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**PALEONTOLOGY**

# A new species of *Darwinopterus* (Wukongopteridae, Pterosauria) from western Liaoning provides some new information on the ontogeny of this clade

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**Abstract:** The Wukongopteridae is an important pterosaur clade from the Yanliao Biota, combining features of basal and derived pterosaurs. So far, the Wukongopteridae consists of five species divided into three genera: *Wukongopterus lii*, *Darwinopterus modularis*, *Darwinopterus linglongtaensis*, *Darwinopterus robustodens*, and *Kunpengopterus sinensis*. Here we report a new species, *Darwinopterus camposi* sp. nov., based on an almost complete skeleton (IVPP V 17957). The new species is referred to *Darwinopterus* due to the presence of an elongated posterior region of the skull and the bony premaxillary crest that starts about the anterior margin of the nasoantorbital fenestra. It differs from all other wukongopterids by having the dorsal margin of the premaxillary crest straight, without an extensive dorsal projection and presenting a smooth lateral surface. Furthermore, *D. camposi* sp. nov. has eighteen and fourteen teeth on each side of the upper and lower jaws, respectively, and the fourth phalanx of the wing finger shorter than the first. IVPP V 17957 shows some fused postcranial bones, like the extensor tendon process to the first wing finger phalanx, but also has unfused premaxilla and frontal, which provides further information about wukongopterid ontogeny.

**Key words:** Pterosauria, Wukongopteridae, ontogeny, Yanliao Biota, Middle-Late Jurassic, China.

## INTRODUCTION

China has been a hotspot for pterosaur research for quite some time, presenting new discoveries that have fostered the study of these extinct flying reptiles. New localities were reported (e.g., Andres et al. 2010, Wang et al. 2014a, Ji 2020) and many taxa were discovered from the western Liaoning in the last decade (Cheng et al. 2012, 2015, Wang et al. 2008, 2012, 2014b, 2020, Jiang et al. 2014, Rodrigues et al. 2015, Zhang et al. 2019), some showing close relationships with faunas from other continents (e.g., Wang & Zhou 2003a, b, Rodrigues et al. 2011, Holgado et al. 2019, Kellner et al. 2019).

Among the most interesting discoveries are the specimens referred to the Yanliao Biota, which were distributed in almost the same regions as the Jehol Biota, but are older in age being regarded as the Middle to Late Jurassic (e.g., Zhou & Wang 2010, Cheng 2013, Sullivan et al. 2014, Wang et al. 2014c, Cheng et al. 2017a).

Perhaps the most conspicuous pterosaurs from the Yanliao Biota are the Wukongopteridae (Wang et al. 2009, 2010, 2015, Lü et al. 2010, 2011a, b, Cheng 2013, Cheng et al. 2016, 2017a, b, Jiang et al. 2021), which show a combination of features of non-pterodactyloid and pterodactyloid pterosaurs (Wang et al. 2009, Lü et al. 2010).

So far, three genera and five species have been described, including *Wukongopterus lii*, *Darwinopterus modularis*, *Darwinopterus linglongtaensis*, *Darwinopterus robustodens*, and *Kunpengopterus sinensis*, as well as an unnamed wukongopterid specimen (Wang et al. 2009, 2010, 2015, Lü et al. 2010, 2011a, b, Cheng et al. 2016, 2017a, b). All these specimens were collected from the Middle to Upper Jurassic Tiaojishan Formation in Linglongta, Jianchang (e.g., Zhou & Wang 2010, Cheng 2013, Sullivan et al. 2014, Wang et al. 2014c, Cheng et al. 2017a, Jiang et al. 2021). Except the materials from China, some potential members of this clade were found in Europe (Martill & Etches 2013, Martin-Silverstone et al. 2024).

Here we report a new wukongopterid species, *Darwinopterus camposi* sp. nov., discovered from the Tiaojishan Formation in Linglongta, which provides new information regarding the Wukongopteridae, such as the complete teeth series and the fusion of some skull elements.

Institutional Abbreviations: HGM-Henan Geological Museum, Zhengzhou, Henan Province, China; IVPP-Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; ZMNH-Zhejiang Museum of Natural History, Hangzhou, Zhejiang Province, China.

