

An Upper Cretaceous lizard with a lower temporal arcade

Jun-chang Lü · Shu-an Ji · Zhi-ming Dong ·
Xiao-chun Wu

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Abstract The reduced lower temporal arcade of the skull and the movable quadrate are the most distinctive features of squamates. Up to now, no exception has been documented for any fossil or extant squamates. We report here a new fossil lizard that possesses a complete lower temporal arcade and an unmovable quadrate. The anatomical relationships indicate that those two modifications were secondarily obtained in the new lizard. The complete lower temporal bar and the firm contact between the pterygoid and quadrate may have served as a brace to support the quadrate jaw articulation and thus prevent it from twisting anteriorly rather than posteriorly during the bite cycles. This represents an entirely new pattern of jaw muscle functions within the Squamata.

Keywords Squamate · Lizard · Upper Cretaceous · Henan · China

Introduction

Squamata (including lizards, snakes, and legless lizards) form a large group of the Diapsida (also including dinosaurs (plus birds), crocodiles, and pterosaurs). All fossil or extant squamates have an incomplete or totally missing lower temporal arcade and a quadrate potentially movable (streptostylic) relative to the skull and mandible (Frazzetta 1962; Rieppel 1978; Carroll 1988). It has been documented that the mandible protracts anteriorly at the beginning of the bite cycles and retracts posteriorly at the end of the cycles in many lizards (Throckmorton 1976, 1980; Smith 1980, 1982; Herrel and De Vree 1999; Herrel et al. 1998, 1999; Metzger 2002) because strong jaw ligaments connecting the jugal and quadrate or the surangular of the lower jaw prevent the mandible from retracting posteriorly when the jaws open (Throckmorton 1976, 1980; Iordansky 1996) and because the M. pterygoideus atypicus (MPTA) or the anterior portion of the M. pterygoideus (APMP) is entirely lost (Oelrich 1956, Haas 1973), which would make the anterior protraction of the mandible impossible at the beginning of the bite cycles if the muscle were present (Wu 2003). It has been recently well demonstrated that the mandible does not have such a fore–aft motion during the bite cycles in many lizards; this is because the quadrate is stabilized by the jaw ligaments in those lizards (De Vree and Gans 1987; Herrel et al. 1998; Metzger 2002). A new fossil lizard, *Tianyusaurus zhengi* gen. et sp. nov., that was recently discovered from China possessed a complete lower temporal arcade and an essentially unmovable quadrate. This is the first squamate with such a morphotype, which is superficially similar to that of *Sphenodon*, the only living taxon of the Rhynchocephalia (Carroll 1985; Whiteside 1986; Wu 1994, 2003) and indicates a new pattern of the jaw muscle function within the Squamata.

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J.-c. Lü · S.-a. Ji
Geological Institute, Chinese Academy of Geological Sciences,
26 Baiwanzhuang Road,
Beijing 100037, People's Republic of China

Z.-m. Dong
Institute of Vertebrate Paleontology and Paleoanthropology,
Chinese Academy of Sciences,
P.O. Box 643, Beijing 100044, People's Republic of China

X.-c. Wu (✉)
Earth Science, Canadian Museum of Nature,
PO Box 3443 STN 'D', Ottawa ON K1P 6P4, Canada
e-mail: xcwu@mus-nature.ca

