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A revision of *Campyloprion* Eastman, 1902 (Chondrichthyes, Helicoprionidae), including new occurrences from the Upper Pennsylvanian of New Mexico and Texas, USA

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ABSTRACT:

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Campyloprion Eastman, 1902 is a chondrichthyan having an arched symphyseal tooth whorl similar to that of *Helicoprion* Karpinsky, 1899, but less tightly coiled. The holotype of *Campyloprion annectans* Eastman, 1902, the type species of *Campyloprion*, is of unknown provenance, but is presumed to be from the Pennsylvanian of North America. *Campyloprion ivanovi* (Karpinsky, 1922) has been described from the Gzhelian of Russia. A partial symphyseal tooth whorl, designated as *Campyloprion* cf. *C. ivanovi*, is reported from the Missourian Tinajas Member of the Atrasado Formation of Socorro County, New Mexico, USA. Partial tooth whorls from the Virgilian Finis Shale and Jacksboro Limestone Members of the Graham Formation of northern Texas, USA, are designated as *Campyloprion* sp. Two partial tooth whorls from the Gzhelian of Russia that were previously referred to *C. ivanovi* are designated as *Campyloprion* cf. *C. annectans*. The age of *Toxoprion lecontei* (Dean, 1898), from Nevada, USA, is corrected from the Carboniferous to the early Permian. An alternative interpretation of the holotype of *T. lecontei* is presented, resulting in a reversal of its anterior-to-posterior orientation. The genera *Helicoprion*, *Campyloprion*, and *Shaktauites* Tchuvashov, 2001 can be distinguished by their different spiral angles.

Key words: Carboniferous; Permian; Eugeneodontiformes; Helicoprionidae; Edestoidea; Chondrichthyes; Geometric morphometrics.

INTRODUCTION

The Helicoprionidae Karpinsky, 1911 is a family of chondrichthyans in the order Eugeneodontiformes Zangerl, 1981. Helicoprionids are characterized by having large symphyseal tooth whorls containing sharply-pointed, laterally-compressed crowns that have rostrally extended lateral spurs (Lebedev 2009). *Helicoprion* Karpinsky, 1899, the best-known member of the family, has a spiral-shaped tooth whorl in which all teeth are retained, the earliest-formed teeth being buried inside the spiral.

Campyloprion annectans Eastman, 1902 was described from an incomplete symphyseal tooth whorl lacking locality information (Eastman 1902a, b). Its presumed Pennsylvanian or Permian age appears to have been based on its resemblance to both *Edestus* Leidy, 1856 and *Helicoprion* Karpinsky, 1899, not on any independent evidence. *Campyloprion annectans* was designated as the type species of the genus.

Edestus davisi Woodward, 1886 and *Edestus lecontei* Dean, 1898 were assigned to *Campyloprion* at the same time (Eastman 1902a), but were later removed from the genus. The holotype of *Helicoprion ivanovi* Karpinsky, 1922 consists of a tooth whorl containing only a few teeth. The species has since been referred to *Campyloprion* Eastman, 1902. Two species of *Campyloprion* (*C. annectans* and *C. ivanovi*) are currently recognized (Obruchev 1964; Zangerl 1981; Ginter *et al.* 2010). The present revision of *Campyloprion* was prompted by the discovery of new specimens from New Mexico and Texas. To complete the revision, the type and referred specimens of *Campyloprion* at Harvard University, the University of California, Berkeley, and the Paleontological Institute, Moscow, were examined.

The Eugeneodontiformes Zangerl, 1981 are an order of chondrichthyans united by possession of large symphyseal tooth whorls. Zangerl (1981) and Ginter *et al.* (2010) divided the Eugeneodontiformes into two superfamilies, the Caseodontoidea Zangerl, 1981 and the Edestoidea Hay, 1929, with the latter sub-divided into two families, the Agassizodontidae Zangerl, 1981 and the Edestidae Jaekel, 1899 (the latter including *Edestus*). Lebedev (2009) argued that the Agassizodontidae is a junior synonym of the Helicoprionidae Karpinsky, 1911 because Zangerl (1981) gave no reason for erecting the new family.

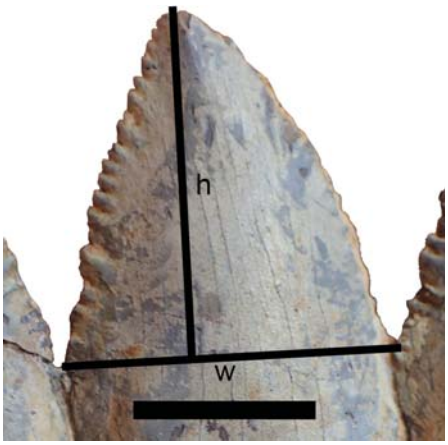
Relationships of the Eugeneodontiformes are poorly understood, particularly since fossil remains other than teeth are rare. Studies of tooth histology are potentially of use in clarifying phylogenetic relationships of chondrichthyans (Gillis and Donoghue 2007; Enault *et al.* 2015). However, convergence (e.g., shared presence of tubular dentine due to adaptation to a durophagous diet) may be present and can lead to misleading results (Radinsky 1981). The teeth of the eugeneodontiform genera *Edestus*, *Sarcoprion* Nielsen, 1952, *Fadenia* Nielsen,1932, and *Erikodus* Nielsen, 1952 were recently studied by scanning electron microscopy (SEM). The teeth were found to share the following properties: (1) complete absence of an enameloid layer, with only a compact form of dentine present, and (2) presence of a thin, outer, compact layer of single crystallites, each about 0.5 µm in length (Duffin 2016). These properties have not been reported in any other chondrichthyan teeth (C. Duffin, pers. comm. 2015). Shared presence of this unusual tooth histology among these genera supports monophyly of the Eugeneodontiformes.

Institutional abbreviations: AMNH, American Museum of Natural History, New York, NY, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; NHMUK, Natural History Museum, London, United Kingdom; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, NM, USA; PIN, A.A. Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; UCM, University of Colorado Natural History Museum, Boulder, CO, USA; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA; USNM, National Museum of Natural History, Washington, DC, USA; URAS, Institute of Geology and Geochemistry, Ural Division, Russian Academy of Sciences, Yekaterinburg, Russia.

