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

I.G. Danilov*, J. Claude and V.B. Sukhanov

1Zoological Institute of the Russian Academy of Sciences, Universitetskaya Emb. 1, 199034 Saint Petersburg, Russia; e-mail: igordanilov72@gmail.com
2Institut des sciences de l’Evolution, UMR 5554 CNRS, Université de Montpellier 2, 2, Place Eugène Bataillon, 34095 Montpellier cedex 5, France; e-mail: julien.claude@um2.fr
3Paleontological Institute of the Russian Academy of Sciences, Profsoyuznaya Str., 123, 117997 Moscow, Russia; e-mail: sukhanovturtle@yandex.ru

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

И.Г. Данилов*, Ж. Клод и В.Б. Суханов

1Зоологический институт Российской академии наук, Университетская наб. 1, 199034 Санкт-Петербург, Россия; e-mail: igordanilov72@gmail.com
2Institut des sciences de l’Evolution, UMR 5554 CNRS, Université de Montpellier 2, 2, Place Eugène Bataillon, 34095 Montpellier cedex 5, France; e-mail: julien.claude@um2.fr
3Палеонтологический институт Российской академии наук, ул. Профсоюзная 123, 117997 Москва, Россия; e-mail: sukhanovturtle@yandex.ru

РЕЗЮМЕ

В этой работе мы даем переописание типовой серии *Elkemys australis*, плохо известной базальной тестицинной черепахи (‘Lindholmemydidae’) из палеоцен 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 схож с *Gravemys barsboldi* из позднего мела.
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 persistence 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 difficult 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* Khusatzky et Mlynarski, 1971 from the Late Cretaceous of Mongolia, as described by Khusatzky and Mlynarski (1971), Sukhanov (2000) and personal 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


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); vertebrales 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 hypoplastra 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, 11, 10, 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)

*Elkemys 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.


**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 36 to 59% of its width. This is the widest nuchal plate known within the ‘lindholmemydid’ group. The anterior lateral 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 median 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 trap-
pezoidal, widened posteriorly, slightly narrower than in *Gravemys barsboldi*. In IVPP V3107.1, suprapygal
1 is divided by a suture into two parts: a smaller ante-
rior and the larger posterior. This is probably an ab-
normal 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 ‘lindhol-
memydids’, *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 V3107.2. 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
goemydids, emydids, and testudinids and in *Grave-
mys 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 later-
ally (IVPP V3107.1). This pattern is more close to test-
udinids 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 V3107.3, V3107.2 and partially in
IVPP V3107.3, whereas posterior peripherals are
exposed in IVPP V3107.6 and V3107 (Ye 1974, pl.
I: 1). The ventral parts of bridge peripherals are vis-
able in IVPP V3107.1, V3107.2 and V3107.3; they
are wider than long. Peripherals 3 and 7 contact
butterxes 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 *Mon-
goemys elegans*, and longer than wide and rectangu-
lar 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 g&oacute;bi-
sis* 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. Verte-
brals 2 and 3 are relatively narrow and rectangular
with almost straight lateral borders like in *Grave-
mys barsboldi*, *Achilemys cassouleti*, some species
of *Palaeoemys* and *Echmatemys*, and some modern
goemydids. In other ‘lindholmemydids’, and many
emydids, these vertebrales 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 ‘lindhol-
memydids’, vertebral 5 is wider than the anterior
vertebrales, 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 parallelepips 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 suprapyagal 2. This
condition is similar to other basal testudinoids, platy-
sterids and emydids. In *Gravemys barsboldi*, geo-
emydids and some testudinids marginals 12 extend
on to suprapyagal 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* (Yéh, 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 – sulcus dermo-scuti; sp – suprapygal. Arabic numerals designate element numbers.
Redescription of *Elkemys australis* (Yéh, 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. *Elkomys 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 (A₁, B₁) and explanatory drawings of the same (A₂, B₂); C, D – IVPP V3107.5, posterior portion of the shell in dorsal (C) and ventral (D) views, photographs (C₁, D₁), explanatory drawings of the same (C₂, D₂); 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.
Redescription of *Elkemys australis*.

