# Chapter 10
# Turtles from the Jurassic Shishugou Formation of the Junggar Basin, People's Republic of China, with Comments on the Basicranial Region of Basal Eucryptodires

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**Abstract** Five fossil turtle species (?*Sichuanchelys* sp., three species of *Xinjiangchelys*, and an indeterminate species of *Annemys*) are present in the Shishugou Formation (late Middle to early Late Jurassic) of the Junggar Basin, northwestern China. Two of these, *X. radiplicatoides* sp. nov. and *Annemys* sp., are each represented by an associated skull and shell. These demonstrate that the Xinjiangchelyidae, as currently defined, encompasses different grades of evolution. *X. radiplicatoides* is primitive in features of the basicranial region, lack of emargination of the skull roof, and presence of an inflated postorbital region. *Annemys* sp., which has a low skull with deeply emarginated temporal and cheek regions and large foramina palatinum posterius, is similar to basal eucryptodires from the Early Cretaceous of Asia, particularly *Hangaiemys*. Early stages in the evolution of the basicranial region in eucryptodires are documented by the well-preserved basicranial region of *X. radiplicatoides* and *Annemys* sp. The slit-like structure of the foramen palatinum posterius in *X. radiplicatoides* is consistent with the interpretation that this opening developed by closure of the interpterygoid vacuity around the palatine artery. Processes of the basisphenoid that extend laterally into the pterygoid, identified here as basipterygoid processes, are well developed in *Xinjiangchelys* and most Early Cretaceous sinemydids/macrobaenids. Although a high taxonomic diversity of turtles is present in the Shishugou Formation, diversity at individual localities is low, often with a single taxon being present or overwhelmingly dominant, and most localities differ in the kinds of turtles that are dominant at that locality. This pattern of high alpha diversity (total diversity within a unit), low diversity within individual localities, and high beta diversity (between-locality diversity within a unit) is unusual in turtle assemblages, and suggests that the paleoecology of the Shishugou Formation has unusual aspects compared to similarly diverse turtle assemblages, where diversity at a locality typically reflects total diversity within the unit.

**Keywords** *Annemys* • China • Junggar Basin • Jurassic • *Sichuanchelys* • Shishugou Formation • Xinjiangchelyidae • *Xinjiangchelys*

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## Introduction

Fossil turtles from Asia are important to our understanding of the rise of modern turtle clades and assemblages, because many extant groups of eucryptodires are thought to have originated there (Hutchison 2000; Hirayama et al. 2000; Sukhanov 2000). These include testudinoids, which first occurred in Asia in the Early Cretaceous (Brinkman et al. 2008), and trionychians, which were present in Asia in the Jurassic (Gaffney and Meylan 1992a; Danilov and Parham 2006). In addition, fossil turtles from Asia have shown that a diverse assemblage of eucryptodires existed there during the Middle-Late Jurassic (Danilov and Parham 2008; Rabi et al. 2010). Thus, the Jurassic of Asia is key for understanding the initial stages of eucryptodire evolution.

Jurassic turtles were first reported from Asia by Young and Chow (1953), who described six taxa on the basis of seven specimens recovered in 1951 during construction of the Chengdu–Chungking Railway in the Province of Sichuan, southern China. Three of these species were placed in monospecific genera: *Chengyuchelys baenoides* Young and Chow 1953; *Tienfuchelys tzuyangensis* Young and Chow 1953; and *Sinaspideretes wimani* Young and Chow 1953. The remaining three were included in the genus *Plesiochelys* Rütimeyer 1873, a basal eucryptodire largely based on plesiomorphic features of the shell and otherwise known from the Jurassic of Europe. The species referred to *Plesiochelys* were *P. latimarginalis* Young and Chow 1953, *P. radiplicatus* Young and Chow 1953, and *P. chungkingensis* Young and Chow 1953. The ages of the specimens described by Young and Chow (1953) are uncertain, because the Chengdu–Chungking Railway cuts through both Middle and Upper Jurassic sediments and detailed locality information was not recorded for any of the specimens. Subsequent papers further documented the diversity and distribution of turtles in the Jurassic of Sichuan (Ye 1963, 1973; Ye and Fang 1982; Fang 1987; Ye and Pi 1997). Four additional taxa were recognized from the Late Jurassic: *Plesiochelys tatsuensis* Ye 1963; *P. kwanganensis* Ye 1963; *P. oshanensis* Ye 1973; and *P. jingyanensis* Ye and Fang 1982. Documentation of Middle Jurassic turtles in China was greatly increased by the discovery of a rich vertebrate assemblage in Zigong, Sichuan, from which three new turtle taxa were described on the basis of shells: *Chengyuchelys zigongensis* Ye 1982; *C. dashanpuensis* Fang 1987; and *Sichuanchelys chowi* Ye and Pi 1997. The Zigong taxa are distinctly more primitive compared with the Late Jurassic forms in their retention of a mesoplastron, and this feature was used to place them in a separate family, the Chengyuchelyidae Ye 1990.

The first Chinese Jurassic turtle recognized from outside of Sichuan, *Xinjiangchelys junggarensis* Ye 1986a, was described on the basis of a complete carapace from a locality near Jiangjunmiao, in the northern part of the Junggar Basin, Xinjiang Uygur Autonomous Region, in the northwestern part of the country. This specimen was regarded as Middle Jurassic in age because of the associated fauna, particularly the presence of tritylodonts (Zhao 1980); that age estimate has been corroborated by later geological studies (Eberth et al. 2001).

The description of *Xinjiangchelys junggarensis* in northwestern China and subsequent discoveries of Middle Jurassic turtle material from elsewhere in central Asia (Kaznyshkin 1988), led to the recognition that the Jurassic eucryptodires from Asia were part of a distinct radiation of primitive eucryptodires not directly related to the European *Plesiochelys*. Kaznyshkin (1988) accordingly transferred all Asian material previously included in *Plesiochelys* to the genus *Xinjiangchelys*. In a later paper, *Xinjiangchelys* was also placed in its own family, the Xinjiangchelyidae Nessov 1990 (in Kaznyshkin et al. 1990).

Explorations by the Canada–China Dinosaur Project, an international expedition that worked in the Junggar Basin of Xinjiang from 1987 to 1990, led to discoveries in the northern part of the basin, north of Qitai, of additional Jurassic turtle-bearing localities clustered in two areas about 90 km apart. Here we refer these as the "Jiangjunmiao field area" and the "Wucaiwan field area", the former near the abandoned settlement of Jiangjunmiao and the latter near Huoshaoshan (see Fig. 10.1a–c). The Jiangjunmiao field area includes the holotype locality of *Xinjiangchelys junggarensis*. No additional material was collected from that quarry but two additional localities of comparable age were identified. The first yielded a non-diagnostic carapace found during explosive excavation of a large sauropod. The second comprised a rich bone bed (herein called the ''Jiangjunmiao turtle bonebed'') dominated by disarticulated and partially articulated turtle elements in a small channel setting. Variation in surface texture of shell elements indicates that at least two kinds of turtles are present, although most belong to a turtle with distinctive plications on the carapace. In addition to shell elements, significant cranial remains were recovered. In the Wucaiwan field area, remains of at least 14 individuals were collected from a single stratigraphic interval near Pingfengshan (see locality map and detailed description in Peng and Brinkman 1993, Fig. 1, p. 2016). Exposures in this area originally were referred to the Qigu Formation by Peng and Brinkman (1993); subsequently it was recognized that the Qigu Formation is restricted to the southern margin of the Junggar Basin and the temporally equivalent sediments from the northern margin of the basin instead belong to the Shishugou Formation (Fig. 10.1d). Two turtle taxa were recognized by Peng and Brinkman (1993) from Pingfengshan: *X. latimarginalis*, represented by 12 specimens, including a nearly complete carapace and some associated postcrania, and an indeterminate eucryptodire, provisionally identified as "*Xinjiangchelys* sp.", represented by a single plastron.

Peng and Brinkman (1993) followed Kaznyshkin (1988) in placing *Xinjiangchelys junggarensis*, the type specimen of "*Plesiochelys*" *latimarginalis*, and an incomplete shell and series of isolated elements from a Middle Jurassic locality in Kirgizstan within the species *X. latimarginalis*. Subsequent studies concluded that the range of variation in *X. latimarginalis*, as defined by Peng and Brinkman (1993), exceeded that expected for a single turtle species (Matzke et al. 2004, 2005; Nessov 1995). Consequently, Nessov (1995) erected the species *X. tianshanensis* for material from Kirgizstan and Matzke et al. (2004) partitioned the Junggar material into two species: *X. junggarensis*, which they restricted to the holotype specimen, and an unnamed congener for the Pingfengshan specimens originally assigned to *X. latimarginalis* by Peng and Brinkman (1993).
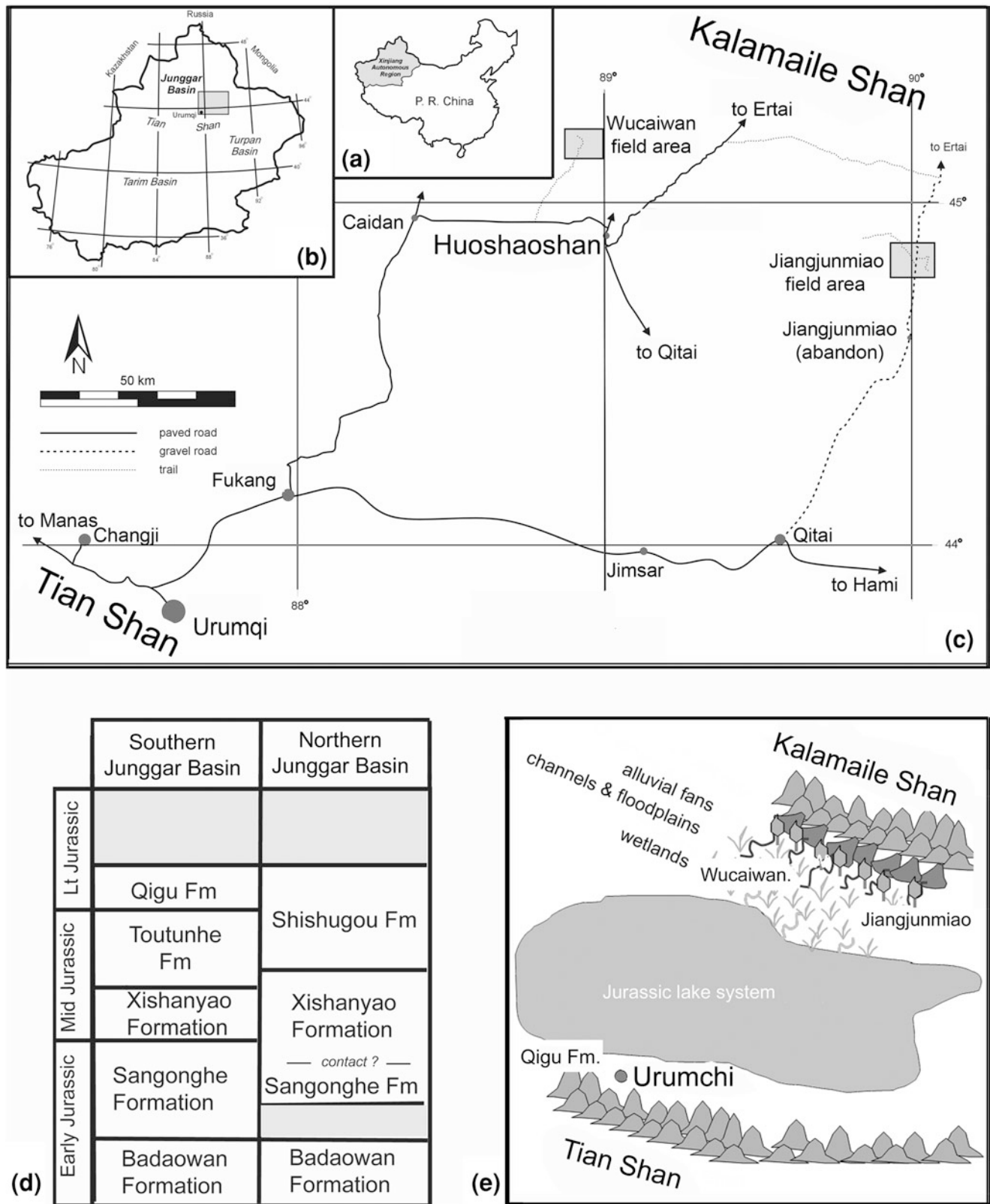
**Fig. 10.1** Locality, stratigraphic, and depositional information for Jurassic turtle-bearing localities in Junggar Basin. **a–c** locality maps: **a** location of Xinjiang Uygur Autonomous Region in northwestern People's Republic of China; **b** location of Junggar Basin within Xinjiang; **c** locations of Wucaiwan and Jiangjunmiao field areas in northern part of Junggar Basin. **d** Stratigraphic chart showing Jurassic formations in northern and southern parts of the Junggar Basin; note that the Middle-Late Jurassic boundary lies within the Shishugou Formation. **e** Paleoenvironmental reconstruction of the Junggar Basin during the time of deposition of the upper part of the Shishugou Formation, showing approximate positions of present-day Wucaiwan and Jiangjunmiao field areas

Brinkman et al. (2008) partially supported Matzke et al. (2004) approach by recognizing *X. latimarginalis* as a distinct taxon, but felt that that the Pingfengshan specimens could not be distinguished from *X. junggarensis* and, contrary to Matzke et al. (2004), included them in the latter species.

Matzke et al. (2004, 2005) documented the presence of three additional *Xinjiangchelys* species from the southern Junggar Basin, in the Qigu Formation: *X.* cf. *radiplicatus*; *X. qiguensis* Matzke et al. 2004; and *X. chowi* Matzke et al. 2005. *X.* cf. *radiplicatus* shared with *X. radiplicatus* from the Late Jurassic of Sichuan the presence of strong plications on the carapace. *X. qiguensis* and *X. chowi* were distinguished on the basis of features of the shell. As a result, Brinkman et al. (2008) concluded that five species of *Xinjiangchelys* are present in the Jurassic formations of the Junggar Basin: *X. junggarensis*; *X.* cf. *radiplicatus*; *X. qiguensis*; *X. chowi*; and *X.* sp. A slightly greater diversity was reported by Rabi et al. (2010), who recognized another two additional genera, *Sichuanchelys* and *Annemys*.

Expeditions to the Junggar Basin co-led by two of us (JC and XX) from 2000 to 2007 collected a series of turtle specimens, including two incomplete skeletons from the Shishugou Formation in the Wucaiwan field area. Those specimens, along with the previously undescribed fragmentary remains from the turtle-dominated bone bed at Jiangjunmiao, provide significant new information on the anatomy, diversity, and relationships of turtles from the Junggar Basin and allow a reevaluation of the patterns of diversification of early eucryptodires in Asia.

## Osteological Terminology

Aside from two exceptions, here we follow the anatomical terminology for turtle skulls developed by Gaffney (1972, 1979b). The first exception is the term "foramen caroticum laterale". That term has been used to refer both to a foramen opening into the braincase and to a more posterior foramen opening through the roof of the palate, although in recent papers (e.g., Gaffney et al. 2007) the former definition has been adopted. Because this term has been used to apply to non-homologous structures, Sterli et al. (2010) proposed a new term, the "foramen caroticum cerebralis posterior", for the posterior opening. We follow Sterli et al. (2010), although for consistency we adhere to Gaffney (1972, 1979b) in using Latin terms for anatomical structures in the turtle skull and, thus, prefer the modified term "foramen posterius canalis carotici cerebralis (fpccc)".

The second exception concerns the "basipterygoid process". A basipterygoid process was not recognized in turtles by Gaffney (1972, 1979b), but a laterally projecting triangular process of the basisphenoid in the Early Cretaceous paracryptodire *Pleurosternon bullockii* was identified as a basipterygoid process by Evans and Kemp (1975). Gaffney (1979a) questioned that identification, arguing that the structure was unlikely to be homologous to the basipterygoid process of primitive reptiles because of its position relative to the dorsum sellae and foramen anterius canalis carotici interni—in primitive reptiles, the basipterygoid process is anterior to these structures, whereas the process identified by Evans and Kemp (1975) as a "basipterygoid process" is more posterior. Subsequently, it has been recognized that a basipterygoid process is widespread among early turtles, being present in, for example, *Proganochelys* and *Kayentachelys* among others (Gaffney 1990; Sterli and Joyce 2007). Because of the widespread presence of a basipterygoid process in those basal turtles, we feel that the triangular process present in *Pleurosternon* and other basal turtles is correctly identified as the basipterygoid process and refer to it by that term, although to recognize that this identification remains to be confirmed, here we enclose that term in quotes.