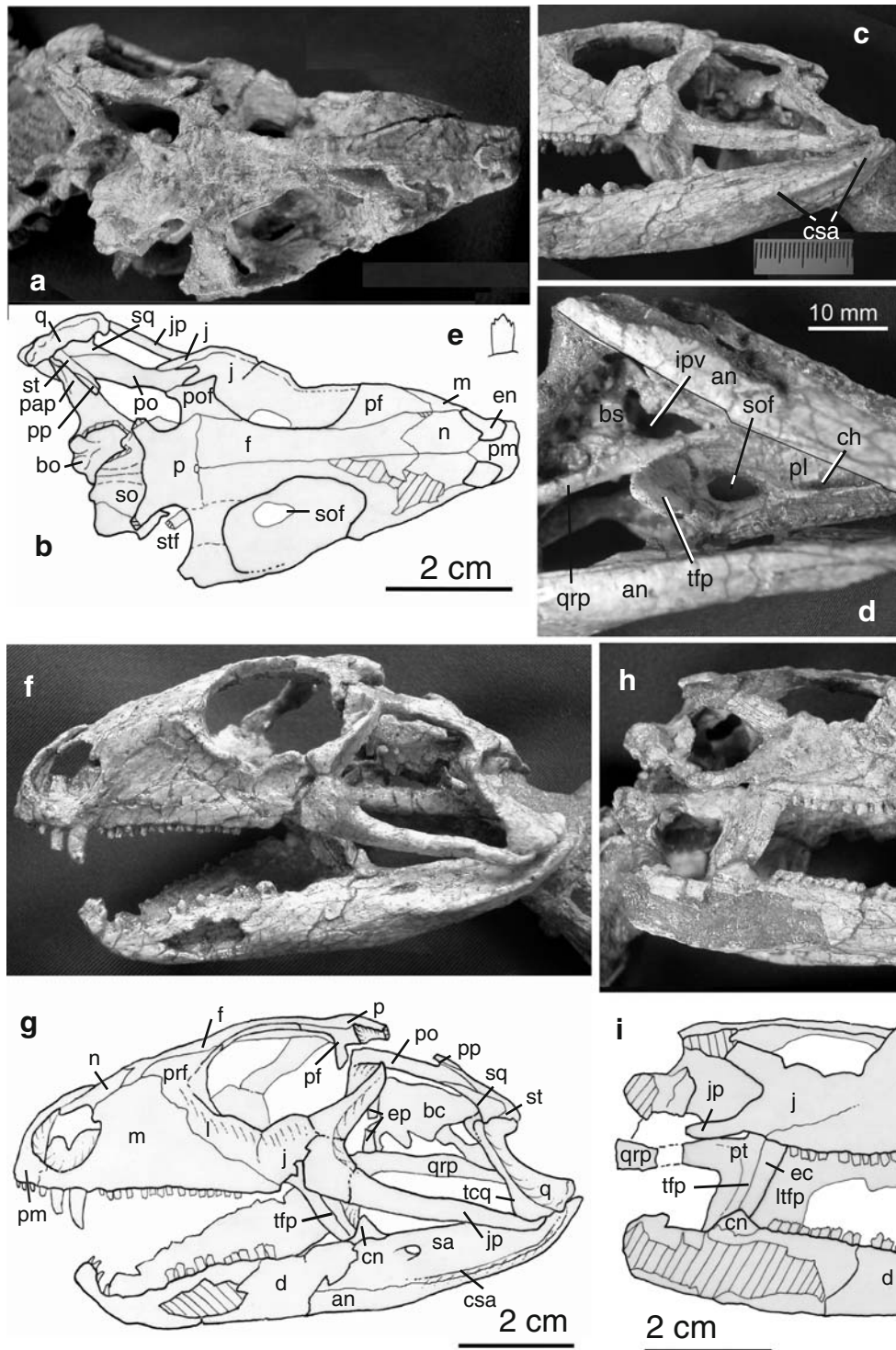
Description of specimen

Etymology

Taxonomy

Generic name is derived from “Tianyu,” the name of the museum in which the specimen is housed; the specific name is in honor of Mr. Xiao-ting Zheng, the director of the museum.

Squamata Merrem, 1820
T. zhengi gen. et sp. nov.



Holotype

Shandong Tianyu Natural Museum-05-f702 (Pingyian, Shandong Province, China), a skull and mandible articulated with the first eight cervical vertebrae and the nearly complete pectoral girdles

Locality and horizon

Near Qiupa, Luanchuan Basin, Henan Province, the Late Cretaceous Qiupa Formation

Diagnosis

A medium-sized squamate, with a skull about 67 mm long along the dorsal midline, differing from all other squamates in the following combination of derived characters: elongate posterior process of jugal forming complete lower temporal arcade; transverse flange of pterygoid extremely large; lateral surface of posterior portion of mandible strongly arched to form a pronounced longitudinal ridge on surangular; pterygoids meeting each other anteriorly; tympanic crest of quadrate strong, with broadened ventral end; third maxillary tooth large, caniniform; and clavicle with greatly expanded lateral end.