Fig. 4. Shells of some 'lindholmydids' (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* Khosatzy et Mlynarski, 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.
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 suturedly 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 ‘lindholmemydid’. 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* differs 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 ‘lindholmemydid’ (*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 hyoplastron 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 ento-
plastron (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 hypo-
plastron 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 ingui-
nal 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 humer-
als 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 Elke-
mys 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: medi-
ral ridge on the carapace (present/absent), neu-
ral 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 charac-
terized by three pairs of inframarginals. Variation in
neutral 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 an-
terior 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, wid-
ened 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 hy-
poplastron. 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.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>V3107.1</th>
<th>V3107.2</th>
<th>V3107.3</th>
<th>V3107.5</th>
<th>V3107.6</th>
<th>V3107.7</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carapace (length/width)</td>
<td></td>
<td></td>
<td></td>
<td>?</td>
<td></td>
<td>?</td>
</tr>
<tr>
<td>Nuchal (length/width)</td>
<td>33/56</td>
<td>31.7/55</td>
<td>28.5/50</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neural 1</td>
<td>26.5/15.7</td>
<td>24.0/18.0</td>
<td>25.3/18.5</td>
<td></td>
<td></td>
<td>?/18</td>
</tr>
<tr>
<td>Neural 2</td>
<td>22/19.2</td>
<td></td>
<td>?</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neural 3</td>
<td>22.5/?</td>
<td>21.3/15.3</td>
<td></td>
<td></td>
<td>20.8/14.3</td>
<td></td>
</tr>
<tr>
<td>Neural 4</td>
<td>22/?</td>
<td>17.5/15.6</td>
<td></td>
<td></td>
<td>19.7/16.5</td>
<td></td>
</tr>
<tr>
<td>Neural 5</td>
<td>20/15</td>
<td>18.0/16.6</td>
<td>20/18.5</td>
<td>?</td>
<td>16.8/17.4</td>
<td></td>
</tr>
<tr>
<td>Neural 6</td>
<td>15/16.2</td>
<td>14.0/16.5</td>
<td>12.2/16</td>
<td>13.8/18</td>
<td>12.2/18.5</td>
<td></td>
</tr>
<tr>
<td>Neural 7</td>
<td>11.3/12.5</td>
<td>11.3/16.7</td>
<td></td>
<td>9.5/17.5</td>
<td>10.7/20</td>
<td></td>
</tr>
<tr>
<td>Neural 8</td>
<td>9.8/13</td>
<td>10.4/15.0</td>
<td>?</td>
<td>?</td>
<td>8/17.5</td>
<td></td>
</tr>
<tr>
<td>Suprapygal 1</td>
<td>8.5/13.5</td>
<td>17.0/30.0</td>
<td>18/26</td>
<td>?</td>
<td>15.2/29</td>
<td></td>
</tr>
<tr>
<td>Suprapygal 2</td>
<td>13/27</td>
<td>?</td>
<td>16/43</td>
<td>?</td>
<td>16/44.4</td>
<td></td>
</tr>
<tr>
<td>Pygal (length/width)</td>
<td></td>
<td></td>
<td>?/24</td>
<td>?</td>
<td>13.5/23</td>
<td></td>
</tr>
<tr>
<td>Costal 1</td>
<td>26.5/44/58</td>
<td>22/39.4/58.2</td>
<td>?</td>
<td></td>
<td></td>
<td>?/25/61.5</td>
</tr>
<tr>
<td>Costal 2</td>
<td>23.5/29/65</td>
<td>?</td>
<td>?</td>
<td></td>
<td>17/18/68</td>
<td></td>
</tr>
<tr>
<td>Costal 3</td>
<td>20/23/68</td>
<td>?</td>
<td>?</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Costal 4</td>
<td>22.5/29/71</td>
<td>?</td>
<td>?</td>
<td>?</td>
<td>?</td>
<td></td>
</tr>
<tr>
<td>Costal 5</td>
<td>19/16.5/67</td>
<td>?</td>
<td>?</td>
<td>?</td>
<td>?</td>
<td></td>
</tr>
<tr>
<td>Costal 6</td>
<td>18/25.5/51</td>
<td>?</td>
<td>?</td>
<td>?</td>
<td>11.5/7/46</td>
<td></td>
</tr>
<tr>
<td>Costal 7</td>
<td>10/20.5/41.5</td>
<td>?</td>
<td>?</td>
<td>?</td>
<td>11.5/7/38.5</td>
<td></td>
</tr>
<tr>
<td>Peripheral 1</td>
<td></td>
<td>?</td>
<td>?</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Peripheral 2</td>
<td>23/?</td>
<td>?</td>
<td>?</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Peripheral 3</td>
<td>29.5/?</td>
<td>?</td>
<td></td>
<td></td>
<td></td>
<td>?</td>
</tr>
<tr>
<td>Peripheral 4</td>
<td>27.2/23</td>
<td>?</td>
<td>?</td>
<td></td>
<td></td>
<td>?</td>
</tr>
<tr>
<td>Peripheral 5</td>
<td>24/?</td>
<td>?</td>
<td>?</td>
<td></td>
<td></td>
<td>?</td>
</tr>
<tr>
<td>Peripheral 6</td>
<td>25/?</td>
<td>?</td>
<td></td>
<td></td>
<td></td>
<td>?</td>
</tr>
<tr>
<td>Peripheral 7</td>
<td>28/?</td>
<td>?</td>
<td></td>
<td></td>
<td></td>
<td>?</td>
</tr>
<tr>
<td>Peripheral 10</td>
<td></td>
<td>?</td>
<td>?</td>
<td></td>
<td>22/18.5</td>
<td></td>
</tr>
<tr>
<td>Peripheral 11</td>
<td></td>
<td>?</td>
<td>?</td>
<td>?</td>
<td>23.7/18.5</td>
<td></td>
</tr>
<tr>
<td>Plastron (length at the midline/width)</td>
<td>185/120</td>
<td>160/136</td>
<td>152/110</td>
<td>?</td>
<td>?/126</td>
<td>173.6/126</td>
</tr>
<tr>
<td>Bridge (length)</td>
<td>84.5 (left)</td>
<td>80 (right)</td>
<td>71 (left)</td>
<td>–</td>
<td>–</td>
<td>72 (left)</td>
</tr>
</tbody>
</table>
Redescription of *Elkhemys australis* 235