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## SYSTEMATIC PALEONTOLOGY

**Pterosauria** Kaup 1834

**Wukongopteridae** Wang, Kellner, Jiang and Meng 2009

***Darwinopterus*** Lü, Unwin, Jin, Liu and Ji 2010

***Darwinopterus camposi* sp. nov.**

ZooBank Life Science Identifier (LSID) - urn: lsid:zoobank.org: act:D3F60252-DF79-4254-ADA1-9C42708F429C.

Etymology: In honor to Dr. Diogenes de Almeida Campos, an important geologist and vertebrate paleontologist who has contributed to pterosaur research and the cooperation between Brazilian and Chinese paleontologists.

Holotype: Almost complete skeleton lacking the distal end of the tail and hindlimbs, housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, under the number IVPP V 17957 (Figs. 1-4).

Locality and horizon: Linglongta, Jianchang County, Liaoning, China, Tiaojishan Formation, Middle to Late Jurassic (Zhou & Wang 2010, Cheng 2013, Sullivan et al. 2014, Wang et al. 2014c, Jiang et al. 2021).

Diagnosis: *Darwinopterus* with the following combination of characters that distinguishes it from other members of this clade (autapomorphies are marked with an asterisk): premaxillary crest starting close to the anterior margin of the nasoantorbital fenestra; dorsal margin of premaxillary crest almost straight and lacking an extensive dorsal projection*; lateral surface of premaxillary crest smooth*; eighteen and fourteen teeth on each side of upper and lower jaws, respectively*; the fourth phalanx of the wing finger shorter than the first*.

## DESCRIPTION AND COMPARISON

The holotype of *D. camposi* sp. nov. is a middle-sized wukongopterid with an estimated wingspan of 75 cm, preserved in a slab of grey-green shale (Fig. 1). The specimen is composed of an almost complete skeleton with the skull and the lower jaw, including several displaced cervical vertebrae, articulated dorsal vertebrae, sacral vertebrae, anterior portion of the tail, partial pectoral girdle, all elements of the forelimbs

