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Theropod teeth from the Lower Cretaceous Ilek Formation of Western Siberia, Russia

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ABSTRACT

A sample of 136 isolated theropod teeth from nine vertebrate localities within the Lower Cretaceous (Barremian-Aptian) Ilek Formation in West Siberia, Russia, can be separated into five dental morphotypes referred to five or six theropod taxa based on morphological characters. The Morphotype A includes small to large lateral teeth with relatively large distal denticles and smaller mesial denticles. Some of these teeth can be attributed to the Dromaeosauridae, while other teeth may belong to a basal member of the Tyrannosauroidea. The distinctly smaller lateral teeth referred to the Morphotype B are similar with Morphotype A in most respects but differ in the lack of mesial denticles and mesial carina, or having a lingually displaced mesial carina. These teeth may belong to juvenile individuals of the same dromaeosaurid taxon. The teeth belonging to Morphotype C also lack mesial denticles and differ from Morphotype B by a flattened area on the lingual side, which is also often present on the labial side. These teeth may belong to either Troodontidae or Microraptorinae, or to both groups. The mesial and lateral teeth of Morphotype E are characterized by unserrated mesial and distal carinae. These teeth most likely belong to a distinct taxon of Troodontidae with unserrated dentition. The teeth of the Morphotype D include mesial teeth with the mesial carina displaced lingually at various extent and denticles present on both carinae. The teeth with moderately displaced lingual carina can be referred to the same dromaeosaurid taxon, which lateral teeth represented by Morphotype A. The teeth with more displaced mesial carina and deeply U-shaped basal crown section belong to an indeterminate Tyrannosauroidea.

Key words: Cretaceous, Dinosauria, Ilek Formation, Russia, Theropoda

Зубы теропод из нижнемеловой илекской свиты в Западной Сибири, Россия

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РЕЗЮМЕ

Выборка из 136 изолированных зубов из девяти местонахождений нижнемеловой (баррем-апт) илекской свиты Западной Сибири, Россия, может быть разделена на основании морфологических признаков на пять зубных морфотипов, относящихся к пяти или шести таксонам теропод. К морфотипу A отнесены мелкие и крупные боковые зубы со сравнительно крупными дистальными зубчиками и мелкими мезиальными зубчиками. Некоторые их этих зубов могут относиться к Dromaeosauridae, другие – к базальным членам Tyrannosauroidea. Намного меньшие по размерам зубы, отнесенные к морфотипу B, в основном схожи с зубами морфотипа A, но отличаются отсутствием мезиальных зубчиков и мезиальной кариной, либо лингвально смещенной мезиальной кариной. Эти зубы могут принадлежать молодым особям того же таксона дромеозаврид. Зубы отнесенные к морфотипу C также не имеют мезиальных зубчиков и отличаются от зубов морфотипа B уплощенной площадкой на лингвальной стороне, которая также часто имеется и на лабиальной стороне. Эти зубы могут принадлежать либо Troodontidae, либо Microraptorinae, или обоим группам. Мезиальные и латеральные зубы морфотипа E характеризуются отсутствием зубчиков как на мезиальной, так и на дистальной карине. Эти зубы скорее всего принадлежат особому таксону Troodontidae с озублением без зубчиков. Зубы морфотипа D включают мезиальные зубы с мезиальной кариной смещенной лингвально в различной степени и с зубчиками на обоих каринах. Зубы с умеренно смещенной лингвальной кариной могут принадлежать тому же таксону дромеозаврид, к которому относятся боковые зубы морфотипа A. Зубы с более смещенной мезиальной кариной и U-образной формой базального сечения коронки отнесены к неопределимым Tyrannosauroidea.

Ключевые слова: меловой период, Dinosauria, илекская свита, Россия, Theropoda

INTRODUCTION

The Lower Cretaceous Ilek Formation, widely distributed in Western Siberia, Russia (Fig. 1), recently yielded an important vertebrate fauna, including fishes, amphibians, squamates, choristoderes, crocodyliforms, pterosaurs, various dinosaurs, birds, tritylodontids, and mammals (Maschenko and Lopatin 1998; Alifanov et al. 1999; Tatarinov and Maschenko 1999; Averianov and Voronkevich 2002; Maschenko et al. 2003; Averianov et al. 2005, 2015, 2017, 2018; Lopatin et al. 2005, 2009, 2010a, b; Kurochkin et al. 2011; O'Connor et al. 2014; Skutschas 2014, 2016; Averianov and Lopatin 2015; Skutschas and Vitenko 2015, 2017; Skutschas et al. 2017). Dinosaurs are represented by fragmentary remains of a titanosauriform sauropod *Sibirotitan astrosacralis*, theropods, stegosaurs, and ornithopods, as well as by several complete and well-preserved skeletons of the basal ceratopsian *Psittacosaurus sibiricus* from the Shestakovo 3 locality (Averianov et al. 2006, 2018; Lopatin et al. 2015).

The theropod skeletal remains are particularly rare and fragmentary in the Ilek Formation, represented by few caudal vertebrae and isolated pedal or manual bones. As it is often the case in Mesozoic fluvial deposits, isolated theropod teeth are, however, abundant in the screen-washing samples. Important and reliable information on the composition of the theropod assemblages can be provided based on these isolated teeth (Currie et al. 1990; Baszio 1997; Csiki and Grigorescu 1998; Sankey 2001, 2008; Rauhut 2002; Sankey et al. 2002; Smith et al. 2005; Fanti and Therrien 2007; Larson and Currie 2013; Sues and Averianov 2013; Hendrickx et al. 2015a; Larson et al. 2016). The theropod remains from the Ilek Formation have previously received a preliminary treatment. Alifanov et al. (1999) reported skeletal fragments of an indeterminate Troodontidae from Shestakovo 3 locality. Leshchinskiy et al. (2000) described some isolated teeth from Shestakovo 1 locality they assigned to an indeterminate Velociraptorinae. Averianov et al. (2004) mentioned isolated teeth they referred to cf. *Prodeinodon* (?Dromaeosauridae), a dorsal vertebra to cf. Dromaeosauridae from Shestakovo 1 locality, as well as isolated teeth ascribed to cf. *Paronychodon* from Bol'shoi Kemchug 3 locality. Averianov and Sues (2007: fig. 5A–C) figured an isolated tooth from Shestakovo 1 locality which they attribute to an indeterminate Troodontidae. Here we provide a detailed study of all available theropod teeth recovered by screen-washing from various sites within the Lower Cretaceous Ilek Formation.

Institutional abbreviations. LMCCE, Laboratory of Mesozoic and Cenozoic Continental Ecosystems, Tomsk State University, Tomsk, Russia; PM TGU, Paleontological Museum, Tomsk State University, Tomsk Russia.

GEOGRAPHIC AND GEOLOGICAL SETTINGS

Deposits of the Ilek Formation are widely spread in the south-east of West Siberia from Krasnoyarsk to Novokuznetsk in Kuznetsk, Chulym-Eniseisk, and Nazarovo depressions (Fig. 1). The time of deposition of the Ilek Formation is poorly constrained and currently estimated as Barremian-Aptian (see review in Averianov et al. 2018). The Ilek Formation overlies Jurassic deposits as well as some folded heterogeneous Paleozoic and pre-Cambrian geological structures. The Ilek Formation consists of poorly lithified greenish-yellow sandstones, light greenish-grey siltstones and reddish-brown argillites of fluvial-lacustrine and fluvial-deltaic genesis. The natural outcrops of the

Fig. 1. Map of Russia, showing position of the inset B, and distribution of the Ilek Formation (green) in the study area (B), with position of the vertebrate localities: 1, Shestakovo 1 and 3; 2, Smolenskii Yar; 3, Ust'-Kolba; 4, Novochernorechenskii; 5, Bol'shoi Kemchug 3 and 4; 6, Bol'shoi Terekhtyul' 2 and 4.

Ilek Formation are exposed along the Kiya River and Serta River, near the village of Shestakovo in the Kemerovo Province, along the Chulym and Uryup rivers near the town of Achinsk and the village of Skripachi, respectively, and in the basin of Bol'shoi Kemchug and Bol'shoi Terekhtyul' rivers of Krasnoyarsk Territory. Vertebrate microfossils are mostly produced in these outcrops. We studied isolated theropod teeth from the screen-washing samples made at nine microvertebrate localities within the Ilek Formation which are briefly described below.

Shestakovo 1. One of the main outcrops of the Ilek Formation is situated near the village of Shestakovo, Chebula District of Kemerovo Province, along the right bank of the Kiya River (N 55°54'29.5'', E 87°57'06.5''). The deposits observed in the section present up to three cycles of alluvial-floodplain-lacustrine origin, starting with gravel conglomerates and coarse-grained cross-bedded sandstones, covered with silt- and mudstones. Each cycle includes fossil vertebrate remains associated with some lenses and layers of conglomerates and sandstones.