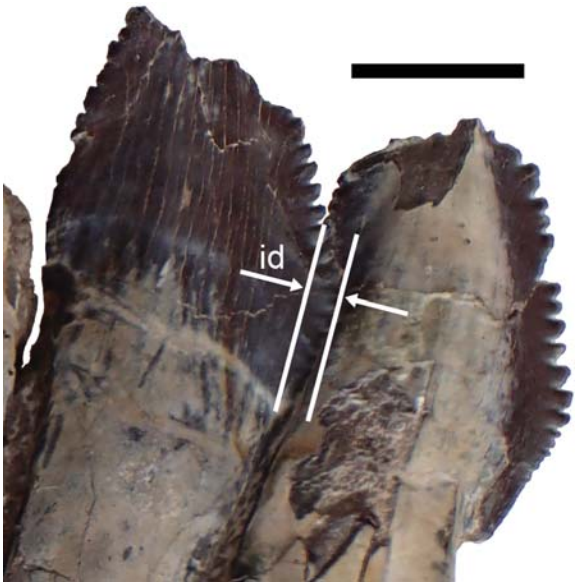
Abbreviations related to tooth measurements: w, width – measured between points of intersection with neighboring crowns; h, height – measured from apex to line segment joining points of intersection with neighboring crowns along a perpendicular line segment (Text-fig. 1); id, imbrication distance between adjacent crowns (Text-fig. 2); ss, serration separation (Text-fig. 3A); sd, serration depth (Text-fig. 3B).

SPIRAL ANGLE OF TOOTH WHORL AS A TAXONOMIC CRITERION

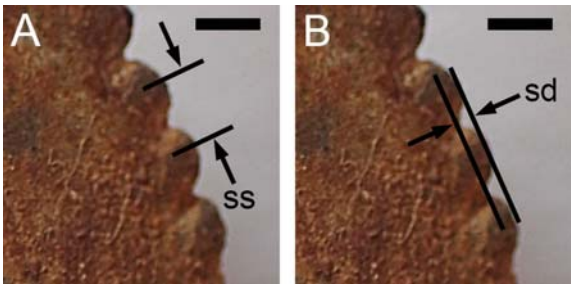
Many biological objects, such as the shell of *Nautilus* Linnaeus, 1758, are shaped like logarithmic (equiangular) spirals (Raup 1961, 1966). A logarithmic spiral has the property that it maintains its shape as it grows, with only a change in scale. In polar coordinates (R, θ), the equation that defines the locus of



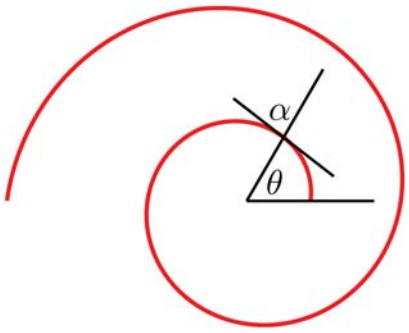
Text-fig. 1. *Campyloprion* cf. *C. annectans* Eastman, 1902, a crown of PIN 1655/1 from the Gzhelian Stage, Dobryatino Horizon at Rusavkino, Balashikha District, Moscow region, Russia (twelfth crown from right end of larger tooth whorl fragment in Text-fig. 13B), with h (height) and w (width) marked. Scale bar = 1 cm



Text-fig. 2. *Campyloprion ivanovi* (Karpinsky, 1922), two crowns of PIN 1655/132 from the Gzhelian Stage, Dobryatino Horizon at Rusavkino, Balashikha District, Moscow region, Russia, with id (imbrication distance) marked. Scale bar = 1 cm



Text-fig. 3. *Campyloprion* cf. *C. annectans* Eastman, 1902, serrated edge of a crown of PIN 1655/1 from the Gzhelian Stage, Dobryatino Horizon at Rusavkino, Balashikha District, Moscow region, Russia (fifth crown from left end of smaller tooth whorl fragment in Text-fig. 13B). A – ss (serration separation) marked; B – sd (serration depth) marked. Scale bars = 1 mm



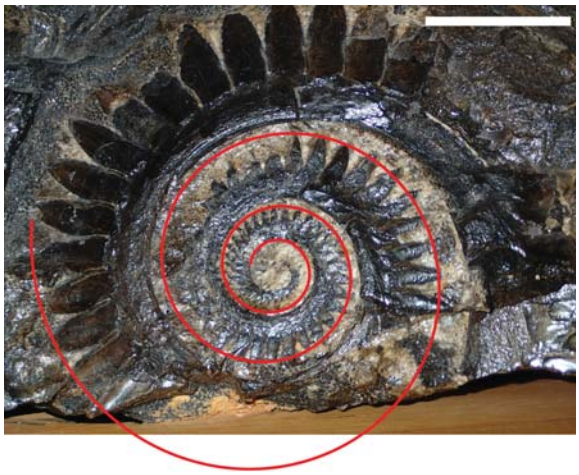
Text-fig. 4. A logarithmic spiral. The parameter α characterizing the spiral is the angle between a radius and a tangent to the spiral. This angle is independent of the polar angle θ, which increases as the spiral expands counterclockwise

a logarithmic spiral is $R = R_0 \exp(\theta \cot\alpha)$. Here, R_0 is an overall scale parameter. The shape of the spiral is determined by the single parameter α. Geometrically, α corresponds to the angle between a radius and a tangent to the spiral, which, for a logarithmic spiral, is independent of the polar angle θ (Text-fig. 4). As α approaches 90º, the spiral approaches a circle (more tightly coiled). As α decreases from 90º, the spiral expands more rapidly for a given change in θ and also appears more open, or loosely coiled.

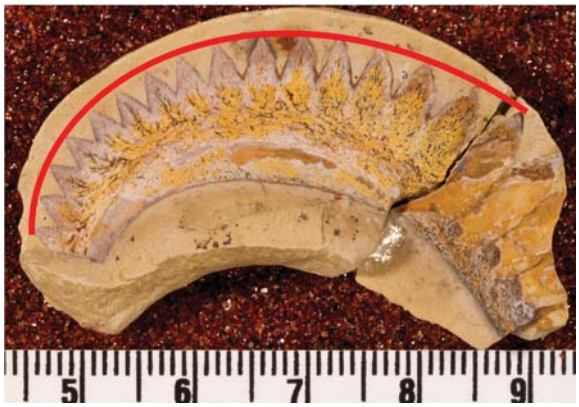
The geometrical method for determining α requires knowledge of the location of the center of the spiral, which might not be known for an incomplete specimen. Computer programs can be used to determine the value of α for an observed shape that approximates a logarithmic spiral, even when the location of the center is not known a priori (Kimberley 1989). In the present study, the Matlab program fit_logspiral.m (Sommer 1998) was used to determine α for the spiral shapes of several tooth whorls. A set of points to which to fit the spiral can be derived from any convenient landmark that repeats from one tooth to the next, such as the apices of the crowns. If the apices are mostly missing, points from the basal margin can be used instead. Whether and how closely a tooth whorl conforms to a logarithmic spiral can only be determined by experiment.