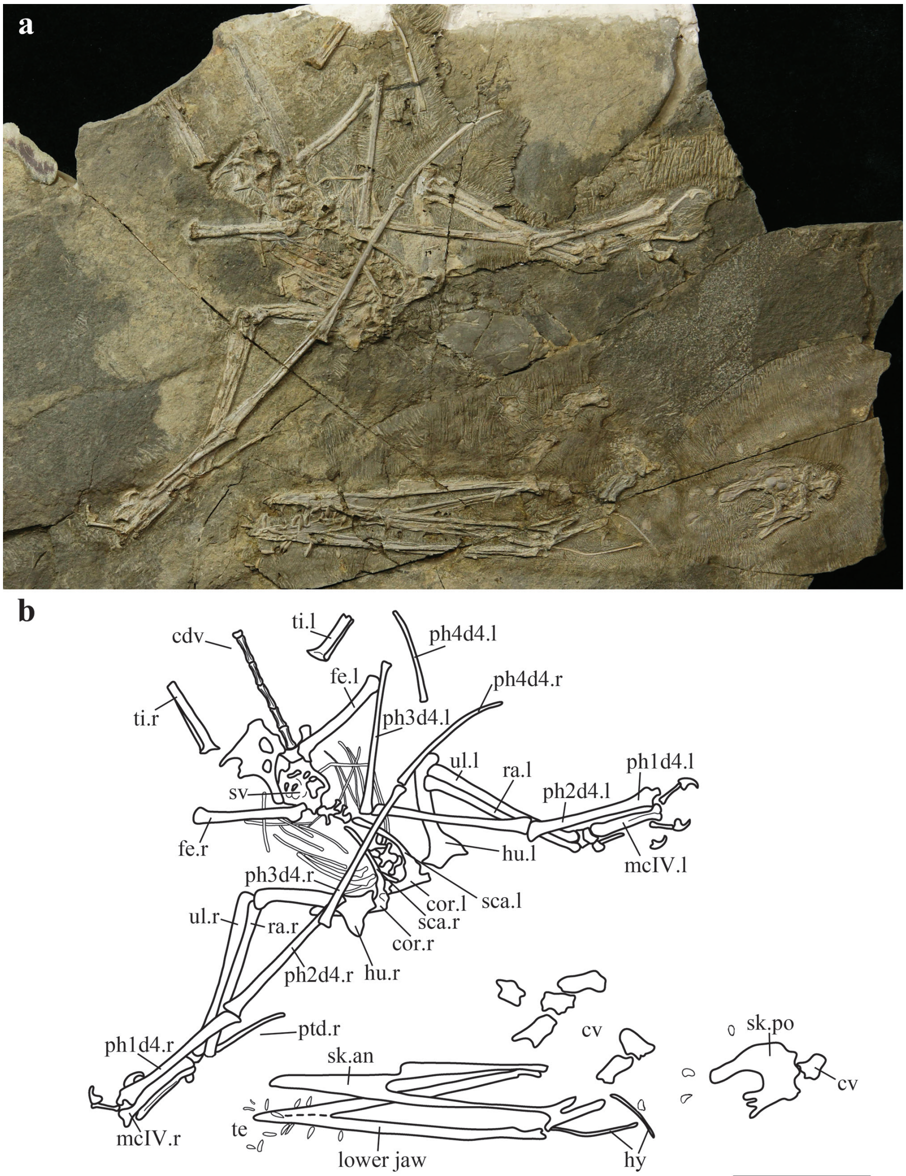


**Figure 1.** The holotype of *Darwinopterus camposi* sp. nov. (IVPP V 17957). (a) Photo and (b) line drawing of the whole skeleton. Scale bar: 50 mm. Abbreviations: cdv, caudal vertebra; cor, coracoid; cv, cervical vertebra; fe, femur; hu, humerus; hy, hyoid; l, left; mcIV, metacarpal IV; ph1-4d4, first to fourth wing phalanx; ptd, pteroid; r, right; ra, radius; sca, scapula; sk.an, anterior region of skull; sk.po, posterior region of skull; sv, sacral vertebra; te, teeth; ti, tibia; ul, ulna.

from both sides, incomplete pelvic girdle, both femora, and both tibiae (lacking the distal ends).

The skull is separated at the orbit, where some bones are broken or missing (Fig. 2). It is preserved in left lateral view. Several small pieces of bones supposed to be the elements of the sclerotic ring are present around the position of the orbit. The posterior part of the skull is elongated, a typical feature of *Darwinopterus* and is flat as that of *D. linglongtaensis*, which is different from *D. modularis*, *D. robustodens*, and *K. sinensis* (Lü et al. 2010, 2011b, Wang et al. 2010, Cheng et al. 2017a).

The premaxilla and maxilla are fused. The premaxilla bears a crest extending backwards, diagnostic for *Darwinopterus*, and differs from the flat dorsal margin of the skull of *K. sinensis* (Lü et al. 2010, 2011b, Wang et al. 2010, Cheng et al. 2017a) and also from IVPP V 17959. The latter is an undetermined wukongopterid, in which the cranial crest is confined to the anterior portion of skull (Cheng et al. 2016). The premaxillary crest

