LETTERS

An ancestral turtle from the Late Triassic of southwestern China

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The origin of the turtle body plan remains one of the great mysteries of reptile evolution. The anatomy of turtles is highly derived, which renders it difficult to establish the relationships of turtles with other groups of reptiles. The oldest known turtle, *Proganochelys* from the Late Triassic period of Germany[1], has a fully formed shell and offers no clue as to its origin. Here we describe a new 220-million-year-old turtle from China, somewhat older than *Proganochelys*, that documents an intermediate step in the evolution of the shell and associated structures. A ventral plastron is fully developed, but the dorsal carapace consists of neural plates only. The dorsal ribs are expanded, and osteoderms are absent. The new species shows that the plastron evolved before the carapace and that the first step of carapace formation is the ossification of the neural plates coupled with a broadening of the ribs. This corresponds to early embryonic stages of carapace formation in extant turtles, and shows that the turtle shell is not derived from a fusion of osteoderms. Phylogenetic analysis places the new species basal to all known turtles, fossil and extant. The marine deposits that yielded the fossils indicate that this primitive turtle inhabited marginal areas of the sea or river deltas.

New fossil turtles have been collected from the lower Carnian[2,3] near Guanling in Guizhou Province, China. The sediments were deposited in the Nanpanjiang Trough Basin, which during the early to middle Carnian marine transgression remained surrounded by the Sichuan–Yunnan–Guizhou Old Land on three sides, opening into the Palaeotethys towards the southwest[3,4]. Sedimentological clues indicate anoxic conditions for the bottom water, and driftwood as well as other plant remains indicate the relative proximity of coastal waters[3]. Vast outcrops yielded a rich fauna of invertebrates and marine reptiles[3,5], but turtles from the Guanling Biota are reported here for the first time.

Order Testudinata
New Family Odontochelyidae
Odontochelys gen. nov.

Etymology. '*odonto-*' (comb. form of 'odoús', Greek): tooth; *chelys* (Greek): lyre of ancient Greece, or tortoise.
Type species. *Odontochelys semitestacea* sp. nov.
Distribution. Late Triassic, Guizhou Province, China.
Diagnosis. As for species.

Odontochelys semitestacea sp. nov.

Etymology. *testaceus* (*-um*) (Latin): of animals, covered with shell; semi- (Latin, as prefix): half.
Holotype. IVPP (Institute of Vertebrate Paleontology and Paleoanthropology) V 15639.
Paratype. IVPP V 13240.
Referred specimen. IVPP V 15653.
Location. Guanling, Guizhou Province, southwestern China.
Horizon. Wayao Member of the Falang Formation.
Diagnosis. A turtle of relatively small size; teeth present on upper and lower jaws, and on kinetic dermal palate; snout elongate and pointed; plastron elongated oval, with four frilled lateral spines; epiplastral dorsal process present; two pairs of mesoplastra; hypoischium butterfly-shaped, closing anal opening behind ischium; only neural plates ossified in carapace; dorsal ribs broadened.

The skull of *Odontochelys* shows an elongate preorbital region forming a pointed snout (Fig. 1a, b). Small and peg-like, pointed teeth are present on premaxilla, maxilla, dentary, pterygoid and vomer (Figs 1b, c and 2c, d). The jugal shows a rounded posteroventral margin, indicating a weak ventral excavation of the cheek. The skull table is not excavated posteriorly. The temporal region is not fenestrated. Distinct basipterygoid processes form an open basicranial articulation with the pterygoids. The pterygoid shows a distinct transverse process that may have separated a subtemporal fenestra from a suborbital fossa (Fig. 2c, d). The quadrate is weakly concave posteriorly; a cavum tympani is absent.

