, 20, 22, 26. In addition, it can be differentiated from *Gravemys* by characters 1, 6, 10, 11, 15, 18; from *Lindholmemys* by characters 2, 3, 8, 11, 12, 14, 17, 19, 23–25; and from *Mongolemys* by characters 2, 3, 6, 7, 8, 10, 11, 13–15, 17–19, 21, 23, 25. For comparison see also Table 2.

Elkemys australis (Yeh, 1974)
(Figs 1–3)

Mongolemys australis: Yeh 1974, p. 26, fig. 1, pls I–III, IV: 3, 4; Sun et al. 1992, p. 30, fig. 33; Yeh 1994, p. 35, fig. 17.
Elkemys australis: Chkhikvadze 1976, p. 746; 1987, p. 65–66, fig. 7; Hervet 2004, p. 14, 17; Brinkman et al. 2008, p. 76, fig. 81.

Holotype. IVPP-V3107, posterior two thirds of the shell.
Material. See Material section above.
Locality and horizon. Chishapai, Hukou, Nanxiong, Guangdong Province, China. Shanghuan (= Lofochai) Formation, Early Paleocene (Lucas 2001).

Diagnosis. As for the genus.
Description. *Shell.* Most shells are depressed, but they were probably rather low as it can be seen in the less deformed specimen IVPP V3107.6 (see Fig. 2E, F). Shell surface is unsculptured but growth lines are visible in the pleural and marginal areas of the carapace. Sutures and scute sulci are easily observable. Although the specimens are rather small (about 20 cm in length), no fontanelles are present, indicating that they were adult or subadult. In addition, there is no indication of marked sexual dimorphism.

Carapace. The carapace is a wide oval in dorsal view (width is about 90% of length, remind that specimens are flattened to some extent and that they may appear wider than when living). The anterior margin of the carapace is truncated and has a large nuchal emargination visible in IVPP V3107.1 and V3107.2 (Fig. 1A, C). The truncated carapace with a large nuchal emargination is known exclusively in *Gravemys barsboldi* (see Danilov 2003) within basal testudinoids. There is a posterior medial ridge on neurals in some specimens (see below), but no lateral ridges appear on costal as in tricarinate geoemydids (Claude and Tong 2004).

Plates of the carapace. The nuchal is preserved in IVPP V3107.1, V3107.2 and V3107.3. It is relatively wide: its width is about 35% of the shell width. The length of the nuchal reaches 56 to 59% of its width. This is the widest nuchal plate known within the 'lindholmemydid' group. The anterolateral borders of the nuchal converge forward as in most other testudinoids, but unlike *Mongolemys elegans*, where these borders are almost parallel.

The neurals are represented by complete series in IVPP V3107.1 and V3107.2 and only partially in the other specimens. Neural 1 is elongated, tetragonal-oval. In most observed specimens, neurals 2–8 are hexagonal and short-sided anteriorly, as in other basal testudinoids. However, in IVPP V3107.6, the posterior part of neural 2 has short sides posteriorly (?hexagonal or octagonal shape), neural 3 and 5 are tetragonal, and neural 4 is octagonal. Neural 8 have a narrower contact with the suprapygal than with neural 7. Neurals 2–5 are similar in size, whereas more posterior neurals get shorter from 6 to 8. In IVPP V3107.1, neurals 6 to 8 bear a clear medial ridge, which is unknown in other basal testudinoids, platysternids and testudinids by contrast to most recent and fossil geoemydids and emydids (Joyce and Bell 2004; Claude and Tong 2004). This ridge is absent

in IVPP V3107.2 and 3107.5 and shorter (limited to neurals 6 and 7) in V3107.6.

Two suprapygals are visible in IVPP V3107.1, V3107.3, V3107.5 and V3107.6. Suprapygal 1 is trapezoidal, widened posteriorly, slightly narrower than in *Gravemys barsboldi*. In IVPP V3107.1, suprapygal 1 is divided by a suture into two parts: a smaller anterior and the larger posterior. This is probably an abnormal morphology as it can be observed sometimes in several individuals of some testudinoid species. Suprapygal 2 is as long as suprapygal 1, but wider; it has the shape of the biconvex lens.

The pygal plate is relatively large (by comparison to posterior peripherals) and wider than long. In caudal view (Fig. 2E) the free edge of the pygal is concave (pygal emargination). Similar morphology of the pygal is observed in other examined 'lindholmemydids', *Pseudochrysemys gobiensis* and emydids. In geoemydids and some testudinids, the pygal is relatively smaller and wider (Claude and Tong 2004).

The whole set of costals are visible in IVPP V3107.1 and V.3107.2. Other specimens demonstrate only parts of the costals. Costal 1 is long, contacting peripherals 1–3, and is nearly or slightly reaching peripheral 4 (Fig. 1A; IVPP V3107.1). The contact between costal 1 and peripheral 4 is known in some geoemydids, emydids, and testudinids and in *Gravemys barsboldi* among basal testudinoids (Danilov 2003). In other basal testudinoids (like *Mongolemys elegans* and *Lindholmemys elegans*) and in many other turtles, costal 1 contacts only peripherals 1–3. Costals 2, 4, 6–8 are longer laterally than medially, whereas costals 3 and 5 are slightly longer medially than laterally (IVPP V3107.1). This pattern is more close to testudinids than to other basal testudinoids and emydids. The buttress-costal relationship is not observable.

Costal-peripheral fontanelles are absent in all the specimens. Free margins of most peripherals are partially broken and thus hardly measurable. The anterior and middle (= bridge) peripherals are visible in IVPP V3107.1, V3107.2 and partially in IVPP V3107.3, whereas posterior peripherals are exposed in IVPP V3107.6 and V.3107 (Yeh 1974, pl. I: 1). The ventral parts of bridge peripherals are visible in IVPP V3107.1, V3107.2 and V3107.3; they are wider than long. Peripherals 3 and 7 contact buttresses and have no musk ducts. The posterior peripherals are not serrated.