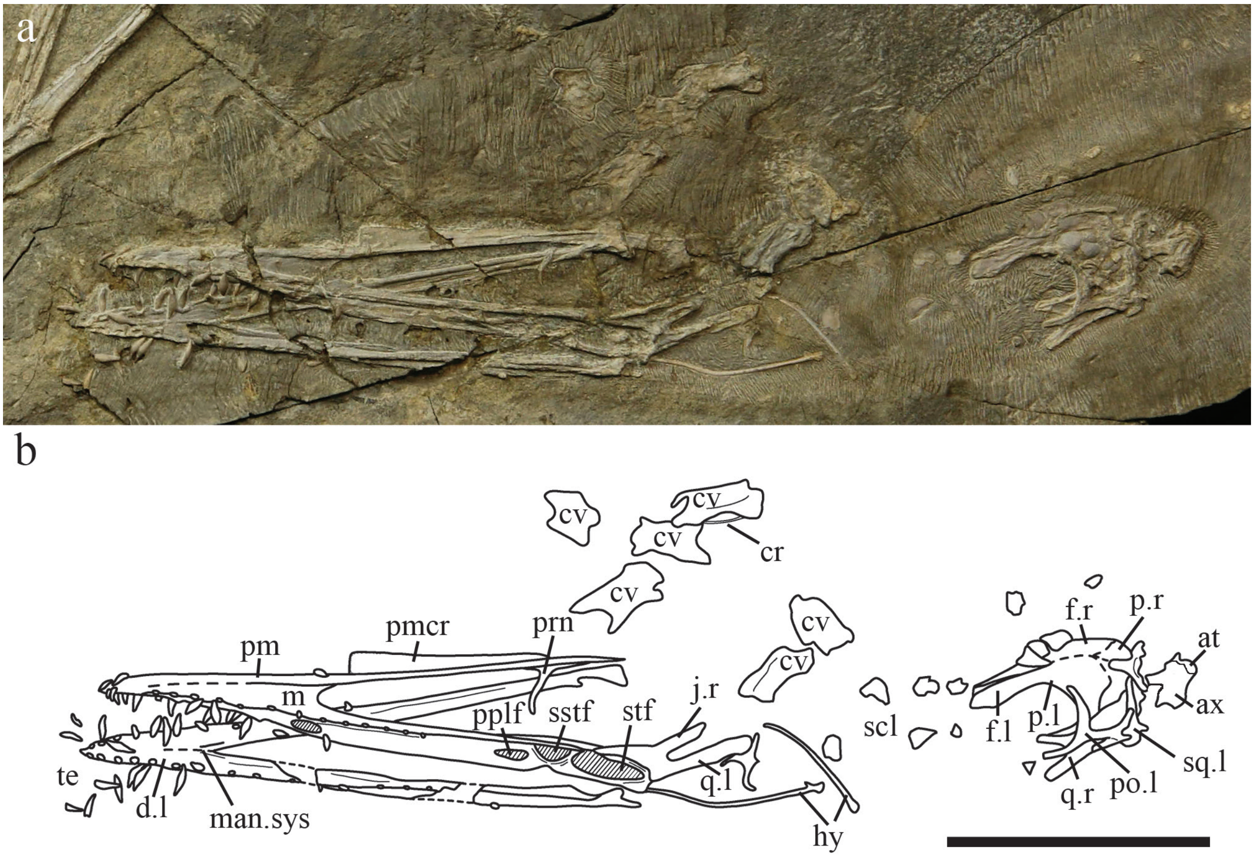


**Figure 2. Details of the skull of the holotype of *Darwinopterus camposi* sp. nov. (IVPP V 17957). (a) Close up of the skull. (b) Line drawing of the skull. Scale bar: 50 mm. Abbreviations: at, atlas; ax, axis; cr, cervical rib; cv, cervical vertebra; d, dentary; f, frontal; hy, hyoid; j, jugal; l, left; m, maxilla; man.sys, mandibular symphysis; p, parietal; pm, premaxilla; pmcr, premaxillary crest; po, postorbital; pplf, postpalatine fenestra; prn, nasal process; q, quadrate; r, right; scl, sclerotic ring; sq, squamosal; sstf, second subtemporal fenestra; stf, subtemporal fenestra; te, teeth.**

starts posterior to the anterior margin of the nasoantorbital fenestra, has a smooth lateral surface of the crest, and shows a straight dorsal margin. The anterior portion of the crest lacks an extensive dorsal projection. These features distinguish *D. camposi* sp. nov. from other members of this genus (Lü et al. 2010, 2011b, Wang et al. 2010, see Cheng et al. 2017b for a detailed comparison on the cranial crest of the Wukongopteridae).

Due to poor preservation, bones forming the orbit and posterior region of the skull are displaced, broken, or missing (Fig. 2). The nasal process is directed anteroventrally, differing from IVPP V 17959 (Cheng et al. 2016). The distal end of the nasal process is slightly curved, which might be caused due to taphonomy. No foramen can be identified on the nasal process. Only a partial portion of the right jugal is preserved. The maxillary process of jugal is straight and fused with the maxilla, which is thinner than the one of *D. linglongtaensis* (Wang et al. 2010). The postorbital process of the jugal is inclined backwards, which gives the orbit a rounded posteroventral shape. The frontals form the largest part of the skull roof and the dorsal margin of the orbit. The postorbital takes part in the orbit, and participates in the upper and the lower temporal fenestrae. The upper temporal fenestra is oblate. The lower temporal fenestra