Shestakovo 3. The site is confined to the artificial outcrop of the road cut, two kilometers southeast of the Shestakovo Village, Chebula District of Kemerovo Province (N 55°52'58.08'', E 87°59'42.0''). The stratigraphic section of this locality is divided into six layers. They are represented by fine to medium-grained greenish-grey sandstones in the bottom of the section covered with irregular beds and lenses of greenish-brown siltstones, deposits of the complicated genesis composed of the mixture of reddish-brown clay (more than 70%) and fine-grained blueish-grey sand (less than 30%) with numerous carbonate concretions, pinkish-brown and chocolate colored argillites. The fossil vertebrates are associated with sandstones and two layers of siltstone of complex genesis. The total thickness of the outcrop is 7.5 m. The section is described in details in Lopatin et al. (2015) and Skutschas et al. (2017).

Smolenskii Yar. The outcrop is situated along the right bank of the Serta River, 500 m downstream from Kursk-Smolenka Village, Chebula District of Kemerovo Province (N 55°58'23.9'', E 88°05'35.9''). The section is described in Averianov et al. (2015). The deposits of Ilek Formation are represented by interbedding of yellow-green polymictic sandstone with gravels and clayish pebbles, dark-grey and reddish-brown argillites and blueish-grey siltstones. These deposits are characterized by a relatively smaller size of clastic material with a large amount of silt and clay. The total height of the outcrop is around 30 m and most of the vertebrate remains are associated with fine-grained sandstones in the basal part of the section.

Ust'-Kolba. The site is located in the 15-meter high artificial outcrop of the sand quarry on Serta River near the mouth of the Kolba River, in the vicinity of the village of Ust-Kolba, Tisul' District of the Kemerovo Province (N 55°52'36.2'', E 88°19'07.6''). The section, which is described in details by Averianov et al. (2015), is almost entirely composed of yellow-green polymictic inequigranular sandstones. Fossil remains are found within the layer of sandstone with gravel-size carbonate concretions and pebbles of argillite intraclasts. In this bed the fossil vertebrate remains are observed visually and collected after being screen-washed.

Novochernorechenskii. The site is associated with a series of sand quarries along the right bank of the Berezovaya River valley (the basin of Bol'shoi Ului River), in the suburbs of Novochernorechensk settlement, Kozulsk District of Krasnoyarsk Territory. The single premaxillary tooth was collected from the outcrop 6 (N 56°16'23.24'', E 91°7'3.98''). Only the upper part of this outcrop is currently accessible due to the talus accumulation along the slope. The complete section described in 2000 was represented by alluvial channel facies of yellowish-grey poorly lithified inequigranular sandstones with layers of gravels and lenses of argillite pebbles. The fossil vertebrate remains are associated with the layers of sandstone in the bottom of the section (up to 5 m from the base of the section) and in several ten-centimeter thick lenses in the top of the section.

Bol'shoi Kemchug 3. The section of the outcrop, exposed on the right bank of the Bol'shoi Kemchug River (N 56°31'38'', E 91°48'49'') of Emelyanovo District, Krasnoyarsk Territory, consists of yellowish to greenish-grey and poorly lithified inequigranular polymictic sandstones with inclusions of argillite pebbles. The lower part of the section is relatively massive, with rare coalified trunks and branches up to 0.8 m in diameter. The overlaying strata were deposited with discordancy, represented by an uneven erosional surface and poorly rounded argillite pebbles up to 0.5 m in diameter, corresponding to coastal deposits. The upper part of the section is a series of lenses with a thickness of up to 2 m. Microvertebrate remains were accumulated in the lowermost parts of the lenses, in yellowish-grey sandstones with small argillite pebbles.

Bol'shoi Kemchug 4. The natural outcrop is exposed on the right bank of the Bol'shoi Kemchug River (N 56°33'56.85", E 91°50'45.22"), Emelyanovo District, Krasnoyarsk Territory. The section is composed of horizontally and cross-bedded yellowish to greenish-grey inequigranular polymictic sandstones with argillite pebbles and carbonate cement. The lowermost part of the section is composed of poorly sorted inequigranular clayish sandstones with pebbles of argillite as well as rare poorly rounded gravel clasts of white, smoky or transparent quartzite. It is formed by a series of irregular-shaped lenses that infill an uneven erosional surface. The upper bedding of lenses is traced by trunks and branches of fossil trees oriented parallel to the paleoflow (azimuth around 273°). The original color of the deposits was most likely blueish-grey due to the anoxic conditions of the sedimentation, as revealed by druses of marcasite in the fossil wood and argillite pebbles. Microvertebrate remains are concentrated within 1.3 meters thick bonebed at the bottom of the section.

Bol'shoi Terekhtyul' 2 and 4. A series of natural outcrops along the right bank of the Bol'shoi Terekhtyul' River is best represented by the outcrop of Bol'shoi Terekhtyul' 3 which is situated one kilometer downstream from the abandoned village of Alekseevka (N 56°38', E 91°59.4'), Emelyanovo District, Krasnoyarsk Territory. The outcrop is represented by three cycles of sedimentation composed of inequigranular light yellowish-grey sandstones with quartz gravels and small pebbles, and siltstones interbedded with fine-grained sandstones. The vertebrate fossil remains are found within the sandstones of the first cycle.

Abbreviations for vertebrate localities. BK-3, Bol'shoi Kemchug 3; BK-4, Bol'shoi Kemchug 4; BT-2, Bol'shoi Terekhtyul' 2; BT-4, Bol'shoi Terekhtyul' 4; Nch, Novochernorechenskii; SmY, Smolenskii Yar; Sh-1, Shestakovo 1; Sh-3, Shestakovo 3; UKo, Ust'-Kolba.

MATERIAL AND METHODS

Intensive screen-washing between 1997 and 2016 at various vertebrate localities within the Ilek Formation produced several hundreds of isolated theropod teeth and tooth fragments. Many teeth are moderately to heavily worn, which prevents accurate measurements. 136 complete to roughly complete and perfectly preserved to slightly worn teeth can be confidently attributed to dental morphotypes (Table 1). Among them, 90 teeth are complete enough for accurate measurements (Table 2). Most analyzed teeth only preserve the basal portion of the root and were likely shed during lifetime. Few specimens with preserved root come from dead animals.

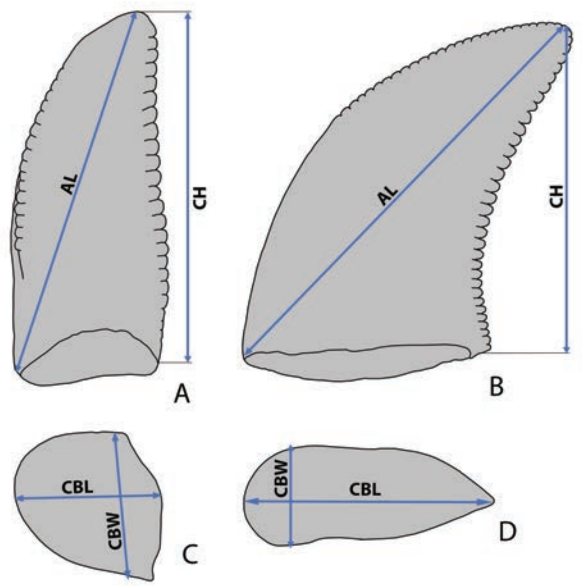

Fig. 2. Scheme of measurements for the mesial (A, C) and lateral (B, D) teeth. AL, crown apical length; CBL, crown base length; CBW, crown base width; CH, crown height.

The anatomical terminology and measurements in most cases follow Hendrickx et al. (2015b). The scheme of measurements is represented in Fig. 2. The following measurements were taken: AL, crown apical length; CBL, crown base length; CBW, crown base width; CH, crown height; DD, distal denticle density (number of denticles per 5 mm measured in the center of carina); MD, mesial denticle density (number of denticles per 5 mm measured in the center of carina). Also, we calculated two indices: CBR, crown base ratio (CBW divided by CBL); CHR, crown height ratio (CH divided by CBL).

Tooth measurements were taken with a dial calliper for the larger teeth (CH > 1 cm) and with a calibrated ocular micrometer using a binocular microscope for the smaller teeth (CH ≤ 1 cm). The denticles were measured in the middle part of the carina with an ocular micrometer under magnification of x6 for 2 mm in most teeth, or for 1 mm for the very

Table 1. Distribution of theropod tooth morphotypes (A-E) by vertebrate localities of the Lower Cretaceous Ilek Formation (BK-3, Bol'shoi Kemchug 3; BK-4, Bol'shoi Kemchug 4; BT-2, Bol'shoi Terekhtyul' 2; BT-4, Bol'shoi Terekhtyul' 4; Nch, Novochernorechenskii; SmY, Smolenskii Yar; Sh-1, Shestakovo 1; Sh-3, Shestakovo 3; UKo, Ust'-Kolba).