All vertebrae are weakly amphicoelous. The vertebral count is eight cervicals, nine dorsals, two sacrals, and minimally 20 caudals. The cervical centra are distinctly keeled ventrally. Cervical ribs are small, knob-like structures. Eight dorsal ribs are distinctly broadened, single-headed, and articulate in facets located at the middle of the centrum. The last dorsal rib is slender. The distally expanded sacral ribs are not fused with the sacral vertebrae (Fig. 1d). The caudal transverse processes likewise are free. Chevrons articulate on the posteroventral aspect of the preceding centrum (Fig. 2a). A tail-club is absent.

The epiplastral dorsal process shows no trace of a suture at its base. The scapular dorsal blade is rod-like, without an acromial process (Figs 1d and 3c). The broad, curved and plate-like coracoid shows a foramen with its anterior margin open (Fig. 3c). The humerus is more massively built than the femur, but of equal length. The proximal end of the humerus shows well-developed medial and lateral processes, separated by the intertubercular fossa (Fig. 2a, b). The distal expansion of the humerus carries double articulations for the radius and ulna. The radius is slightly shorter and more lightly built than the ulna; the ulna lacks an ossified olecranon. Eight to nine ossifications are present in the carpus: a radiale seems to be fused with the intermedium (in the paratype, absent in the holotype), ulnare, pisiforme, lateral and medial centralia, and five distal carpals (Fig. 2a, b). The metacarpals are proximally overlapping, the third and the fourth being the longest in the series. The phalangeal formula in the manus is 2-3-4-4-3.

The ilium is stout, with a short dorsal shaft (Fig. 1d). Pubes and ischia form a pubo-ischial plate with a medioventral ridge terminating in a posterior ischial tubercle (Fig. 2a, b); the thyroid foramen is present in the referred specimen (Fig. 3d). The pubis carries a ventrally projecting lateral process that articulates with the plastron (Fig. 3d). The ischium is located behind the plastron, and carries a

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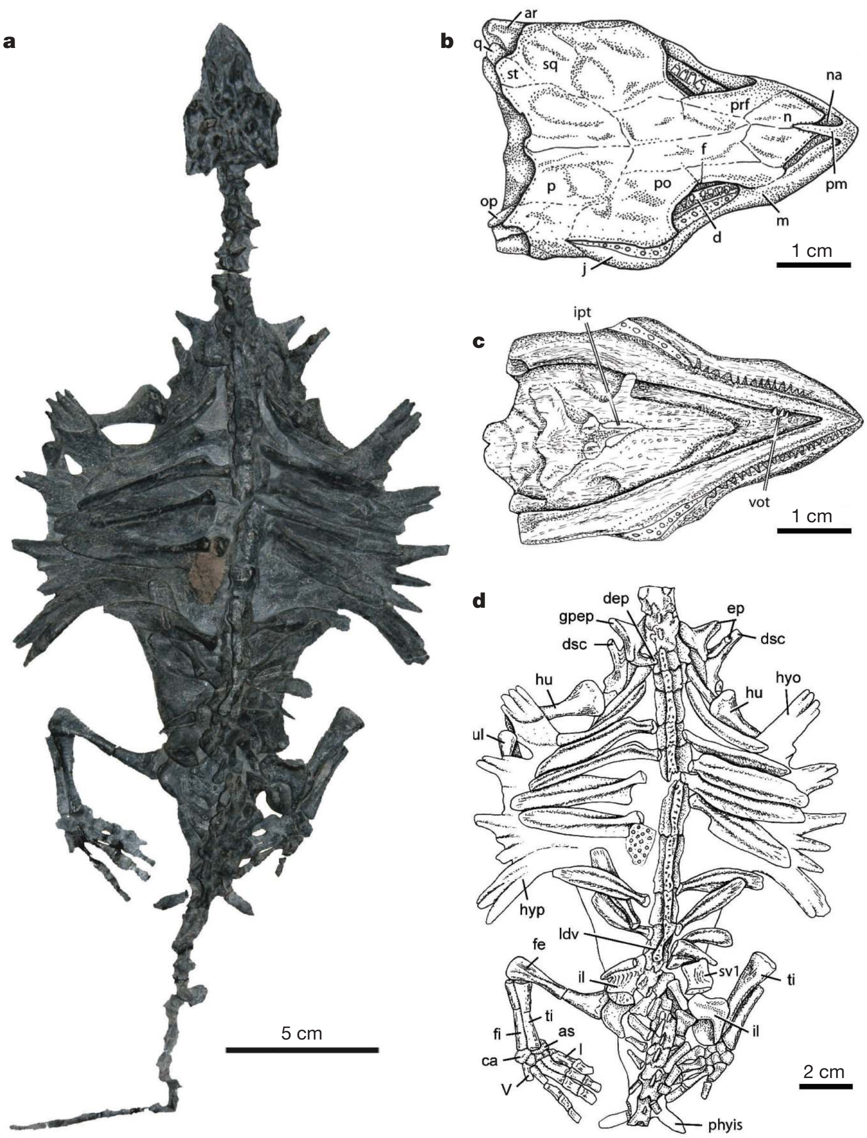