Institutional abbreviations used in this paper are: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; WCW, Wucaiwan (used as part of the field number for specimens collected from the Wucaiwan field area).

## Geology

The Shishugou Formation consists of a 450 m thick sequence dominated by fluvial-lacustrine beds. Fossil turtle remains described here are from exposures of the Shishugou Formation in the Jiangjunmiao and Wucaiwan field areas (Fig. 10.1a–c). In both field areas, the formation is dominated by alluvial facies (Eberth et al. 2001). The Jiangjunmiao Formation is considered to span the Middle-Late Jurassic boundary (Eberth et al. 2001), and unpublished radiometric dates from the middle and top of the formation indicate the upper Jurassic section is restricted to the Oxfordian (Clark et al. 2006) Although turtle material was found below and above the boundary, most of the identifiable specimens that could be placed in stratigraphic position are from the upper portion of the formation and, thus, are Oxfordian in age (Fig. 10.1d).

During the Jurassic, the highlands bordering the Junggar Basin (Kalamaili Shan Mountains in the north and Tian Shan Mountains in the south) drained into the central part of the basin. The Shishugou Formation was deposited in wetlands between the Kalimeili Mountains in the north and a central lake, whereas the Qigu Formation was deposited farther to the south along the margins of the Tian Shan

**Fig. 10.2** Carapaces of ?*Sichuanchelys* sp., Wucaiwan field area, northern Junggar Basin, Xinjiang, China; upper part of Shishugou Formation; Middle (Callovian) and/or Late (Oxfordian) Jurassic.
**a–c** Photographs of original specimens, all in dorsal view: **a** holotype (IVPP V18101); **b** referred specimen (IVPP V18102); **c** referred specimen (IVPP V18103).
**d** Reconstruction of carapace in dorsal view, based on all three of the figured specimens. Images at different scales
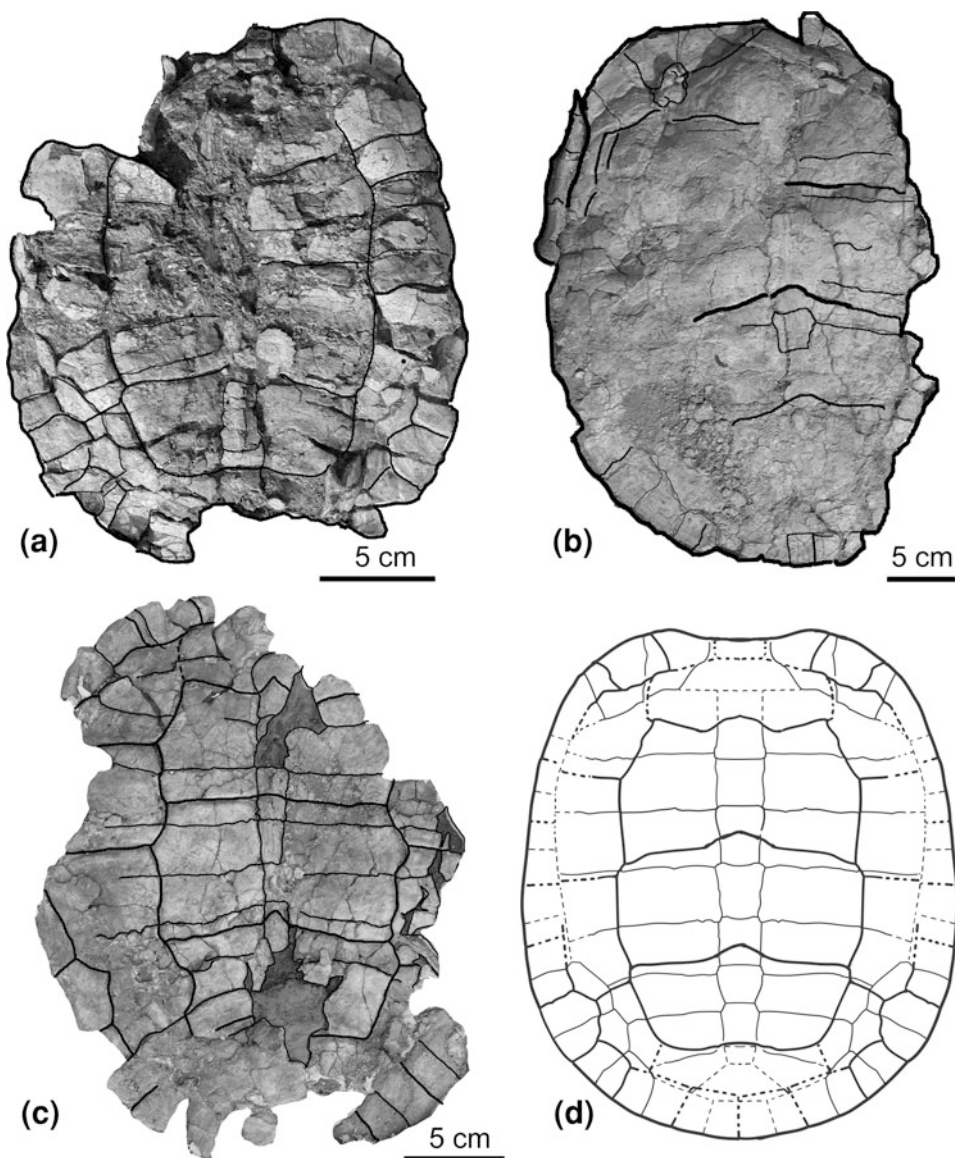


Mountains (Fig. 10.1e). The climate was seasonally dry (Eberth et al. 2001).

## Systematic Paleontology

Order Testudines Batsch 1788
Megaorder Cryptodira Cope 1868
?*Sichuanchelys* sp.
(Fig. 10.2)

**Unit**, **locality and age**: Shishugou Formation, Wucaiwan field area, northern Junggar Basin, Xinjiang Uygur Autonomous Region. The stratigraphic position of the holotype relative to the Middle-Late Jurassic boundary is not known, so it may be either late Middle (Callovian) or early Late (Oxfordian) Jurassic in age.

**Referred specimens**: Three incomplete carapaces, both with their dorsal surfaces exposed: IVPP V18101 (field number WCW-04-57), incomplete carapace missing portions of margins and with dorsal surface exposed (Fig. 10.2a); IVPP V18102 (field number WCW-01-5), missing about the lateral half of its right side (Fig. 10.2b); and IVPP V18103 (field number WCW-03-33), missing much of its margins (Fig. 10.2c). Both specimens are from exposures of the Shishugou Formation in the Wucaiwan field area.

**Occurrence**: Known only from the Shishugou Formation in the Wucaiwan field area, northern Junggar Basin, Xinjiang. Stratigraphic positions for all three specimens within the Shishugou Formation relative to the Middle-Upper Jurassic boundary are uncertain; consequently, the temporal range of this species can only be listed as Callovian and/or Oxfordian.

**Description**: ?*Sichuanchelys* sp. is represented by three carapaces of moderate size, ranging from 22.5 to 36 cm long (Fig. 10.2a–c). Although none is complete, together they allow for the major carapacial features to be reconstructed (Fig. 10.2d).

The carapace is sub-rectangular in shape, with the width being about 80% of its length. A nuchal emargination is weakly developed (Fig. 10.2a) or absent (Fig. 10.2b). Peripherals one and two are expanded to form a flange along the anterolateral edge of the carapace, giving the anterior end of the carapace a truncated appearance. These peripherals lack the thickened, upturned edge present in many species of *Xinjiangchelys*. The posterior end of the carapace is rounded.

A prominent feature of the carapace is the presence of extremely wide vertebral scutes (Fig. 10.2a–c). In the case of the third vertebral scute, the maximum width is nearly three times the length. The presence of greatly expanded vertebral scutes is associated with correspondingly reduced (i.e., narrow) pleural scutes. In the holotype, the maximum width of the third pleural scute is less than a third the width of the third vertebral scute (Fig. 10.2a). The remaining scutes are incompletely documented by the available material. The cervical scute is not preserved in any of the specimens. The marginal series is most completely preserved in IVPP V18102 (Fig. 10.2b). The anterior and posterior marginal scutes are both restricted to the peripherals and are broadly exposed dorsally.

Sutures are largely obscured but those on the anterior portion of the shell are distinct on IVPP V18103 (Fig. 10.2c). As well, sutures between most of the costals and the anterolateral peripherals can be identified on either the holotype or IVPP V18103, allowing the reconstruction shown in Fig. 10.2d.

**Remarks**: ?*Sichuanchelys* sp. is distinctive in the presence of unusually wide vertebral scutes. In the proportions of the vertebral and pleural scutes, ?*Sichuanchelys* sp. is similar to *Sichuanchelys chowi* from the Middle Jurassic of Sichuan: both taxa have exceptionally broad vertebral scutes and narrow pleural scutes. They differ in that *Sichuanchelys chowi* has a deep nuchal emargination, whereas that feature is reduced or absent in ?*Sichuanchelys* sp. As well, the shape of the vertebral scutes differs and the pleural scutes are relatively larger in ?*Sichuanchelys* sp. The morphology of the plastron, which currently is unknown in ?*Sichuanchelys* sp., will provide a test of the inclusion of this species in

*Sichuanchelys* rather than *Xinjiangchelys*, because the former primitively retains a mesoplastron, indicating that it is basal relative to *Xinjiangchelys* and other Jurassic turtles from Xinjiang, all of which have lost the mesoplastron.

Capaxorder Eucryptodira Gaffney 1975
Family Xinjiangchelyidae Nessov in Kaznyshkin et al. 1990

**Remarks**: Xinjiangchelyidae are basal eucryptodires from the Middle Jurassic-Early Cretaceous of Asia that have a plastron that articulates with the peripherals via a series of peg- and socket-joints. They are derived relative to Chengyuchelyidae in the absence of mesoplastra. They can be differentiated from members of the Plesiochelyidae, a group of basal eucryptodires from the Jurassic of Europe, on the basis of a series of features of the plastron and carapace (Peng and Brinkman 1993). These include the presence of a plastron in which the inguinal and axillary buttresses are in the same plane as the bridge and do not, or only slightly, contact the costals, the presence of a weak connection between the carapace and plastron via a series of peg and socket joints, the extension of the pleural-marginal sulcus onto the antero-lateral peripheral, the presence of a significant dorsal thickening of the lateral edge of peripherals two to seven, and highly expanded seventh to eleventh peripherals. In these features xinjiangchelyids are similar to Early Cretaceous sinemydids/macrobaenids such as *Dracochelys* Gaffney and Ye 1992 and *Hangaiemys* Sukhanov and Narmadakh 1974. Xinjiangchelyids are primitive relative to sinemydids/macrobaenids, in the presence of amphicoelous cervical vertebrae, a more robust plastron with large anterior and posterior lobes, and epiplastra that are large and bear distinct dorsal epiplastral processes. Thus the Xinjiangchelyidae are best interpreted as a paraphyletic group that includes basal members of a radiation of eucryptodires, with the Sinemydidae and Macrobaenidae as successively more derived grades (Rabi et al. 2010).

Genus *Xinjiangchelys* Ye 1986a

**Type species**: *Xinjiangchelys junggarensis* Ye 1986a.
**Referred species**: *Xinjiangchelys chowi* Matzke et al. 2005; *X. chungkingensis* (Young and Chow 1953); *X. jinyanensis* (Ye and Fang 1982); *X. latimarginalis* (Young and Chow 1953); *X. oshanensis* (Ye 1973); *X. qiguensis* Matzke et al. 2004; *X. radiplicatus* (Young and Chow 1953); *X. radiplicatoides* sp. nov.; and *X. tianshanensis* Nessov 1995.

**Occurrence**: Middle Jurassic-Early Cretaceous of Asia: Xinjiang (Middle Jurassic-Early Cretaceous) and Sichuan (Middle and Late Jurassic), People's Republic of China; Fergana Basin (Middle Jurassic), Kirgizstan; and Krasnoyarski Kria, Siberia (Middle Jurassic), Russia (see Rabi et al. 2010, Tables 1, 2 and references therein).

**Revised diagnosis**: Genus of Xinjiangchelyidae characterized by the following unique combination of shell features: carapace thick; vertebral scutes subequal in width and
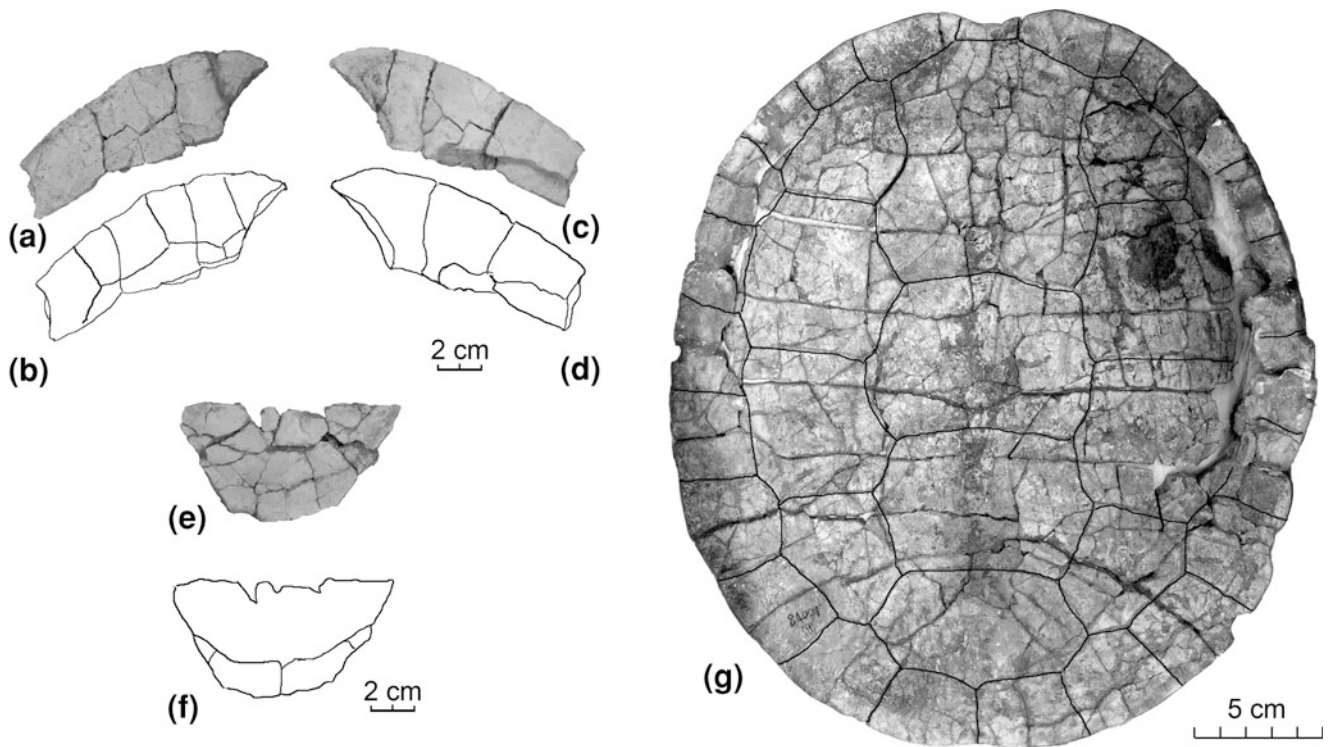
**Fig. 10.3** Carapaces of *Xinjiangchelys junggarensis* Ye 1973 (Xinjiangchelyidae); northern Junggar Basin, Xinjiang, China; upper part of Shishugou Formation; Late Jurassic (Oxfordian). **a–f** Referred and fragmentary carapace (IVPP V18100), from the Pingfengshan locality, Wucaiwan field area: **a–d** first to third left peripherals: **a** photograph and **b** interpretive drawing, both in dorsal view; **c** photograph and **d** interpretive drawing, both in ventral view; **e, f** suprapygal 2: **e** photograph and **f** interpretive drawing, both in dorsal view. **g** Holotype and nearly complete carapace, (IVPP V7648), from the Jiangjunmiao field area, in dorsal view. Images at different scales

length or wider than long; and epiplastra form a transversely-oriented bar across anterior lobe of plastron.

**Remarks**: *Annemys* was included in *Xinjiangchelys* by Matzke et al. (2004), but is excluded here because it has a relatively thin shell and narrow vertebral scutes. *Xinjiangchelys* is similar to *Shartagemys* Sukhanov and Narmandakh 2006 in the pattern of scutes on the carapace, but we also recognize the latter as a distinct genus because the orientation of its epiplastra differs.