Table 1. (Continued)

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

<table>
<thead>
<tr>
<th>Characters</th>
<th><em>Mongolemys elegans</em></th>
<th><em>Lindholmemydidae</em></th>
<th><em>Gravemys barsboldi</em></th>
<th><em>Elkemys australis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Shell height</td>
<td>About 1/3 of its width</td>
<td>Up to 55% of its width</td>
<td>No more than 1/2 of its width</td>
<td>?</td>
</tr>
<tr>
<td>Shell surface</td>
<td>Smooth or with sculpturing of tubercles and ridges</td>
<td>Smooth or with sculpturing of tubercles and ridges</td>
<td>With sculpturing of tubercles and ridges</td>
<td>Smooth</td>
</tr>
<tr>
<td>Carapace in dorsal view</td>
<td>Oval, slightly widened posteriorly</td>
<td>Oval, slightly widened posteriorly</td>
<td>Oval, truncated anteriorly</td>
<td>Oval, truncated anteriorly</td>
</tr>
<tr>
<td>Nuchal emargination</td>
<td>Absent</td>
<td>Small</td>
<td>Large</td>
<td>Large</td>
</tr>
<tr>
<td>Nuchal width</td>
<td>About 30% of shell width</td>
<td>About 30% of shell width</td>
<td>About 25% of shell width</td>
<td>About 35% of shell width</td>
</tr>
<tr>
<td>Costal 1/peripheral 4 contact</td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
<td>Present or absent</td>
</tr>
<tr>
<td>Thoracic rib 1</td>
<td>Not shortened</td>
<td>Shortened</td>
<td>Shortened</td>
<td>?</td>
</tr>
<tr>
<td>Cervical</td>
<td>Wide and rectangular, covers no more than 1/4 of the nuchal length</td>
<td>Wide and trapezoid-shaped, covers 1/4 – 1/3 of the nuchal length</td>
<td>Square-shaped, covers no less than 1/3 of the nuchal length</td>
<td>Wide and trapezoid-shaped, covers about 1/4 of the nuchal length</td>
</tr>
<tr>
<td>Vertebral 1</td>
<td>Strongly widened anteriorly and contacts marginals 2</td>
<td>Narrowed or slightly widened anteriorly and does not contact marginals 2</td>
<td>Almost rectangular and does not contact marginals 2</td>
<td>Narrowed anteriorly and does not contact marginals 2</td>
</tr>
<tr>
<td>Vertebrals 2 and 3</td>
<td>Relatively wide</td>
<td>Relatively wide</td>
<td>Relatively narrow</td>
<td>Relatively narrow</td>
</tr>
<tr>
<td>Vertebral 5</td>
<td>Reaches about middle part of marginals 11</td>
<td>Reaches about middle part of marginals 11</td>
<td>Reaches about middle part of marginals 11</td>
<td>Reaches or almost reaches marginals 10</td>
</tr>
<tr>
<td>Extension of marginals 11 on to costals 8</td>
<td>Absent</td>
<td>Present or absent</td>
<td>Present</td>
<td>Absent</td>
</tr>
<tr>
<td>Extension of marginals 12 on to suprrapygal 2</td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
<td>Absent</td>
</tr>
<tr>
<td>Plastral buttresses</td>
<td>Weak</td>
<td>Strong</td>
<td>Moderate or strong</td>
<td>Weak or moderate</td>
</tr>
<tr>
<td>Minimal length of the bridges</td>
<td>50–57% of plastron width</td>
<td>About 65% of plastron width</td>
<td>60–72.5% of plastron width</td>
<td>60–70% of plastron width</td>
</tr>
<tr>
<td>Contribution of hyo- and hypoplastra to the minimal length of the bridges</td>
<td>Approximately equal</td>
<td>Approximately equal</td>
<td>Greater in hyoplastra</td>
<td>Greater in hyoplastra</td>
</tr>
<tr>
<td>Length of the anterior plastral lobe</td>
<td>About 30% of plastron length</td>
<td>About 25% of plastron length</td>
<td>22–24% of plastron length</td>
<td>About 25% of plastron length</td>
</tr>
<tr>
<td>Length of the posterior plastral lobe</td>
<td>About 35% of plastron length</td>