Scutes of the carapace. The cervical is trapezoid-shaped, wider than long and similar to *Lindholmemys*

elegans. Its length is about 1/4 of the nuchal length. In *Gravemys barsboldi*, the cervical is larger (about 1/3 of the nuchal length) and almost quadrate. The cervical is wider than long and rectangular in *Mongolemys elegans*, and longer than wide and rectangular in *Pseudochrysemys gobiensis*.

Vertebral 1 is much narrower than the nuchal, lyre-shaped (narrowed anteriorly). A similar shape of the vertebral 1 is known in *Pseudochrysemys gobiensis* and species of *Lindholmemys* (as a variation); this pattern can be observed in geoemydids and emydids within modern testudinoids. In *Gravemys barsboldi*, vertebral 1 is narrow, but has convex lateral borders, whereas in *Mongolemys elegans*, vertebral 1 is always wider than the nuchal, contacting marginal 2. Vertebrals 2 and 3 are relatively narrow and rectangular with almost straight lateral borders like in *Gravemys barsboldi*, *Achilemys cassouleti*, some species of *Palaeoemys* and *Echmatemys*, and some modern geoemydids. In other 'lindholmemydids', and many emydids, these vertebrals are relatively wider and more hexagonal in shape. Vertebral 4 is narrowed in its posterior half. As visible in IVPP V3107.6 (Fig. 2C), vertebral 5 is very wide, has a shape of biconvex lense and reaches marginal 10 on the right side and is separated from it by a short contact between pleural 4 and marginal 11 on the left side. In other 'lindholmemydids', vertebral 5 is wider than the anterior vertebrals, but usually reaches only about middle part of marginals 11.

Pleural 1 is the largest. Pleurals 2–4 get smaller caudally. Pleural 2 is longer laterally than medially. Pleurals 3 and 4 have oblique parallelepipeds shapes. Pleural 2 contacts marginals 5–7, and pleural 3 contacts marginals 7–9 as in other basal and most modern testudinoids.

Most marginals are unmeasurable. The marginals are narrow (low), excluded from costals, overlapping lateral halves of the anterior peripherals, and get closer to the costal-peripheral suture in the bridge and posterior peripherals. Marginals 12 are restricted to the pygal, not extending on to suprapygal 2. This condition is similar to other basal testudinoids, platysternids and emydids. In *Gravemys barsboldi*, geoemydids and some testudinids marginals 12 extend on to suprapygal 2. The ventral parts of the bridge marginals are narrow, restricted to peripherals and contacting the inframarginals.