*Xinjiangchelys junggarensis* Ye 1973
(Fig. 10.3)

**Synonymies**: *Xinjiangchelys latimarginalis* (in part): Kaznyshkin 1988, p. 28; Peng and Brinkman 1993, p. 2016, Figs. 3–12; Sukhanov 2000, pp. 313–314, Fig. 17.1; Rabi et al. 2010, p. 262, Fig. 1, Table 1. *Xinjiangchelys junggarensis*: Matzke et al. 2004, p. 1295, Figs. 12, 14; Brinkman et al. 2008, pp. 42–43, Fig. 42.

**Referred specimens**: Thirteen specimens: IVPP V18100 (field number WCW-04-36): fragmentary carapace consisting of first three left peripherals in articulation, an incomplete costal, and second suprapygal (Fig. 10.3a–f); and a dozen IVPP specimens (IVPP V9537-1 to -9 and -11 to -13), shell

and postcranial material, originally described and assigned to *Xinjiangchelys latimarginalis* (Peng and Brinkman 2003, pp. 2016–2022, Figs. 3–11). All referred specimens are from the Pingfengshan locality, Wucaiwan field area, northern Junggar Basin, Xinjiang Uygur Autonomous Region; upper part of Shishugou Formation; Late Jurassic (Oxfordian).

**Occurrence**: Known from two localities in the upper part (Oxfordian) of the Shishugou Formation, in the northern Junggar Basin, Xinjiang: holotype locality in the Jiangjunmiao field area (Ye 1973); and Pingfengshan locality (for the above-listed, referred specimens) in the Wucaiwan field area.

**Revised diagnosis**: Species of *Xinjiangchelys* different from *X. latimarginalis*, *X. tianshanensis*, *X. qiguensis*, *X. chowi*, and *X. jinyanensis* in having a carapace that is an elongate oval, rather than round, in outline. Different from *X. tianshanensis* and *X. qiguensis* in having strongly expanded anterolateral peripherals and the first peripheral having a contact with the first costal. Different from *X. chungkingensis*, *X. radiplicatus*, and *X. radiplicatoides* in having carapace with unornamented, smooth external surface; also differs from last two species in having vertebral scutes that are wider than long. Different from *X. oshanensis* in having a larger entoplastron that is located largely posterior to the epiplastra.

**Description**: IVPP V18100 is a fragmentary, disarticulated carapace (Fig. 10.3a–f). Individual elements are well preserved. The first three left peripherals (Fig. 10.3a–d) are preserved in articulation. Their proportions match those in the holotype carapace of *Xinjiangchelys junggarensis* (Fig. 10.3g) and the other referred specimens from the Pingfengshan locality originally described as *X. latimarginalis* by Peng and Brinkman (1993, Figs. 3a, 4a, 5a, 6). The first peripheral is mediolaterally expanded and, therefore, is longer than wide. The suture for the nuchal is curved and its articular surface for the first costal is short. The second peripheral is more nearly equi-dimensional and its articular surface for the first costal is longer than that on the first peripheral. Ventrally, the articular surface for the axillary buttress of the hyoplastron is represented by a distinct groove that extends well onto the second peripheral. This groove just meets the medial edge of the peripheral, indicating that the axillary buttress would have contacted the first costal. Costal fragments are present, but cannot be accurately positioned and are not figured here. The second suprapygal (Fig. 10.3e–f) is nearly complete. Distinct sutural surfaces for the pygal and eleventh peripherals are present. The sulci show that the twelfth marginal scute extended onto the posterior edge of the element and the eleventh marginal scute overlapped the lateral corner.

**Remarks**: IVPP V18100 is interpreted as an additional specimen of the taxon that Peng and Brinkman (1993) included in the species *Xinjiangchelys latimarginalis*. Matzke et al. (2004, 2005) argued that the Pingfengshan population was incorrectly identified as *X. latimarginalis* and, instead, provisionally referred those specimens to *X. 'latimarginalis'* sensu Peng and Brinkman (1993). The Pingfengshan taxon differs from unequivocal specimens of *X. latimarginalis* most distinctly in the proportions and outline of the carapace, which is elongate and oval in the Pingfengshan taxon versus more rounded in the holotype of *X. latimarginalis* (cf., Peng and Brinkman 1993, Figs. 3a, 4a vs. Young and Chow 1953, plates 2–3). The carapace of the Pingfengshan taxon is most similar to the holotype carapace of *X. junggarensis* (cf., Peng and Brinkman 1993, Figs. 3a, 4a vs. Fig. 10.3g), which prompted Brinkman et al. (2008) to transfer the Pingfengshan specimens to that species. In addition, the Pingfengshan carapaces and holotype of *X. junggarensis* differ from *X. latimarginalis* and *X. tianshanensis* in having a subrectangular first peripheral with a distinct contact with the first costal. In *X. latimarginalis* and *X. tianshanensis*, the first peripheral is more triangular in shape and has, at most, a point contact with the first costal. The most nearly carapace from Pingfengshan (IVPP V9537-1; Peng and Brinkman 1993, Fig. 3a, b, 4a, b) differs from the holotype of *X. junggarensis* in having greatly expanded anterolateral peripherals giving a truncated anterior edge; the possibility that this difference is taxonomically significant was considered by Peng and Brinkman (1993). As noted by Rabi et al. (2010), variation of characters within a species must be considered in evaluating their taxonomic significance. Variation in the shape of the anterior end of the carapace is documented by six specimens from Pingfengshan: IVPP V9537-1, -13, -9, -5, and -3 (Peng and Brinkman 1993, Figs. 4a, 5a, 6a, b, d, respectively) and IVPP V18100 (Fig. 10.3a–d). These all have an elongate first peripheral that only barely contacts the first costal. The greatly expanded anterolateral peripherals are present in only one specimen (IVPP V9537-1), so rather than being a taxonomically significant feature as Peng and Brinkman (1993) initially considered, that feature more likely is just an individual variant. Both IVPP V9537-13 and IVPP V18100 show a more rounded anterior end, like the holotype of *X. junggarensis*. Thus, we follow Brinkman et al. (2008) in including the 12 Pingfengshan specimens previously referred to *X. latimarginalis* by Peng and Brinkman (1993) and the newly reported specimen IVPP V18100 in *X. junggarensis*.

*Xinjiangchelys radiplicatoides* sp. nov.
(Figs. 10.4, 10.5, 10.6, 10.7, 10.8, 10.9, 10.10)

**Holotype**: IVPP V18104 (field number WCW-01-19): incomplete skeleton consisting of the shell and skull in association and incomplete left shoulder girdle, femur, and tibia preserved in place within the body cavity (Figs. 10.4, 10.5). Surfaces of the shell have been cleaned of matrix, so the dorsal surface of the carapace and the ventral surface of the plastron are visible. The carapace and plastron are largely complete, although the carapace has been distorted post-mortem. The skull is relatively complete, but distorted, and many of its sutures are obscured by poor preservation of the bone surfaces.

**Holotype unit**, **locality**, **and age**: Upper part of Shishugou Formation; Wucaiwan field area, northern Junggar Basin, Xinjiang Uygur Autonomous Region; Late Jurassic (Oxfordian).

**Etymology**: Species name refers to the morphological similarity to *Xinjiangchelys radiplicatus*.

**Referred specimens**: Less nearly complete specimens (isolated shell plates, girdle and skull bones, and fragmentary skulls) of *Xinjiangchelys radiplicatoides* sp. nov. are abundant in the Jiangjunmiao turtle bonebed. Costal plates with the diagnostic plicate ornament dominate the locality. Other elements from the locality are identified through comparisons with the holotype skeleton. Referred specimens from the Jiangjunmiao turtle bonebed are included in the catalogue number IVPP V9539, with individual specimens being designated by a unique suffix, as follows: IVPP V9539-1, braincase (Fig. 10.6); IVPP V9539-2, isolated parietal (Fig. 10.7a, b); IVPP V9539-3, isolated postorbital (Fig. 10.7e, f); IVPP V9539-4, isolated quadrate (Fig. 10.7c, d); IVPP V9539-5, isolated dentary
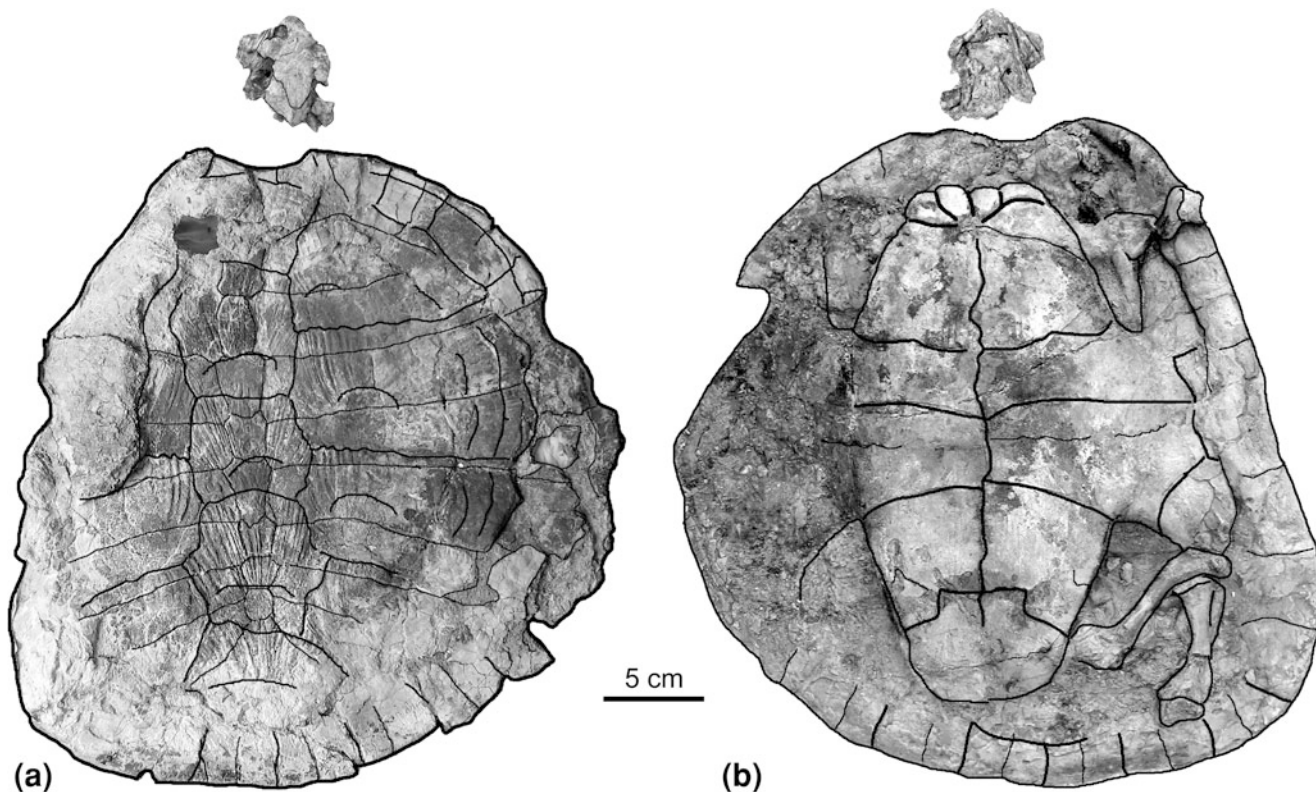
**Fig. 10.4** Holotype skeleton (IVPP V18104) of *Xinjiangchelys radiplicatoides* sp. nov. (Xinjiangchelyidae); Wucaiwan field area, northern Junggar Basin, Xinjiang, China; upper part of Shishugou Formation; Late Jurassic (Oxfordian). **a** Dorsal view; and **b** ventral view. Images at same scale
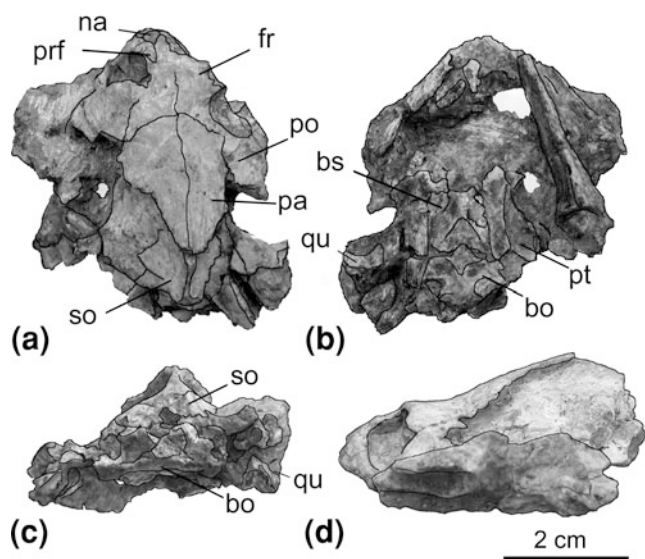


**Fig. 10.5** Skull and lower jaws of holotype (IVPP V18104) of *Xinjiangchelys radiplicatoides* sp. nov. (Xinjiangchelyidae); Wucaiwan field area, northern Junggar Basin, Xinjiang, China; upper part of Shishugou Formation; Late Jurassic (Oxfordian). **a** Dorsal view; **b** ventral view; **c** occipital view; and **d** left lateral view. Abbreviations: *bo* basioccipital; *bs* basisphenoid; *fr* frontal; *na* nasal; *pa* parietal; *po* postorbital; *prf* prefrontal; *pt* pterygoid; *qu* quadrate; *so* supraoccipital. Images at same scale

(Fig. 10.7g, i); IVPP V9539-6, nuchal (Fig. 10.8a); IVPP V9539-7, first peripheral (Fig. 10.8b); IVPP V9539-8, second peripheral (Fig. 10.8c); IVPP V9539-9, first costal (Fig. 10.8d, e); IVPP V9539-10, first and second costals in articulation (Fig. 10.8f, g); IVPP V9539-11, isolated third costal (Fig. 10.8h); IVPP V9539-12, isolated third costal (Fig. 10.8i); IVPP V9539-13, pygal, second suprapygal, and eleventh peripheral in articulation (Fig. 10.8j, k); IVPP V9539-14, right and left epiplastra (Fig. 10.9a, b and c, d, respectively); IVPP V9539-15, hyoplastron (Fig. 10.9e); IVPP V9539-16, humerus (Fig. 10.10a–c); IVPP V9539-17, scapula (Fig. 10.10d, e). CT scans of the referred braincase, IVPP V9539-1, are available on the Digimorph Web site at: http://digimorph.org/specimens/Xinjiangchelys_radiplicatoides/.

**Occurrence**: Known from two localities in the Shishugou Formation, northern Junggar Basin, Xinjiang: holotype locality (Oxfordian) in Wucaiwan field area; and Jiangjunmiao turtle bonebed (Callovian or Oxfordian) in Jiangjunmiao field area.