	BK-3	BK-4	BT-2	BT-4	Nch	SmY	Sh-1	Sh-3	UKo	Total
A	5	8	1	2	1	0	31	5	3	56
B	7	8	1	1	0	0	10	0	0	27
C	7	8	3	0	0	1	14	0	2	35
D	0	1	0	1	1	0	7	0	0	10
E	0	0	1	1	0	0	5	0	1	8
Total	19	25	6	5	2	1	67	5	6	136

small teeth, and this value was multiplied by 2.5 or 5, respectively, to get denticles density for 5 mm.

A discriminant function analysis (DFA) was performed using PAST3 (Hammer et al. 2001). We used four morphometric variables (CBL, CBH, CH, and AL) and two meristic variables (MD and DD). All measurements were log-transformed to better reflect a normal distribution. The mesial and distal denticle density were log transformed using the formula log(x+1) to account for values of 0 in the morphotypes which lack denticles on mesial or distal carina. Missing data were coded as a question mark in the dataset. In PAST3 DFA the missing data supported by column average substitution.

The teeth were separated into morphotypes based on qualitative instead of quantitative data. Morphotypes A, B, and C are lateral teeth and morphotype D include mesial teeth. Morphotype E comprises both mesial and lateral teeth. The most important dental characters considered to separate each morphotype is the presence of a mesial carina and a flat area on the lingual side, the lingual displacement of mesial carina, and cross-section outline of the crown base. The mesial and distal denticle morphology does not vary between morphotypes. The absence of mesial denticles is characteristic of Morphotype B and C, yet some teeth attributed to Morphotype A also lack mesial denticles. Morphotype E includes unserrated teeth.

There are several published datasets containing tooth measurements of various predominantly Late Cretaceous theropods taken in situ or from isolated teeth (Smith et al. 2005; Smith and Lamanna 2006; Larson and Currie 2013; Hendrickx et al. 2015a). However, these datasets contain predominantly measurements of much larger teeth than the small theropod teeth, recovered by screen-washing from the Ilek Formation. Because of this, the Ilek theropod teeth are placed in DFA plot separately from the most theropod taxa included in those datasets.

DESCRIPTION OF MORPHOTYPES

Morphotype A. This is the most common morphotype in all localities within the Ilek Formation (Table 1). It includes ziphodont and mesiodistally compressed teeth, with a CBR varying between 0.41 and 0.65 (Table 2). The teeth are strongly to moderately elongated, with an average CHR of 1.83 (Table 2). The mesial carina varies greatly in length, generally it occupies about half of the crown height. The distal carina extends apicobasally along the entire distal margin of the crown; sometimes it is not developed in the vicinity of the crown apex. Usually both mesial and distal carinae occupy mesialmost and distalmost edges of the crown, respectively, and are not displaced lingually. Rarely the basalmost part of the mesial carina is slightly displaced lingually, with a tiny longitudinal groove along the mesial carina on the lingual side (four specimens). On more distal teeth, the distal profile of the crown is less curved compared than the mesial profile. Both mesial and distal carinae are serrated in most teeth, except two mesial and seven distal teeth that lack mesial denticles. One of these distal teeth (LMCCE 004-20, former number PM TGU 16/5-124, from Sh-1) was previously described and identified as Troodontidae indet. (Averianov and Sues 2007: fig. 5A–C). The size of the distal denticles decreases towards the apical and basal ends of the crown (about 24 denticles per 5 mm in central part of the crown; Table 2). The mesial denticles are more constant in size and about 1.5 times smaller than the distal denticles (about 30 denticles per 5 mm in central

Table 2. Tooth measurements for theropod dental morphotypes from the Lower Cretaceous Ilek Formation.

	Limits	M±m	n	CV
		Morphotype A		
CBL	1.5–12.3	5.47±0.48	40	55.56
CBW	0.75–6.8	2.75±0.26	40	59.38
CH	2.5–30.1	10.51±1.17	40	70.17
AL	3.0–34.5	12.44±1.28	40	65.06
MD*	17–47.5	29.61±1.53	27	26.72
DD	15.8–60.0	24.07±0.69	40	30.21
CBR	0.41–0.65	0.50±0.01	40	11.12
CHR	1.24–2.49	1.83±0.06	40	20.94
		Morphotype B		
CBL	1.3–4.1	2.34±0.17	19	31.39
CBW	0.7–2.8	1.53±0.11	19	32.10
CH	1.8–9.8	4.83±0.49	19	44.47
AL	2.1–10.8	5.64±0.54	19	41.75
MD	0	0	18	
DD	25–65	34.08±2.47	18	30.76
CBR	0.52–0.85	0.66±0.02	19	15.97
CHR	1.18–2.57	2.00±0.10	19	20.83
		Morphotype C		
CBL	1.4–3.2	1.87±0.11	18	24.92
CBW	0.7–1.3	0.88±0.04	18	17.54
CH	1.9–5.3	3.006±0.21	18	29.62
AL	2.75–6.3	3.63±0.23	18	26.43

	Limits	M±m	n	CV
		Morphotype C (continued)		
MD	0	0	18	
DD	0–70	40.00±4.44	18	47.11
CBR	0.41–0.57	0.48±0.01	18	12.11
CHR	1.19–2.2	1.61±0.06	18	17.02
		Morphotype D		
CBL	1.5–7.3	2.68±0.93	6	84.50
CBW	1.2–5.3	2.14±0.64	6	73.00
CH	3.55–17.3	6.081±2.25	6	90.59
AL	4.0–18.1	6.57±2.31	6	86.09
MD	25.0–42.5	32.96±3.12	5	21.14
DD	17.5–40.0	30.60±3.67	5	26.83
CBR	0.73–0.95	0.83±0.03	6	8.76
CHR	2.00–2.41	2.22±0.08	6	8.56
		Morphotype E		
CBL	1.3–1.7	1.50±0.07	7	11.55
CBW	0.7–1.1	0.91±0.06	7	17.55
CH	2.35–3.00	2.61±0.10	7	10.28
AL	2.4–3.1	2.71±0.10	7	9.32
MD	0	0	7	
DD	0	0	7	
CBR	0.50–0.71	0.60±0.03	7	13.95
CHR	1.47–2.14	1.76±0.09	7	13.14

*Calculated for teeth with mesial denticles present.

part of the crown; Table 2). In some specimens, the basalmost part of the mesial carina lacks denticles. The crown cross-section at cervix can be elliptical, lanceolate, or figure-8-shaped, with rounded mesial margin and pointed distal margin (the mesial carina usually does not extend to the cervix). In the specimens with figure-8-shaped crown-section there are usually shallow lateral and lingual depressions. In other teeth, usually there are flat areas on lingual and labial sides in the place of such depressions. The cervix line is perpendicular to the crown longitudinal axis or oblique, with the enamel extending more basally along the distal carina. The enamel is smooth or has a very fine irregular texture. Some specimens show slight transverse undulations, which are more pronounced in the basal half of the crown (LMCCE 004-27, 004-58, 004-86 from Sh-1; Fig. 3N).

The distal denticles are subrectangular in shape, with the height about twice greater than their length, and oriented perpendicular to the crown edge. The external margin of denticles is symmetrical or slightly pointed apically. In distal teeth, this asymmetry can be more pronounced. The interdenticular space occupies about one quarter of the denticle length. There are no interdenticular sulci (blood grooves). However, the caudae of distal denticles often extend proximally to some distance from the interdenticular diaphysis. The mesial denticles are subquadrangular in shape and usually worn to various extent. Their external margin is symmetrical.

Morphotype B. The Morphotype B includes ziphodont mesial and lateral teeth similar to Morphotype A but differing in having a labiolingually broad mesial margin and either no mesial carina (nine