Plastron. The proportion of the plastron on the carapace lengths is the same as in *Gravemys barsboldi*
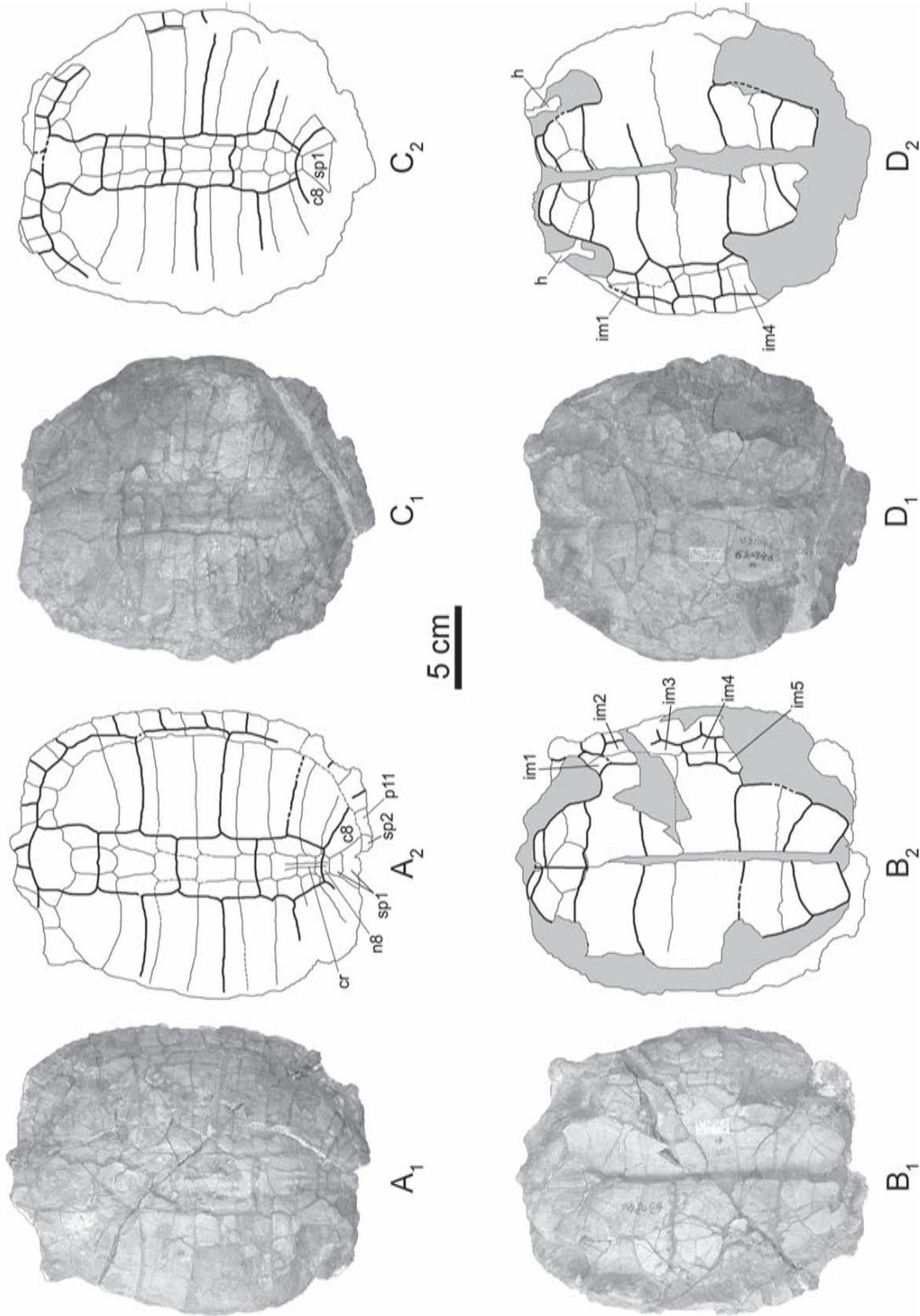
Fig. 1. *Elkemys australis* (Yeh, 1974): A, B – IVPP V3107.1, shell in dorsal (A) and ventral (B) views, photographs (A₁, B₁) and explanatory drawings of the same (A₂, B₂); C, D – IVPP V3107.2, shell in dorsal (C) and ventral (D) views, photographs (C₁, D₁) and explanatory drawings of the same (C₂, D₂). Matrix is filled with grey. Tentative sutures and sulci are shown with dashed lines. Abbreviations: ab – axillary buttress; as – additional scute; c – costal; co – coracoid; cr – carapacial ridge; h – humerus; ib – inguinal buttress; im – inframarginal; m – marginal; n – neural; p – peripheral; py – pygal; s – suprapygal; sp – suprapygal. Arabic numerals designate element numbers.
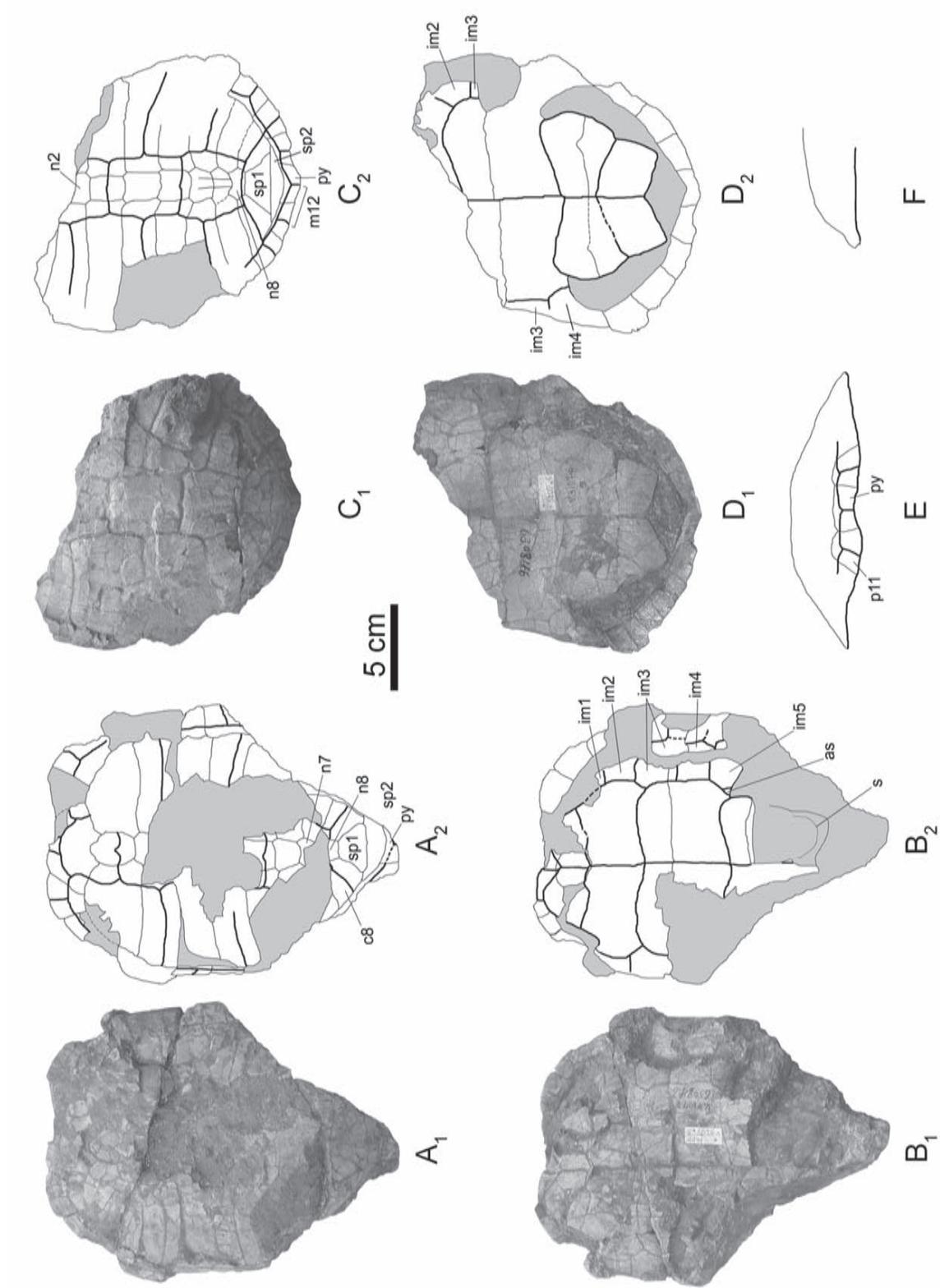
Fig. 2. *Elkemys australis* (Yeh, 1974): A, B – IVPP V3107.3, shell in dorsal (A) and ventral (B) views, photographs (A₁, B₁) and explanatory drawings of the same (A₂, B₂); C–F, – IVPP V3107.6, posterior portion of the shell in dorsal (C), ventral (D), posterior (E) and right lateral (F) views, photographs (C₁, D₁) and explanatory drawings of the same (C₂, D₂) and schematic drawings (E, F). Matrix is filled with grey. Tentative sutures and sulci are shown with dashed lines. For abbreviations see Fig. 1.
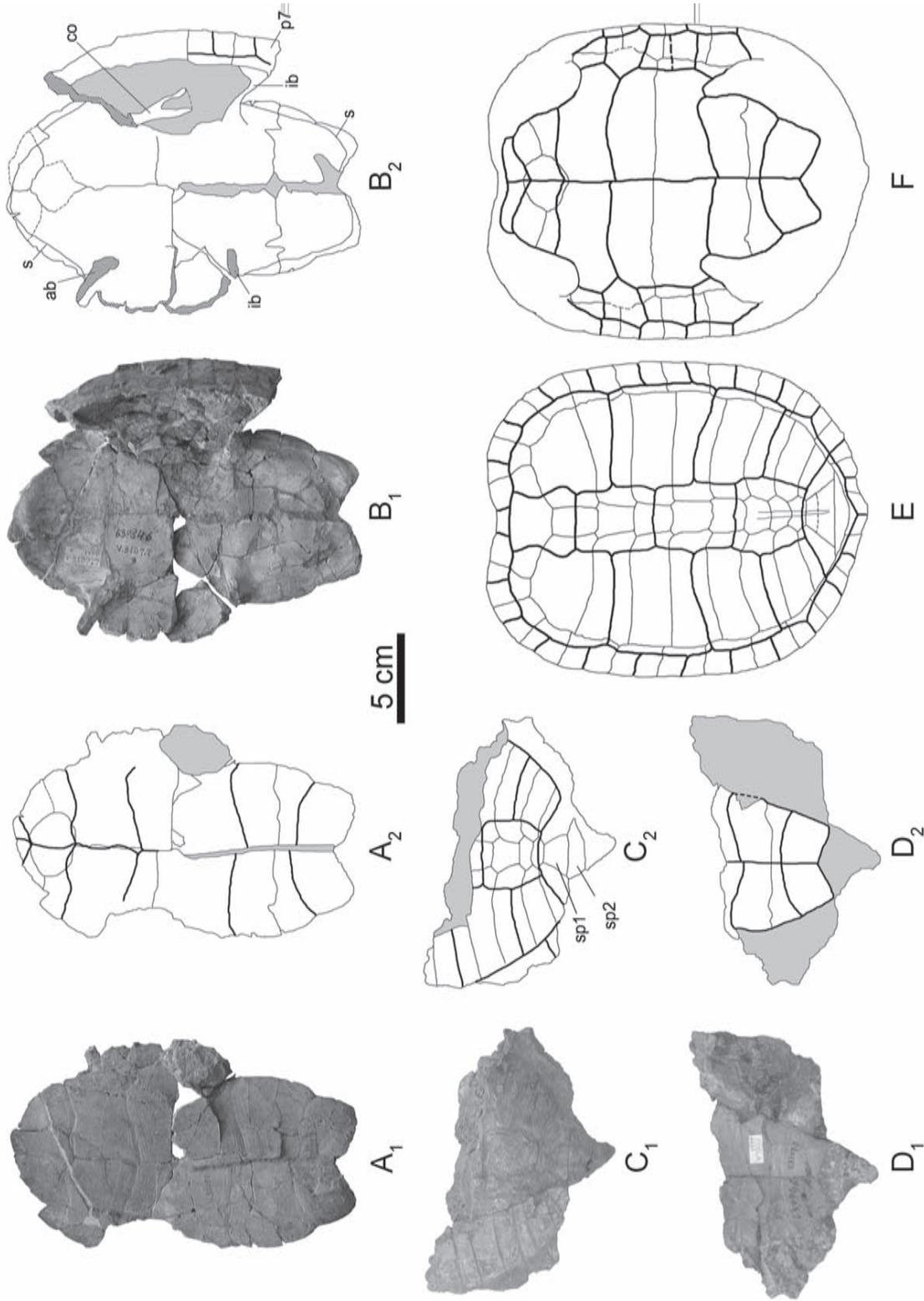