**Diagnosis**: Species of *Xinjiangchelys* similar to *X. radiplicatus* and different from other congeners in having carapace ornamented with plications extending forward
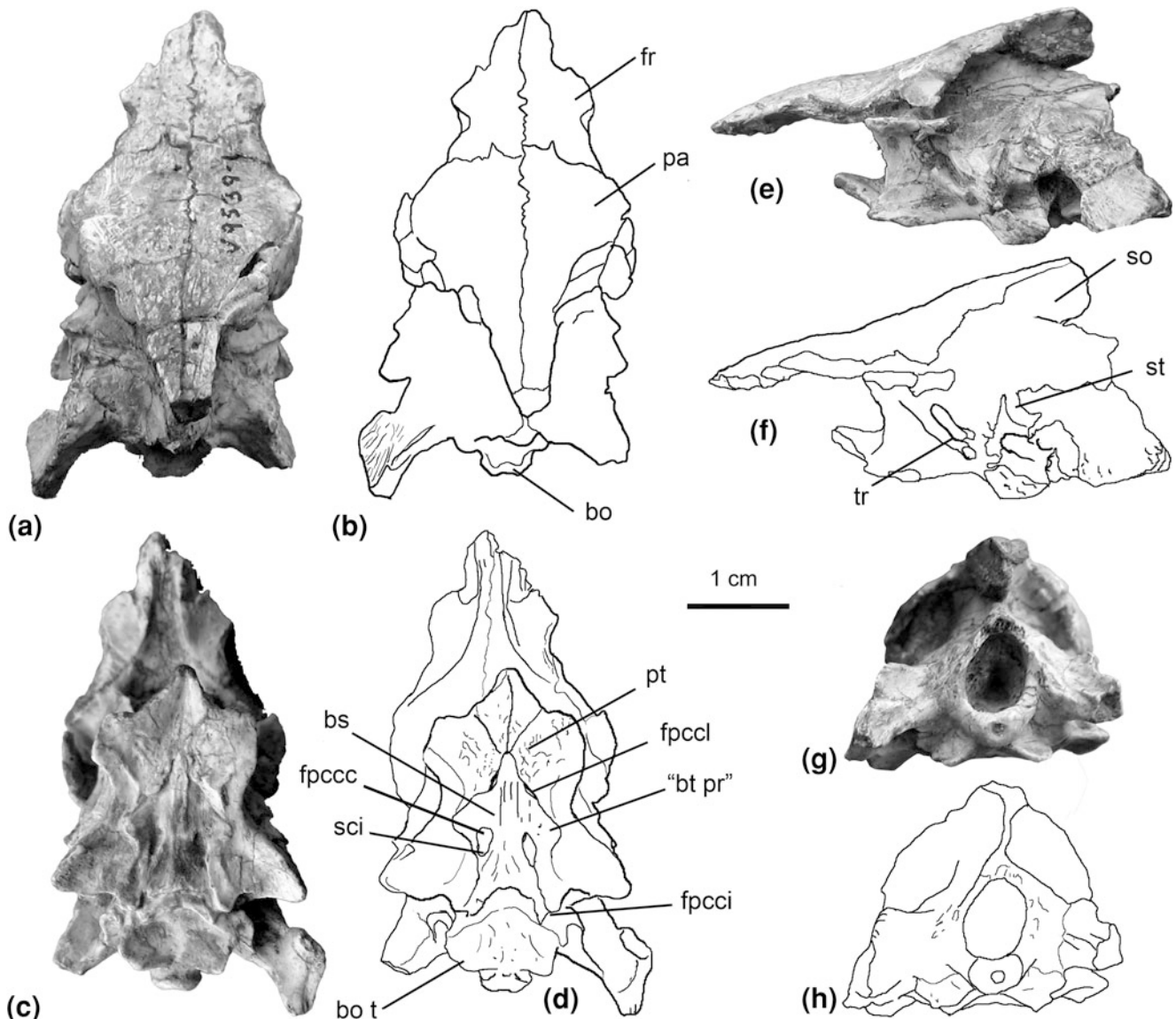
**Fig. 10.6** Incomplete, referred skull (IVPP V9539-1) of *Xinjiangchelys radiplicatoides* sp. nov. (Xinjiangchelyidae); Jiangjunmiao turtle bonebed, Jiangjunmiao field area, northern Junggar Basin, Xinjiang, China; upper part of Shishugou Formation; Middle (Callovian) or Late (Oxfordian) Jurassic. **a**, **b** Dorsal view: **a** photograph and **b** interpretive drawing; **c**, **d** ventral view: **c** photograph and **d** interpretive drawing; **e**, **f** left lateral view: **e** photograph and **f** interpretive drawing; **g**, **h** posterior view: **g** photograph and **h** interpretive drawing. Note that the size of the foramen palatinum posterius is inferred from the portion of the border for the foramen preserved on the pterygoid. Abbreviations: *bo* basioccipital; *bo t* basioccipital tubercula; *bs* basisphenoid; *bt pr* basipterygoid process; *fpccc* foramen posterior canalis caroticus cerebralis; *fr* frontal; *fpccl* foramen posterius canalis caroticus lateralis; *fpcci* foramen posterius canalis caroticus internus; *fpp* foramen palatinum posterius; *pa* parietal; *pt* pterygoid; *sci* sulcus caroticus internus; *so* supraoccipital; *st* medial edge of canalis stapedio-temporalis; *tr* trigeminal foramen. Images at same scale

from growth centers on the posterior of the vertebral and pleural scutes and the presence of vertebral scutes in adults that are subequal in width and length. Differs from *X. radiplicatus* in that plications forming the carapace ornament are more numerous and less distinct, radiate outwards from a smooth area on the posterior portions of the vertebral and pleural scutes, and are crossed by ridges that parallel the margins of the scutes.

## Description

**Skull**: The skull is triangular in dorsal view and nearly as wide as it is long (Figs. 10.5, 10.6). The orbits are located far forward and are well exposed dorsally. The skull roof slopes upwards from the orbit, so that in lateral profile the skull appears wedge-shaped. As well, in dorsal view, the lateral edge
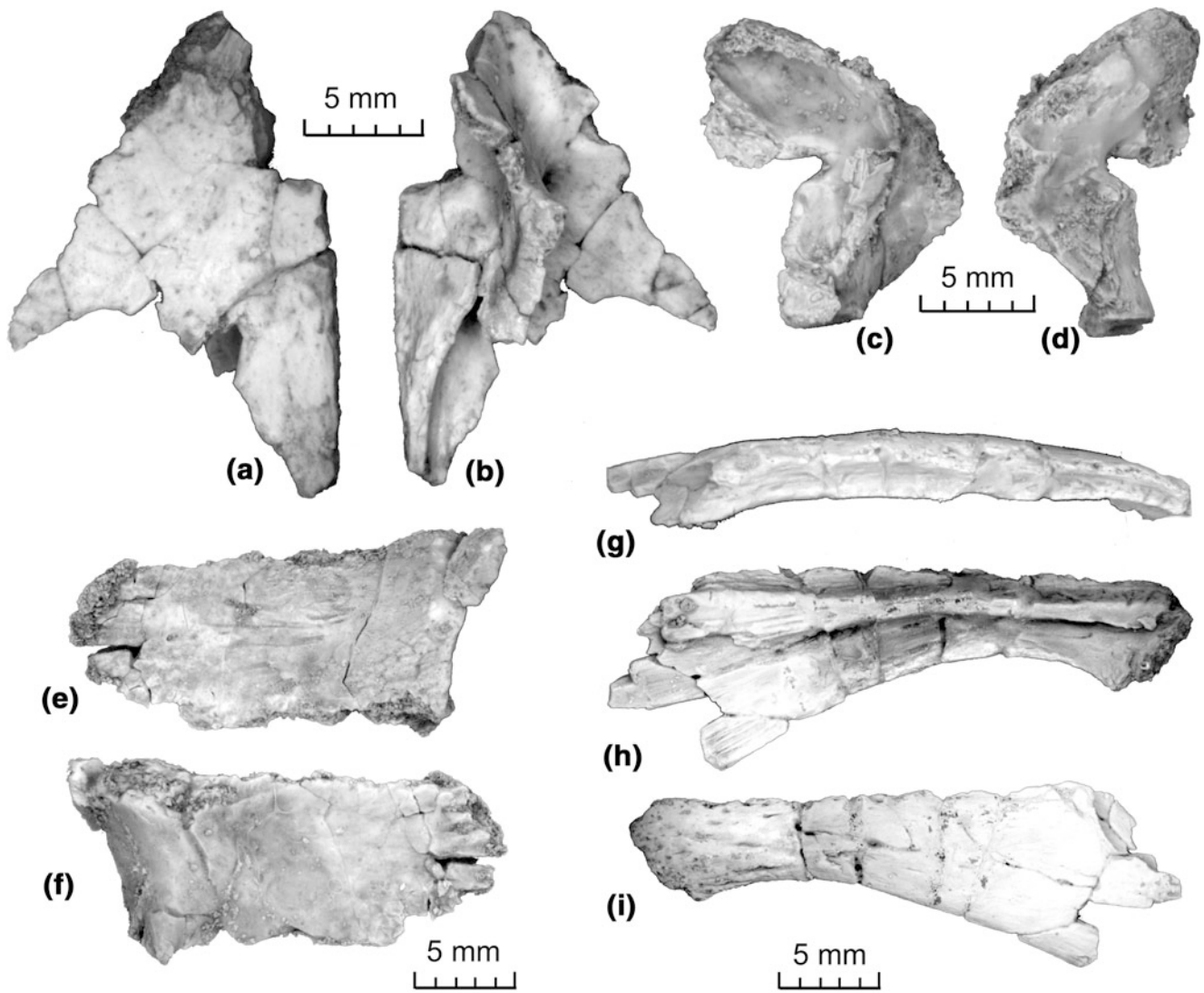
**Fig. 10.7** Isolated, referred skull elements of *Xinjiangchelys radiplicatoides* sp. nov. (Xinjiangchelyidae); Jiangjunmiao turtle bonebed, Jiangjunmiao field area, northern Junggar Basin, Xinjiang, China; upper part of Shishugou Formation; Middle (Callovian) or Late (Oxfordian) Jurassic. **a**, **b** Right parietal (IVPP V9539-2) in **a** dorsal view and **b** ventral view; **c**, **d** left quadrate (IVPP V9539-4) in **c** lateral view and **d** medial view; **e**, **f** right postorbital (IVPP V9539-3) in **e** dorsal view and **f** ventral view; **g**–**i** left dentary (IVPP V9539-5) in **g** occlusal view, **h** medial view, and **i** external view. Images at different scales

of the skull slopes outwards so that the posterior end of the skull is wider than the orbital region. As a result, the height and width of the posterior end of the skull are both approximately double the equivalent dimensions in the region of the orbits.

The skull roof is incompletely preserved, meaning the degree of emargination of the temporal and cheek regions is uncertain. However, at their greatest extent, the emargination of these regions is less than in *Annemys* (see below, *Annemys* sp. account).

Nasals, visible in IVPP V18104, are triangular bones wedged between the frontals and prefrontals. A small contact is present between opposite nasals anterior to the frontals.

Frontals are large elements that contact the nasals anteriorly, the maxilla and prefrontal anterolaterally, the parietal posteriorly, and the postorbital posterolaterally. A lateral lappet extends between the prefrontal and postorbital to form a portion of the orbital border. Narrow anterior processes of the frontals separate the prefrontals, as is typical for basal eucryptodires.

The parietal is the largest element in the skull roof. The frontal–parietal suture extends transversely across the skull roof well posterior to the orbits. Laterally the parietal has a long contact with the postorbital. An isolated parietal, IVPP V9539-2 (Fig. 10.7a, b), preserves a long lateral end that extended past the deepest point of the temporal emargination. Thus, a contact with the squamosal is likely, although the presence of a contact between these bones cannot be directly confirmed. The descending branch of the parietal, fully preserved in IVPP V9539-2 and visible in lateral
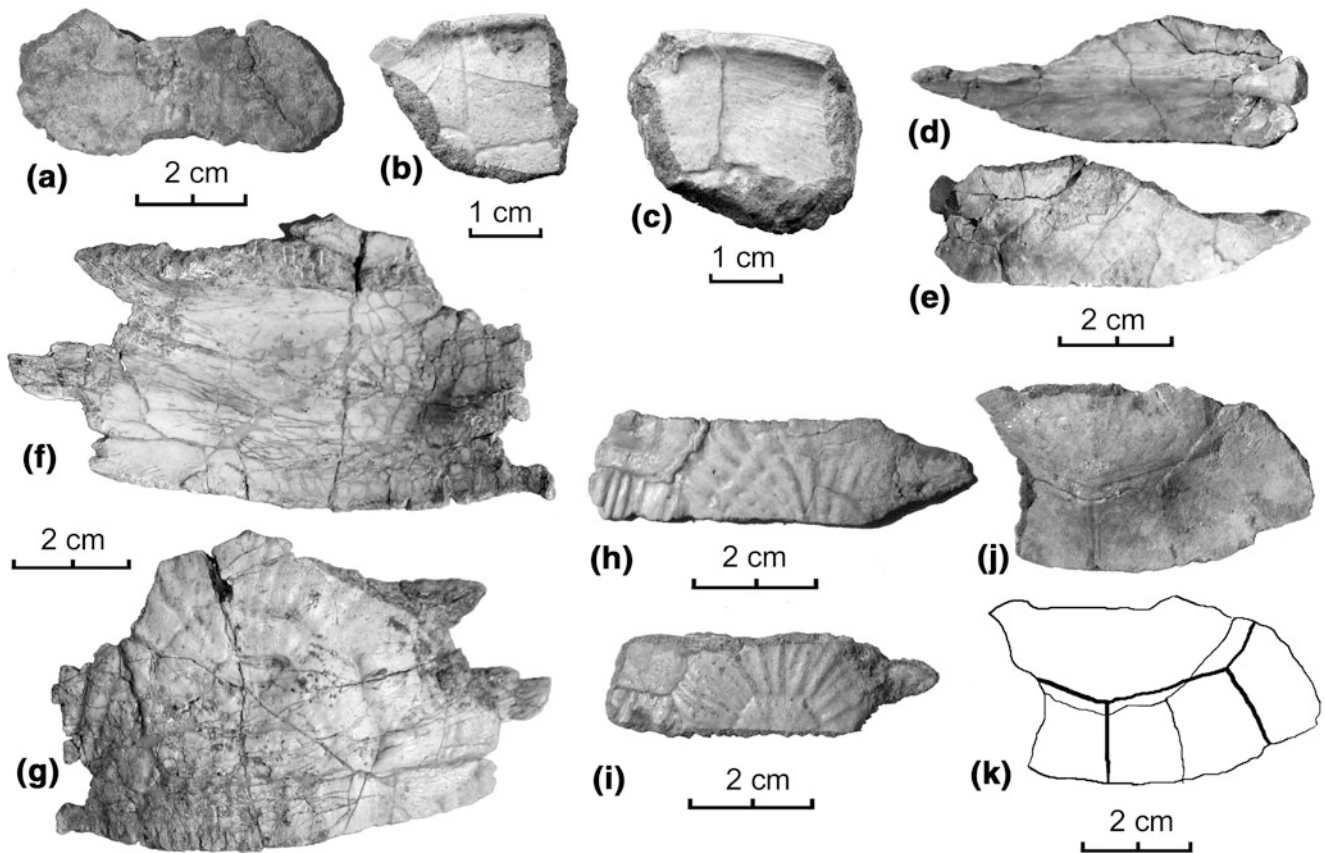
**Fig. 10.8** Referred carapace elements of *Xinjiangchelys radiplicatoides* sp. nov. (Xinjiangchelyidae); Jiangjunmiao turtle bonebed, Jiangjunmiao field area, northern Junggar Basin, Xinjiang, China; *upper part* of Shishugou Formation; Middle (Callovian) or Late (Oxfordian) Jurassic. **a** Nuchal (IVPP V9539-6) in dorsal view; **b** first peripheral (IVPP V9539-7) in dorsal view; **c** second peripheral (IVPP V9539-8) in dorsal view; **d**, **e** first right costal (IVPP V9539-9) in **d** visceral view and **e** dorsal view; **f**, **g** first and second right costals in articulation (IVPP V9539-10) in **f** visceral view and **g** dorsal view; **h** third right costal (IVPP V9539-11) in dorsal view; **i** third right costal (IVPP V9539-12) in dorsal view; **j**, **k** pygal, second suprapygal, and eleventh peripheral in articulation (IVPP V9539-13): **j** photograph and **k** interpretive drawing, both in dorsal view. Images at different scales

view in IVPP 9539-1, is well developed (Fig. 10.6e, f). This contacted the pterygoid and epipterygoid, contributing to a fully enclosed trigeminal foramen.

The postorbital is poorly preserved in IVPP V18104 and missing in IVPP V9539-1, but IVPP V9539-3, an isolated postorbital from the Jiangjunmiao turtle bonebed, shows that this is an elongate, rectangular element with a thickened area bordering the orbit (Fig. 10.7e, f).

The portions of the skull formed by the jugal, maxilla, premaxilla, and prefrontal are present in IVPP V18104, but because the sutures delineating these bones could not be identified the exact contacts of these bones are unknown. The squamosal and quadratojugal are not preserved.

The anterior end of the palate is not preserved in any of the available specimens. The posterior portion is preserved in both IVPP V18104 and IVPP V9539-1 (Figs. 10.5, 10.6). In IVPP V9539-1 the palatines form a triangular area anterior to the basisphenoid and pterygoid (Fig. 10.6c, d). The palatines barely contact the basisphenoid, preventing a

midline contact between the pterygoids. The posterior edge of the foramen palatinum posterius is present on the anterior edge of the pterygoid and that foramen is of moderate size.

The pterygoids are nearly completely preserved in IVPP 9539-1, missing only the processus pterygoideus externus and their posterolateral tips (Fig. 10.6c, d). The pterygoids extend posteriorly along the basisphenoid, just contacting the anterolateral corner of the basioccipital.