Description

T. zhengi is referred to the Squamata because it shares with the members of the latter a set of diagnostic features (see the caption of Fig. 1). The phylogenetic position of *T. zhengi* within the Squamata awaits detailed study of the specimen although the heterodont dentition, nearly vertically oriented maxilla, and large postorbital forming the entire lateral margin of the supratemporal fenestra suggest a close relationship with the Teiidae (Estes 1983). It is easily distinguishable from other known squamates in that the lower temporal arcade is complete, the lateral surface of the surangular strongly arched to form a pronounced longitudinal ridge, and the pterygoid flange is extremely large (Fig. 1).

The large, nearly round external nares face laterally. The oval orbit faces more dorsally than laterally. The small supratemporal fenestra (incomplete) is obliquely oriented. The large lower temporal fenestra is much broader ventrally than dorsally. The posttemporal fenestra is dorsoventrally shallow. The snout is box like and slightly shorter than the rest of the skull, and the postorbital region of the skull is evidently expanded laterally. The interorbital region is narrower than the region between the supratemporal fenestrae. The premaxillae and parietals are fused. In lateral view, the premaxillary–maxillary suture is partly traceable. The vertically oriented maxilla has a broad dorsal process. The large prefrontal–lacrimal complex has a plate-like ventral process contacting the palate. The postorbital, separate from the postfrontal, is very elongate, well beyond the supratemporal fenestra. The lateral margin of the orbit is dorsoventrally broad. The jugal has an elongate, bar-like posterior process which is bulged laterally and extends posteriorly to underlie the distolateral surface of the tympanic crest of the quadrate. The quadratojugal is entirely reduced as in other squamates. The quadrate is characterized by a thickened tympanic crest on the lateral side and a large lappet-like process on the medial side. The lappet-like process (dorsally incomplete) is tightly articulated with the quadrate ramus of the pterygoid (Fig. 2a), which, with the complete lower temporal arcade, firmly anchors the quadrate. In dorsal view, the small squamosal has a peg-like lateral process fitting into the dorsal notch of the quadrate. The strap-like supratemporal enters the supratemporal fenestra. In palatal view, the pterygoids meet each other along the midline anterior to the narrow interpterygoid vacuity and are separated from the vomers anteriorly by the palatines. The pterygoid flange, missing the distal tip, is very large, bending downward and slightly backward (Figs. 1c,f–i,f; 2c,d). It differs from that of other diapsid reptiles such as *Sphenodon*, crocodiles, or fossil *Youngina* (see Figs. 12B, C; 16A, G in Wu 2003) in that it

◀ **Fig. 1** The skull and mandible of *T. zhengi* in dorsal (a, b), lateral (c, i), ventral (d), lateral and slightly dorsal (f, g), and posterior (h) views. e Outline of a postconical tooth (not to scale). It was excavated from the Qiupa Formation of the Upper Cretaceous (Bureau of Geology and Mineral Resources of Henan Province 1989) in the Luanchuan Basin, Henan, China. It is a squamate based on the possession of the following character states: reduced size of nasals with a width not as broad as distance across conjoined nares; frontoparietal suture more or less transverse in dorsal view and broader than nasofrontal suture; supratemporal displaced to a deep position, wrapping around ventral surface of parietal and developed prominently on anterior face of supratemporal process of parietal; paroccipital process expanded distally and taking part in support of quadrate dorsally, rather than being a simple contact of roof bones; loss of descending ramus of squamosal; quadrate notch on dorsal surface of quadrate head for a peg-like process of squamosal; columelliform epipterygoid with a narrow base, not contacting quadrate; quadratojugal and quadrate foramen absent, and coronoid eminence formed uniquely by coronoid bone (Estes et al. 1988; Gauthier et al. 1988). Abbreviations: *an* angular, *bc* braincase, *bo* basioccipital, *bs* basisphenoid, *ch* choana, *cn* coronoid, *csa* crest on surangular, *d* dentary, *ec* ectopterygoid, *ep* epipterygoid, *f* frontal, *ipv* interpterygoid vacuity, *j* jugal, *jp* posterior process of jugal, *m* maxilla, *n* nasal, *p* parietal, *pap* paroccipital process, *pf* prefrontal, *pl* palatine, *pm* premaxilla, *po* postorbital, *pof* postfrontal, *pp* posterior process of parietal, *q* quadrate, *qrp* quadrate ramus of pterygoid, *so* supraoccipital, *sof* suborbital fenestra, *sq* squamosal, *st* supratemporal, *tcq* tympanic crest of quadrate, *tff* transverse flange of pterygoid