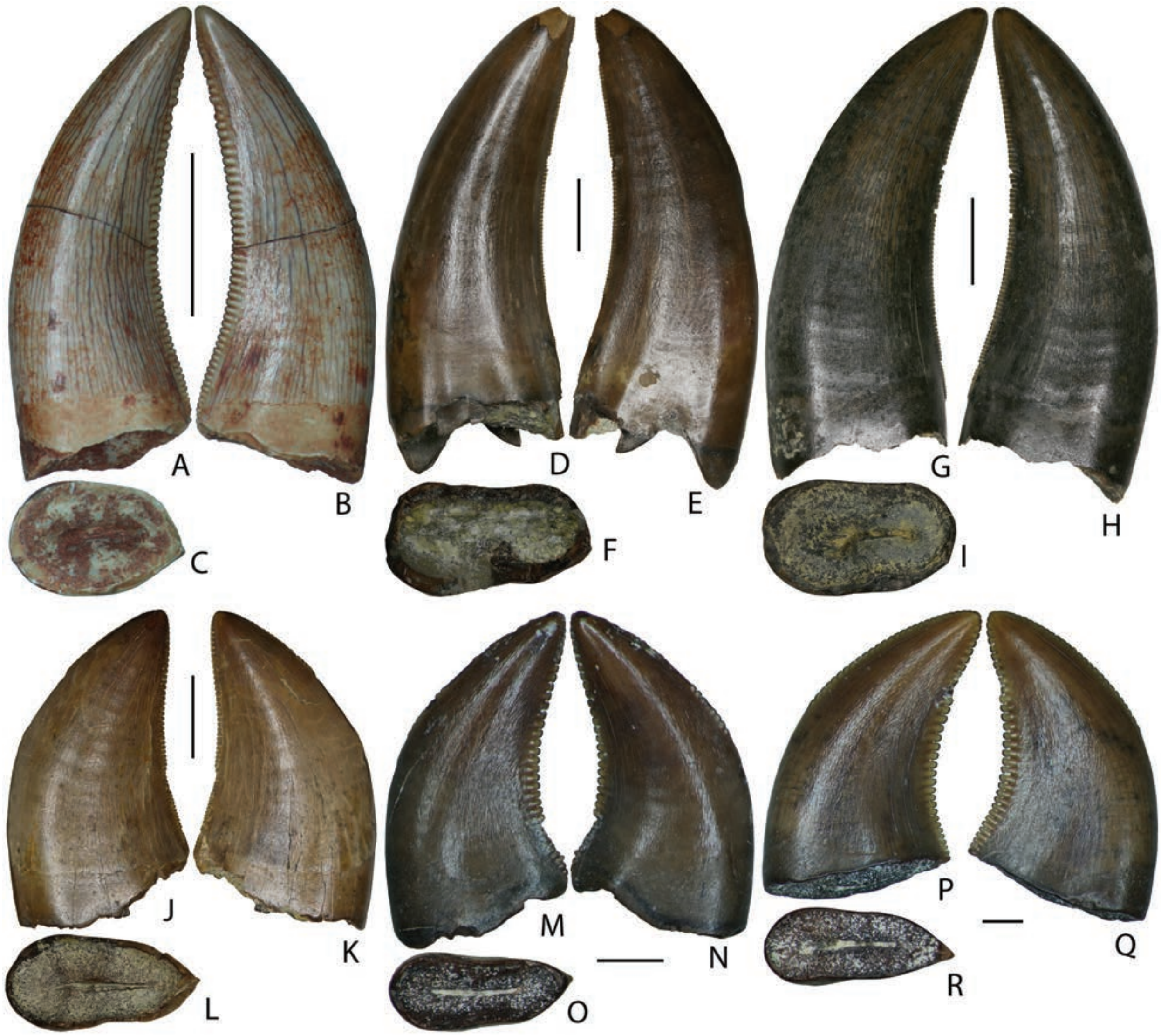

Fig. 3. Theropod lateral teeth included in Morphotype A (Dromaeosauridae indet. or Tyrannosauroidea indet.) from the. Ilek Formation, Lower Cretaceous (Barremian Aptian). A–C, LMCCE 006/1 (Shestakovo 3), in lingual or labial (A, B) and basal (C) views; D–F, LMCCE 004/125 (Shestakovo 1), in lingual or labial (D, E) and basal (F) views; G–I, LMCCE 005/35 (Bol'shoi Kemchug 3), in lingual or labial (G, H) and basal (I) views; J–L, LMCCE 004/5 (Shestakovo 1), in lingual or labial (J, K) and basal (L) views; M–O, LMCCE 004/86 (Shestakovo 1), in lingual (M), labial (N), and basal (O) views; P–R, LMCCE 004/53 (Shestakovo 1), in lingual or labial (P, Q) and basal (R) views. Scale bars equal 5 mm for A–L and 1 mm for M–R.

specimens; Fig. 4) or a lingually displaced and unserrated mesial carina along most of the crown height. These teeth are distinctly smaller than those from Morphotype A, with an average CH of 4.83 mm (Table 2). The crown cross-section at the cervix varies from oval to subrectangular, with round mesial and pointed distal ends. Some, presumably more mesial teeth, have an almost circular crown cross-section outline. The CBR varies from 0.52 to 0.85 (Table 2). The mesial carina usually does not extend basically towards the cervix. In six specimens it occupies about half of the crown height. There is no direct correlation between the crown cross-section and lingual displacement of the mesial carina. Some specimens with nearly circular cross-section may have mesial carina not deflected lingually. The enamel is smooth

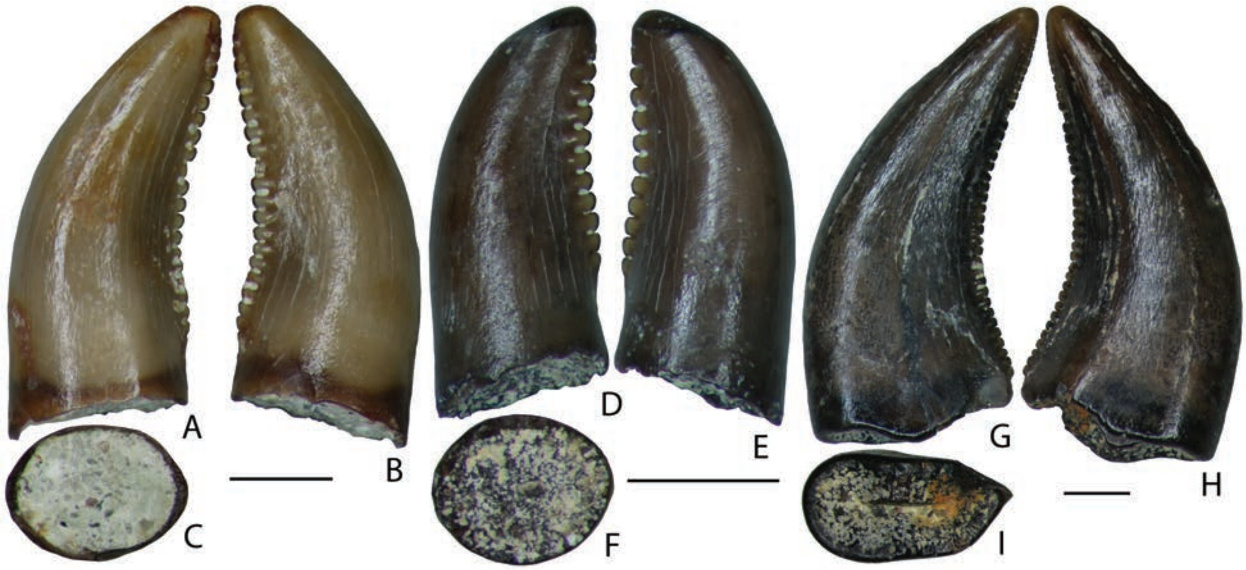

Fig. 4. Theropod mesial and lateral teeth included in Morphotype B (juvenile teeth of Dromaeosauridae indet. or Tyrannosauroidea indet.). Ilek Formation, Lower Cretaceous (Barremian Aptian). A–C, LMCCE 004/74 (Shestakovo 1), in lingual or labial (A, B) and basal (C) views; D–F, LMCCE 004/83 (Shestakovo 1), in lingual or labial (D, E) and basal (F) views; G–I, LMCCE 005/14 (Bol'shoi Kemchug 3), in lingual or labial (G, H) and basal views. Scale bars equal 1 mm.

or finely striated. The distal denticles are similar in size with those of Morphotype A, although they are more often asymmetrical, with an apically pointed external margin.

Morphotype C. Morphotype C includes mostly small teeth, with a CH ranging between 1.9 and 5.3 mm (Fig. 5; Table 2). It is similar with Morphotype B in that it also has an unserrated mesial carina but differs in having a well-pronounced longitudinal groove on the lingual side, adjacent to the mesial carina. This morphotype is also distinct in the presence of a roughly to strictly flat triangular area on the lingual surface of the crown side, which extends from the cervix to the crown apex. Often a similarly flat area is present on the labial surface of the crown. In these specimens, the crown cross-section at cervix is subrectangular, with rounded mesial and pointed distal ends. Some specimens have a figure-8-shaped basal crown cross-section due to the presence of marked lingual and labial depressions. A poorly defined longitudinal ridge may be present on the flat lingual surface of the crown (LMCCE 005-9 from BK-3). The CBR varies from 0.41 to 0.57, and CHR ranges between 1.19–2.2 (Table 2). The mesial carina either extends basally to the cervix, or at a certain distance from it. The basal part of the mesial carina is slightly displaced lingually in six specimens. In some teeth (LMCCE 005/111 from BK-3), the mesial crown base is convex basally and distinctly mesiodistally longer than the root. The enamel surface is smooth or, rarely, finely braided. In LMCCE 005/116 from BK-3 there are two to three poorly pronounced vertical ridges. Some teeth show distinct transverse undulations. The distal denticles decrease in size apically and basally. The denticles morphology is similar to that of Morphotype A, although there is a greater proportion of denticles with asymmetrical and apically pointed external margins.