The basisphenoid is an elongate element that separates the pterygoids and has a broad contact with the basioccipital (Fig. 10.6c, d). The V-shaped anterior end of the basisphenoid separates the pterygoids at the midline. Ventrally an elongate, rounded ridge extends posteriorly from this process to the posterior edge of the basisphenoid. A prominent feature of the basisphenoid is the "basipterygoid process," a triangular lateral processes that underlies the pterygoid, extending laterally to a ridge that runs posteriorly from the lateral tip of the processus pterygoideus externus. The ventral surface of the basisphenoid lacks the distinct
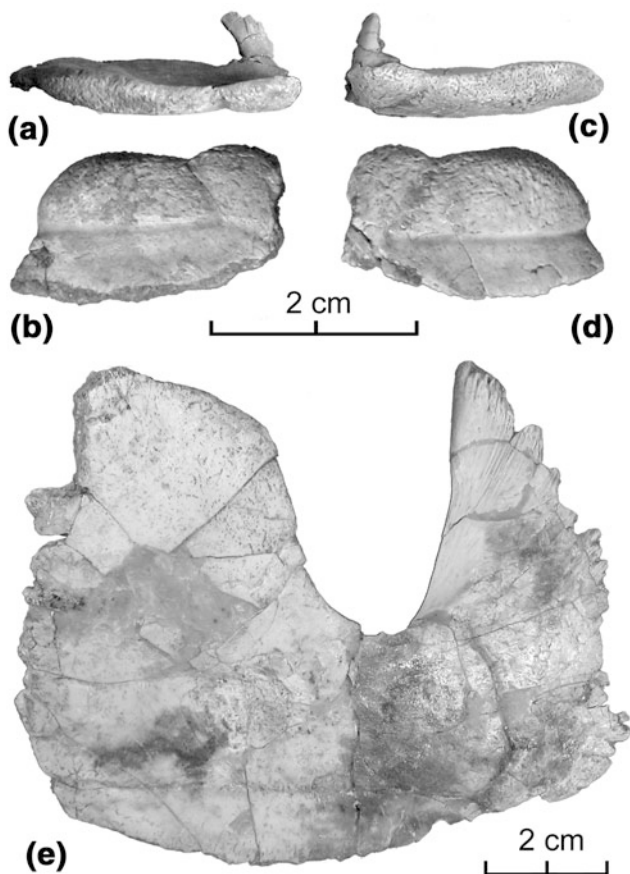
**Fig. 10.9** Isolated, referred plastral elements of *Xinjiangchelys radiplicatoides* sp. nov. (Xinjiangchelyidae); Jiangjunmiao turtle bonebed, Jiangjunmiao field area, northern Junggar Basin, Xinjiang, China; upper part of Shishugou Formation; Middle (Callovian) or Late (Oxfordian) Jurassic. **a**–**d** Epiplastra (IVPP V9539-14): **a**, **b** right epiplastron in **a** anterior view and **b** ventral view; **c**, **d** left epiplastra in **c** anterior and **d** ventral view; **e** left hyoplastron (IVPP V9539-15) in ventral view. Images at different scales



**Fig. 10.10** Isolated, referred humerus and scapula of *Xinjiangchelys radiplicatoides* sp. nov. (Xinjiangchelyidae); Jiangjunmiao turtle bonebed, Jiangjunmiao field area, northern Junggar Basin, Xinjiang, China; upper part of Shishugou Formation; Middle (Callovian) or Late (Oxfordian) Jurassic. **a**–**c** right humerus (IVPP V9539-16) in **a** posterior view, **b** dorsal view, and **c** ventral view; **d**, **e** left scapula (IVPP V9539-17) in **d** anterior view and **e** posterior view. Images at different scales

pits like those present in *Ordosemys leios* Brinkman and Peng 1993b (Brinkman and Wu 1999).

The foramina and canals of the basicranial region are distinct in IVPP V9539-1. CT scans of this specimen allow the relative size and position of the common carotid artery and its major branches to be identified (Fig. 10.6d). The foramen posterius canalis caroticus internus is located at the posterior end of the contact between the pterygoid and basisphenoid. The canalis caroticus internus runs forward between the basisphenoid and pterygoid to open into groove in the basisphenoid, referred to as the sulcus caroticus internus by Sukhanov (2000). This groove extends forward to the foramen posterius canalis carotici cerebralis (fpccc in Fig. 10.6d). Because the foramen posterius canalis carotici cerebralis is the opening in the basisphenoid through which the cerebral branch of the internal carotid artery would have entered the sella turcica, this groove would have been occupied by the internal carotid artery. Slit-like openings between the basisphenoid and the
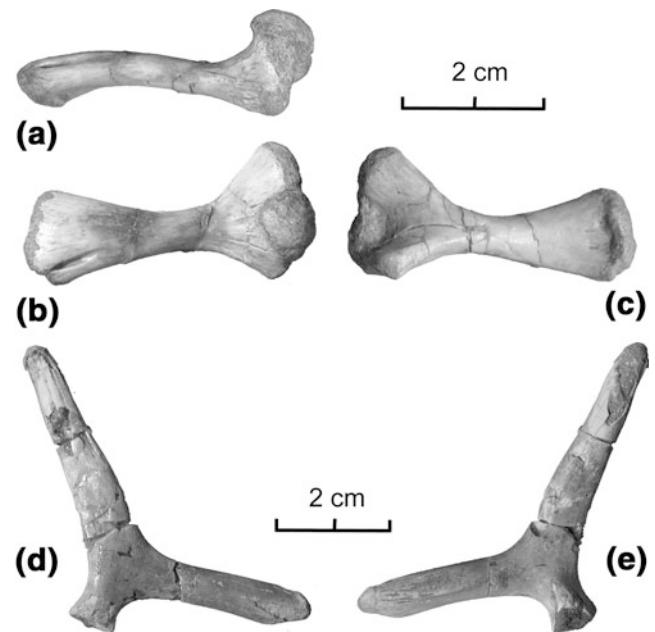
pterygoid anterior to the "basipterygoid processes" are identified as the foramen posterius canalis caroticus lateralis, the opening through which the palatine artery enters the skull. Thus the palatine artery would have branched off from the internal carotid artery in the area of the sulcus caroticus internus and passed ventral to the basisphenoid to reach the foramen palatinum posterius. A shallow groove leads from the anterior end of the sulcus caroticus internus to the foramen posterius canalis caroticus lateralis. This likely marks the path of the palatine artery in this region.

The braincase and otic capsule are visible in dorsal view in IVPP V18104 (Fig. 10.5a). The external surface of the braincase is fully exposed in IVPP V9539-1 (Fig. 10.6), although sutures are difficult to identify and the elements lateral to the stapedial foramina are missing. Reflecting the inflated posterior region of the skull, the supraoccipital crest is tall (Figs. 10.5c, 10.6g, h). Although the posterior end is not preserved, it would have extended at most only a short distance past the occipital condyle. The presence of a short supraoccipital crest is a widespread feature of basal cryptodires, also being present for example in *Kayentachelys* Gaffney et al. 1987, *Kallokibotion* Nopcsa 1923, and *Chubutemys* Gaffney et al. 2007. In IVPP V9539-1 the medial edge of the left stapedial foramen is present, showing that this foramen was large in diameter compared

to the foramen posterius canalis carotici interni. The trigeminal opening is an elongate, narrow opening bordered by the pterygoid, epipterygoid, and parietal.

The basioccipital and exoccipitals are fused. Ventrally this element has a broad, area that is shallowly concave. The anterior edge of the concave area is marked by a distinct ridge that lies just posterior to the basioccipital-basisphenoid suture. The lateral edges of the concave area are identified as the basioccipital tubercula, although these are little differentiated relative to the more medial surface. The basioccipital tubercula floor a space into which a pair of foramina nervi hypoglossi open. The occipital condyle is located dorsal to the ventral surface of the basioccipital.

The prootic forms the anterior margin of the foramen stapedio-temporale and the anterior edge of the otic capsule. However, the sutures delineating this element cannot be distinguished from fractures so its full extent cannot be determined.

The opisthotic, as seen in ventral view, is largely situated posterior to the pterygoid and slopes posteriorly so that its lateral tip is posterior to the occipital condyle. The fenestra postotica, which is bordered by the opisthotic, exoccipital, pterygoid, and quadrate, is a circular opening that faces primarily ventrally.

The quadrate is best represented by an isolated element from the Jiangjunmiao turtle bonebed (IVPP V9539-4; Fig. 10.7c, d). This is rather tall, with a shallow incisura columellae auris. The cavum tympani has a gently curved anterior edge. The anterior surface of the quadrate bears a pitted area indicating that it contributed to the processus trochlearis oticum. Features on the internal surface of the quadrate can be identified through comparison with *Chelydra* as illustrated by Gaffney (Gaffney 1972, Fig. 18). A dorsal groove leading from the insisura columellae auris is identified as the canalis stapedio-temporalis, and a ventrally oriented groove is identified as the canalis cavernosus. Below the canalis cavernosus a sutural surface for the pterygoid is present.

An isolated dentary (IVPP V9539-5; Fig. 10.7g, i) is long and slender, and has a narrow triturating surface. Sutural surfaces show that the splenial extended about halfway along the medial surface of the dentary. The coronoid did not contribute to the formation of the triturating surface. The anterior end of the dentary is expanded, so the ventral surface of the element is concave in lateral view.

**Vertebrae**: The vertebral column is poorly represented in the available material. Although the skull was preserved in association with the shell in IVPP V18104, no cervical or caudal vertebrae are apparent in that specimen. Isolated cervical centra of two distinct morphologies are present in the Jiangjunmiao turtle bonebed, but there is no way of associating either of those cervical morphs with *Xinjiangchelys radiplicatoides*.

**Carapace**: The carapace of IVPP V18104 is complete, but distorted, with the left posterolateral edge expanded relative to the right (Fig. 10.4a, b). Based on this specimen numerous isolated shell elements from the Jiangjunmiao turtle bonebed are referred to *Xinjiangchelys radiplicatoides* (Figs. 10.8, 10.9). The undistorted right side of the carapace indicates that the shell is subcircular in outline and is approximately as wide as it is long. In its strongly rounded profile, the carapace of *X. radiplicatoides* is similar to *X. chowi*, *X. qiguensis*, *X. tianshanensis*, and *X. latimarginalis*. The carapace of *X. junggarensis* differs in being more rectangular. Plications on the external surface of the carapace extend forward and outward from a hexagonal smooth area near the posterior edge of each of the vertebral and pleural scutes. The plications are crossed by ridges paralleling the smooth hexagonal area. As demonstrated by isolated costal elements from the Jiangjunmiao turtle bonebed, both the plications and ridges are most strongly developed in juvenile individuals and become subdued with age (Fig. 10.8).

The nuchal is best documented by IVPP V9539-6, from the Jiangjunmiao turtle bonebed (Fig. 10.8a). This short and wide element bears a distinct nuchal emargination anteriorly and a concave notch on its posterior edge for the first neural.

Eight neurals are present. The first is hexagonal with short posterolateral edges, the second is rectangular, the third to seventh are hexagonal and have short anterolateral edges, and the eighth is rectangular. The lengths of the neurals decrease posteriorly, with the sixth neural being only slightly longer than wide.

The first costal is subrectangular in shape and bears a sharp ridge ventrally that extends along the length of the element (Fig. 10.8d–g). The sutural surface on the anterior face of this ridge shows that the first thoracic rib was elongate and reached the lateral edge of the bone. No evidence for a contact of the costal with the hyoplastron is present. Costals two to six extend relatively straight laterally and show little expansion of their lateral ends (Fig. 10.8h, i). Costals eight differ in that they curve posteriorly and have an expanded lateral edge. The shape of costals seven is intermediate between costals six and eight.

Peripherals one to three and nine to eleven are preserved in IVPP V18104; additionally, an isolated first peripheral (IVPP V9539-7; Fig. 10.8b) and an isolated second peripheral (IVPP V9539-8; Fig. 10.8c) are available from the Jiangjunmiao turtle bonebed. The anterior peripherals have thickened lateral edges, like those of *Xinjiangchelys junggarensis*. This extends at least to the fourth peripheral and likely farther. The first peripheral has a broad area of contact with the first costal. The axillary buttress extends onto the second peripheral. Posterolateral peripherals are thin elements that are nearly square in dorsal view. The anterior extend of the bridge is unclear, however, posteriorly it extends to the eighth peripheral.

The posterior end of the carapace is best documented by an articulated second suprapygal, pygal, and eleventh peripheral (Fig. 10.8j, k). Two suprapygals are present. The first is narrow relative to the second and does not contact the peripherals. The second suprapygal extends to the tenth peripheral and has a short area of contact with the eighth costal. The pygal is nearly square.

The pattern of scutes on the carapace is documented by IVPP V18104 (Fig. 10.4a). The cervical scute is wide. Vertebral scutes are approximately square and are much narrower than the pleural scutes. The lateral edges of the second and third vertebral scutes are nearly straight. The fourth vertebral scute has a more distinctly angled lateral edge. The fifth vertebral scute is only slightly wider than the fourth. For the fifth vertebral scute, its posterior edge crosses the second suprapygal, whereas its anterior edge crosses the first suprapygal. The first pleural extends onto peripherals one and two. The lateral margin of the pleural scutes posterior to this could not be followed on IVPP V18104, but isolated posterolateral peripherals from the Jiangjunmiao turtle bonebed show that the lateral tip of the pleural scutes extended onto the peripherals in the posterior region of the shell. Both the eleventh and twelfth marginal scutes extend onto the second suprapygal. The pygal is subdivided by the sulcus separating the twelfth marginal scutes.

**Plastron**: The plastron of *Xinjiangchelys radiplicatoides* is documented by the holotype skeleton (Fig. 10.4b) and by the isolated elements from the Jiangjunmiao turtle bonebed (Fig. 10.9). The anterior lobe, posterior lobe, and bridge are subequal in length. Both the anterior and posterior lobes have truncated ends. Plastral fenestrae are absent in adults, although these were well developed in juveniles.

As in other species of *Xinjiangchelys*, the epiplastra are short and wide, so together they form a transversely-oriented bar that extends across the anterior lobe of the plastron. Isolated epiplastra (Fig. 10.9a–d) from the Jiangjunmiao turtle bonebed show that distinct dorsal epiplastral processes are present. The entoplastron is a large, shield-shaped element. Its anterior end is continuous with the anterior edge of the hyoplastron, so together the entoplastron and hyoplastron form a nearly straight sutural surface for the epiplastra.

The hyoplastron has a rectangular ventral surface and a bridge area that is weakly angled relative to this surface. The inguinal buttress and the bridge are differentiated by the texture of the bone: the bridge area, like the ventral surface, has weakly developed texture but the inguinal buttress is smooth, likely because this area is not covered by scutes. These two areas are in approximately the same plane. The lateral edge of the hyoplastron bears a series of pegs that fit in sockets in the bridge peripherals. These are best developed anteriorly, but extend along the full length of the lateral edge of the hyoplastron. The buttress does not extend onto the costals.

The hypoplastron largely mirrors the hyoplastron in general shape, although the bridge portion of the hypoplastron is narrower than the bridge portion of the hyoplastron. The axillary buttress, which is differentiated from the bridge area by the smooth surface, is in about the same plane as the bridge region. The buttress extends to the eighth peripheral, but does not extend onto the costals.

Xiphiplastra are present in IVPP V18104, and these form the posterior half of the posterior lobe of the plastron.

Sulci are generally distinct. The gular and intergular scutes are located entirely on the epiplastra and are transversely oriented. The mid-line sulcus is weakly sinusoidal anteriorly and nearly straight posteriorly. The humeral-pectoral sulcus extends transversely across the base of the anterior lobe. The pectoral-abdominal sulcus is located near the posterior edge of the hyoplastron. The abdominal-femoral sulcus crosses the base of the posterior lobe; this sulcus is gently convex and curves forward. The femoral-anal sulcus has a blunt anterior end located just anterior to the hypoplastron–xiphiplastron suture. Four inframarginals are present, each extending about halfway up the bridge region.

**Pectoral girdle**: The acromion process of the scapula is preserved in specimen IVPP V18104; based on that specimen, an isolated scapula from the Jiangjunmiao turtle bonebed is referred to *Xinjiangchelys radiplicatoides* (Fig. 10.10d, e). The acromion and scapular processes are rod-like and between them form an obtuse angle. The acromion process is slightly shorter than the humerus.

**Fore limb**: The humerus is visible in ventral view in IVPP V18104; based on that skeleton, isolated humeri from the Jiangjunmiao turtle bonebed are referred to *Xinjiangchelys radiplicatoides* (Fig. 10.10a–c). The humerus is a stout bone, with a slightly upturned head. In end view, the two trochanters form nearly a $90^{\circ}$ angle with one another. The ectepicondylar foramen is fully enclosed.

**Hind limb**: The hind limb is represented by a left femur and tibia of IVPP V18104, preserved in articulation (Fig. 10.4b). The femur is longer than the humerus and has a less distinctly upturned head. The tibia is shorter than the femur.

**Remarks**: *Xinjiangchelys radiplicatoides* sp. nov. is one of the most osteologically fully documented basal eucryptodires and it provides the best evidence for a close affiliation between *Xinjiangchelys* species from Xinjiang and Sichuan. *X. radiplicatus* was erected by Young and Chow (1953) on the basis of the central part of a carapace from the Late Jurassic of Sichuan. Later, a complete shell was described by Ye (1986b). The latter specimen is here interpreted as a juvenile, because of its relatively small size and well developed costal-peripheral fenestrae. *X. radiplicatus* was diagnosed largely on the basis of a distinctive ornamentation on the carapace. This consists of ridges extending forwards from the middle of the posterior edges

of the scutes. The presence of a closely related taxon in the southern part of the Junggar Basin was reported by Maisch et al. (2003), who referred fragmentary carapace elements from the Toutunhe and Qigu formations with a similar distinctive plicated surface texture to *X. cf. radiplicatus*. Specimen IVPP V18104 and the isolated elements from the Jiangjunmiao turtle bonebed confirm that the Xinjiang species is similar to *X. radiplicatus*, but specifically distinct.