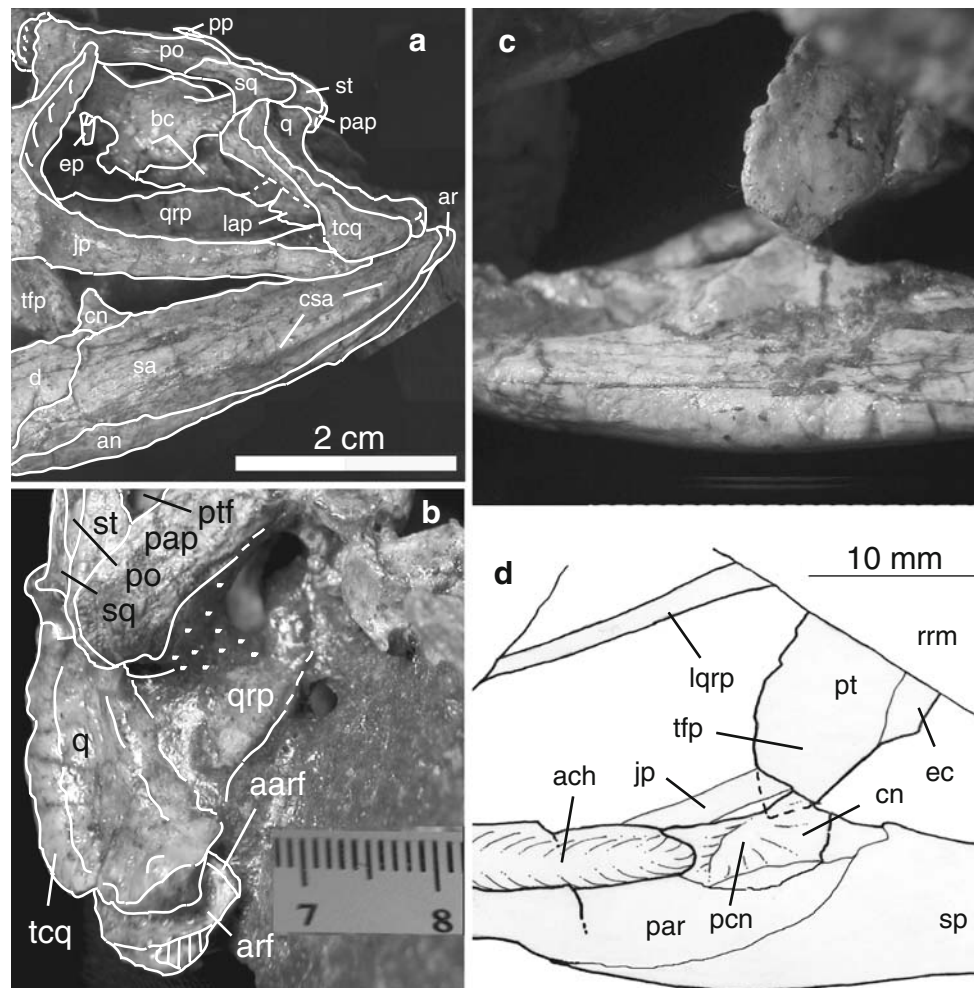


Fig. 2 Regional details of the skull and mandible of *T. zhengi*. **a** Right temporal region in lateral view. **b** Right side of the skull and mandible in posterior view. **c, d** The posterior portion of the left ramus of the mandible and the transverse flange of the left pterygoid in medial view. It is well documented that the pterygoid flange serves as a pulley for the APMP or the MPTA in crocodiles and *Sphenodon* (Haas 1973, Gorniak et al. 1982, Cong et al. 1988, Wu 2003). Such a pterygoid flange is dorsoventrally flat and transversely broad, with a trunked distal margin and a thickened lateral margin terminated by a distolateral tip (for the insertion of the lateral part of the MPTT) in nonlizard diapsids, such as crocodiles, *Sphenodon*, and fossil *Youngina* (see Figs. 11–9, 11–17 in Carroll 1988; Figs. 7, 8a, 12, 16 in Wu 2003). As described in the text, the large pterygoid flange of *T. zhengi*