The tooth whorls of both *Campyloprion* and *Helicoprion* are shaped approximately like logarithmic spirals, but with different values of α. Text-fig. 5 shows a fitted spiral overlaid on a photograph of a specimen of *Helicoprion* cf. *H. ferrieri* (Hay, 1907) from the Permian Phosphoria Formation near Soda Springs, Idaho, USA (Hess 2013). According to Tapanila and Pruitt (2013), *H. ferrieri* is a junior synonym of *H. davisi* (Woodward, 1886). The fitted spiral is chosen to give a good overall fit to the shape of the tooth whorl, but deviates systematically in the innermost and outermost parts of the tooth whorl, reflecting the changes in tooth form from early to late ontogeny. The value of α determined by fit_spiral.m is 82º. This confirms earlier work by Tapanila and Pruitt (2013, table 2), who found that the mean value of α varied from 81.3º to 83.8º in a set of 11 *Helicoprion* tooth whorls.

Fits of several *Campyloprion* tooth whorls yielded values of α of approximately 60º. An example of such a fit is shown in Text-fig. 6. The partial tooth whorl, USNM PAL330003, is from the Jacksboro Limestone Member of the Graham Formation, Virgilian (Gzhelian) Stage near Jacksboro, Texas, USA. It is here identified as *Campyloprion* sp. The fitted spiral corresponds to a value of α = 58º. The process of fitting the tooth whorls to determine α makes more quantitative



Text-fig. 5. Logarithmic spiral characterized by α = 82º overlaid on a photograph of a tooth whorl of *Helicoprion* cf. *H. ferrieri* (Hay, 1907), from the Phosphoria Formation (Permian) near Soda Springs, Idaho, USA (Hess 2013). The polar angle increases as the spiral expands clockwise. Specimen is property of the Geological Society of America. Gift of the Department of Geology, Idaho State University, Pocatello, Idaho, through H. Thomas Ore. Photograph by W.M. Itano used with permission of the Geological Society of America. Scale bar = 4 cm



Text-fig. 6. Logarithmic spiral characterized by α = 58º overlaid on photograph of *Campyloprion* sp., USNM PAL330003, from the Jacksboro Limestone Member of the Graham Formation, early Virgilian (= early Gzhelian) Stage, near Jacksboro, Texas, USA. Anterior end to left. The polar angle increases as the spiral expands clockwise. Scale in cm. Image copyrighted, Smithsonian Institution, all rights reserved (used with permission)

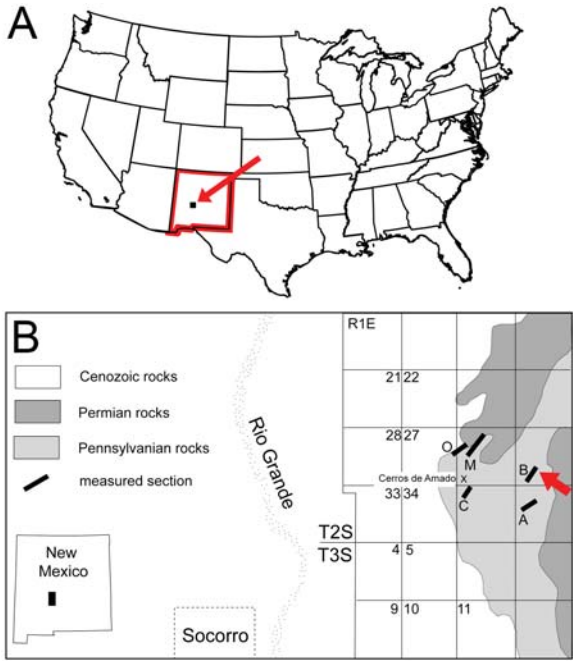
the observation that tooth whorls of *Campyloprion* are more loosely coiled than those of *Helicoprion*.

The uncertainty in the determination of α for a tooth whorl depends on the completeness of the specimen. The apices of the crowns, which are the landmarks most suited to the determination, are often missing. For a relatively complete specimen, the uncertainty in the determination of α is less than 1º, but for an incomplete specimen, the computer program might fail to determine α. There is a limit in principle to the determination, because the tooth whorl might not be a perfect logarithmic spiral.

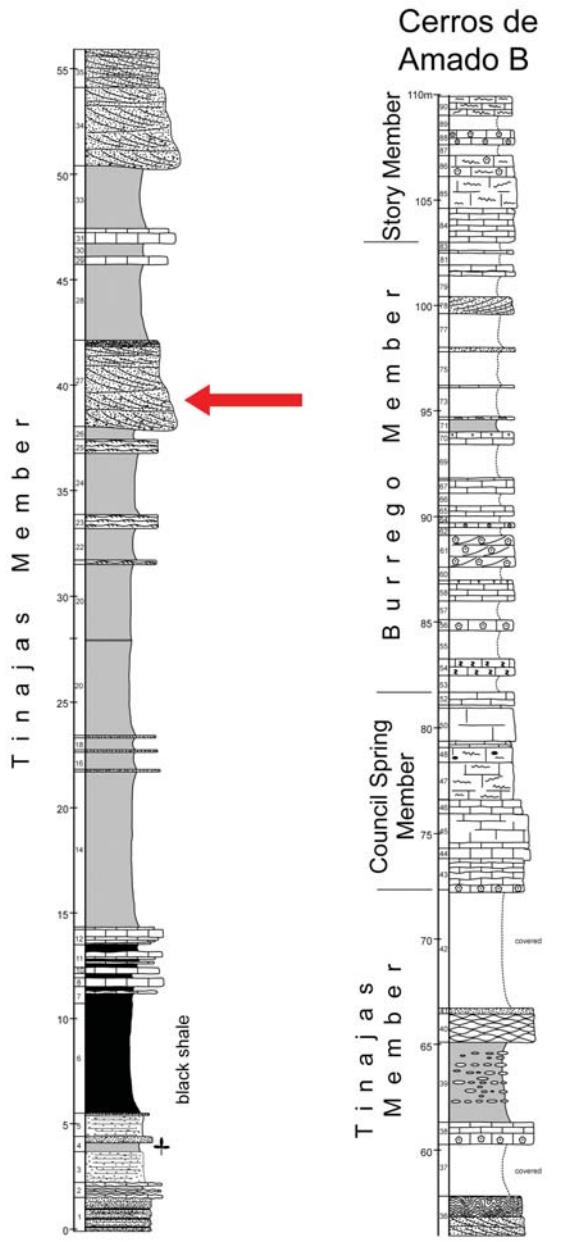
Text-fig. 7 shows the holotype, specimen number URAS P-214-1, of *Shaktauites seywi* Tchuvashov, 2001. The specimen is from the upper part of the Sakmarian Stage (Sterlitamakian Substage) at Shakh-Tau quarry, 12 km east of Sterlitamak, Russia (Tchuvashov 2001). The curve is a logarithmic spiral characterized by α = 76º. This value of α is clearly different from the values for either *Campyloprion* (approximately 60º) or for *Helicoprion* (approximately 82º) and supports the validity of *Shaktauites* as a distinct genus. The fossil is preserved in two discontinuous pieces. The fact that the extrapolation of the spiral fitted to the inner part of the tooth whorl closely fits the outer part of the tooth whorl, without any further adjustment, suggests that the two pieces were once part of the same tooth whorl and that they are in their original positions with respect to each other.