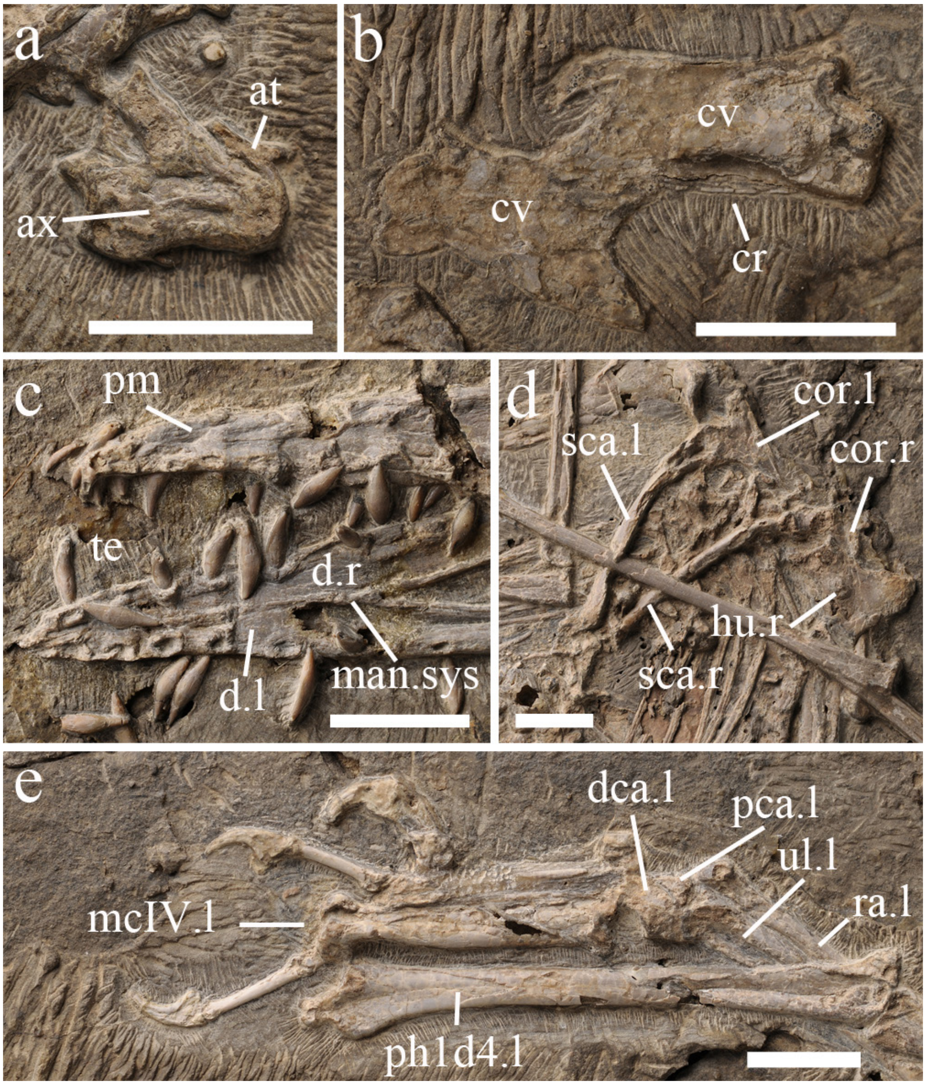


**Figure 3.** **Details of the holotype of *Darwinopterus camposi* sp. nov. (IVPP V 17957). (a) Close up of the atlas and axis. (b) Close up of middle cervical vertebrae. (c) Close up of the tip of upper and lower jaws. (d) Close up of the pectoral girdle. (e) Close up of the left manus. Scale bar: 10 mm. Abbreviations: at, atlas; ax, axis; cor, coracoid; cr, cervical rib; cv, cervical vertebra; d, dentary; dca, distal syncarpal; hu, humerus; l, left; man.sys, mandibular symphysis; mcIV, metacarpal IV; pca, proximal syncarpal; ph1d4, first wing phalanx; pm, premaxilla; r, right; ra, radius; sca, scapula; te, teeth; ul, ulna.**

is elongated, with the dorsal margin wider than the ventral one. The right quadrate is exposed medially and inclined backwards for about 155° (Fig. 2).

The left portion of the palate is exposed (Fig. 2), showing that this new taxon bears a comparably larger subtemporal fenestra, located posterior to two smaller fenestrae, which might be the second subtemporal fenestra and the postpalatine fenestra (Fig. 2).