Fig. 3. *Elkemys australis* (Yeh, 1974): A, B – IVPP V3107.7, plastron and part of the bridge in ventral (A) and dorsal (B) views (the bridge is removed on A), photographs (A_1, B_1) and explanatory drawings of the same (A_2, B_2); C, D – IVPP V3107.5, posterior portion of the shell in dorsal (C) and ventral (D) views, photographs (C_1, D_1), explanatory drawings of the same (C_2, D_2); E, F – reconstruction of the shell in dorsal (E) and ventral (F) views, without scale. Matrix is filled with grey. Tentative sutures and sulci are shown with dashed lines. For abbreviations see Fig. 1.
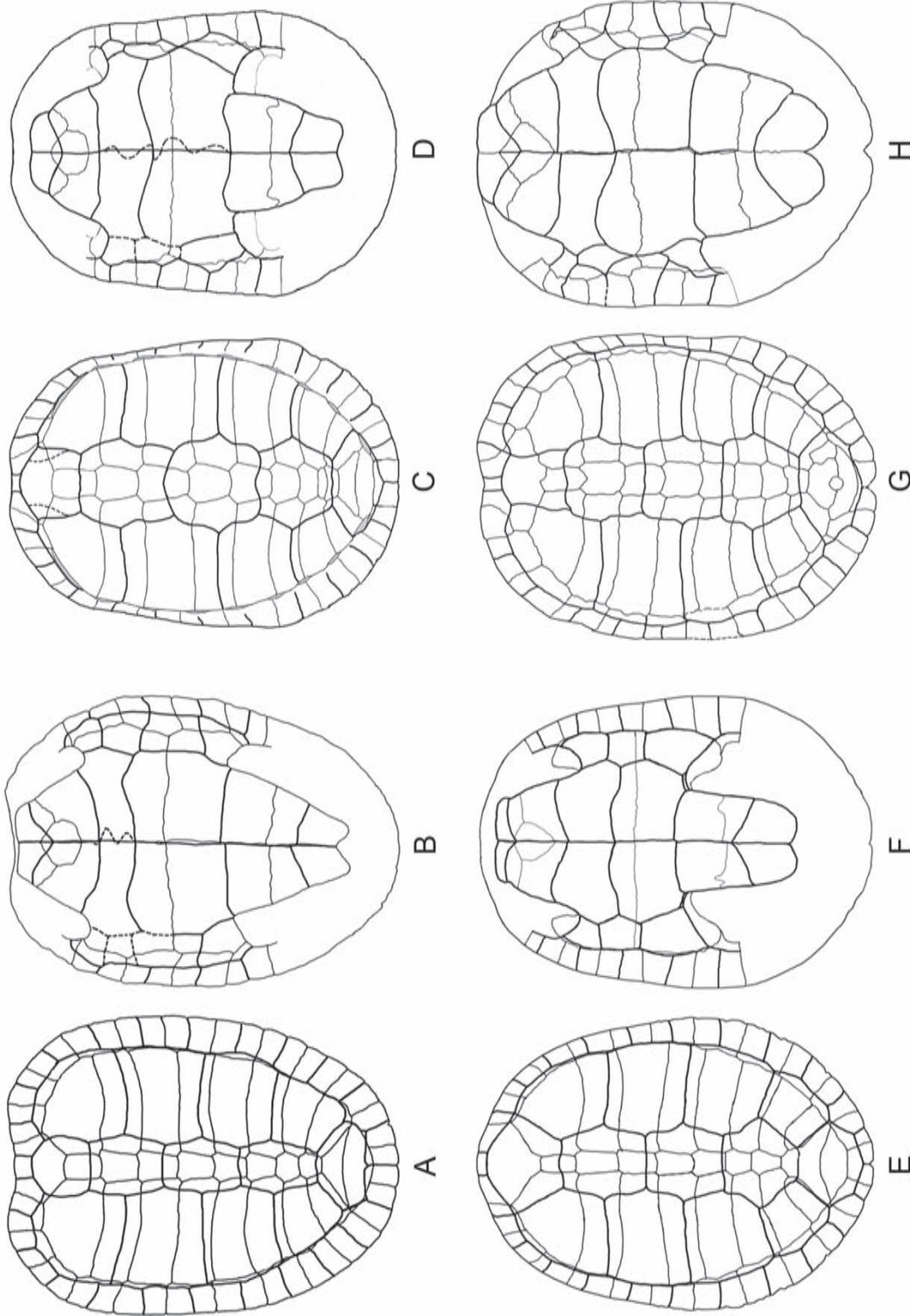
Fig. 4. Shells of some 'lindholmemydids' (A–F) and *Pseudochrysemys gobiensis* (G, H) in dorsal (A, C, E, G) and ventral (B, D, F, H) views: A, B – *Gravemys barsboldi* (Sukhanov et Narmandakh, 1974) (reconstruction based on several specimens; after Danilov 2003, with small changes); C, D – *Lindholmemys elegans* Riabinin, 1935 (reconstruction based on the holotype shell and isolated plates; fontanelles are filled with grey, variation is shown by dashed line); E, F, – *Mongolemys elegans* Khosatzky et Młynarski, 1971 (dorsal view based on PIN 4693-22 and ventral view based on the holotype plastron and several additional specimens; after Danilov 2003); G, H – *Pseudochrysemys gobiensis* Sukhanov et Narmandakh, 1976 (reconstruction based on PIN without number). Without scale.