*Xinjiangchelys radiplicatoides* differs from *X. radiplicatus* in the pattern of ornament on the carapace. In *X. radiplicatoides* the plications are more numerous and less distinct and extend outward from a smooth rectangular area near the posterior end of the carapace. In *X. radiplicatus* the plications are coarser and converge on a point near the posterior edge of the carapace. As well, these species differ in that *X. radiplicatoides* has ridges paralleling the margin of the scutes crossing the plications. These differences are interpreted here as specifically significant, rather than a result of variation within a species, because the range of variation present in specimens from the Jiangjunmiao turtle bonebed does not include any examples of the ornament pattern seen in *X. radiplicatus*.

As well as being similar in their development of plications on the surface of the carapace, adults of *Xinjiangchelys radiplicatus* and *X. radiplicatoides* are similar to one another and different from other species of *Xinjiangchelys* in having vertebral scutes that are subequal in width and length and smaller than the pleural scutes. In other species of *Xinjiangchelys*, the vertebral scutes generally are twice as wide as they are long and are larger than the pleural scutes.

As indicated by the undistorted left half of the holotype, the carapace in *Xinjiangchelys radiplicatoides* was distinctly round in outline. The presence of a round carapace is widespread in *Xinjiangchelys*, also being present in *X. chowi*, *X. tianshanensis*, *X. qiguensis*, and *X. latimarginalis*. This shape differs from that of *X. junggarensis* which has a more elongate, oval carapace. However, the carapace in the juvenile specimen of *X. radiplicatus* described by Ye (1986b) is oval and longer than wide, indicating that the proportions of the shell in that species changes during growth.

Two specimens, IVPP V18104 and IVPP V9636-1, provide the first evidence of a relatively complete skull for a species of *Xinjiangchelys*. The skull differs in its proportions from that of *Annemys levensis*, described by Sukhanov (2000) and *Annemys* sp. described below, which are the only other Asian Jurassic cryptodires represented by relatively complete cranial material. In *Annemys* the height and width of the postorbital portion of the skull does not expand posteriorly, so that the post-orbital region is more parallel sided. The presence of an inflated post-temporal region can be interpreted as a primitive feature, because that is widespread in basal cryptodires, being present for example in *Kallokibotion* (Gaffney and Meylan 1992b) and *Chubutemys* (Gaffney et al. 2007).

Expansion of the temporal region likely was a strategy for increasing the mass of the adductor musculature in the absence of an elongate supraoccipital crest.

The skull of *Xinjiangchelys radiplicatoides* is notably primitive in its basicranial region. The pointed anterior end of the basisphenoid is reminiscent of the cultriform process of primitive reptiles and the slit-like shape of the foramen caroticum laterale is suggestive of a reduced interpterygoid vacuity. The latter identification is consistent with the interpretation presented by Sterli et al. (2010) that in basal turtles, such as *Proganochelys*, the palatine artery would have entered the skull through the interpterygoid vacuity and that the canalis caroticus lateralis formed as a result of closure of the interpterygoid vacuity around that artery.

The basicranial region of *Xinjiangchelys radiplicatoides* is similar to that of *Chubutemys* in the shape and proportions of the basisphenoid, presence of a slit-like opening between the basisphenoid and the pterygoid, and presence of a distinct sulcus carotici leading to the canalis caroticus cerebralis. They differ in that the "basipterygoid process" of *Chubutemys* is relatively smaller and the posterior portion of the canalis caroticus cerebralis is less fully covered. The similarities between these two taxa are consistent with the interpretation that *Chubutemys* is a eucryptodire at about the same grade of evolution as *X. radiplicatoides*, but may also be because they are both plesiomorphic (Smith and Kear 2012).

The quadrate is different from that of *Annemys* and similar to *Kayentachelys* in having a shallow incisura columellae (Sterli and Joyce 2007; Gaffney and Jenkins 2010). Thus, in this feature as well, *Xinjiangchelys radiplicatoides* is primitive relative to *Annemys*. Although the anterior edge of the otic capsule of *X. radiplicatoides* is not completely visible on either specimen, the rugose anterior surface on the quadrate demonstrates that a processus trochlearis oticum was present, as would be expected in a basal eucryptodire.

*Xinjiangchelys chowi* Matzke, Maisch, Sun, Pfretzschner, and Stöhr 2005
(Fig. 10.11)

**Referred specimen**: IVPP V18105 (field number WCW-02-61): incomplete carapace, preserving the left half and much of the median area, exposed in dorsal view (Fig. 10.11a, b), plus associated postcranial elements, including an incomplete cervical vertebra (Fig. 10.11c, d). From "Pingfen Shan J23" locality, Wucaiwan field area, northern Junggar Basin, Xinjiang Uygur Autonomous Region; upper part of Shishugou Formation; Late Jurassic (Oxfordian). This is the only referred specimen known for the species.

**Occurrence**: Known from two localities in the Junggar Basin, Xinjiang: holotype locality near Urumqi, southern part of basin, in the Middle Jurassic (Callovian) Toutunhe
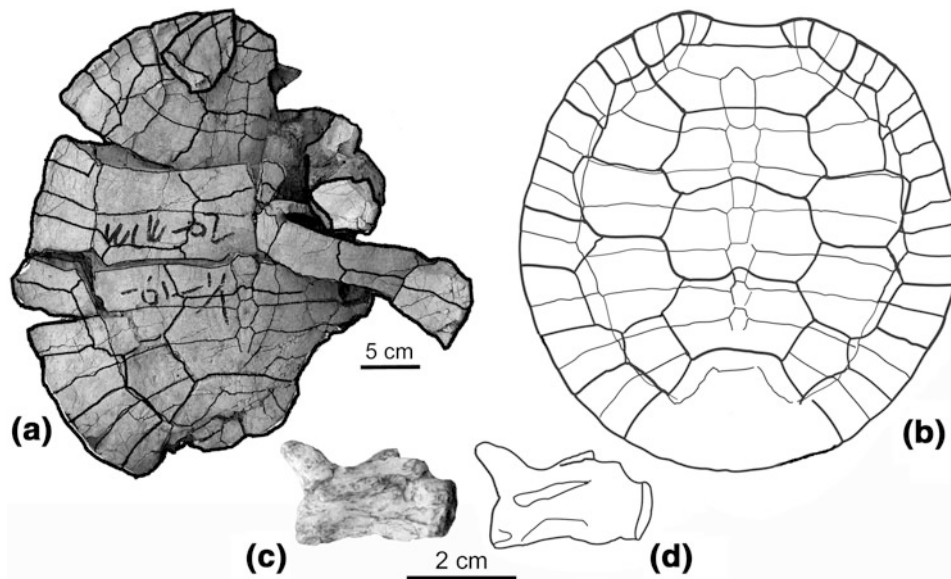
**Fig. 10.11** Associated carapace and cervical vertebra (IVPP V18105) of *Xinjiangchelys chowi* Matzke et al. 2005 (Xinjiangchelyidae); "Pingfen Shan J23" locality, Wucaiwan field area, northern Junggar Basin, Xinjiang, China; upper part of Shishugou Formation; Late Jurassic (Oxfordian). **a** Carapace in dorsal view; **b** reconstruction of carapace, based on figured specimen, in dorsal view; **c, d** cervical vertebra in left lateral view: **c** photograph and **d** interpretive drawing. Images at different scales

Formation (Matzke et al. 2005); and "Pingfen Shan J23" locality (for above-listed referred specimen), Wucaiwan field area, northern part of basin, in the Upper Jurassic (Oxfordian) upper part of the Shishugou Formation.

**Diagnosis**: See Matzke et al. (2005)

**Description**: The carapace of the referred specimen, IVPP V18105, is of moderate size, low domed, and round in outline, with a weakly developed nuchal emargination (Fig. 10.11a, b). The external surface of the carapace is smooth and sulci on the carapace are generally distinct.

The carapace is partially disarticulated, allowing many of the sutures to be identified with confidence. The nuchal is broad and relatively short. Seven neurals can be identified, of which the posterior six are strongly hexagonal. The sutures delineating the eighth costal and suprapygals cannot be differentiated, so it is uncertain if an eighth neural was present and if the neural series contacted the suprapygals. The first nine peripherals can be differentiated. The first peripheral has only a very narrow area of contact with the first costal. A striking feature of the carapace is the presence of wide bridge peripherals that are approximately as wide as long and are broadly exposed in dorsal view. This is in contrast to the typical xinjiangchelyid condition, in which the bridge peripherals are narrower than they are long and are poorly exposed in dorsal view.

Sulci generally are distinct. The cervical scute is short and wide. The vertebral scutes are wider than long and have strongly angled lateral edges. Unlike ?*Sichuanchelys* sp., which also has wide vertebral scutes, the pleural scutes are also wide, their maximum width being about a half the

maximum width of the vertebral scutes. The pleural scutes extend onto the peripheral series and the fourth, seventh, and ninth marginal scutes extend onto the costals.

A single cervical vertebra (Fig. 10.11c, d) was found in association with the carapace. The centrum is amphicoelous and elongate. The transverse process is a short, flange-like structure that extends from about the middle of the centrum to its anterior end. A sharp mid-ventral ridge is present. Both in its proportions and development of the transverse process, the cervical vertebrae are similar to those of *Xinjiangchelys junggarensis* as described by Peng and Brinkman (1993, Figs. 3e–g, 8).

**Remarks**: *Xinjiangchelys chowi* was described by Matzke et al. (2005) on the basis of a shell from the Middle Jurassic (Callovian) Toutunhe Formation on the southern margin of the Junggar Basin. It was diagnosed largely on the basis of the presence of large plastral fenestrae. Matzke et al. (2005) considered this to be a diagnostic feature of the species, rather than a developmental feature, because the carapace was of large size. However subsequent studies have questioned the diagnostic reliability of that feature (Rabi et al. 2010), because in turtles the size of plastral fenestrae typically changes during development. Despite uncertainty about the taxonomic significance of the presence of large plastral fenestrae in the holotype, *X. chowi* is here considered a valid species because of the presence of mediolaterally expanded bridge peripherals that are broadly exposed in dorsal view. This is most strongly expressed by the fifth and sixth peripherals, which are wider than they are long. These proportions contrast with the typical condition
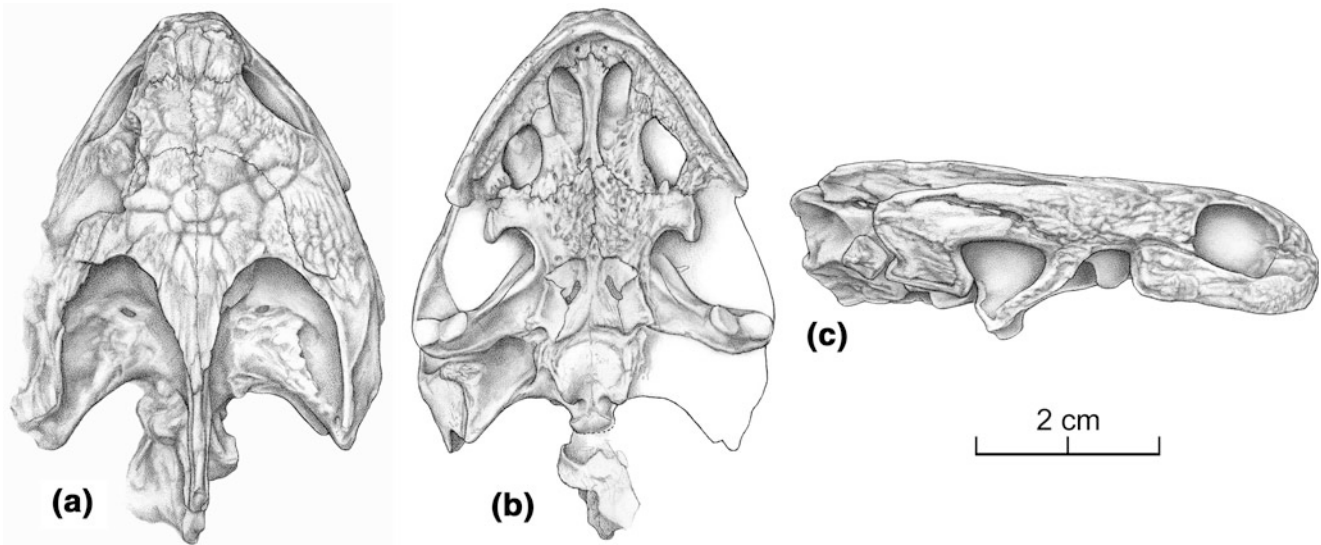
**Fig. 10.12** Illustration of skull (part of skeleton IVPP V18106) of *Annemys* sp. (Xinjiangchelyidae); Wucaiwan field area, northern Junggar Basin, Xinjiang, China; upper part of Shishugou Formation; Middle (Callovian) or Late (Oxfordian) Jurassic. **a** Dorsal view; **b** ventral view; **c** right lateral view. Matrix adhering to skull is not fully illustrated. Images at same scale

in basal cryptodires, in which the bridge peripherals are narrower than long and poorly exposed in dorsal view. In having wide peripherals, *X. chowi* is most similar to *X. qiguensis*. However *X. qiguensis* has distinct plications extending posteriorly from the vertebral and pleural sulci. Specimen IVPP V18105 is included in *X. chowi*, because no such plications are present.

The occurrence of *Xinjiangchelys chowi* in both the upper beds of the Shishugou Formation of the Wucaiwan area, which are Late Jurassic (Oxfordian) in age, and the Middle Jurassic (Callovian) Toutunhe Formation suggests there was no major change in turtle assemblages across the Middle-Late Jurassic boundary in the present-day Junggar Basin region.

Genus *Annemys* Sukhanov and Narmandakh 2006
*Annemys* sp.
(Figs. 10.12, 10.13, 10.14, 10.15)

**Synonymy**: *Annemys* sp.: Rabi et al. 2010, p. 263, Fig. 1g, h, Table 1.

**Referred specimens**: IVPP V18106 (field number WCW-04-10), incomplete skeleton consisting of a moderately complete skull (Figs. 10.12, 10.13, 10.14), four cervical vertebrae in articulation (Fig. 10.15), and an incomplete carapace (not figured) in two parts, the first part including four disarticulated anterior costals and a series of anterolateral peripherals in articulation and the second part including a series of posterolateral peripherals in articulation. CT scans of the skull from this specimen are available on the Digimorph Web site at: http://digimorph.org/specimens/Annemys_sp/. IVPP V18107 (field number WCW05A-30), fragmentary carapace consisting of the nuchal and first peripheral in articulation and two disarticulated costals (not figured). Both specimens are from the

Wucaiwan field area, northern Junggar Basin, Xinjiang Uygur Autonomous Region, and their positions within the Shishugou Formation relative to the Middle-Upper Jurassic boundary are uncertain.

**Occurrence**: *Annemys* sp. (sensu this study) is known only from the Middle (Callovian) and/or Upper (Oxfordian) Jurassic Shishugou Formation, in the Wucaiwan field area, northern Junggar Basin. Outside of the Jungarr Basin, the genus is known from the Late Jurassic both in the nearby Turpan Basin, Xinjiang, and in Mongolia (Rabi et al. 2010, Table 1 and references therein).