Figure 1 | Holotype (IVPP V 15639) of *Odontochelys semitestacea* gen. et sp. nov. a, Skeleton in dorsal view. **b**, Skull in dorsal view. **c**, Skull in ventral view. **d**, Body in dorsal view. Teeth on the upper jaw and palatal elements were scratched out during excavation. Abbreviations: ar, articular; as, astragalus; ca, calcaneum; d, dentary; dep, dorsal process of epiplastron; dsc, dorsal process of scapula; ep, epiplastron; fe, femur; fi, fibula; gpep, gular projection of epiplastron; hu, humerus; hyo, hyoplastron; hyp, hypoplastron; il, ilium; ipt, interpterygoid vacuity; j, jugal; ldv, last dorsal vertebra; m, maxilla; n, nasal; na, naris; op, opisthotic; p, parietal; phyis, posterolateral process of hypoischium; pm, premaxilla; po, postorbital; prf, prefrontal; q, quadrate; sq, squamosal; st, supratemporal; sv1, 1st sacral vertebra; ti, tibia; ul, ulna; vot, vomerine teeth; I, V, 1st and 5th metatarsals.

posterolaterally projecting ischial process. These processes, together with hypoischium, enclose a rounded anal opening (Fig. 2b). The hypoischium extends into posterolaterally projecting processes. The femur is slender and sigmoidally curved; its proximal articular head is angled away from its long axis. The internal trochanter is distinct. The distal articulations on the femur are confluent. The fibula is more lightly built than the tibia. Astragalus and calcaneum are sutured in the holotype but fused in the paratype; no perforating foramen is located between them (Fig. 2b). No centralia are ossified in the tarsus; four distal tarsals are preserved. The metatarsals are proximally overlapping; the fifth metatarsal is angulated (hooked). The pedal phalangeal formula is 2-3-4-4-?.

Costal and marginal carapacial plates are absent, but neural plates are ossified. The neural plates are not fused with broadened neural spines of dorsal vertebrae but were displaced laterally during fossilization (Fig. 3a, b). The plastron is composed of epiplastra and entoplastron, one pair of hyoplastra, two pairs of mesoplastra, one pair of hypoplastra and one pair of xiphiplastra. The entoplastron is heart-shaped, with well-developed anterolateral facets receiving the epiplastra (Fig. 2b). Hyoplastron, mesoplastron and hypoplastron each bear laterally projecting frilled spines. No osteoderms are present on the neck, trunk, tail and limbs.