(about 80–90%). The minimal length of the bridge makes up about 60–70% of the plastron width and about 40–50% of the plastron length, which is similar to *Gravemys barsboldi* and *Lindholmemys elegans*, and greater than in *Mongolemys elegans*. The plastron is suturally connected to the carapace. The plastral buttresses, partially observable in IVPP V3107.7 (Fig. 3B), are vertically orientated, implying contact with costals. The bases of the axillary and inguinal buttresses extend for 1/4–1/3 distance from the free edge of the plastron to the midline, implying that the buttresses were weakly or moderately developed.

The plastral lobes are relatively wide with small or absent gular notch and a well developed anal notch. The anterior lobe is expanded in the humeral part and narrowed in the gular part, forming a short and narrow but clearly separated gular projection. Posterior to this projection, the humeral margin is slightly convex and not straight as it is in some other 'lindholmemydids'. The length of the anterior lobe is about 47–51% of width at its posterior edge (base) and about 24–26% of the plastron length. In IVPP V3107.1, the widths of the anterior lobe at the gular-humeral sulcus (= width of the gular projection) and at the epi-hyoplastral suture make up 52% and 76% of the lobe width at its posterior edge respectively (in *Gravemys barsboldi* the same ratios are about 49% and 51% respectively). A small gular notch is present in IVPP V3107.1 and V3107.2, but it is almost absent in IVPP V3107.3. Among examined testudinoids, a gular notch is present in *Gravemys* spp., *Hokouchelys chenshuensis* and some specimens of *Palaeoemys* spp. and *Echmatemys* spp.

The length of the posterior lobe makes up 55–69% of the width at its anterior edge (base) and about 30–32% of the plastron length (in *Gravemys barsboldi* the same ratios are 76% and 37–41% respectively). Thus, the posterior lobe is slightly longer than the anterior one. The posterior lobe is expanded and convex in the femoral part, incised in the femoral-anal sulcus and straight in the anal part. The femoral convexity of the posterior lobe is better developed in IVPP V3107.6 (Fig. 2D), whereas in IVPP V3107.5, it is less pronounced or absent (Fig. 3D). In IVPP V3107.1, the widths of the posterior lobe at the hypo-xiphiplastral suture and at the femoral-anal sulcus are respectively 102% and 84% of the width at its anterior edge (in *Gravemys barsboldi* the same ratios are 77% and 54% respectively). As visible from the above ratios, *Elkemys australis* dif-

fers from *Gravemys barsboldi* in expanded (convex) humeral and femoral parts of the plastral lobes, and shorter posterior lobe. A well developed anal notch (wide with pointed xiphiplastral processes) is present in *Gravemys barsboldi*, geoemydids, platysternids and testudinids. Other basal testudinoids, have no (*Mongolemys elegans*) or very weakly developed (*Gravemys hutchisoni*, *Lindholmemys elegans*, *Pseudochrysemys gobiensis*) anal notch.