<td>About 35% of plastron length</td>
<td>About 40% of plastron length</td>
<td>About 30% of plastron length</td>
</tr>
<tr>
<td>Shape of the posterior plastral lobe</td>
<td>Relatively narrow at the base and slightly narrowed posteriorly</td>
<td>Relatively narrow at the base and slightly narrowed posteriorly</td>
<td>Relatively wide at the base and strongly narrowed posteriorly</td>
<td>Relatively wide at the base and strongly narrowed posteriorly</td>
</tr>
<tr>
<td>Lateral borders of the posterior plastral lobe</td>
<td>Straight</td>
<td>Convex in femoral part and straight in anal part</td>
<td>Straight</td>
<td>Convex in femoral part and straight in anal part</td>
</tr>
<tr>
<td>Anal notch</td>
<td>Small or absent</td>
<td>Small</td>
<td>Large</td>
<td>Large</td>
</tr>
<tr>
<td>Epiplastra</td>
<td>Relatively small</td>
<td>Relatively small</td>
<td>Relatively small</td>
<td>Relatively large</td>
</tr>
<tr>
<td>Entoplastron</td>
<td>Diamond-shaped longer than wide or as long as wide</td>
<td>Diamond-shaped longer than wide, or hexagonal wider than long</td>
<td>Hexagonal wider than long</td>
<td>Hexagonal wider than long</td>
</tr>
<tr>
<td>Extension of pectorals on to entoplastron</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
</tr>
<tr>
<td>Number of inframarginals</td>
<td>Three pairs</td>
<td>Three pairs</td>
<td>Four pairs</td>
<td>Four or five pairs</td>
</tr>
<tr>
<td>Inframarginals</td>
<td>Wide</td>
<td>Narrow</td>
<td>Wide</td>
<td>Wide</td>
</tr>
<tr>
<td>Extension of inframarginals on to peripherals</td>
<td>Weak or absent</td>
<td>Weak or absent</td>
<td>Strong</td>
<td>Strong</td>
</tr>
<tr>
<td>Position of skin-scute sulcus on the plastron</td>
<td>Close to the free margin</td>
<td>Close to the free margin</td>
<td>Close to the free margin</td>
<td>Distant from the free margin</td>
</tr>
</tbody>
</table>
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 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 vertebrae 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 chenshuenensis*, 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. chenshuenensis* (large anal notch and relatively narrow vertebrae 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 1999, 2005a, b). Thus, we partially agree with some previous authors (Chkhikvadze 1987; Lapparent de Broin 1999, 2005a, b). This study is done under financial support of grants of the President of the Russian Federation (NSh-6560.2012.4 and MK-330.2006.5) and grant of the Russian Foundation for Basic Research (04-05-65000-a) to IGD. This research was supported by the Ministry of Education and Science of the Russian Federation to IGD.

**ACKNOWLEDGMENTS**

IGD thanks Professor J. Li, Dr. Y. Wang and Ms. F. Zheng (IVPP, Beijing) for access to turtle collection of IVPP and hospitality. Ted Papenfuss (Berkeley, USA) provided invaluable assistance to IGD and without him this project would be impossible. JC thanks Haiyan Tong provided data concerning morphology of Chinese Late Cretaceous and Paleocene testudinoids for comparisons. This study is done under financial support of grants of the President of the Russian Federation (NSh-6560.2012.4 and MK-330.2006.5) and grant of the Russian Foundation for Basic Research (04-05-65000-a) to IGD. This research was supported by the Ministry of Education and Science of the Russian Federation to IGD.

**REFERENCES**


Submitted 15 June, 2012; accepted 15 August, 2012.