The lower jaw is exposed in dorsal view (Figs. 2, 4). At the anterior tip, a small, pointed projection can be observed that is shorter than the first lower tooth and different from the elongated anteriorly projected tip of *Rhamphorhynchus* (Wellnhofer 1991). Both mandibular rami are straight, fused anteriorly, and form an angle of 15°. The symphysis occupies less than 25% of the lower jaw length (Table I). There are no sutures to distinguish dentary, surangular, angular, or articular. One socket is present at the posterior end of lower jaw in the medial side, which is the adductor fossa. Two slender elements preserved posterior to the lower jaw are interpreted as the hyoid bones.

The holotype of *D. camposi* sp. nov. presents nearly complete teeth series (Figs. 2, 4). A few teeth were still in their alveoli and others fell

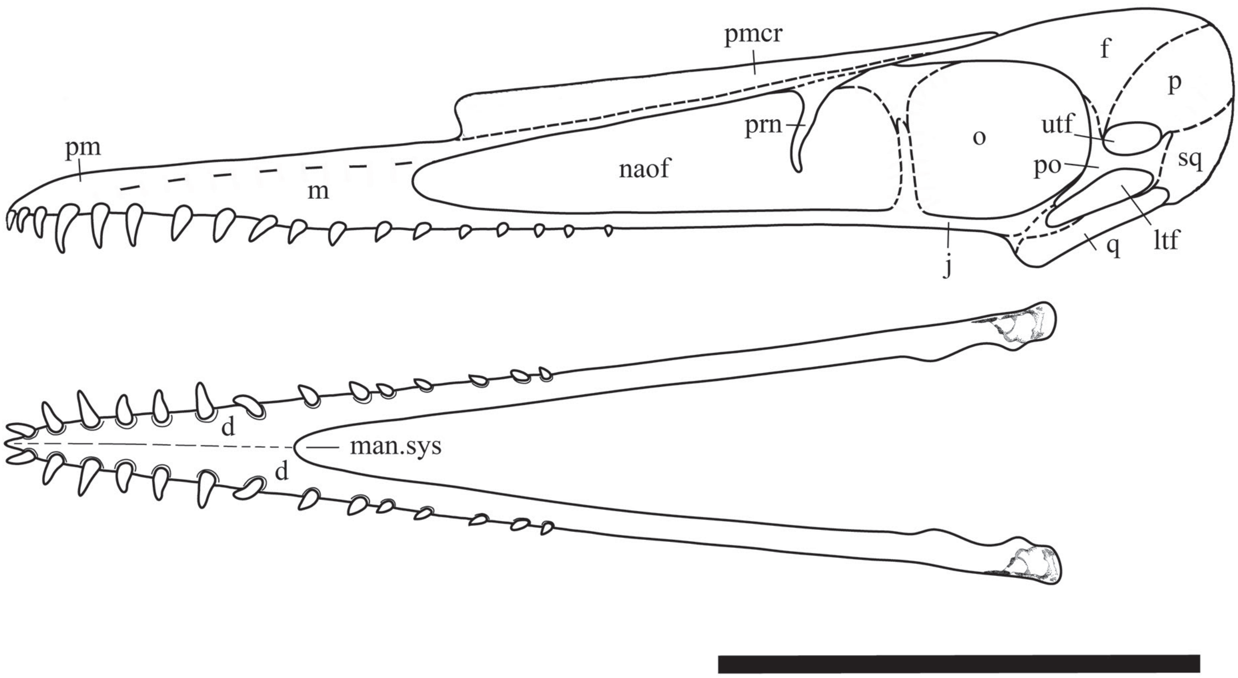


**Figure 4. The reconstruction of the skull and lower jaw of the holotype of *Darwinopterus camposi* sp. nov. (IVPP V 17957). Scale bar: 50 mm. Abbreviations: d, dentary; f, frontal; j, jugal; ltf, lower temporal fenestra; m, maxilla; man. sys, mandibular symphysis; naof, nasoantorbital fenestra; o, orbit; p, parietal; pm, premaxilla; pmcr, premaxillary crest; po, postorbital; prn, nasal process; q, quadrate; sq, squamosal; utf, upper temporal fenestra.**

out during the fossilization process, but most were preserved close to the respective alveoli. The teeth are generally short, cone-shaped, and inflated at the middle portion. The root is slightly thicker than the crown. The color of the tooth surface becomes gradually darker from the root to the tip (Fig. 3c).