Odontochelys is more primitive than *Proganochelys*[1] in presence of teeth on premaxilla, maxilla and dentary; relatively long preorbital skull; distinct transverse process on pterygoid; absence of fully formed carapace; no acromial process on scapula; dorsal ribs articulating at midline of centrum; free sacral ribs; free caudal transverse processes; presence of long tail; four (rather than three) phalanges in digits III and IV of manus and pes; absence of osteoderms and tail-club. *Odontochelys* shares with *Proganochelys* primitive features that are absent in Casichelydia: teeth on vomer and pterygoid; open basicranial articulation; dorsal epiplastral process (also present in

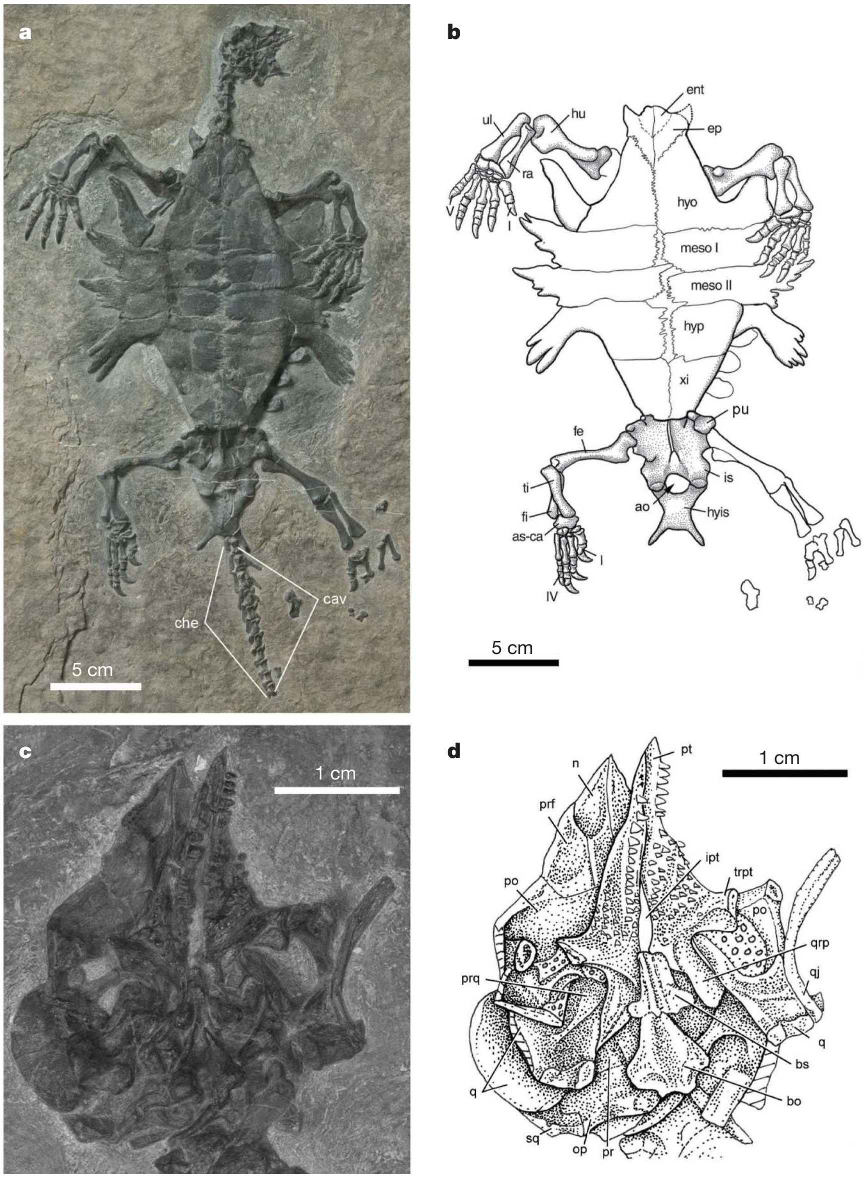

Figure 2 | Paratype (IVPP V 13240) of *Odontochelys semitestacea* gen. et sp. nov. a, Skeleton in ventral view. **b**, Body in ventral view. **c**, **d**, Skull in ventral and slightly lateral views. Abbreviations as in Fig. 1, plus: ao, anal opening; bo, basioccipital; bs, basisphenoid; cav, caudal vertebrae; che, chevron; ent, entoplastron; hyis, hypoischium; is, ischium; meso I and II, mesoplastra 1 and 2; pr, prootic; prq, pterygoid ramus of quadrate; pt, pterygoid; pu, pubis; qj, quadratojugal; qrp, quadrate ramus of pterygoid; ra, radius; trpt, transverse process of pterygoid; xi, xiphiplastron; I, IV and V, 1st, 4th and 5th digits.