Plates of the plastron. The epiplastra are preserved in IVPP V3107.1, V3107.2, V3107.3 and V3107.7. They are rather large and make up about half of the lateral edge of the anterior lobe, which is more similar to modern testudinoids and *Pseudochrysemys gobiensis*, than to most basal testudinoids having smaller epiplastra making up one third or less of the lateral edge of the anterior lobe. Anterior epiplastral lips are present, as in most modern testudinoids and *Pseudochrysemys gobiensis*, although they are smaller (Fig. 3B). The entoplastron is roughly hexagonal externally, wider than long, similar to some other 'lindholmemydids' (*Gravemys* spp., *Hokouchelys chenshuensis* and some *Lindholmemys elegans*) and most modern testudinoids. *Mongolemys elegans* and some *Lindholmemys elegans* have more elongated diamond-shaped entoplastron, while *Pseudochrysemys gobiensis* has slightly wider than long diamond-shaped entoplastron. Internally the entoplastron of *Elkemys australis* is more elongated than externally (Fig. 3B).

The hyoplastron is shorter than the hypoplastron at the midline, but it contributes more largely to the length of the bridge as in *Gravemys* spp., *Pseudochrysemys gobiensis* and many modern testudinoids (especially geoemydids and testudinids). In *Mongolemys elegans* and *Lindholmemys elegans*, platysternids and in some emydids, the hyo- and hypoplastron have similar contributions to the bridge. The contribution of the hyoplastron to the anterior lobe is relatively small: 35% (IVPP V3107.1) of the maximum length of the hyoplastron (this ratio is about 40% in *Gravemys barsboldi* and about 50% in *Mongolemys elegans*). The contribution of the hypoplastron to the posterior lobe is about 38–43% (IVPP V3107.6) of the maximum length of the hypoplastron (this ratio is about 45% in *Gravemys barsboldi* and about 43% in *Mongolemys elegans*).

The xiphiplastron is relatively short, making up 18% (IVPP V3107.1) of the plastron and 58% of the posterior lobe length at the midline. In *Gravemys*

barsboldi, these ratios are 22% and 69%, whereas in *Mongolemys elegans*, 23% and 62% respectively.

Scutes of the plastron. The plastral formulae are Gu<Hu<Pe<Ab>Fe=An (most specimens) or Gu<Hu<Pe<Ab>Fe<An (IVPP V3107.6). The gulars are short medially, extending on to the entoplastron (IVPP V3107.2), touch it (IVPP V3107.7) or lie anteriorly to it (IVPP V3107.1). The humerals are shorter than the pectorals. The humeral-pectoral sulcus lies on the entoplastron along its posterior border. The abdominals are very long. The femorals are equal or shorter than the anals. Midline sulcus between the anals is long as in *Mongolemys elegans*, *Lindholmemys elegans*, *Pseudochrysemys gobiensis* and emydids; they eventually contact the hypoplastron in IVPP V3107.4. The inframarginals are represented by four (IVPP V3107.2) or five (IVPP V3107.1 and V3107.3) pairs. All inframarginals strongly extend on to the peripherals. Among 'lindholmemydids', this condition is observed only in *Gravemys* spp. and also present in *Hokouchelys chenshuensis* Yeh, 1974 (Yeh 1974, 1994); the inguinal scute (homologous to a posterior inframarginal scute in basal testudinoids) overlaps peripherals only in geoemydids and testudinids, while it is restricted to the plastron in emydids. The last inframarginal (4 or 5) is separated from the femoral by a gap. In IVPP V3107.3, this gap is filled with a small additional scute also known in *Mongolemys elegans* (Fig. 4F). As visible in IVPP V3107.7 (Fig. 3B), the plastral scutes strongly overlap on to the dorsal surface of the plastron and the skin-scute sulcus is distant from the free margin of the plastral lobes. In all other basal testudinoids, except *Pseudochrysemys gobiensis*, this overlap is very small and the skin-scute sulcus is located very close to the free margin of the plastral lobes. In *Pseudochrysemys gobiensis*, like in most other modern testudinoids, the overlap is strong and the skin-scute sulcus is distant from the free margin of the plastral lobes.

Other elements of the skeleton. Parts of two humeral bones are visible in IVPP V3107.2 (Fig. 1D) and a distal portion of the right coracoid is observable in IVPP V3107.7 (Fig. 3B). No differential diagnostic characters appear from these bones.

DISCUSSION

We consider all the examined specimens of *Elkemys* as belonging to a single species, *E. australis*, based on their general similarity and low variation, within the limits common in other testudinoid species. The observed variation include the following characters: medial ridge on the carapace (present/absent), neural formula (see Description), gular notch (present/absent), shape of the posterior plastral lobe (more or less incised in the femoral-anal sulcus and more or less widened in the femoral part), and number of inframarginals (four or five pairs). The number of inframarginals was previously considered as a very stable character among basal testudinoids (Danilov 2003). For instance, examination of more than a hundred specimens of *Mongolemys* spp. by one of us (IGD) showed that this genus is invariably characterized by three pairs of inframarginals. Variation in neural formula is not well described in other basal testudinoids, but rather common is modern members of this group (Pritchard 1988; Joyce and Bell 2004). No marked sexual differences were observed on the examined specimens.

According to the reconstruction of Yeh (1974, fig. 1; 1994, fig. 17; Sun et al. 1992, fig. 30; Brinkman et al. 2008, fig. 81), *Elkemys australis* is characterized by an oval shell without nuchal emargination, rounded anterior margin of the plastron, long cervical, long anals and four pairs of the inframarginals laying entirely on the plastron. Based on examination of figures in the Yeh's (1974) paper, Chkhikvadze (1987, fig. 7) published a new reconstruction of the plastron of this taxon, which differs from the original reconstruction by the truncated anterior lobe of the plastron, widened posterior lobe, longer entoplastron, shorter anals and presence of only three pairs of the inframarginals, of which inframarginals 1 and 2 slightly extend on to the peripherals and inframarginal 3 lies on the hypoplastron. In addition, Chkhikvadze (1987) noted strong overlap of the scutes on the dorsal surface of the plastron. According to our observations and in contrast to Yeh (1974) and Chkhikvadze (1987), *E. australis* is characterized by presence of a large nuchal emargination in the carapace, a shorter cervical, a gular notch sometimes present in the plastron, four to five pairs of the inframarginals strongly extending on to the peripherals. We agree with Yeh (1974) in the size of entoplastron and with Chkhikvadze (1987) in the shape of the posterior lobe, size of the anals and in the presence of the overlapping of the scutes on to the visceral surface of the plastron. New observations for *E. australis* include presence of the medial ridge in the posterior part of the carapace and absence of musk

Table 1. Measurements (in mm) of the specimens of *Elkemys australis* (Yeh, 1974). Notations: "?", element unmeasurable; "–", element is not preserved.