Determination of the angle α thus can be used to aid in distinguishing tooth whorls of *Helicoprion*,

Text-fig. 7. Logarithmic spiral characterized by α = 76º overlaid on photograph of the holotype of *Shaktauites seywi* Tchuvashov, 2001, specimen number URAS P-214-1, from the upper part of the Sakmarian Stage (Sterlitamakian Substage) at Shakh-Tau quarry, 12 km east of Sterlitamak, Russia. The polar angle increases as the spiral expands counterclockwise. Scale bar = 5.5 cm. Photograph after Kulagina *et al.* (2015, p. 62)



Text-fig. 8. Locality where NMMNH P-68551 was found. A – Map of United States, with state of New Mexico (NM) outlined. Arrow points to locality. B – Simplified geologic map of the locality area. Grid shows legal land survey. Numbered squares are sections, approximately one mile (1.6 km) on a side. Arrow points to measured section B, shown in detail in Text-fig. 9. After Lucas *et al.* (2009, fig. 1)



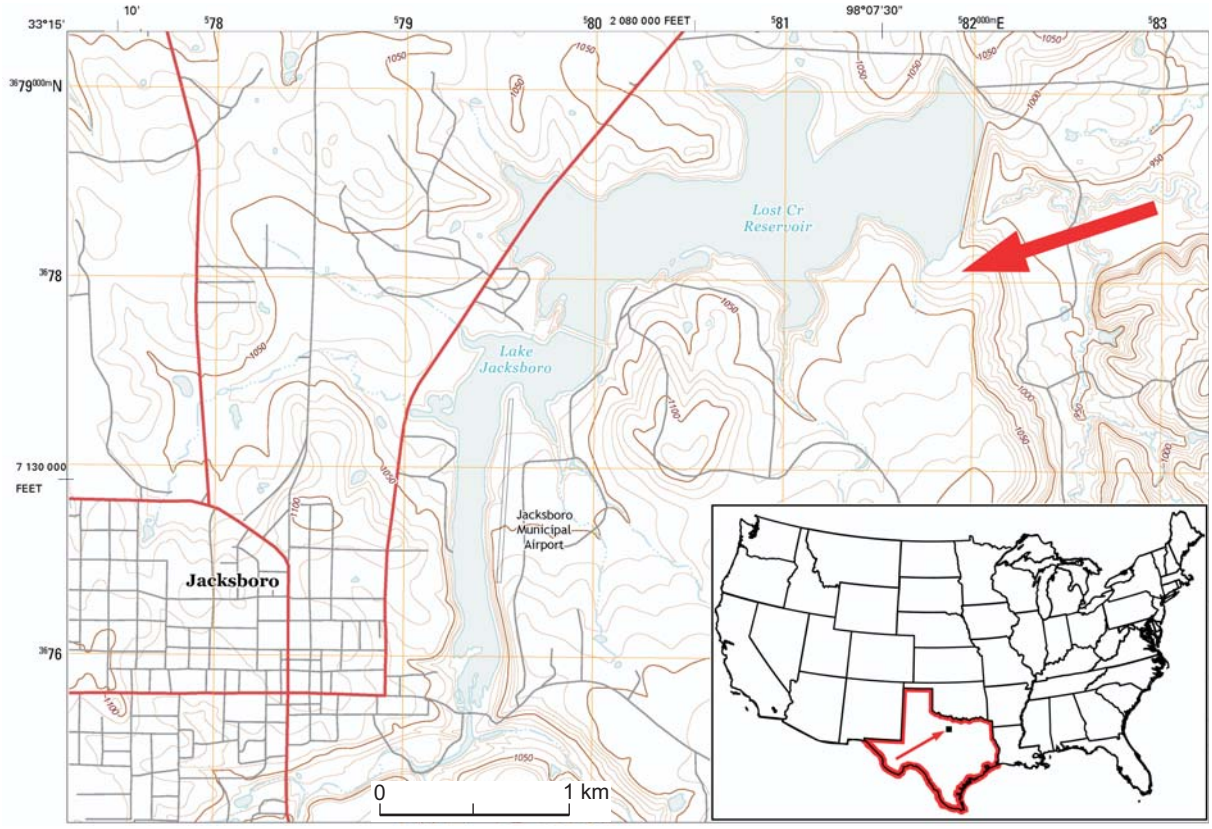
Text-fig. 9. Measured section B (see Text-fig. 8 for location), with arrow showing horizon at which NMMNH P-68551 was found. After Barrick *et al.* (2013, fig. 4)

Campyloprion, and *Shaktauites* from each other, even from very incomplete material, such as the holotype of *Helicoprion davisi* (Woodward, 1886). This possibility was anticipated by Tapanila and Pruitt (2013, p. 970), who observed that the "Spiral geometry appears to be conservative within the genus (referring to *Helicoprion*) and may be a useful generic taxobase." Determination of α may also be useful for inferring the relative positions of disarticulated parts of a single tooth whorl or for reconstructing missing parts of a tooth whorl.

GEOLOGIC SETTINGS OF THE NEWLY-REPORTED SPECIMENS FROM NEW MEXICO AND TEXAS

New Mexico locality

A partial chondrichthyan tooth whorl, NMMNH P-68551, was discovered in early 2013, at NMMNH locality 9095 in Socorro County, southern New Mexico, USA (Text-fig. 8A, B). Detailed map coordinates of the locality are on file and available to qualified researchers. The sandstone bed that produced the chondrichthyan fossil is a coarse-grained, trough-cross-bedded, crinoidal sandstone stratigraphically high in the Tinajas Member of the Atrasado Formation (Text-fig. 9). Lucas *et al.* (2009) interpreted such sandstones in the Tinajas Member as the deposits of subtidal marine channels. Conodonts



Text-fig. 10. Topographic map of area near Jacksboro, Jack County, Texas, where UCM 109521 and UCM 109522 were found. The locality is marked by an arrow. Map data from United States Geological Survey Jacksboro and Jacksboro NE Quadrangles, Texas, Jack County, 7 1/2 Minute Series (2016). Inset shows map of United States, with state of Texas outlined and locality area marked with arrow

from the Tinajas Member indicate that the upper part of the member, including the bed that produced the chondrichthyan fossil, is of late Missourian (late Kasimovian) age, close to the Missourian–Virgilian boundary (Lucas *et al.* 2009; Barrick *et al.* 2013).