Morphotype D. The teeth of Morphotype D are generally similar to those of Morphotype A but differ in having the mesial carina displaced lingually to some extent and J-, D-, or U-shaped basal crown cross-section (Fig. 6). At least some teeth referred to Morphotype D belong to the mesial dentition (i.e., premaxillary, anterior maxillary and anterior dentary teeth), which lateral dentition is represented by the Morphotype A. The teeth vary in size, with a CH ranging from 3.55 to 17.3 mm (Table 2). There is typically a prominent longitudinal groove on the lingual side and adjacent to the mesial carina (Fig. 6B, F, I). The mesial carina extends along the apical mid-height of the mesial margin (LMCCE 004-26 from Sh-1; Fig. 6K), or further basally. The lingual side of the crown is convex and typically includes a longitu-

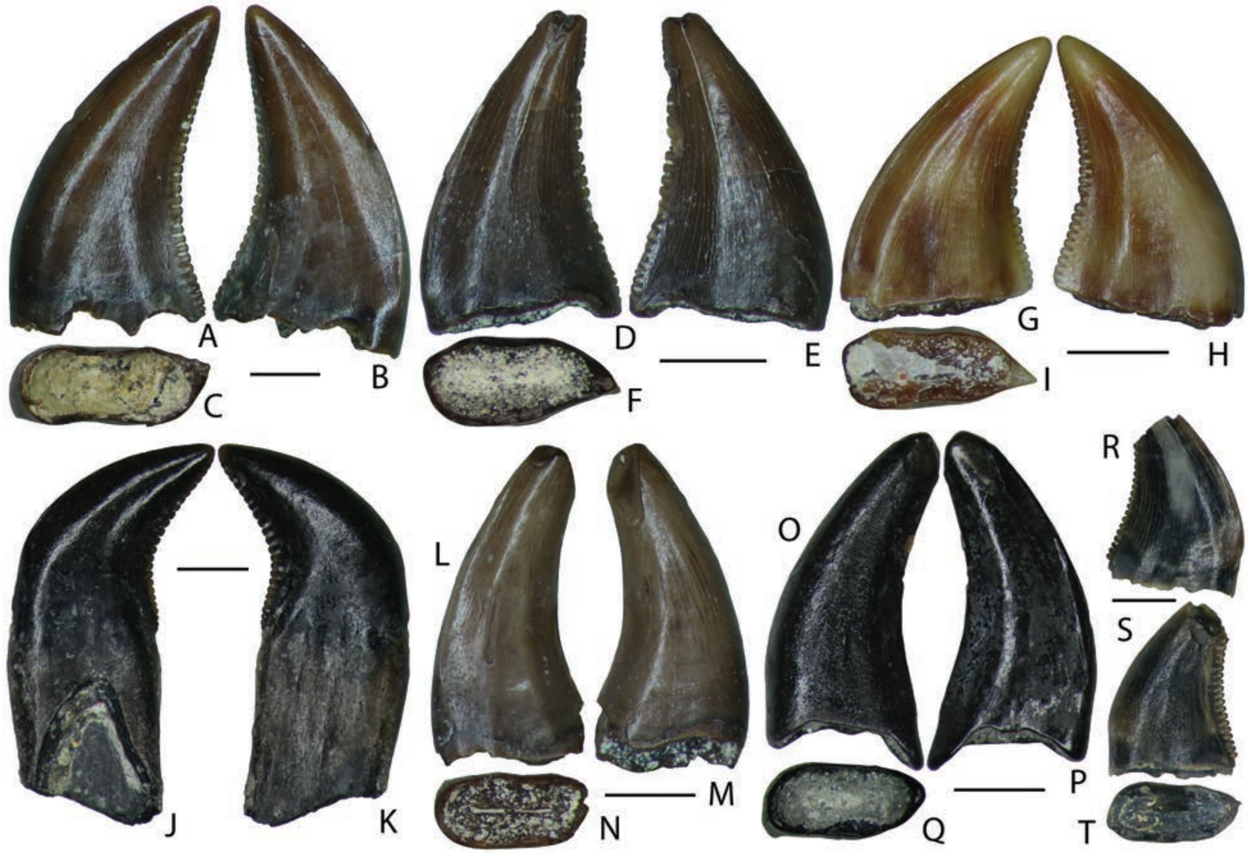

Fig. 5. Theropod lateral teeth included in Morphotype C (Microraptorinae indet. or Troodontidae indet.) from the Ilek Formation, Lower Cretaceous (Barremian-Aptian). A–C, LMCCE 004/32 (Shestakovo 1), in labial (A), lingual (B), and basal (C) views; D–F, LMCCE 004/61 (Shestakovo 1), in lingual (D), labial (E), and basal (F) views; G–I, LMCCE 004/44 (Shestakovo 1), in lingual (G), labial (H), and basal (I) views; J, K, LMCCE 005/44 (Bol'shoi Kemchug 4), in lingual (J) and labial (K) views; L–N, LMCCE 004/62 (Shestakovo 1), in lingual (L), labial (M), and basal (N) views; O–Q, LMCCE 005/65 (Bol'shoi Kemchug 4), in labial (O), lingual (P), and basal (Q) views; R–T, LMCCE 001/14 (Ust' Kolba), in lingual (R), labial (S), and basal (T) views. Scale bars equal 1 mm.

dinal ridge in the middle. In LMCCE 004-116 from Sh-1 a small longitudinal ridge on lingual surface is confined to the basal part of the crown, basal to the denticles. The enamel is smooth. Both mesial and distal carina are serrated. The morphology of mesial and distal denticles is the same as in Morphotype A.

Morphotype E. These are the most distinctive theropod teeth from the Ilek Formation (Fig. 7). The teeth are small, with CH varying between 2.35 and 3.0 mm (average 2.61 mm; Table 2). The crown is lanceolate, with a flat lingual margin and a strongly convex labial surface. The mesial margin is slightly to moderately convex and the distal margin is slightly concave or straight. There is no denticles on both mesial and distal carinae, except LMCCE 004-78 from Sh-1, where there are small denticles in the basal half of the distal carina (Fig. 7B). LMCCE 004-78 is the most anterior tooth in the sample (Fig. 7A–C) based on the fact that the crown is sub-symmetrical, with almost round basal crown cross-section. Both carinae are facing lingually. The basal crown cross-section is oval in other specimens. In two specimens (LMCCE 004-107 and 004-124 from Sh-1), the mesial carina projects lingually while the distal carina is linguodistally oriented. In what is assumed to be a more distal tooth LMCCE 001-4 from UKo, the mesial and distal carinae face mesiolingually and linguodistally, respectively (Fig. 7I). In four remaining teeth in the sample (LMCCE 003-3 and 003-27 from BT-4, and 004-1 and 004-29 from Sh-1) the mesial carina projects lingually while the distal carina faces distally (Fig. 7F, L). A median ridge of variable development

Fig. 6. Theropod mesial teeth included in Morphotype D (Dromaeosauridae indet. and Tyrannosauroidea indet.) from the Ilek Formation, Lower Cretaceous (Barremian-Aptian). A–D, LMCCE 004/51 (Shestakovo 1), in distal (A), lingual (B), mesial (C), and basal (D) views; E–G, LMCCE 004/13 (Shestakovo 1), in distal (E), lingual (F), and basal (G) views; H–J, LMCCE 004/52, in distal (H), lingual (I), and basal (J) views; K, L, LMCCE 004/26 (Shestakovo 1), in lingual (K) and labial (L) views; M–Q, LMCCE 003/19 (Bol'shoi Terekhtyul' 4), in lingual (M), mesial (N), labial (O), distal (P), and basal (Q) views; R–U, LMCCE 004/116 (Shestakovo 1), in distal (R), lingual (S), mesial (T), and basal (U) views; V–Y, LMCCE 006/6 (Shestakovo 3), in distal (V), lingual (W), mesial (X), and basal (Y) views. Scale bars equal 1 mm.

is present on the lingual surface of the crown. It is, however, absent in LMCCE 004-78. In LMCCE 004-124, this median ridge extends onto the root, while in LMCCE 003-27 it terminates some distance distal to the cervix. Both mesial and distal carina are worn out and the typical wear facet extends onto the crown apex. In LMCCE 004-78 and 001-4 there is a separate wear facet on the apex (Fig. 7B, K). The crown is slightly to distinctly wider (mesiodistally) than the root.

MORPHOMETRIC ANALYSIS

The largest sample (Morphotypes A) is rather heterogeneous, including large and small teeth of different proportions. Thus, the morphometric variables for this sample have a relatively large coefficient of variation (CV; Table 2). This variation apparently reflects position variation of the teeth within the tooth row, as well as an ontogenetic variation. The second and third largest samples (morphotypes B and C) include predominantly small teeth of similar size and show less variation (Table 2).