Eighteen teeth and alveoli can be recognized on the left side of upper jaw (Figs. 2, 4). The 1$^{st}$ tooth is remarkably close to the 2$^{nd}$ one and much smaller than the latter. The 2$^{nd}$ tooth is subequal in size to the 3$^{rd}$ one. The 4$^{th}$ tooth is the biggest, after which upper teeth become smaller gradually posteriorly. Some anterior upper teeth, such as the 2$^{nd}$, 3$^{rd}$, 4$^{th}$ and 6$^{th}$ of the right side are still in their alveolus and almost vertically directed. The 8$^{th}$ and 9$^{th}$ right teeth are also in their original position, but inclined anteriorly. The last tooth is positioned almost under the middle part of the nasoantorbital fenestra. A total of 12 pairs of upper teeth are present anterior to the nasoantorbital fenestra. In the holotype of *W. lii* (IVPP V 15113) and in ZMNH M8802, there are 10 teeth anterior to the nasoantorbital fenestra, while in the holotype of *D. robustodens* (HGM 41HIII-0309A) there are 11. The holotype of *D. modularis* (ZMNH M8782) has been reported of having only 9 pairs of teeth under the nasoantorbital fenestra, but based on our observation, the total number is most likely 11.

On each side of the lower jaw, fourteen teeth and alveoli can be determined (Fig. 2, 4). The 1$^{st}$ pair of alveoli is close to the anterior projection of the lower jaw. The distance between the 1$^{st}$ and 2$^{nd}$ teeth is only half of that between the 2$^{nd}$ and 3$^{rd}$ ones. The space between alveoli increases after the 5$^{th}$ one to over two alveolus width, except the 10$^{th}$ and 14$^{th}$ that are quite close to the tooth in front of them. The

**Table I. Measurements of the holotype of *Darwinopterus camposi* sp. nov. (IVPP V 17957).**

| Bones | Length (mm) |
|---|---|
| Skull | 130.0 est |
| Rostrum | 40.1 |
| Lower jaw | 106.8 |
| Symphysis | 25.5 |
| Scapula | 32.3 l, 31.8 r |
| Coracoid | 28.4 r |
| Humerus | 43.6 l, 44.9 r |
| Ulna / Radius | 62.4 l, 62.8 r |
| Metacarpal IV | 26.6 l |
| 1st wing phalanx | 53.3 l, 54.1 r |
| 2nd wing phalanx | 58.6 l, 59.5 r |
| 3rd wing phalanx | 57.7 l, 58.5 r |
| 4th wing phalanx | 49.4 r |
| Femur | 42.7 l, 42.2 r |

**est: estimated; l: left; r: right.**

4th, 5th and 6th teeth on the right side are still in their alveoli and pointing laterally. The 7th pair of teeth also remains in their alveoli, but they are pointing anteriorly and are quite smaller than the 4th, 5th and 6th ones.

The postcranial elements are nearly complete and articulated, but the poor preservation limits the available information that can be retrieved from these elements (Figs. 1, 2). The atlas and axis are preserved at the right edge of the slab (Fig. 2). Both bones are connected, but show a clear suture, indicating that they are not fused. The atlas is much shorter than the axis and bears a smaller neural spine. It is worth to point out that the neural spine of the atlas shows an anterior projection (Fig. 3a), which is similar to that reported in the unnamed wukongopterid specimen IVPP V 17959 (Cheng et al. 2016).

Besides atlas and axis, six cervical vertebrae are exposed around the skull (Fig. 2). Only one of them, probably the 8th cervical element, is remarkable short and others are elongated with a length over two times of its width. One slender cervical rib can be observed associated with one elongated cervical vertebra (Figs. 2, 3b). The dorsal and sacral vertebrae are preserved underneath other bones. The five caudal vertebrae that are complete are elongated and enclosed by rod-like bony extension, formed by the zygapophyses. There are three other caudal elements, covered by bones.