Texas locality

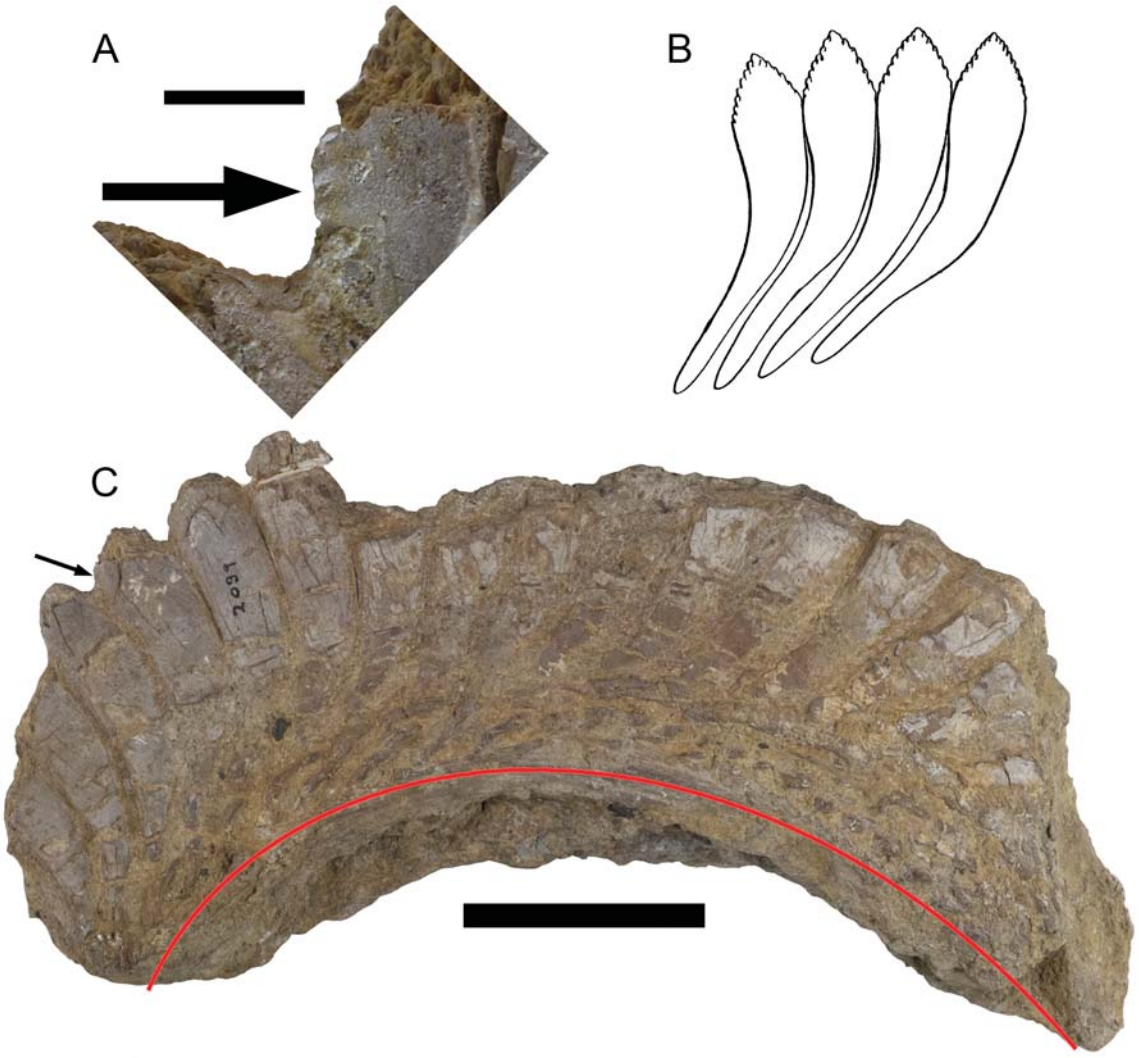
Two fragments of chondrichthyan symphyseal tooth whorls, UCM 109521 and UCM 109522, were discovered in 2001, at UCM locality 2015123 at the Lost Creek Reservoir Spillway locality, 4 km northeast of Jacksboro, Jack County, Texas (Text-fig. 10). The stratigraphic unit is the "Core" black shale facies of the Finis Shale Member of the Graham Formation (Cisco Group) (McKinzie and McLeod 2003). The locality has been described by McKinzie and McLeod (2003, fig. 4.1), although the circle on their published map indicating the specific site is slightly misplaced (M. McKinzie, pers. comm. 2017).

The age of the Finis Shale is early Virgilian (Boardman and Heckel 1989). Presence of the conodont *Idiognathus simulator* (Ellison, 1941) in the Finis Shale places this unit above and near the base of the global Gzhelian Stage (Barrick *et al.* 2013). The first appearance of *I. simulator* has been accepted as the event marker for the base of that stage (Barrick *et al.* 2013).

SYSTEMATIC PALEONTOLOGY

Class Chondrichthyes Huxley, 1880
Subclass Euchondrocephali Lund and Grogan, 1997
Order Eugeneodontiformes Zangerl, 1981
Family Helicoprionidae Karpinsky, 1911
Genus *Campyloprion* Eastman, 1902

TYPE SPECIES: *Campyloprion annectans* Eastman, 1902 (Eastman 1902a).



Text-fig. 11. Holotype of *Campyloprion annectans* Eastman, 1902, MCZ 2039 from an unknown locality and horizon. A – Arrow indicates crenulated area of crown resulting from remains of serrations. Scale bar = 5 mm; B – Reconstructed outline of four teeth. After Eastman (1902b, text-fig. 3). Mirror-reversed to aid comparison with photograph; C – Lateral view of entire tooth whorl. Anterior end to left. Arrow indicates remains of serrations. Curve is a logarithmic spiral characterized by $\alpha = 60^{\circ}$. The polar angle increases as the spiral expands clockwise. Scale bar = 5 cm. Museum of Comparative Zoology, Harvard University. © President and Fellows of Harvard College. Used with permission

REFERRED SPECIES: The type species and *Helicoprion ivanovi* Karpinsky, 1922.

EMENDED DIAGNOSIS: Known only from symphyseal tooth whorls. Teeth with pointed, laterally compressed crowns and tapered, labially projecting crown spurs. Crowns serrated. Basal surface of tooth whorl concave. In lateral view, tooth whorl shaped like a logarithmic spiral having a spiral angle of approximately 60º.