Parameters	V3107.1	V3107.2	V3107.3	V3107.5	V3107.6	V3107.7
Carapace						
Carapace (length/width)	225/205	205/184	190/?	?	?	?
Plates of the carapace						
Nuchal (length/width)	33/56	31.7/55	28.5/50	–	–	–
Neurals (length/width)						
Neural 1	26.5/15.7	24.0/18.0	25.3/18.5	–	–	–
Neural 2	22/19.2	?	?	–	?/18	–
Neural 3	22.5/?	21.3/15.3	–	–	20.8/14.3	–
Neural 4	22/?	17.5/15.6	–	–	19.7/16.5	–
Neural 5	20/15	18.0/16.6	20/18.5	?	16.8/17.4	–
Neural 6	15/16.2	14.0/16.5	12.2/16	13.8/18	12.2/18.5	–
Neural 7	11.3/12.5	11.3/16.7	?	9.5/17.5	10.7/20	–
Neural 8	9.8/13	10.4/15.0	?	?	8/17.5	–
Suprapygals (length/width)						
Suprapygal 1	8.5/13.5	17.0/30.0	18/26	?	15.2/29	–
Suprapygal 2	13/27	?	16/43	?	16/44.4	–
Pygal (length/width)	?	?	?/24	?	13.5/23	–
Costals (medial length/lateral length/width along posterior border)						
Costal 1	26.5/44/58	22/39.4/58.2	?	–	?	–
Costal 2	23.5/29/65	?	?	–	?/25/61.5	–
Costal 3	20/23/68	?	?	–	17/18/68	–
Costal 4	22.5/29/71	?	?	?	?	–
Costal 5	19/16.5/67	?	?	?	?	–
Costal 6	18/25.5/51	?	?	?	11.5/?/46	–
Costal 7	10/20.5/41.5	?	?	?	11.5/?/38.5	–
Costal 8	6.5/15.5/31	?	?	?	10/17.5/28	–
Peripherals (length along free edge/width)						
Peripheral 1	?	?	?	–	–	–
Peripheral 2	23/?	?	?	–	–	–
Peripheral 3	29.5/?	?	–	–	–	?
Peripheral 4	27.2/23	?	?	–	?	?
Peripheral 5	24/?	?	?	–	?	?
Peripheral 6	25/?	?	–	–	–	?
Peripheral 7	28/?	?	–	–	–	?
Peripheral 10	?	?	–	?	22/18.5	–
Peripheral 11	?	?	?	–	23.7/18.5	–
Plastron						
Plastron (length at the midline/width)	185/120	160/136	152/110	?	?/126	173.6/126
Bridge (length)	84.5 (left)	80 (right)	71 (left)	–	–	72 (left)
Anterior lobe of the plastron						
Length at the midline	44	40	39	–	–	46
Width at the base	87	84	76	–	–	98

Table 1. (Continued)

Parameters	V3107.1	V3107.2	V3107.3	V3107.5	V3107.6	V3107.7
Width at the humeral-pectoral sulcus	80	80	68	–	–	82
Width at the gular-humeral sulcus	45	48	32	–	–	?
Posterior lobe of the plastron						
Length at the midline	56.5	51.5	47	45.5	48	52.5
Width at the base	82	90.5	77	73	87.5	94.3
Width at the hypo-xiphiplastral suture	84	87	?	70	88	93
Width at the femoral anal sulcus	69	70	?	57	64	74
Plates of the plastron						
Epiplastron (length)	7.7	6.4	8.4	–	–	~7
Entoplastron (length/width)	24.5/32.5	25/32	20/23.4	–	–	28/35.5
Hyoplastron (length)	53.8	50	45	–	–	52
Hypoplastron (length)	62.5	53	50	~25	50	57
Xiphiplastron (length)	33.0	32.6	27	?	30	35
Scutes of the carapace						
Cervical (length/width)	8/12.5	7/12.3	9.7/9	–	–	–
Vertebral 1 (length/width anteriorly/width posteriorly)						
Vertebral 1	41/36/31.5	37/26/31.5	?	–	–	–
Vertebrals 2–5 (length/width maximal/width posteriorly)						
Vertebral 2	44.5/39/28	36.5/34/28.5	?	–	?/40/29	–
Vertebral 3	44/39.5/32	36/34/32	?	–	41/37/32	–
Vertebral 4	39.5/37/20	37.8/37/17.5	?	?	33.2/40/26	–
Vertebral 5	?/63	40.5/64	?	?	37.5/62	–
Pleurals (length medial/length lateral/width along posterior border)						
Pleural 1	23.5/77.5/59	?	?	–	?	–
Pleural 2	46.3/56.5/?	?	?	–	?	–
Pleural 3	40/48.5/?	?	?	?	?	–
Pleural 4	23/?/?	?	?	?	?	–
Marginals (length along free edge/width)						
Marginal 11	?	?	–	–	20.7/14	–
Marginal 12	?	?	?	–	24.5/13.2	–
Scutes of the plastron						
Gular (length)	5	11	11	–	–	9
Humeral (length)	26.6	17.5	16.2	–	–	26
Pectoral (length)	35.4	31.3	29.5	–	–	34
Abdominal (length)	57	53.5	47		53	57 (left)
Femoral (length)	27	29	28.2	23.2	21	27.5 (left)
Anal (length)	29	23.3	21	20.5	24.5	24.3 (left)
Inframarginals (length at border with marginals/width posteriorly)						
Inframarginal 1	?	?/14.6	?	–	?	?
Inframarginal 2	?	25/19	?	–	?	?
Inframarginal 3	?	26/20	?	–	?	?