The scapula and coracoid are preserved in contact, with the scapula slightly longer than the coracoid (Fig. 3d, Table I). No suture between these elements can be observed, suggesting that they are fused. The scapula bears a dorsoventrally compressed distal plate. The humerus bends anteriorly that shows a short deltopectoral crest, which is broken and placed proximally. The ulna and radius are straight and similar in length, with the radius being thicker than half the width of the ulna. Proximal and distal carpal series are fused, with the proximal syncarpal much thinner than the distal one in lateral view. The middle portion of the right pteroid is preserved, which is straight like that of *D. linglongtaensis* (Wang et al. 2010) but different from the curved one of IVPP V 17959 (Cheng et al. 2016). The left metacarpal IV shows a deep furrow between the condyles (Fig. 3e). The proximal end of both wing fingers is preserved in dorsal view. The extensor tendon process and first wing phalange are entirely fused (Fig. 3e). The first wing phalanx is shorter than the second and third ones, but longer than the fourth one, which is unique in *Darwinopterus* (Table I). The fourth wing phalange is slightly bended and showing a pointed distal end.

The pelvic girdle is badly preserved, and only fragments can be observed (Fig. 1). Both femora are straight and bear a short neck. Only the proximal parts of both tibiae are preserved.

## DISCUSSION

*D. camposi* sp. nov. is classified as a wukongopterid due to the combination of the following characters: confluent naris and antorbital fenestra, quadrate inclined backwards, elongated cervical vertebrae, reduced cervical ribs, length of the wing metacarpal about half the length of the first wing phalange, and elongated tail enclosed by rod-like bony extensions of the zygapophyses (Wang et al. 2009, 2010, Cheng et al. 2016). Furthermore, the new species is referred to *Darwinopterus* by the following combination of features: posterior region of the skull elongated, and the presence of a bony premaxillary crest that starts about the anterior margin of the nasoantorbital fenestra (Wang et al. 2010). *D. camposi* sp. nov. shows several anatomical details that distinguish it from other species of this genus, such as the straight dorsal margin of the cranial crest that starts about the anterior margin of the nasoantorbital (see Cheng et al. 2017b for a detailed comparison on the cranial crest of the Wukongopteridae), the number of teeth, and the fourth wing phalanx being shorter than the first one.

According to the ontogenetic studies done so far in Pterosauria (Bennett 1993, Kellner & Tomida 2000, Kellner et al. 2013, Kellner 2015), the holotype of *D. camposi* sp. nov. shows evidences that it might be an adult animal (at least reaching OS5), such as a fused scapula and coracoid. It also shows the extensor tendon process fused to the first phalanx of the wing finger (Figs. 3d, e).

Based on the preservation of the holotype of *D. camposi* sp. nov., we infer that the carcass was not transported for a long distance during the fossilization process or submitted to great disturbance during burial. It is interesting to point out that IVPP V 17957 has the posterior part of the skull separated from the anterior one, dividing the orbit (Fig. 2). This condition indicates that several cranial elements are not fused, such as the premaxilla and the frontal, as well as the jugal and the postorbital.

Although admittedly difficult to establish the ontogenetic sequence within pterosaurs, there is some suggestions that the skull would fuse quite early in pterosaur ontogeny (e.g., Kellner & Tomida 2000). However, regarding the postcranial elements, the fusion of the extensor tendon process is regarded to happen rather late in ontogeny (Bennett 1993, Kellner 2015). Based on the information that can be retrieved from the holotype of *D. camposi* sp. nov., there is indication that the fusion of the premaxilla and frontal might happen after the fusion of the extensor tendon process with the first wing finger phalanx. Therefore it is possible that the complete fusion of the skull elements was probably concluded extremely late during pterosaur ontogeny, or at least in some members of the Wukongopteridae.

## CONCLUSIONS

Based on a combination of distinctive anatomical features, a new species, *D. camposi* sp. nov. from the Linglongta region is established and regarded a new species of *Darwinopterus*, of the clade Wukongopteridae. Among the main features that differ the new species from other wukongopterids is the premaxillary crest that shows a quite distinct straight dorsal margin and a smooth lateral surface, the number of teeth, and the shorter fourth wing phalanx compared to the first. The skull of the holotype of *D. camposi* sp. nov. shows that some cranial elements only fuse at an extremely late stage during ontogeny. More specimens and a closer look at the fusion of bones are needed to gain a better understanding of the ontogeny of the species that make up this interesting clade of pterosaurs.

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