Kayentachelys[6]); broad and plate-like coracoid; ilium with short dorsal shaft; hypoischium present; distinct gular projections on epiplastra. Testing the phylogenetic relationships (see Supplementary Information) of *Odontochelys* confirms its position as basal to all other known turtles, fossil or extant (Fig. 3e). The relationships of turtles with other amniotes have been controversial[1,7–11]. The inclusion of *Odontochelys* in the analysis of turtle relationships within amniotes (see Supplementary Information) supports the position of turtles within diapsid reptiles.

Odontochelys provides documentation that in turtles, the plastron evolved before the carapace. This corresponds to the ossification of plastral before carapacial elements in embryonic turtles[12–14]. The new taxon also shows that the neural plates were the first to evolve among the carapacial elements. The neural plates remained separate from the underlying dorsal neural spines in *Odontochelys*, as was also reported for a juvenile *Testudo loveridgii*[15]. This differs from other turtles[12,16,17], in which neural plate formation expands from the perichondral ossification of the vertebral neural arch. The dorsal ribs of *Odontochelys* are characteristically broadened, resembling the ribs of *Chelydra serpentina* at the Yntema[18] embryonic stage 23; that is, at a stage before marginal, nuchal and pygal elements start ossification[12,14]. In extant turtles[12–14,16,17,19,20], ossification of costal plates spreads from the perichondral ossification of the dorsal ribs through the adjacent dermis of the carapacial disk. *Odontochelys* resembles embryonic stages of extant turtles in that there is only some broadening and consequent flattening of the dorsal ribs, which do not expand into costal plates. That *Odontochelys* should be represented by juvenile specimens can be rejected, given the fusion of the astragalus and calcaneum. Carapace reduction in fossil and extant turtles[21] never restores the embryonic morphology of the ribs, and is generally correlated with the formation of fontanelles in the plastron that are larger than the narrow midline fontanelle seen in the plastron of *Odontochelys*.

Osteoderms of reptiles form through metaplastic ossification[22–27]. Both dermal sclerification[22] and osteoblast activity contribute to