In spite of difference in size, the crown height ratio (CHR) is similar in the morphotypes A and B (Fig. 8). The average CHR is 1.83 for the Morphotype A and 2.00 for the Morphotype B (Table 2). The Morphotype C contains teeth with generally smaller CHR (Fig. 8). The average CHR for the Morphotype C is 1.61 (Table 2). The morphotypes A and C are

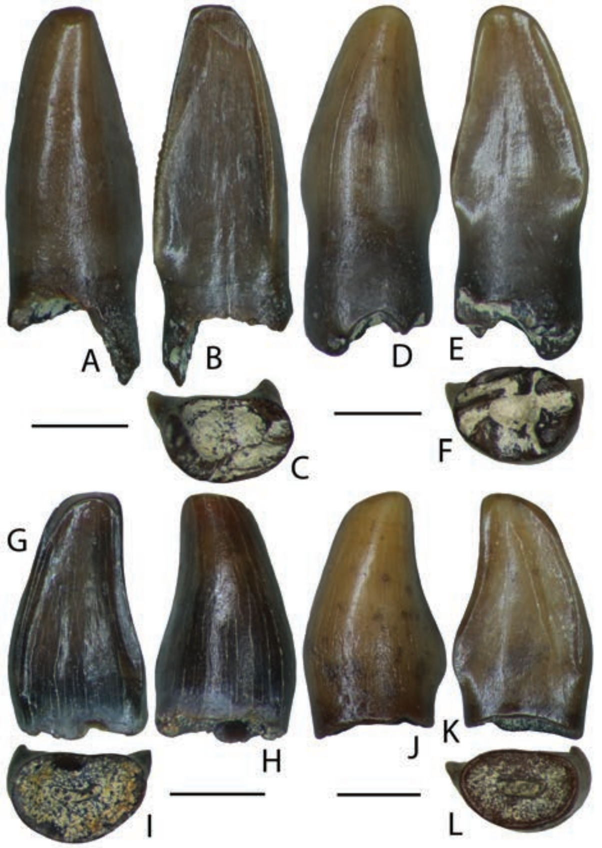

Fig. 7. Theropod mesial and lateral teeth included in Morphotype E (Troodontidae indet. cf. *Urbacodon* sp.) from the Ilek Formation, Lower Cretaceous (Barremian-Aptian). A–C, LMCCE 004/78 (Shestakovo 1), in labial (A), lingual (B), and basal (C) views; D–F, LMCCE 004/29 (Shestakovo 1), in labial (D), lingual (E), and basal (F) views; G–I, LMCCE 001/4 (Ust' Kolba), in lingual (G), labial (H), and basal (I) views; J–L, LMCCE 004/1 (Shestakovo 1), in labial (J), lingual (K), and basal (L) views. Scale bars equal 1 mm.

similar in the crown base ratio (CBR) and almost completely overlap in the CBR-CHR morphospace (Fig. 8). The average CBR is 0.50 for the Morphotype A and 0.48 for the Morphotype C (Table 2). The Morphotype B includes some teeth with a greater CBR (Fig. 8), and the average CBR is larger (0.66; Table 2). Consequently, the Morphotype B partly overlaps the morphotypes A and C in the CBR-CHR morphospace and approximates the morphospace of the Morphotype D (Fig. 8). The morphospace of the mesial teeth (Morphotype D) in CBR-CHR plot is most remote from the other Morphotypes marginally overlapping only with the Morphotype B (Fig. 8). The morphospace of the Morphotype E in CBR-CHR plot is placed within the morphospace of the Morphotype B (Fig. 8).

The denticle density on distal carina (DD) strongly correlated with the tooth size, as exemplified by crown height (CH) (Fig. 9). This correlation was noted by previous authors (Farlow et al. 1991; Rauhut and Werner 1995). In particular, large teeth of the Morphotype A have DD around 20 (Fig. 9). The smallest teeth of the Morphotype A also have DD around 30, with one specimen having DD of 60 (Table 2). The teeth from the morphotypes B and C with similarly small CH have value of DD between 30 and 70 (Fig. 9). This may indicate that the low value of DD is a diagnostic character for the theropod taxon represented by the Morphotype A. The Morphotype C, with the smallest teeth (CH 1.9–5.3 mm, Table 2), has the greatest range of DD, from 0 to 70 denticles per 5 mm (Table 2; Figure 9). The morphospaces of the morphotypes A and C only marginally overlap in the CH-DD plot (Figure 9). The morphospace of the Morphotype B largely overlaps with the morphospace of the Morphotype C and partially with the Morphotype A. The mesial teeth (Morphotype D) are distributed between morphotypes A, B, and C in the CH-DD plot (Fig. 9).

The DFA of 90 theropod teeth from the Ilek Formation returned 80.72% correctly classified teeth. The first and second discriminant functions explain 74.48% of the variance (Table 3). The mesial denticle density (MD) and distal denticle density (DD) have the greatest loading on the first axis (0.194 and 0.181 respectively; Table 3). The morphometric variables CBL, CBW, CH, and AL contribute almost equally to the first axis (0.069–0.087; Table 3). The greatest loading on the second axis also have MD and DD (-0.079 and 0.025 respectively; Table 3). The loadings of CBL and CBW to this axis is similar to that of DD (Table 3).

In the DFA morphospace the morphotypes A, B, and C are partially overlapping (Fig. 10). The morphotypes A and B are separated along the axis 1 and the morphotypes A and C – along the axis 2. The morphospace of the mesial teeth (Morphotype D) is well separated from the other morphotypes along the axis 1 (Fig. 10). On the axis 2 the Morphotype D occupies the spaces between values 1 and 2; this space is occupied also only by Morphotype A. This may indicate that the mesial teeth (Morphotype D) and the lateral teeth of the Morphotype A belong to the same taxon. The Morphotype E, including mesial and

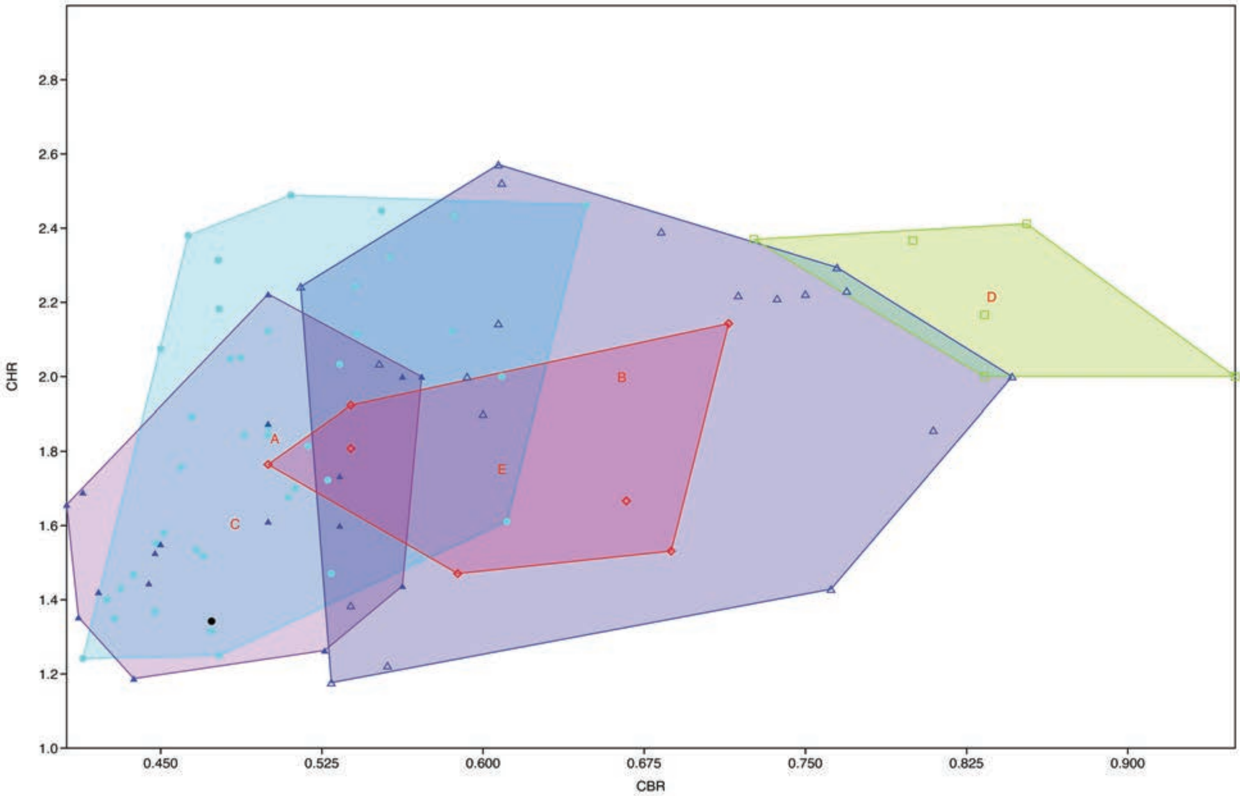

Fig. 8. Crown base ratio (CBR) versus crown height ratio (CHR) bivariate plot for the morphotypes A–E of theropod teeth from the Lower Cretaceous (Barremian-Aptian) Ilek Formation.

Table 3. Axis loadings and eigenvalue data for DFA of isolated theropod teeth from the Lower Cretaceous Ilek Formation.