differs in detail from that of nonlizard diapsid reptiles. It is a twisted triangular plate, with a pointed distal end; it has a thinned medial margin and lacks a thickened distolateral tip (Figs. 1d, 2c, d). Such a pterygoid flange must have had a different function and probably just served for the insertion of the MPTT as in other lizards (such as some chamaeleonids). The large size of the flange may simply indicate a big MPTT rather than the presence of the MPTA in *T. zhengi*. Abbreviations as in Figs. 1 and 2 plus *aarf* anterior edge of articular fossa, *ach* adductor fossa, *ar* articular, *arf* articular fossa, *lap*, lappet-like process of quadrate, *larp* quadrate ramus of left pterygoid, *par* prearticular, *pcn* prominence on medial surface of coronoid, *ptf* posttemporal fenestra, *rrm* eight ramus of mandible, *sp* splenial

is a twisted triangular plate, with the medial margin blade-like and the lateral margin proximally very thick but distally thin (see the caption of Fig. 2 for further comparison). The large pterygoid flange suggests that the new lizard may have had a large *M. pterygoideus typicus* (MPTT) in life. The elongate quadrate ramus of the pterygoid extends posteriorly to overlap the large lappet-like process of the quadrate (Fig. 2b). The ectopterygoid has an elongate anterolateral process and a pronounced posteromedial process bending downward along the prox-

imal half of the lateral side of the pterygoid flange. The small suborbital fenestra is longitudinally oval, enclosed by the palatine, pterygoid, and ectopterygoid. The preserved ventral half of the eipterygoid is columelliform, with its slightly expanded ventral end sitting on the dorsal surface of the pterygoid. The braincase is damaged. The preserved part indicates that the supraoccipital bears a pronounced median ridge. The preserved left paroccipital process is short and robust; its distal end is dorsoventrally expanded and meets the dorsal head of the quadrate. The preserved

left prootic shows a short but broad supratrigeminal process. The preserved basioccipital shows the inner surface, the part of the braincase floor. The ventral surface of the basisphenoid is concave, with a pair of the short and stout basipterygoid processes. The parabasisphenoid process is broken away.