Table 2. Comparison of some genera of 'Lindholmemydidae' in shell characters.

Characters	*Mongolemys elegans*	*Lindholmemys elegans*	*Gravemys barsboldi*	*Elkemys australis*
Shell height	About 1/3 of its width	Up to 55% of its width	No more than 1/2 of its width	?
Shell surface	Smooth or with sculpturing of tubercles and ridges	Smooth or with sculpturing of tubercles and ridges	With sculpturing of tubercles and ridges	Smooth
Carapace in dorsal view	Oval, slightly widened posteriorly	Oval, slightly widened posteriorly	Oval, truncated anteriorly	Oval, truncated anteriorly
Nuchal emargination	Absent	Small	Large	Large
Nuchal width	About 30% of shell width	About 30% of shell width	About 25% of shell width	About 35% of shell width
Costal 1/peripheral 4 contact	Absent	Absent	Present	Present or absent
Thoracic rib 1	Not shortened	Shortened	Shortened	?
Cervical	Wide and rectangular, covers no more than 1/4 of the nuchal length	Wide and trapezoid-shaped, covers 1/4 – 1/3 of the nuchal length	Square-shaped, covers no less than 1/3 of the nuchal length	Wide and trapezoid-shaped, covers about 1/4 of the nuchal length
Vertebral 1	Strongly widened anteriorly and contacts marginals 2	Narrowed or slightly widened anteriorly and does not contact marginals 2	Almost rectangular and does not contact marginals 2	Narrowed anteriorly and does not contact marginals 2
Vertebrals 2 and 3	Relatively wide	Relatively wide	Relatively narrow	Relatively narrow
Vertebral 5	Reaches about middle part of marginals 11	Reaches about middle part of marginals 11	Reaches about middle part of marginals 11	Reaches or almost reaches marginals 10
Extension of marginals 11 on to costals 8	Absent	Present or absent	Present	Absent
Extension of marginals 12 on to suprapygal 2	Absent	Absent	Present	Absent
Plastral buttresses	Weak	Strong	Moderate or strong	Weak or moderate
Minimal length of the bridges	50–57% of plastron width	About 65% of plastron width	60–72.5% of plastron width	60–70% of plastron width
Contribution of hyo- and hypoplastra to the minimal length of the bridges	Approximately equal	Approximately equal	Greater in hyoplastra	Greater in hyoplastra
Length of the anterior plastral lobe	About 30% of plastron length	About 25% of plastron length	22–24% of plastron length	About 25% of plastron length
Length of the posterior plastral lobe	About 35% of plastron length	About 35% of plastron length	About 40% of plastron length	About 30% of plastron length
Shape of the posterior plastral lobe	Relatively narrow at the base and slightly narrowed posteriorly	Relatively narrow at the base and slightly narrowed posteriorly	Relatively wide at the base and strongly narrowed posteriorly	Relatively wide at the base and strongly narrowed posteriorly
Lateral borders of the posterior plastral lobe	Straight	Convex in femoral part and straight in anal part	Straight	Convex in femoral part and straight in anal part
Anal notch	Small or absent	Small	Large	Large
Epiplastra	Relatively small	Relatively small	Relatively small	Relatively large
Entoplastron	Diamond-shaped longer than wide or as long as wide	Diamond-shaped longer than wide, or hexagonal wider than long	Hexagonal wider than long	Hexagonal wider than long
Extension of pectorals on to entoplastron	Absent	Absent	Absent	Present
Number of inframarginals	Three pairs	Three pairs	Four pairs	Four or five pairs
Inframarginals	Wide	Narrow	Wide	Wide
Extension of inframarginals on to peripherals	Weak or absent	Weak or absent	Strong	Strong
Position of skin-scute sulcus on the plastron	Close to the free margin	Close to the free margin	Close to the free margin	Distant from the free margin

ducts in peripherals 3 and 7. A new reconstruction of *E. australis* is shown on the Fig. 3E, F.

Elkemys australis can be considered as a 'lindholmemydid' based on combination of such characters as contact of plastral buttresses with costals (a testudinoid synapomorphy; Gaffney and Meylan 1988) and presence of continuous rows of inframarginal scutes. *Elkemys australis* demonstrates unique combination of characters (see Diagnosis) which confirm its generic distinctness. Some of these characters, like extension of the pectorals on to the entoplastron, and skin-scute sulcus distant from the free margin of plastral lobes in visceral view, are advanced and this combination is unique among known pre-Eocene basal testudinoids. Among 'lindholmemydids', *E. australis* shares many similar features with *Gravemys barsboldi* such as the shape of the carapace in dorsal view, the large nuchal emargination, the relatively narrow vertebrals 2 and 3, the greater contributions of the hyoplastra than hypoplastra to the minimal length of the bridges, proportions of the posterior plastral lobe, the large anal notch, the shape of the entoplastron, and the presence of four (or five) pairs of wide inframarginals which strongly extend on to peripherals (see Table 2). The inframarginal pattern of *E. australis* and *Gravemys* spp., also shared by *Hokouchelys chenshuensis*, is unique among 'lindholmemydids' and testudinoids in general and suggests that these species may form a natural group (either a clade or a grade) of basal testudinoids. Some other characters shared by *E. australis*, *G. barsboldi* and *H. chenshuensis* (large anal notch and relatively narrow vertebrals 2 and 3) remind features of some geoemydids and testudinids, that may indicate closer relations of the three mentioned genera to these groups (Danilov 2005b). Thus, we partially agree with some previous authors (Chkhikvadze 1987; Lapparent de Broin 2001) in that *E. australis* might be somehow related to geoemydids. However, all these considerations are tentative and need to be corroborated with a phylogenetic analysis of basal and modern testudinoids.

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