	Axis 1	Axis 2	Axis 3	Axis 4
logCBL	0.073	0.031	0.090	−0.130
logCBW	0.069	−0.020	0.078	−0.146
logCH	0.079	0.004	0.090	−0.154
logAL	0.087	0.014	0.086	−0.155
log(MD+1)	0.194	−0.079	0.350	0.078
log(DD+1)	0.181	0.025	−0.149	0.104
Eigenvalue	4.05	1.85	1.77	0.25
% of total variance	51.14	23.34	22.35	3.17

lateral unserrated teeth, is distinctly separated from the remaining morphotypes along the axis 2 (Fig. 10). Along the axis 1 the Morphotype E occupies the space between 1 and -2; a similar space is occupied by Morphotypes A (between 2 and -2), B (between 1 and -3), and C (between 3 and 0). Morphotypes D and E are completely separated along the axes 1 and 2.

DISCUSSION

The teeth referred to the Morphotype A are somewhat similar to those of Dromaeosauridae in having relatively large distal denticles (average density is 24 denticles per 5 mm; Table 2). However, they are different from the dromaeosaurid teeth in the morphology of denticles, which are more hook-like in dromaeosaurids (Currie et al. 1990; Currie and Varricchio 2004). The teeth from the Morphotype A clearly differ from the maxillary and dentary teeth of *Dromaeosaurus* and other Late Cretaceous dromaeosaurids (Currie 1995) by the mesial carina not displaced lingually in the basal part of the crown in most of the specimens. The mesial carina is not displaced lingually in the lateral teeth of the Early Cretaceous dromaeosaurids (Microraptorinae). Among the microraptorines, the mesial denticles are present on lateral teeth in *Sinornithosaurus* (Xu and Wu 2001). These denticles are distinctly smaller than the distal denticles, as in the teeth referred to the Morphotype A (Table 2). In the basal mid-Cretaceous tyrannosauroid *Timurlengia*

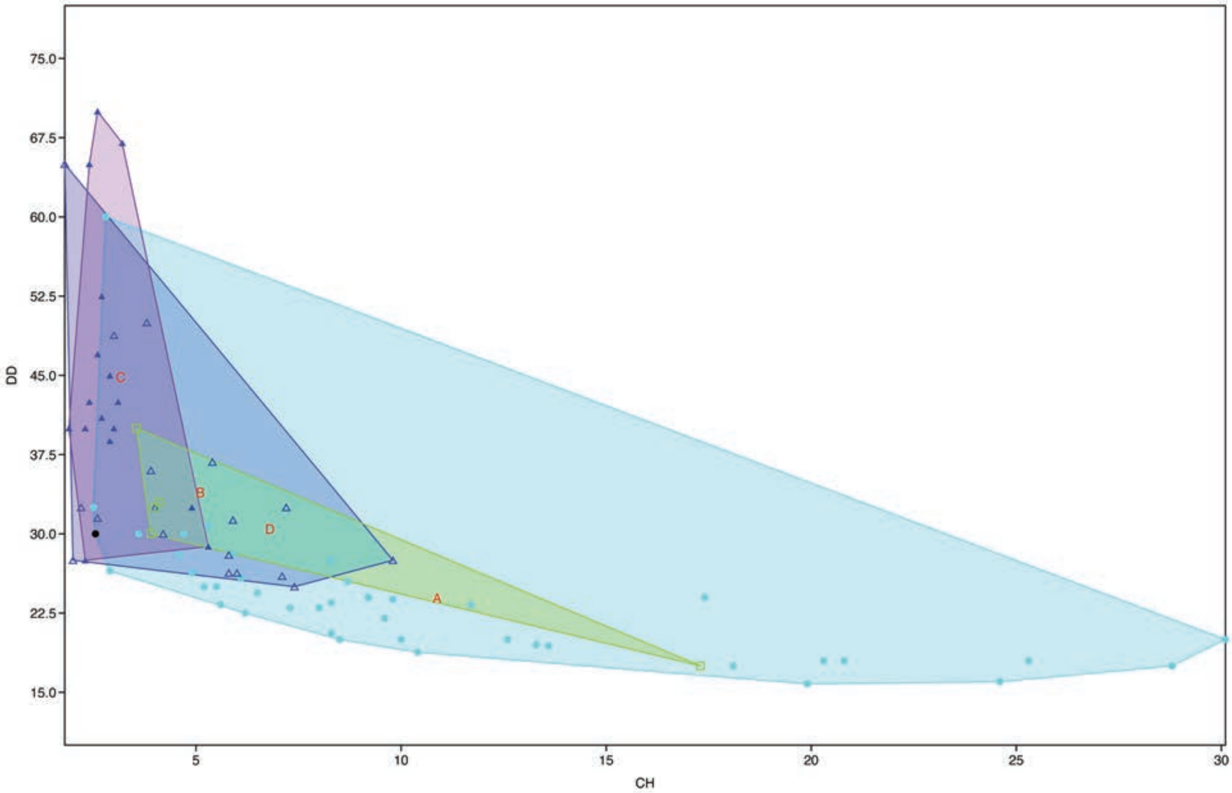

Fig. 9. Distal denticle density (DD; number of denticles per 5 mm) versus crown height ratio (CHR) bivariate plot for the morphotypes A–D of theropod teeth from the Lower Cretaceous (Barremian-Aptian) Ilek Formation. Specimens lacking distal denticles (Morphotype E and some other teeth) are not included.

the mesial and distal denticles are distinctly larger than in Morphotype A (see Table 2): in average 19 denticles per 5 mm on mesial carina and 17.5 denticles on distal carina (Averianov and Sues 2012). The size difference between the mesial and distal denticles is smaller than in the teeth referred to the Morphotype A. The theropod teeth from the Ilek Formation referred to the Morphotype A are most likely belonging to the Dromaeosauridae. However, we cannot exclude referral of some specimens from the Morphotype A to basal tyrannosauroids, which were likely present in the Ilek Formation judging from the U-shaped premaxillary teeth (see discussion of the Morphotype D).

The lateral theropod teeth from the Lower Cretaceous Khilok Formation of Transbaikalia, Russia, identified as '*Prodeinodon*' sp. (Averianov and Skutschas 2009: fig. 2A–G), are very similar with the teeth from the Ilek Formation attributed to the Morphotype A. These teeth might belong to a similar dromaeosaurid taxon.

The teeth of the morphotypes B and C are distinct from Morphotype A in the lack of denticles along the mesial carina. The lateral teeth with only distal denticles are found in compsognathids *Sinosauropteryx*, *Huaxiagnathus*, and *Juravenator* (Stromer 1934; Currie and Chen 2001; Hwang et al. 2004; Chiappe and Göhlich 2011), troodontids *Sinornithoides*, *Daliansaurus*, *Jianianhualong*, and *Saurornithoides* (Currie and Dong 2001; Norell et al. 2009; Shen et al. 2017; Xu et al. 2017), microraptorine *Microraptor* (Xu et al. 2000; Hwang et al. 2002; Pei et al. 2014), and dromaeosaurids *Tsaagan* and *Linheraptor* (Norell et al. 2006; Xu et al. 2010). In a compsognathid *Sinocalliopteryx* only part of the lateral teeth lacks mesial denticles (Ji et al. 2007).

The compsognathids exhibit a tooth shape unique among theropods: the crown base is expanded, the middle part is straight, and the apical two thirds of the crown height is kinked distally (Stromer 1934; Peyer 2006). However, this particular tooth shape could be common to the juvenile theropod teeth (Peyer 2006).