REMARKS: Eastman (1902a) noted a close similarity to *Helicoprion*. The most useful distinguishing characteristic given by Eastman (1902a) was the "lesser degree of curvature" of the tooth whorl of *Campyloprion* compared to that of *Helicoprion*. The curve overlaid on the image of the holotype in Text-fig. 11C corresponds to a logarithmic spiral with $\alpha = 60^{\circ}$. He also noted that it was extremely improbable that the tooth whorl of *Campyloprion* could have been coiled into a "complete spiral," as in *Helicoprion*. The term "complete spiral" is problematic and needs to be clarified.

A spiral is "A continuous curve traced by a point moving round a fixed point in the same plane while

Text-fig. 12. Holotype of *Campyloprion ivanovi* (Karpinsky, 1922), PIN 1655/132, from the Gzhelian Stage, Dobryatino Horizon, quarry near Rusavkino, Balashikha District, Moscow Region, Russia. A– Lateral view. Anterior end to left. Scale bar = 5 cm; B – Lateral view of two crowns, showing serrations and imbrication of adjacent crowns. Scale bar = 1 cm

steadily increasing (or diminishing) its distance from this" (OED Online, 2018). This is the general definition of a spiral, a logarithmic spiral being a special case. A mathematical spiral can be infinite. Any physical representation is finite. Unlike the term "complete circle," the term "complete spiral" has no definite meaning. A "spiral having a range of polar angle of at least one full volution (360º)" might be substituted for "complete spiral." A finite spiral with a range of polar angle of any amount, however small, is still a spiral. In the emended diagnosis of *Campyloprion*, we choose to indicate the nature of the shape of the tooth whorl by describing it as a logarithmic spiral with a particular value of spiral angle, rather than as an "incomplete" vs. "complete" spiral.

The degree of curvature is not easy to determine on an incomplete specimen, and this led to Eastman (1902a, b) referring *Edestus davisi* Woodward, 1886 to *Campyloprion*. The holotype of *Edestus davisi* is now thought to be an incomplete tooth whorl of *Helicoprion* (see e.g., Tapanila and Pruitt 2013). Eastman (1902a, b) also referred *Edestus lecontei* Dean, 1898 to *Campyloprion*. Hay (1910) later erected a new genus, *Toxoprion*, with *Edestus lecontei* as the type and only species.

The holotype of *Helicoprion ivanovi* Karpinsky, 1922 is a partial tooth whorl from Rusavkino near Moscow, Russia (Gzhelian Stage, Dobryatino Horizon), comprising seven teeth (Text-fig. 12A, B). The specimen is too incomplete for the spiral shape to be characterized. Therefore, the assignment to *Helicoprion* was natural. Later, a more complete helicoprionid specimen, PIN 1655/1, was found in deposits of the same age, at Rusavkino (Text-fig. 13A–C; Obruchev 1964, pl. 3, fig. 2). This specimen shows an open spiral form, like that of *Campyloprion* and unlike that of *Helicoprion*. The two helicoprionid specimens were presumed to belong to the same species, and *Helicoprion ivanovi* was transferred to *Campyloprion*. PIN 1655/1 was designated as a topotype of *C. ivanovi* (caption to Obruchev 1964, pl. 3, fig. 2).

Campyloprion annectans Eastman, 1902
(Text-fig. 11A–C)

1902a. *Campyloprion annectans*; Eastman, pp. 148–152, text-fig. 3, pl. 8, fig. 2.
1902b. *Campyloprion annectans*; Eastman, pp. 64–69, text-figs 4, 5, pl. 4.
1903. *Campyloprion annectans*; Eastman, pl. 21, fig. 1.

EMENDED DIAGNOSIS: A species of *Campyloprion* that has serrated crowns with a ratio of height to width (h/w) of approximately 1.0. Little or no imbrication of adjacent crowns. The spiral angle is approximately equal to 60º.

HOLOTYPE: A partial tooth whorl, MCZ 2039.

LOCALITY OF HOLOTYPE: The specimen was ob-

tained by the MCZ from Tufts College with "no clue as to its locality" (Eastman 1902a). It is presumed to be from North America. The age was presumed by Eastman (1902a) to be late Carboniferous or Permian, based on similarity to *Edestus* and *Helicoprion*.

REMARKS ON THE HOLOTYPE AND ONLY KNOWN SPECIMEN: The specimen is sufficiently complete to show the open spiral shape of the tooth whorl. The crowns are all incomplete. None have any part of the edge preserved. However, it is possible to estimate the positions of the missing edges from the tapering of the surfaces. Presumably, Eastman (1902b, text-fig. 3) reconstructed the outlines of four teeth in this way (Text-fig. 11B). Weak crenulations indicating the existence of serrations on the edges are present (Text-fig. 11A). The serration separation (ss) on the crown indicated in Text-fig. 11A is approximately 1 mm. The crown has a width (w) equal to approximately 17 mm. The computer program failed to fit a logarithmic spiral to the shape of this specimen, due the lack of a sufficient number of suitable landmarks, such as crown apices. The spiral angle was determined to be $\alpha = 60^{\circ}$, with an uncertainty of 2º, by comparison with spirals having different values of α, printed onto transparencies (Text-fig. 11C).

Campyloprion ivanovi (Karpinsky, 1922)
(Text-figs 12A, B, 13A in part)

1922. *Helicoprion ivanovi*; Karpinsky, pp. 369–378, figs 1a, b.
1953. *Helicoprion ivanovi*; Obruchev, pl. 5, fig. 1.

EMENDED DIAGNOSIS: A species of *Campyloprion* having crowns with h/w equal to approximately 1.5. Crowns coarsely serrated. Serration separation (ss) approximately 1.2 mm on a crown of width (w) equal to approximately 17 mm. Ratio of serration depth to serration separation (sd/ss) equal to approximately 0.6. Adjacent crowns imbricated. Ratio of imbrication distance to crown width (id/w) equal to approximately 0.12.

HOLOTYPE: A partial tooth whorl, PIN 1655/132.

LOCALITY OF HOLOTYPE: Quarry near Rusavkino Village, Balashikha District, Moscow Region, Russia. Pennsylvanian, Gzhelian, Dobryatino Horizon.

REMARKS ON THE HOLOTYPE AND ONLY KNOWN SPECIMEN: The specimen is not complete enough to show whether the tooth whorl has a spiral shape. All of the crowns are incomplete apically. Thus, the crown heights (h) can only be estimated very roughly. There is enough remaining, however, to show that the crowns are higher than in the holotype and only known specimen of *C. annectans*. The degree of imbrication of adjacent crowns is more pronounced in *C. ivanovi* than in *C. annectans*. Serrations on the holotype of *C. annectans* are too poorly preserved to compare them with those of *C. ivanovi*.