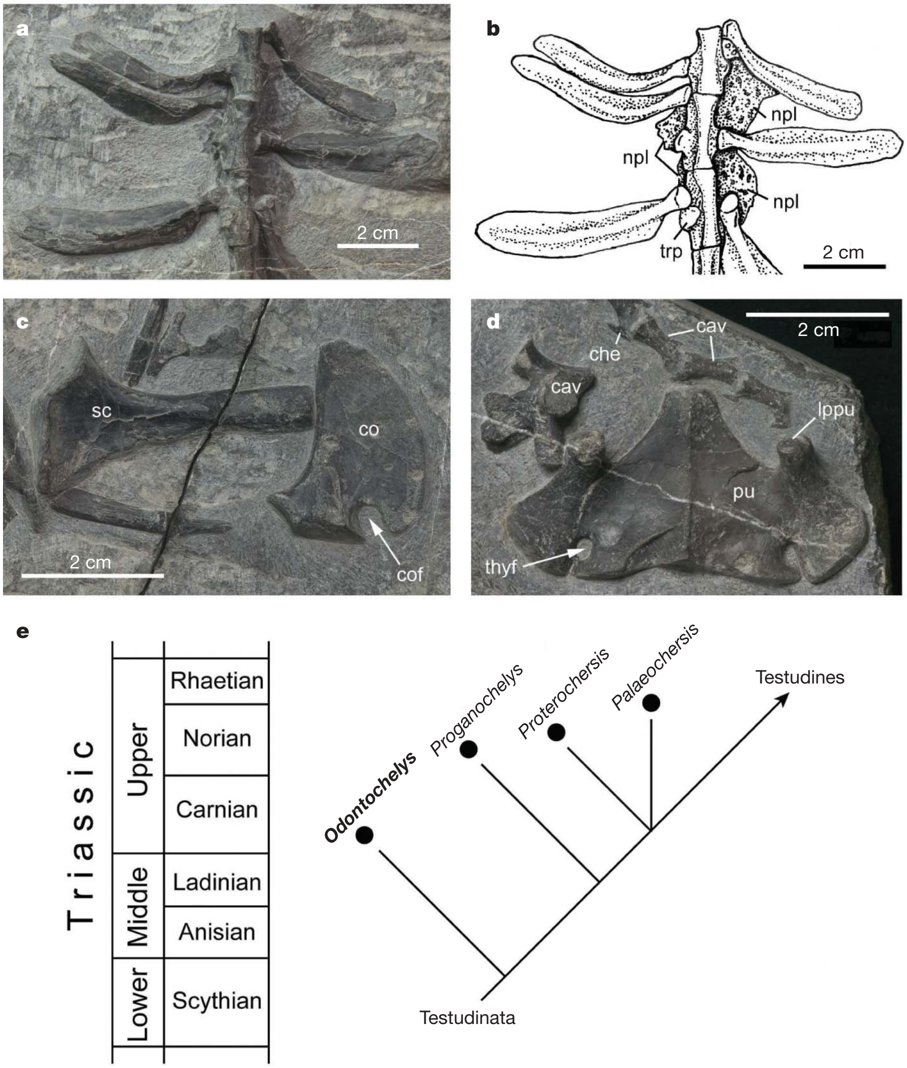

Figure 3 | Referred specimen (IVPP V 15653) of *Odontochelys semitestacea* gen. et sp. nov. a, b, Three dorsal vertebrae, ribs and neural plates (shifted onto one side; others are not exposed) in ventral views. **c,** Scapula and coracoid in medial view. **d,** Two pubes in inner and posterior caudal vertebrae in lateral views. **e,** Geological time table of the Triassic period, showing the stratigraphic distribution of basal members of Testudinata, and a cladogram depicting the phylogenetic relationships of *Odontochelys* with other Triassic turtles. Abbreviations as in Figs 1 and 2, plus: co, coracoid; cof, coracoid foramen; lppu, lateral process of pubis; npl, neural plate; sc, scapula; thyf, thyroid fenestra; trp, transverse process of dorsal vertebrae.

carapace formation in turtles[17,28]. This has led to the hypothesis that turtles evolved from an osteoderm-bearing ancestor[8,17,29]. The evolution of the carapace would thus have involved the shift of endoskeletal neural arches and ribs into the deep dermis of the carapacial disk, followed by fusion of endoskeletal and dermal elements, or a replacement of the former by the latter[17]. The absence of osteoderms in *Odontochelys* indicates that the carapace did not evolve through the fusion of ancestrally present osteoderms[8], but instead formed by intramembranous ossification within the carapacial disk[11,16,19,20].

The evolution of a ventral dermal armor (plastron) has previously been taken to indicate an aquatic origin of turtles[11]. *Odontochelys* may have inhabited marginal areas of the Nanpanjiang Trough Basin, or river delta habitats. Forelimb proportions have been shown to correlate with habitat preferences in living turtles[30]. Studies of primitive fossil turtles such as *Proganochelys* and *Palaeochersis* showed that they were predominantly terrestrial. In addition, shell bone histology[28] was used to support the hypothesis of a terrestrial origin of turtles[30]. However, on the basis of its forelimb proportions, *Odontochelys* compares to living turtles that inhabit 'stagnant or small bodies of water'[30]. This is indicative of primarily aquatic habits and of a possible aquatic origin of turtles.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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