## Description

**Skull**: The skull of IVPP V18106 is nearly complete and little crushed (Figs. 10.12, 10.13, 10.14). It has an elongate, subtriangular shape in dorsal view (Figs. 10.12a, 10.13a). Its width across the quadrates is about two-thirds of its length to the end of the supraoccipital crest. In lateral view (Figs. 10.12c, 10.14), the skull is low, its height being about a quarter of its width across the quadrates. The orbits are large, located far forward, and face primarily anterolaterally. Both the temporal and cheek regions are deeply emarginated: the temporal emargination extends just anterior to the otic capsule and the cheek emargination extends to about midway along the height of the orbit. The supraoccipital crest is an elongate, thin, vertical flange of bone that extends posteriorly beyond the squamosals. The dorsal surface of the skull bears well-defined sulci that show that a complex arrangement of scutes was present on the skull.
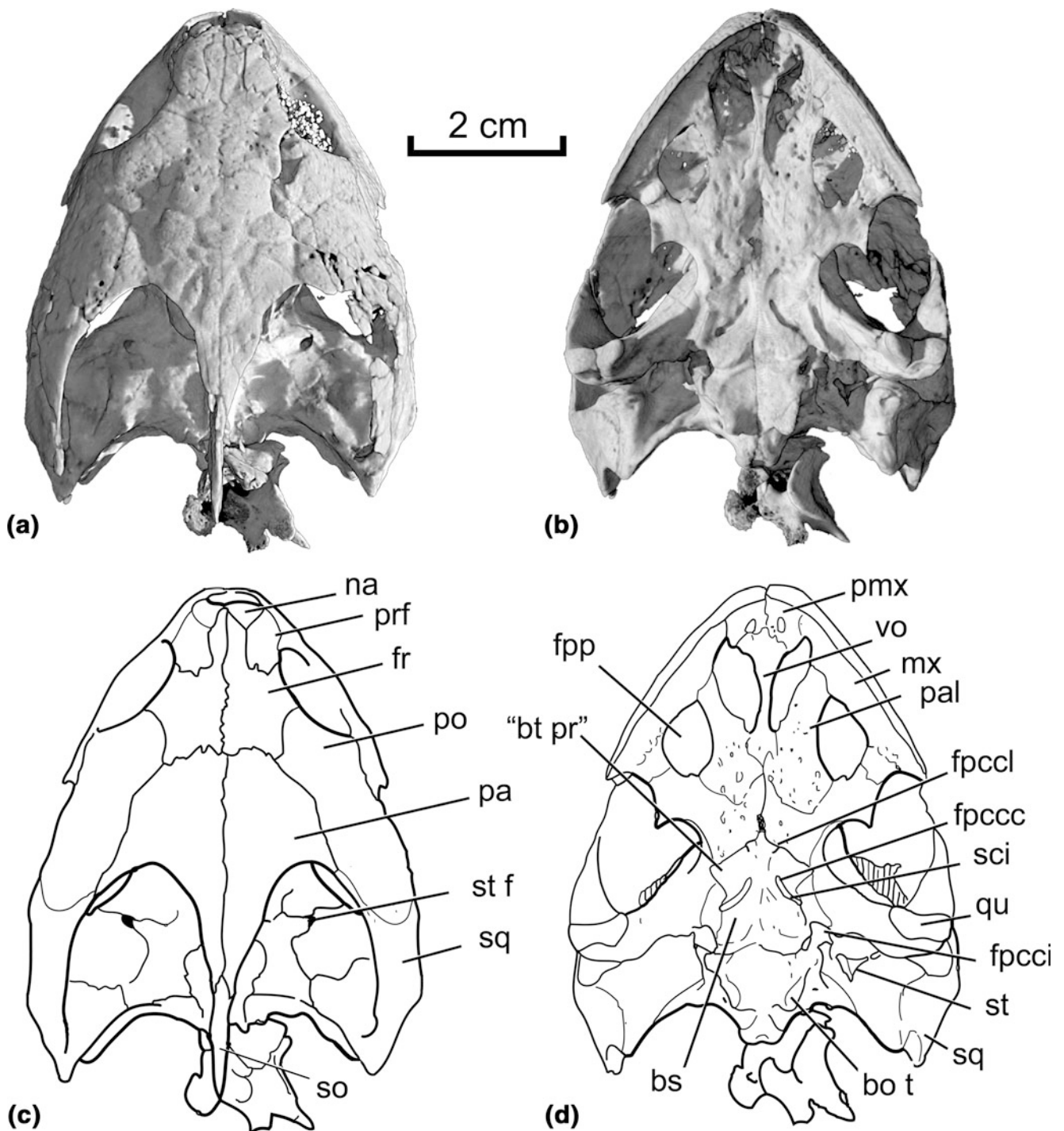
**Fig. 10.13** CT volume renderings and interpretive drawings, in dorsal and ventral views, of skull (part of skeleton IVPP V18106) of *Annemys* sp. (Xinjiangchelyidae); Wucaiwan field area, northern Junggar Basin, Xinjiang, China; upper part of Shishugou Formation; Middle (Callovian) or Late (Oxfordian) Jurassic. **a**, **b** Surface CT scans in **a** dorsal view and **b** ventral view; **c**, **d** interpretive drawings in **c** dorsal view and **d** ventral view. Abbreviations: *bo t* basioccipital tubercula; *bs* basisphenoid; *bt pr* basipterygoid process; *fpccc* foramen posterius canalis caroticus cerebralis; *fpcci* foramen posterius canalis caroticus internus; *fpccl* foramen posterius canalis caroticus lateralis; *fpp* foramen palatinum posterius; *fr* frontal; *mx* maxilla; *na* nasal; *pa* parietal; *pal* palatine; *pmx* premaxilla; *po* postorbital; *prf* prefrontal; *pt* pterygoid; *qu* quadrate; *sci* sulcus caroticus internus; *so* supraoccipital; *sq* squamosal; *st* stapes; *st f* stapedial foramen; *vo* vomer. Images at same scale
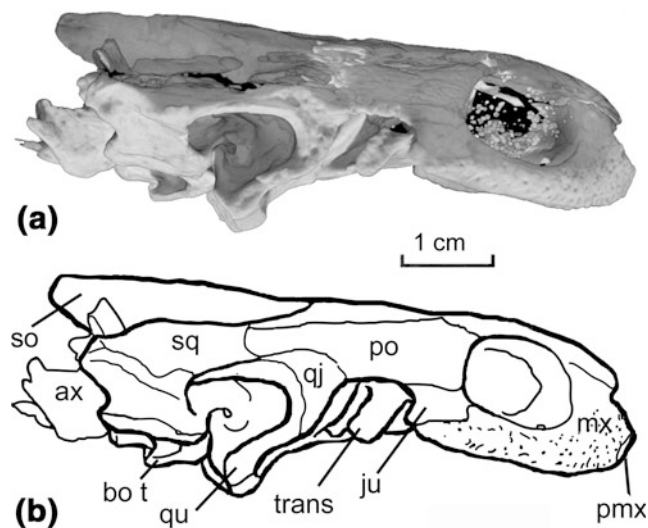
**Fig. 10.14** CT volume renderings and interpretive drawings, in right lateral view, of skull (part of skeleton IVPP V18106) of *Annemys* sp. (Xinjiangchelyidae); Wucaiwan field area, northern Junggar Basin, Xinjiang, China; *upper part* of Shishugou Formation; *Middle* (Callovian) or *Late* (Oxfordian) Jurassic. **a** Surface CT scan; **b** interpretive drawing. Abbreviations: *ax* axis; *bo t* basioccipital tubercula; *ju* jugal; *mx* maxilla; *pmx* premaxilla; *po* postorbital; *qj* quadratojugal; *qu* quadrate; *so* supraoccipital; *pr pt* processus pterygoideus externus. Images at same scale

The nasals are subtriangular elements wedged between the prefrontals and maxilla, where they form the anterior edge of the external narial opening. The nasals barely meet one another at the midline, excluding the frontal and prefrontal from the margins of the external narial openings.

The prefrontals are of moderate size, forming about two-thirds the dorsal surface of the skull anterior to the orbits. In addition to their contact with the nasals anteriorly, they contact the frontals medially and posteriorly, the maxilla laterally, and the vomer and palatine ventrally.

The frontals form the dorsal portion of the skull roof between the orbits. They contact the prefrontals and nasals anteriorly, the parietals posteriorly, and the postorbitals posterolaterally. The frontal has a rectangular posterior portion, and an elongate anterior projection extending between the prefrontals to reach the nasals. A lateral lappet forms the dorsal margin of the orbit, separating the prefrontal from the postorbital. The posterior end of the frontals is located posterior to the orbits.

The parietals are the largest bones in the skull roof. They contact the frontal anteriorly, postorbital laterally, squamosal posterolaterally, and the supraoccipital posteriorly. Although the temporal region is deeply emarginated, the parietal has a lateral process that barely touches the squamosal, excluding the postorbital from the upper temporal emargination.

The postorbital is a large rectangular element that forms a portion of the border of the orbit anteriorly and contacts the
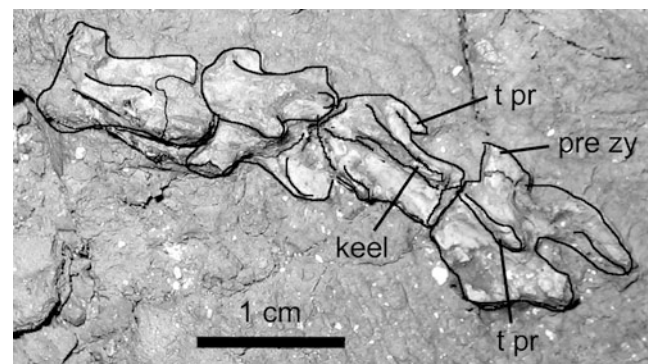


**Fig. 10.15** Photograph of four articulated cervical vertebrae (part of skeleton IVPP V18106) of *Annemys* sp. (Xinjiangchelyidae); Wucaiwan field area, northern Junggar Basin, Xinjiang, China; *upper part* of Shishugou Formation; *Middle* (Callovian) or *Late* (Oxfordian) Jurassic. Vertebrae are partly embedded in *rock slab*; for clarity, outlines and major structures for each vertebra are traced in *black*. Abbreviations: *keel* mid-ventral keel; *pre zy* prezygapophysis; *t pr* transverse process

parietal medially, the quadratojugal and squamosal posteriorly, and the jugal anteroventrally. The postorbital forms a portion of the margin of the border of the ventral margin of the skull, where it separates the jugal and quadratojugal.

The jugal is a triangular element in lateral view that contacts the maxilla anteroventrally and the postorbital dorsally. It forms a portion of the orbital margin, where it separates the maxilla and postorbital. The posterior border of the jugal forms the anterior margin of the lower temporal emargination.

The quadratojugal is a small, crescent-shaped element that borders the anterior margin of the quadrate and contacts the postorbital anteriorly and dorsally. It minimally contacts the squamosal posteriorly. Ventral to its contact with the postorbital, it forms the posterior margin of the cheek emargination.

The squamosal forms the posterolateral corner of the skull, capping the quadrates and anteriorly contacting the parietal, postorbital, and quadratojugal. The posterior tip of the squamosal extends posterior to the level of the occipital condyle. Thus the antrum postoticum would have been large. Medially the squamosal forms the lateral edge of the temporal emargination and it contacts the opisthotic and quadrate.

The premaxilla forms the ventral edge of the external narial opening and the anterior edge of the labial ridge. Ventrally, the premaxilla forms the anterior edge of the palate, contacting the vomer posteriorly and the maxilla laterally. The premaxilla forms a small portion of the margin of the internal narial opening between the vomer and the maxilla. Prepalatine foramina are located within the ventral surface of the premaxilla.

The maxilla forms most of the anterolateral surface of the skull. In external view, the maxilla contacts the jugal

posteriorly, the prefrontal dorsally, the nasal anterodorsally, and the premaxilla anteroventrally. Between the jugal and prefrontal, the maxilla forms the ventral margin of the orbit. The suborbital portion of the maxilla is narrow and has a nearly straight ventral edge. In palatal view, the maxilla forms most of the triturating surface. This is a narrow, flat surface without a distinct lingual ridge. The contacts with the palatine and pterygoids are short and widely separated by the large foramen palatinum posterius.

The palate is completely exposed ventrally and the sutures between individual bones are clear (Figs. 10.12b, 10.13b). The internal narial openings are oval in shape, with their long axis oriented anteroposteriorly. The vomer forms a narrow, flat-topped bar of bone that separates the internal narial openings. The foramen palatinum posterius is large, exceeding the internal narial opening in size. The foramen palatinum posterius is bordered by the pterygoid, palatine, and maxilla. The proportion of the border of the foramen formed by the pterygoid is about half that formed by the palatine. A rugose area is present on the ventral surface of the palate between the foramen palatinum posterius and basisphenoid. This rugose area is largely located on the pterygoid, but also extends onto the palatine and the posterior tip of the vomer.

In ventral view the palatine is a triangular element, wide posteromedially and tapering to a narrow bar that separates the internal narial opening from the foramen palatinum posterius. The palatines contact one another at the midline between the pterygoid and vomer.

The pterygoids form the ventral surface of the palate posterior to the palatines. The pterygoids are very thin at the midline and a small unossified area between the pterygoids is present anterior to the basisphenoid. A midline contact between the pterygoids is present between the basisphenoid and the palatines. The pterygoid extends to the posterior edge of the basisphenoid, but does not contact the basioccipital. The processus pterygoideus externus is well developed and bears a large, flat lateral surface. A ridge extends from the lateral tip of the process to the posterior edge of the pterygoid, presumably marking the medial extent of insertion of the pterygoideus muscle. The posterolateral wing of the pterygoid slopes strongly laterally, so the posterior edge of the pterygoid is located at the level of the posterior edge of the basisphenoid and the jaw joint is located at about the same level as the posterior end of the basisphenoid. A deep fossa is present posterior to the quadrate ramus of the pterygoid.

The basisphenoid is a rectangular element, having a broad contact with the basioccipital. In ventral view the two bones are barely distinguished, but the contact between them can be recognized as following a groove that extends across these elements. The short, V-shaped, anterior end of the basisphenoid separates the pterygoids at the midline. A prominent feature of the basisphenoid is the "basipterygoid processes." These are triangular processes that extend laterally to barely contact the C-shaped ridge that runs posteriorly from the lateral tip of the processus pterygoideus externus. The ventral surface of the basisphenoid lacks a distinct pair of pits like those present in *Ordosemys leios*, although a small, rugose area is present at about the same position.

The canals and foramina in the basicranial region are distinct. As described above for *Xinjiangchelys radiplicatoides*, the foramen posterius canalis carotici interni is located at the posterior end of the contact between the pterygoid and basisphenoid. The canalis caroticus internus runs forward between the basisphenoid and pterygoid to open at the posterior edge of the "basipterygoid process." A deep groove, the sulcus caroticus internus, extends forward from this canal to the foramen posterius canalis caroticus cerebralis. A separate opening for the palatine artery, the foramen posterius canalis caroticus lateralis, is located farther anteriorly between the basisphenoid and the pterygoid. Rather than being a slit-like opening like that of *X. radiplicatoides*, this is a distinct foramen that leads into a well-defined canal. The canalis caroticus cerebralis and the canalis caroticus lateralis are subequal in diameter.

The basioccipital is subrectangular in ventral view, with the basioccipital tubercula oriented anteroposteriorly along the lateral edges of the bone. The basisphenoid–basioccipital suture is located at about the level of the posterior end of the pterygoid, so the basioccipital is located almost entirely posterior to the pterygoid. Also extending well posterior to the pterygoid is the opisthotic, which means the latter bone is largely visible in ventral view.

The quadrate has a complex structure. In lateral view, the quadrate forms the anteroposteriorly elongate and sub-triangular cavum tympani (Fig. 10.14). The incisura columellae auris is open posteriorly and is very narrow. Thus, the Eustachian tube must have been posterior to the quadrate. In ventral view, the quadrate forms the condylus mandibularis, which has the saddle-shaped joint surface typical of turtles.

The otic capsule is fully exposed in dorsal view (Figs. 10.12a, 10.13a). This is elongate and has a flat dorsal surface. A large stapedial foramen is present. The anterior edge of the otic capsule is not exposed, which means the size of the processus trochlearis oticum is uncertain. Sutures between the prootic, opisthotic, and quadrate cannot be identified.

**Cervical vertebrae**: IVPP V18106 includes a cervical series containing four vertebrae preserved in articulation (Fig. 10.15). These vertebrae are amphicoelous and elongate. The transverse processes are short, flange-like structures located near the anterior end of the centrum. A sharp midventral ridge is present. In proportions, the cervical vertebrae are similar to the one described above for

*Xinjiangchelys radiplicatoides* in that the flange-like transverse processes are located near the anterior end of the centrum.

**Carapace**: Carapace elements (not figured) preserved in IVPP V18106 include four disarticulated anterior costals, five anterolateral peripherals in articulation, and the posterior edge of the carapace. A second specimen, IVPP V18107 (also not figured) includes four disarticulated costals, three in exposed in dorsal view and one exposed in ventral view. As in the holotype specimen of *Annemys latiens* Sukhanov and Narmandakh 2006 described by Sukhanov (2000), the carapace is thin and smooth. In dorsal view the carapace is longer than wide and has a rounded posterior end. The anterolateral peripherals are narrow and have an upturned lateral edge.

Also, the pattern of scutes is like that of *A. latiens* in that vertebral scutes two and three are narrow and show little angulation of their lateral edges. In IVPP V18107 low plications extend posteriorly from the anterior edge of the vertebral scutes.