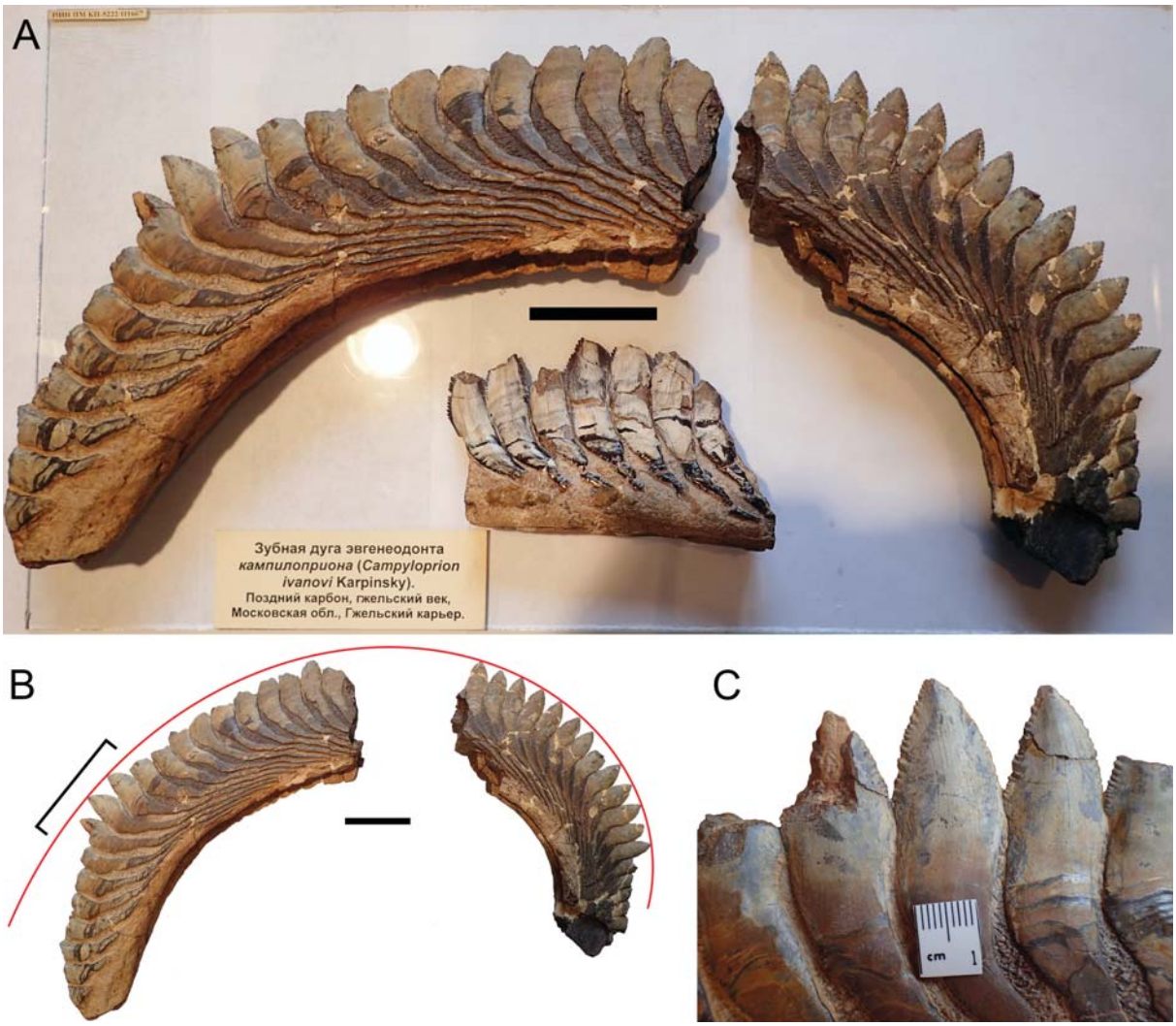
Campyloprion cf. *C. annectans* Eastman, 1902
(Text-figs 13A in part, 13B, C, 14)

1964. *Campyloprion ivanovi*; Obruchev, pl. 3, fig. 2.
1981. *Campyloprion ivanovi*; Zangerl, fig. 98F.
2010. *Campyloprion ivanovi*; Ginter *et al*., fig. 120A.

REMARKS ON SPECIMEN PIN 1655/1: Because of the general similarity of PIN 1655/1 (Text-fig. 13A–C) to PIN 1655/132, the holotype of *C. ivanovi*, and the fact that it was from deposits of the same age and a nearby locality, it was presumed also to belong to *C. ivanovi*. Figures of PIN 1655/1 have been published and identified as *C. ivanovi* (Obruchev 1964, pl. 3, fig. 2; Zangerl 1981, fig. 98F; Ginter *et al*. 2010, fig. 120A).

However, crowns of PIN 1655/1 differ from those of PIN 1655/132. They have values of h/w varying from approximately 1.05 to 1.15, versus approximately 1.5 for PIN 1655/132. They have a value of sd/ss of approximately 0.24, versus approximately 0.6 for PIN 1655/132. The value of h/w is close to that of *C. annectans* (approximately 1.0). The value of sd/ss is not known for *C. annectans*. Imbrication of adjacent crowns is present in PIN 1655/1, but is less pronounced than in PIN 1655/132 (id/w of less than 0.07 versus 0.12 for *C. ivanovi*). Overall, crowns of PIN 1655/1 are similar to those of *C. annectans*, but incompleteness of the holotype and only known specimen of that species prevents definite assignment of PIN 1655/1 to that species.

The relative positions of the two parts of PIN 1655/1 are unknown, because material between them is missing. If the tooth whorl is assumed to have been shaped like a logarithmic spiral, the two pieces can be restored to their original positions with respect to each other. Text-fig. 13B shows a logarithmic spiral characterized by a spiral angle $\alpha = 67.4^{\circ}$ fitted to the crown apices of the two pieces of PIN 1655/1. The fitting procedure was carried out in two steps. First, the computer program fit_logspiral.m was used to fit a logarithmic spiral to the eight most complete apices on the smaller piece. The resulting value of $\alpha = 67.4^{\circ}$



Text-fig. 13. *Campyloprion* cf. *C. annectans* Eastman, 1902, PIN 1655/1, from the Gzhelian Stage, Dobryatino Horizon at Rusavkino, Balashikha District, Moscow Region, Russia. A – Lateral view of entire specimen, in two pieces. Anterior end is to right. Holotype of *C. ivanovi* (Karpinsky, 1922), PIN 1655/132, included for comparison, below PIN 1655/1. Scale bar = 5 cm; B – The two pieces of PIN 1655/1, in their reconstructed original positions with respect to each other. A logarithmic spiral characterized by $\alpha = 67.4^{\circ}$ is fitted to apices of crowns of both pieces. The polar angle increases as the spiral expands counterclockwise. Scale bar = 5 cm; C – Section of PIN 1655/1 including five crowns. This section is indicated by the bracket in Text-fig. 13B. Scale = 1 cm

was extended to larger polar angles, and an image of the larger piece was moved and rotated relative to an image of the smaller piece until a match was obtained between the spiral and the positions of the crown apices (estimated where missing).