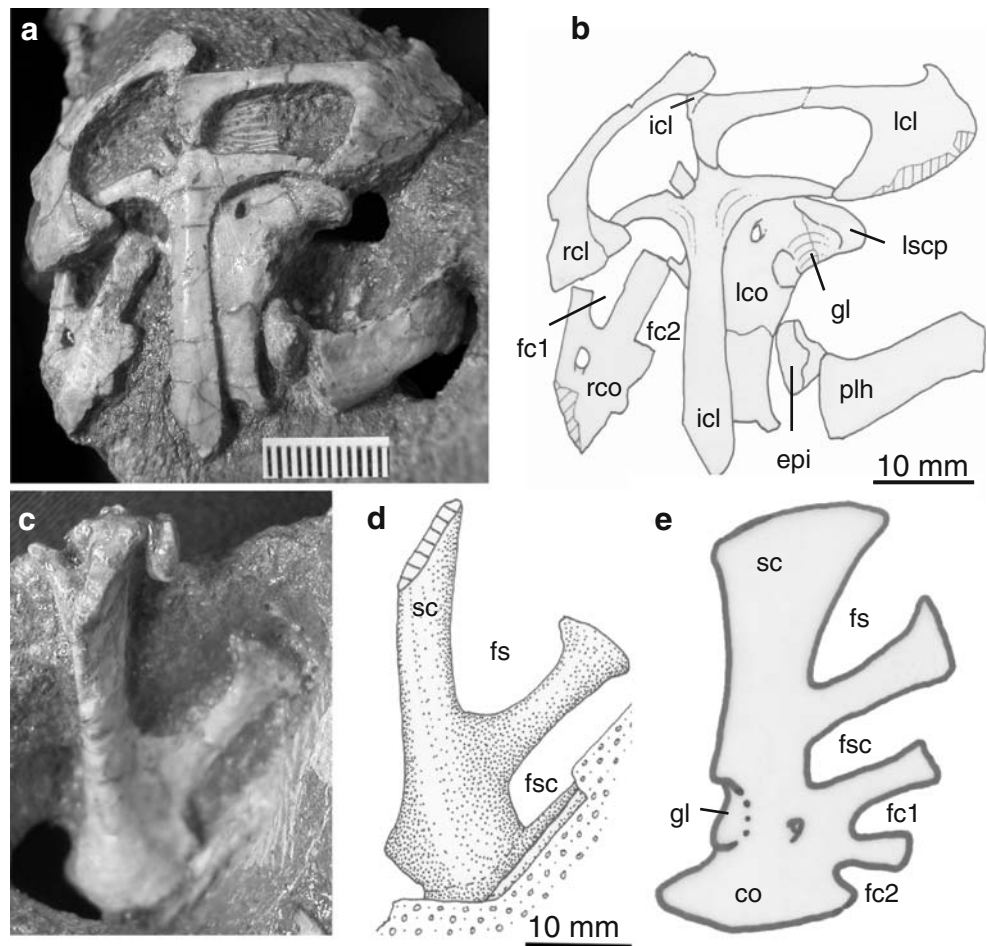
The dentary is short, slightly over the half of the total length of the mandible, and laterally bowed. The postdentary portion of the mandible is strongly arched posterior to the small coronoid eminence and forms a pronounced, longitudinally oriented ridge, which divides the external surface of the posterior portion of the mandible into a dorsolaterally faced upper portion and a ventrolaterally faced lower portion. Consequently, the dorsal margin of the mandible in this area is well medial in position to the bulged lower temporal arcade. In this way, the external surface of the mandible separately provides an area for the lateral attachment of the superficial layer of the *M. adductor mandibulae externus* (MAMES) dorsal to the ridge and for the insertion of the MPTT ventral to the ridge (Figs. 1c,f,g; 2a) as in other lizards. The pronounced ridge reflects that the MAMES and MPTT may have been very large in the new lizard. The surangular extends posteriorly to a level just lateral to the

articular fossa while the angular extends further posteriorly. The articular is partly exposed in posteroventral view (Fig. 2a). The mandibular fossa has a raised anterior border but posteriorly incomplete because of damage (Fig. 2b). In medial view, the large splenial enters the mandibular symphysis anteriorly. The prearticular is broad anteriorly, forming the lower margin of the large and deep adductor chamber (Fig. 2c,d). There is a prominence, extending obliquely on the medial surface of the coronoid, which may have been an insertion scar of the *M. pseudotemporalis* and indicates that the muscle was probably large in the new lizard.

The pleurodont dentition is heterodont (Fig. 1c,f–i). The premaxillary teeth are tiny and pointed. The first three maxillary teeth are conical and the third is large and caniniform. The remaining maxillary teeth are much smaller and uniform in morphology; a newly complete postconical tooth shows that crowns have a slightly narrow base and a serrated tip with five denticles (Fig. 1e). The first three or four dentary teeth are conical too, larger than the premaxillary teeth. The remaining dentary teeth are similar to the postconical teeth of the maxilla in both size and morphology.

The nearly complete cervical vertebrae show procoelous centra, with no foramina on the ventral surface. Among the

Fig. 3 Pectoral girdle of *T. zhengi*. **a, b** Girdle elements in ventral views. **c, d** The left scapula in posteromedial view. **e** The schematic outline of the right scapulocoracoid in lateral view. Abbreviations: *co* coracoid, *epi* epiphysis, *fc1*, *fc2* fenestrations 1 and 2 in coracoid, *fs* fenestration of scapular, *fsc* fenestration of scapulocoracoid, *gl*, glenoid, *icl* interclavicle, *lcl* left clavicle, *lco* left coracoid, *lscp* left scapulocoracoid, *rcl* right clavicle, *rco* right coracoid, *plh* proximal part of left humerus, *sc* scapula



elements of the pectoral girdle, the clavicle is most peculiar in having a greatly expanded lateral end (Fig. 3a,b). The interclavicle is typically cross shaped, with an anterior process fairly long and an elongate shaft which broadens distally before terminating. Its transverse process forms, with the clavicle, a large fenestra. The scapula–coracoid complex is partly covered by the interclavicle on the one side or incomplete on the other. As reconstructed on the basis of the preserved parts on both sides, there have been four embayments along the anterior margin of the complex (Fig. 3c–e).