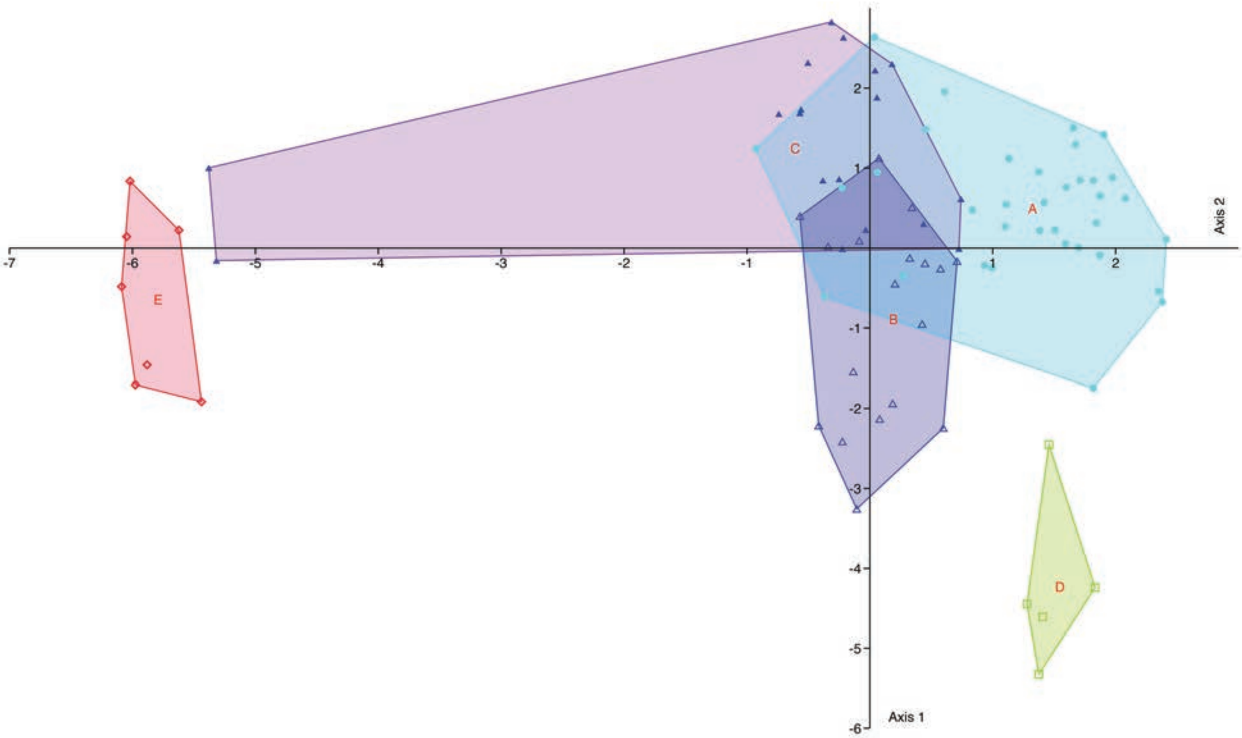

Fig. 10. Results of the discriminant function analysis (DFA) conducted on a dataset of 90 isolated theropod teeth from the Lower Cretaceous Ilek Formation. The first and second discriminant functions explain 51.14% and 23.34% of variance, respectively.

Among the sample from the Ilek Formation, LMCCE 005/44 from BK-4 (Morphotype C; Fig. 5J, K) shows a somewhat similar morphology. This tooth, preserving the complete root with a resorption pit on the lingual side, apparently comes from a dead animal. Its rather small size (CH=2.7) suggests attribution to a juvenile individual. Because of different tooth shape, the teeth from the morphotypes B and C are not attributable to the Compsognathidae.

Presence of only distal denticles on lateral teeth is a common feature for the Early Cretaceous troodontids. This feature is also characteristic for the microraptorine *Microraptor*, which has essentially troodontid-like dentition, similar to that of the Early Cretaceous troodontid *Sinovenator* (Hwang et al. 2002). In *Microraptor* the mesial denticles might be present on posterior dentary teeth in some specimens (Xu and Li 2016). The distal dentary teeth of *Microraptor* have been described as having a constriction between crown and root (Hwang et al. 2002). This constriction is not present in the maxillary teeth of *Microraptor* (Pei et al. 2014). A similar constriction is present in some specimens from Morphotype C (LMCCE 001/14 and 004/61; Fig. 5D, E, R, S). The distal dentary teeth of *Microraptor* have 40 denticles per 5 mm on the distal carina (Hwang et al. 2002). The same value (40) is an average distal denticle density for Morphotype C (Table 2). Notably, the dentary teeth of *Microraptor* have a distinctly flat area on their lingual and labial sides (Hwang et al. 2002: fig. 5; Xu and Li 2016: fig. 3E, F). This flattened lingual side is a defining character of Morphotype C and flat labial side is also frequently present in the teeth from the Ilek Formation attributed to the Morphotype C. The teeth from the Morphotype C may belong to either Troodontidae or Microraptorinae, or to both groups. The teeth from Morphotype B, which have convex mesial, lingual, and lateral margins, can be attributed to the same dromaeosaurid taxon, which is represented by the Morphotype A. Being generally smaller than teeth from the Morphotype A, the teeth of Morphotype B, lacking mesial denticles, may represent the juvenile dentition of this taxon.

Some lateral teeth referred to the Morphotype C and all teeth referred to the Morphotype E are distinct in the absence of denticles from both mesial and distal carinae. In *Compsognathus* the mesial denticles are absent on all teeth and distal denticles may be absent on posterior maxillary teeth (Peyer 2006). In an oviraptorosaur *Incisivosaurus* the lateral teeth lack denticles on both mesial and distal sides (Balanoff et al. 2009). The dentary teeth of *Incisivosaurus* have slightly concave lingual surface and strong mesial and distal carinae (Balanoff et al. 2009). These teeth are not recurved posteriorly, in contrast with the teeth from the Morphotype C. The denticles may be absent from either carina in dentary teeth of *Microraptor* (Pei et al. 2014). The unserrated mesial and lateral teeth are common in troodontids, being found in *Mei*, *Urbacodon*, *Byronosaurus*, *Almas*, *Gobivenator*, and *Xixiasaurus* (Makovicky et al. 2003; Xu and Norell 2004; Averianov and Sues 2007; Lü et al. 2010; Gao et al. 2012; Tsuihiji et al. 2014; Pei et al. 2017). The mesial teeth from the Morphotype E are very similar to the mesial teeth of *Urbacodon* (Averianov and Sues 2007, 2016) and likely belongs to an unserrated troodontid. The two small lateral teeth lacking both mesial and distal denticles, referred to the Morphotype C (LMCCE 005-65 and 005-89; Fig. 5O–Q) come very close to the Morphotype E in DFA morphospace (Fig. 10). These teeth may belong to an unserrated troodontid, although they are quite distinct morphologically from the Morphotype E.

The Morphotype D includes premaxillary and possible mesial dentary teeth with a round or U-shaped basal crown cross section. Some of these specimens have symmetric deeply U-shaped basal crown cross-section and lingual side flat or having only weak median ridge (Fig. 6M–Y). This morphology is most prominent in LMCCE 003/19 from BT-4 (Fig. 6M–Q). A very similar premaxillary tooth, referred to the Tyrannosauridae, is known from the Lower Cretaceous of Japan (Manabe 1999: fig. 1). Both specimens have similar apical wear facets on the labial and lingual sides. A U-shaped premaxillary tooth with a strong median ridge on the lingual side and lack of serrations on both carinae has been reported from the Lower Cretaceous of Wyoming, USA (Zanno and Makovicky 2011: fig. 1). This specimen, referred to Tyrannosauroidea, documents the Early Cretaceous Laurasian interchange event, which saw tyrannosauroids migrating to North America from Asia. The unserrated U-shaped premaxillary teeth are found in primitive tyrannosauroids (Holtz 2004). In the mid-Cretaceous primitive tyrannosauroid *Timurlengia*, the premaxillary teeth have a strong median ridge on lingual side (Averianov and Sues 2012). In *Timurlengia* the smallest premaxillary teeth lack serrations on either carina and larger teeth may lack mesial serrations (Averianov and Sues 2012). Apparently, the absence of serrations on premaxillary teeth is an ontogenetic character characteristic for the juvenile dentition. The teeth from the Ilek Formation, referred to the Morphotype D and having a U-shaped basal crown cross section are likely belonging to the Tyrannosauroidea. The other teeth from the Morphotype D, which have the mesial carina less displaced lingually, might be premaxillary or mesial dentary teeth of Dromaeosauridae, which lateral dentition is represented by the Morphotype A.

CONCLUSIONS

A sample of isolated theropod teeth from the Ilek Formation (n=136) can be distributed into five dental morphotypes based on morphological characters. From this sample, 90 teeth are complete enough for accurate measurements. The Morphotype A includes small to large lateral teeth with relatively large distal denticles (around 24 per 5 mm in average) and smaller mesial denticles (around 30 denticles per 5 mm). Some of these teeth can be attributed to the Dromaeosauridae, while other teeth may belong to a basal member of the Tyrannosauroidea. The Early Cretaceous dromaeosaurids, in contrast with the Late Cretaceous taxa, have the mesial carina not displaced lingually for the whole crown height. The distinctly smaller lateral teeth referred to the Morphotype B are similar with Morphotype A in most respects but differ in the lack of mesial denticles and mesial carina, or having a lingually displaced mesial carina. These teeth may belong to juvenile individuals of the same dromaeosaurid taxon. The teeth belonging to Morphotype C also lack mesial denticles and differ from Morphotype B by a flattened area on the lingual side, which is also often present on the labial side. These teeth may belong to either Troodontidae or Microraptorinae, or to both groups. The mesial and lateral teeth of Morphotype E are characterized by unserrated mesial and distal carinae. These teeth most likely belong to a distinct taxon of Troodontidae with unserrated dentition. The teeth of the Morphotype D include mesial teeth with the mesial carina displaced lingually at various extent and denticles present on both carinae. The teeth with moderately displaced lingual carina can be referred to the same dromaeosaurid taxon, which lateral teeth represented by Morphotype A. The teeth with more displaced mesial carina and deeply U-shaped basal crown section belong to an indeterminate Tyrannosauroidea.

Based on isolated teeth, five–six theropod taxa can be currently identified in the Lower Cretaceous Ilek Formation: Dromaeosauridae indet. (Morphotypes A and B, partially Morphotype D), Troodontidae indet. or Microraptorinae indet. (Morphotype C), Troodontidae indet. cf. *Urbacodon* sp. (unserrated dentition; Morphotype E), and Tyrannosauroidea indet. (partially Morphotype D and possible some teeth from the Morphotype A).

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