**Remarks**: *Annemys* was erected by Sukhanov and Narmandakh (2006) on the basis of specimens from the Late Jurassic of Mongolia. It was differentiated from *Xinjiangchelys* on the basis of features of the carapace, particularly the presence of a relative thin shell with narrow vertebral scutes two and three. In these features it is similar to sinemydids/macrobaenids, but differs from them in having a broader anterior lobe of the plastron. IVPP V18106 is included in the genus *Annemys*, because it is has a relatively thin carapace with narrow vertebral scutes and is Jurassic in age.

Inclusion of IVPP V18106 in *Annemys* also is supported by similarities in the general proportions of the skull with that of *Annemys levensis* as described by Sukhanov (2000). Both are relatively low, have deep temporal and cheek emarginations, and a long supraoccipital crest. In these features, the skull of *Annemys* is different from that of *Xinjiangchelys radiplicatoides*, which has an expanded temporal region, weakly emarginated temporal and cheek region, and a short supraoccipital crest.

Two species of *Annemys* have been named, *A. latiens* and *A. levensis*. These differ primarily in features of the carapace, particularly the presence of a relatively thin shell in *A. latiens* compared to *A. levensis*. The shell of IVPP V18106 is not sufficiently well preserved to be assigned to either species. The skull of IVPP V18106 differs from that of *A. levensis* in that the prefrontals do not contact one another at the midline anterior to the frontals. In *A. levensis* the prefrontals meet at the midline between the frontals and nasals (Sukhanov 2000, Fig. 17.2). Also, in *A. levensis* the postorbital forms a portion of the posterior margin of the skull, thereby separating the parietal and squamosal, whereas in IVPP V18106 the parietal has a long lateral process that contacts the squamosal. As reconstructed, *A. levensis* differs from IVPP V18106

in the presence of a relatively small foramen palatinum posterius. However, as noted by Rabi et al. (2010) the skull of *A. levensis* appears to be rather poorly preserved, so a larger opening is possible. In the basicranial region, IVPP V18106 differs from *A. levensis* in that the carotid canals are closed posteriorly instead of being open as in *A. levensis*. Because the skull of *A. latiens* is not known, it is not possible to resolve whether IVPP V18106 is attributable to that species. Thus, we consider IVPP V18106 to be specifically indeterminate within *Annemys*.

In features of its skull and shell, *Annemys* is at a more derived grade of evolution than *Xinjiangchelys radiplicatoides*. Derived skull features of *Annemys* include the presence of a low temporal region, the deeply emarginate skull, the long and blade-like supraoccipital crest, the long incisura columella, circular shape of the foramen caroticum laterale, and a relatively short basisphenoid that is truncated anteriorly. The carapace of *Annemys* is derived relative to *X. radiplicatoides* in being thin and in having narrow vertebral scutes. In all these features, *Annemys* both is derived relative to *X. radiplicatoides* and is similar to Early Cretaceous eucryptodires from Asia, such as *Ordosemys* Brinkman and Peng 1993a, *Sinemys* Brinkman and Peng 1993b, *Hangaiemys* Sukhanov and Narmandakh 1974, and *Dracochelys* Gaffney and Ye 1992. In addition, as noted by Rabi et al. (2010) *Annemys* shows particularly strong similarities to the Early Cretaceous sinemydid *Hangaiemys* in the proportions of the skull, development of the supraoccipital crest, and presence of a greatly enlarged foramen palatinum posterius; this combination of features suggests a close relationship between the two genera. Whether similarities in the skulls of *Annemys* and *Hangaiemys* compared to *X. radiplicatoides* reflect true relationships must await the discovery of additional cranial material from Jurassic eucryptodires from Asia. At present, however, the substantial similarities between *Annemys* and *Hangaiemys* appear to support a recent suggestion that the Xinjiangchelyidae are a paraphyletic assemblage of basal cryptodires (Rabi et al. 2010).

## Discussion

### *The Shishugou Formation Turtle Assemblage*

Although taxonomic uncertainty remains, a high level of diversity is present among Jurassic turtles in the northern part of the Junggar Basin. At least five species are now known from the Shishugou Formation: ?*Sichuanchelys* sp.; *X. junggarensis*; *X. radiplicatoides*; *X. chowi*; and *Annemys* sp. The plastron described by Peng and Brinkman (1993,

pp. 2023–2025, Figs. 13, 14) as *Xinjiangchelys* sp. may be an additional taxon. One additional taxon has been reported from the Qigu Formation, *X. qiguensis*, although the taxonomic significance of the differences between this and *X. chowi* has been questioned (Rabi et al. 2010). This level of diversity is similar to that of other well-documented Jurassic turtle assemblages. For example, in the Late Jurassic of Sichuan eight named turtle taxa are present. Significantly, in both the Junggar and Sichuan assemblages many of the taxa are represented by single specimens, suggesting that the diversity of these assemblages is not yet fully documented by available samples.

Despite a high level of diversity of turtles in the Shishugou Formation, diversity at individual localities is low. Typically, when multiple individuals are found together, no more than two taxa are present and one of those is overwhelmingly dominant. For example, in the Jiangjunmiao turtle bonebed two taxa are present, but most of the identifiable elements are from *Xinjiangchelys radiplicatoides*. At the Pingfengshan locality Peng and Brinkman (1993) recognized the presence of two taxa based on 14 specimens, with all but one of these being *X. junggarensis*. This pattern appears to be typical for the Late Jurassic of Central Asia. Similarly, in the adjacent Turpan Basin, a locality containing multiple thousand individuals of *Annemys* has been reported (Wings and Joyce 2009). This pattern of high alpha diversity (total diversity within a unit), low diversity within individual localities, and high beta diversity (between-locality diversity within a unit) is unusual when compared with most turtle assemblages of the Cretaceous. The paleoecological significance of this pattern is uncertain. Given the paleoenvironmental and paleoclimatic setting, it is likely that short-term environmental conditions, such as wet intervals following periods of drought, leading to explosive expansion of low diversity communities played a factor. Additional taphonomic and paleoecological studies are necessary to resolve this.

## Implications for Evolution of the Basicranial Region in Basal Eucryptodires

The basicranial region has long been recognized as an important source of information for interpreting the interrelationships of turtles (Gaffney 1979b). Most recently, the evolution of the braincase in turtles was reviewed by Sterli et al. (2010), who placed each of six patterns of carotid circulation described by Sterli and de la Fuente (2010) into a phylogenetic framework. In the most basal pattern, represented by *Proganochelys*, the carotid artery splits into cerebral and palatine branches ventral to the skull, the cerebral branch enters the braincase through a foramen (the

foramen posterius canalis caroticus cerebralis) in the basisphenoid, and the palatine branch extends forward through the interpterygoid vacuity. In a slightly more derived pattern, represented by *Kallokibotion*, the interpterygoid vacuity has closed around the palatine artery so that the artery enters the skull through a distinct canal, called the canalis caroticus lateralis. In pleurodires, the internal carotid and its cerebral and palatine branches are fully encased in bone and a single foramen is present posteriorly. Sterli et al. (2010) interpreted this as a result of expansion of the parasphenoid portion of the basisphenoid, trapping the internal carotid between the basisphenoid and the pterygoid.

In the most basal paracryptodires, such as *Pleurosternon* and *Glyptops*, the carotid artery branches into the cerebral and palatine arteries in a shallow concavity along the side of the basisphenoid and, slightly more anteriorly, the two branches enter canals though separate openings. In baenids, a single opening is present along the side of the basisphenoid. Sterli et al. (2010) hypothesize that the paracryptodire condition also formed by expansion of the parasphenoid portion of the basisphenoid to trap the internal carotid and its bifurcation between the basisphenoid and the pterygoid.

Sterli et al. (2010) did not incorporate the eucryptodire pattern into this evolutionary sequence because the early stages of the evolution of the eucryptodire basicranial region were too poorly documented. The skulls of *Xinjiangchelys radiplicatoides* and *Annemys* sp. described here provide additional data that document the early stages of evolution of the basicranial region in eucryptodires (Fig. 10.16). Specifically, these new skulls show that in the most primitive eucryptodires there is still a recognizable interpterygoid vacuity and the foramen posterius canalis caroticus lateralis is located a long distance from the foramen posterior canalis caroticus cerebralis. Also, as discussed in the next section, the "basipterygoid process" is still well developed.

In eucryptodires, the carotid artery enters the skull through a single foramen, called the foramen posterior canalis caroticus internus, located either between the pterygoid and basisphenoid or within the pterygoid. In basal eucryptodires, such as *Chubutemys* (Fig. 10.16a), xinjiangchelyids (Fig. 10.16b, d), and Early Cretaceous sinemydids/macrobaenids from Asia (Fig. 10.16c, e, f), the canalis caroticus internus does not completely enclose the carotid artery and its branches. Instead, the carotid artery exits ventral to the basisphenoid prior to the point at which the carotid artery branches into the cerebral and palatine arteries. Thus, these arteries are not fully encased in bone. In these turtles, the cerebral artery would have continued forward in the sulcus caroticus internus, a well-defined groove that leads to the foramen posterius canalis caroticus cerebralis. There is no distinct groove for the palatine artery, so the exact course of this artery is unknown. However, it would have branched off from the carotid artery somewhere between the anterior opening of the carotid canal
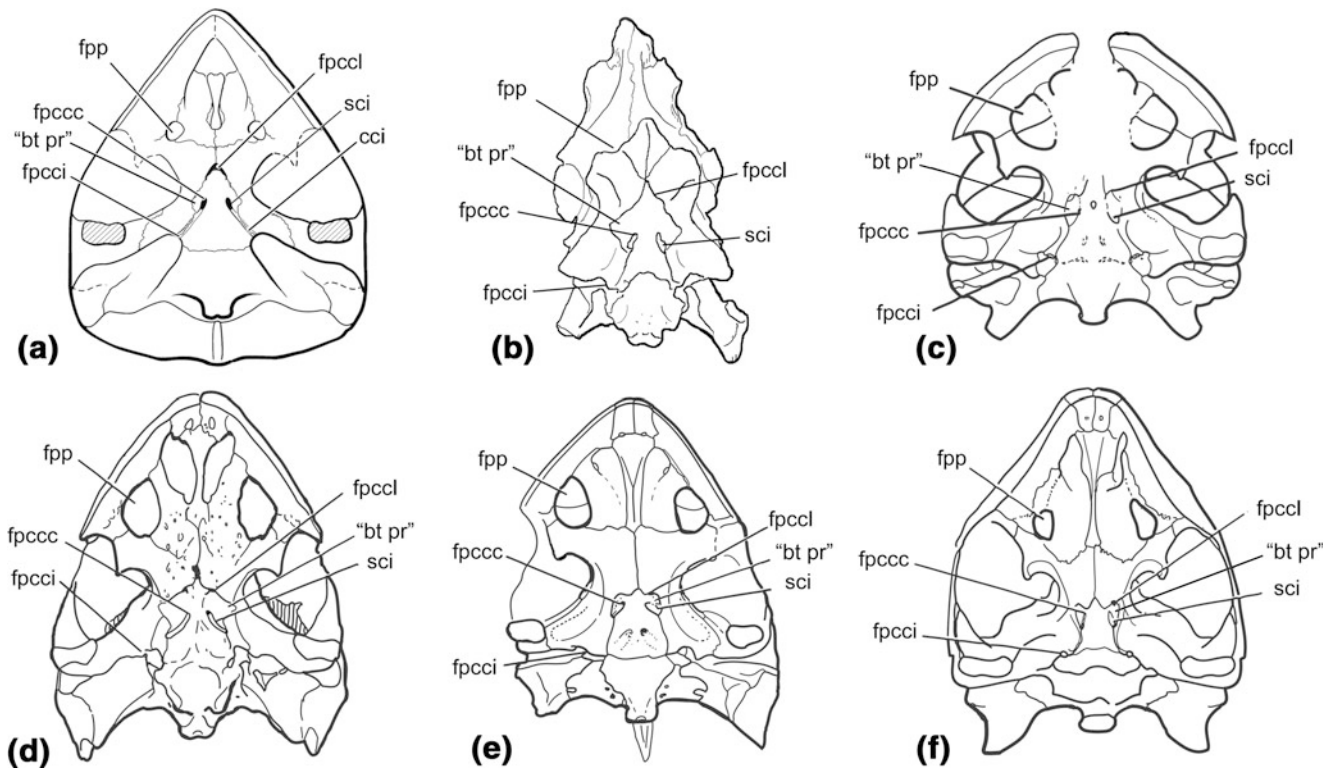
**Fig. 10.16** Palatal views of skulls of reprresentative basal cryptodires to show differences in structure of the basicranial region. **a** *Chubutemys*, redrawn from Gaffney et al. (2007); **b** *Xinjiangchelys radiplicatoides* sp. nov., drawn from IVPP V9539-1 (see Fig. 10.6c, d); **c**, reconstruction of *Sinemys gamera*, based on IVPP V9532-11; **d** *Annemys* sp, drawn from IVPP V18106 (see Fig. 10.13d); **e** *Hangaiemys*, redrawn from Sukhanov (2000); **f** reconstruction of *Ordosemys* sp., based on IVPP V12092. Abbreviations: *bt pr* basipterygoid process; *cci* canalis caroticus internus, *fpccc* foramen posterior canalis carotis cerebralis; *fpcci* foramen posterior canalis caroticus internus; *fpccl* foramen posterior canalis caroticus lateralis; *fpp* foramen palatinum posterior; *sci* sulcus caroticus internus. Images at different scales

and the foramen posterior canalis carotici cerebralis, and passed below the basisphenoid to enter the cranial cavity through the foramen posterior canalis caroticus lateralis, which is located between the pterygoid and basisphenoid. In *Cubutemys* (Fig. 10.16a) and *Xinjiangchelys radiplicatoides* (Fig. 10.16b) the foramen posterior canalis caroticus lateralis is a slit-like space that can be interpreted as a reduced interpterygoid vacuity. This also appears to be the case in *Dracochelys* (Gaffney and Ye 1992, Fig. 5) and *Annemys* (Fig. 10.16d). In contrast, *Ordosemys* (Fig. 10.16f), and *Sinemys* (Fig. 10.16c) are more derived in that the interpterygoid vacuity is more fully constricted to form the canalis caroticus lateralis. Also, these taxa are more derived in that the foramen posterius canalis caroticus lateralis is located closer to the foramen posterius canalis caroticus cerebralis.

A more derived eucryptodire condition is seen in *Adocus* Cope1868 and *Judithemys* Parham and Hutchison 2003, in which the area of exposure of the internal carotid and its branches is restricted to a small foramen-like opening in the area just above the point at which the artery branches (Meylan and Gaffney 1989; Parham and Hutchison 2003). The foramen posterius canalis caroticus lateralis and the foramen posterius canalis cerebralis are visible in this

opening. In the fully derived condition, the carotid artery enters the skull through a foramen on the posterior edge of the skull and the more anterior portion of the artery, and its branches are fully encased in bone. Because the exposed portion of the carotid artery and its branches lie ventral to the basisphenoid, it is likely that restriction of the space between the foramen anterior canalis caroticus internus and the foramen canalis caroticus lateralis was a result of expansion of the pterygoid, rather than the parasphenoid portion of the basisphenoid (Sterli et al. 2010).

## The "Basipterygoid Process" in Basal Eucryptodires

A separate question of significance for interpreting the early evolution of the basicranial region in eucryptodires is the development of the "basipterygoid process." This structure was first documented in *Pleurosternon* by Evans and Kemp (1975) and subsequently recognized in *Glyptops* by Gaffney (1979a). It can also be recognized in *Chubutemys* (Gaffney et al. 2007, Fig. 4). In eucryptodires from Asia, this structure

is present in *Sinemys* (Fig. 10.16c) and *Ordosemys* (Fig. 10.16f), as well as *Xinjiangchelys radiplicatoides* (Fig. 10.16b) and *Annemys* sp. (Fig. 10.16d) as described above. In these xinjiangchelyids and sinemydids/macrobaenids from Asia, the "basipterygoid process" is a large and obvious feature of the basisphenoid. The position of this process relative to the reduced interpterygoid vacuities in *X. radiplicatoides* and *Chubutemys* is consistent with this structure being correctly identified as the basipterygoid process. Gaffney (1979a) noted that its position relative to the dorsum sellae and foramen anterius canalis carotici interni differs from that in primitive reptiles. In primitive reptiles, the basipterygoid process is anterior to these structures, whereas the process that Evans and Kemp (1975) identified as the basipterygoid process is posterior to the same structures. However, it was subsequently recognized that an undoubted basipterygoid process is present in the primitive turtle *Proganochelys* (Gaffney 1990). In *Proganochelys* the basipterygoid process is located posterior to the dorsum sellae (see Gaffney 1990, Fig. 45). Thus, the unusual position of the basipterygoid process in *Proganochelys* can be interpreted as a feature of turtles that is retained in basal cryptodires and the "basipterygoid process" is correctly interpreted as homologous with the basipterygoid process of more basal reptiles.

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