Discussion

The most striking specializations of *T. zhengi* are the complete lower temporal arcade and the unmovable quadrate. With these two structures, the skull of the new lizard appears morphologically similar to that of other diapsid reptiles such as *Sphenodon*. However, this similarity is superficial when compared in detail. The complete lower temporal arcade is formed by the posterior process of the jugal and the anterior process of the quadratojugal in a typical diapsid reptile (a primitive condition) while it is formed by the elongate posterior process of the jugal that articulates the descending process of the squamosal and quadratojugal in *Sphenodon* (a derived condition). In *T. zhengi*, it is formed by the elongate posterior process of the jugal that contacts the quadrate. Although there is no way to determine whether the posterior process of the jugal would be the regrowing of the process once reduced or derived from the ossification of the quadratojugal ligament as seen in extant lizards (such as a scincomorph lizard, *Cordylus cordylus* (see Fig. 1b in Iordansky 1996)), it represents a new morphotype entirely different from the aforementioned two types. The unmovable quadrate is fixed medially by the extensive contact of the large pterygoid ramus with the quadrate ramus of the pterygoid in *Sphenodon* and other diapsid reptiles (a primitive condition). The pterygoid ramus of the quadrate was reduced into a lappet-like process or entirely lost and the quadrate and pterygoid is connected through a ligament or soft tissue in lizards (a derived condition), which is one of the preconditions for a movable quadrate. In *T. zhengi*, the lappet-like process is relatively much larger than in other lizards and appears to be tightly overlapped by the quadrate ramus of the pterygoid (Fig. 2a). Therefore, both sides of the quadrate are fixed in the new lizard although not as rigidly as in *Sphenodon* and other diapsids. Apart from the complete lower temporal arcade and the fixed quadrate, the anatomy of the temporal region in *T. zhengi* changed little from that in other lizards.

Whether the lower temporal arcade is complete or not and whether the quadrate is movable or not is important to the jaw muscle function of diapsid reptiles including lizards (Rieppel 1978, Rieppel and Gronowski 1981; Wu 2003). As mentioned earlier, the mandible protracts first and then retracts during the bite cycles in many lizards, which relies on anatomical specializations of the temporal region of the skull: the reduction of the lower temporal arcade and the development of a movable quadrate. The reduction of the lower temporal arcade allowed the MAMES to insert onto the external surface of the jaw, and the loss of the quadratojugal, the descending process of the squamosal, and the pterygoid ramus of the quadrate led to a quadrate that can or is potentially able to rotate anteroposteriorly relative to the skull. On the other hand, the quadrate keeps static during the bite cycles in some other lizards (such as *Iguana iguana*, *Ploceoderma (Agama) stellio*, helodermatids) although the bone is potentially rotatable backwards in those lizards (Throckmorton 1976, Herrel et al. 1998, Metzger 2002). To prevent the quadrate from the backward rotation, the jaw ligaments, such as the jugomandibular ligament and quadratojugal ligament, played an important role in balancing the acting forces of the jaw adductor muscles during the bite cycles (Herrel et al. 1998). When compared with those lizards, *T. zhengi* may have used the complete lower temporal arcade, together with the firm pterygoid–quadrate contact, to act as a quadrate stabilizer. However, the way to stabilize the quadrate in *T. zhengi* is different from that in those lizards. In the latter lizards, the ligaments provides tension to prevent the quadrate jaw articulation from twisting backwards during the bite cycles while in the former lizard, the solid contacts of the lower temporal bar and the pterygoid with the quadrate provide compression to prevent the quadrate jaw articulation from twisting anteriorly rather than posteriorly. This shows a different pattern of the jaw muscle function from that of all other lizards so far known.

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