REMARKS ON SPECIMEN PIN 1655/653: Following the visit of one of the authors (WMI) to the PIN, Oleg Lebedev located another specimen assignable to *Campyloprion* in the PIN collections and supplied a photograph of it (Text-fig. 14). The specimen, PIN 1655/653, apparently has never been figured or described. It is of same age and is from the same locality as PIN 1655/1 (O. Lebedev, pers. comm. 2016). The authors have not had the opportunity to examine this specimen. However, one of the authors (WMI) located plaster casts of PIN1655/653 at the NHMUK, with specimen numbers NHMUK PV P37768 and PV P37767. The former is a cast of the three fragmentary crowns shown on the right side of Text-fig. 14; the latter is a cast of the remaining part. According to different measures, PIN 1655/653 displays similarities

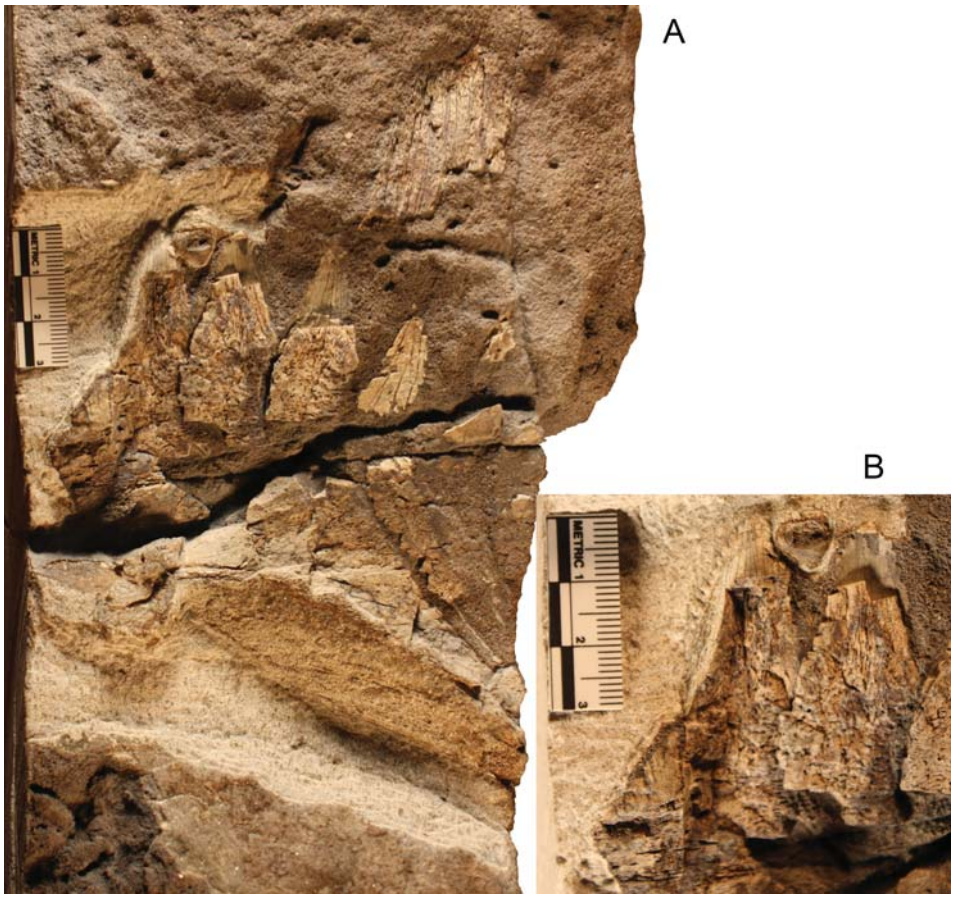
Text-fig. 14. *Campyloprion* cf. *C. annectans* Eastman, 1902, PIN 1655/653, from the Gzhelian Stage, Dobryatino Horizon at Rusavkino, Balashikha District, Moscow Region,, Russia. Scale bar = 5 cm. Photograph by O. Lebedev. Used with permission

to both PIN 1655/1 and to PIN 1655/132. The value of h/w ranges from 1.4 to 1.5, which is similar to the value of h/w estimated for PIN 1655/132. On the other hand, unlike PIN 1655/132, imbrication of adjacent crowns is barely discernible, and sd/ss varies, but averages approximately 0.3. Based on similarity of degree of imbrication and of sd/ss, PIN 1655/653 is judged to be more similar to PIN 1655/1 than to PIN 1655/132 and might belong to the same species as PIN 1655/1.

Given the lack knowledge of intraspecific variability, it is possible that all three of the specimens known from Russia represent variation within a single species, *Campyloprion ivanovi*. It is also possible that *C. ivanovi* is a junior synonym of *C. annectans*.

Campyloprion cf. *C. ivanovi* (Karpinsky, 1922)
(Text-fig. 15A, B)

REMARKS ON SPECIMEN NMMNH P-68551: The specimen preserves only a few teeth, so that the spiral shape cannot be determined. Unlike in the holotypes of *C. annectans* or *C. ivanovi*, one of the crowns has a preserved apex. The poor preservation of all of the teeth makes it difficult to measure the crown height, width, and degree of imbrication. The ratio of crown



Text-fig. 15. Partial tooth whorl of *Campyloprion* cf. *C. ivanovi* (Karpinsky, 1922), NMMNH P-68551, Tinajas Member, Atrasado Formation, late Missourian (= late Kasimovian), Socorro County, New Mexico, USA. A – Whole specimen, lateral view, anterior to right; B – Detail of two crowns, showing serrated edges and imbrication of adjacent crowns. All scales in cm

height to width (h/w) is approximately 1.5. The serration separation (ss) is approximately 1.7 mm on a crown of width (w) equal to approximately 28 mm. The ratio of serration depth to serration separation (sd/ss) is equal to approximately 0.6. Adjacent crowns are noticeably imbricated, but the amount of imbrication cannot be measured accurately due to poor preservation of the specimen. The value of h/w and the degree of imbrication of adjacent crowns are closer to the values for *C. ivanovi* than to those for *C. annectans*. The value of sd/ss is similar to that for *C. ivanovi*. The value of sd/ss is not known for *C. annectans*. Overall, NMMNH P-68551 compares more closely with *C. ivanovi* than with *C. annectans*, but there is insufficient evidence to definitely assign it to *C. ivanovi*. As previously noted, we lack knowledge of intraspecific variability, so the possibility that NMMNH P-68551 belongs to *C. annectans*, the only species described from North America, cannot be discounted.

Campyloprion sp.
(Text-figs 6, 16A, B)

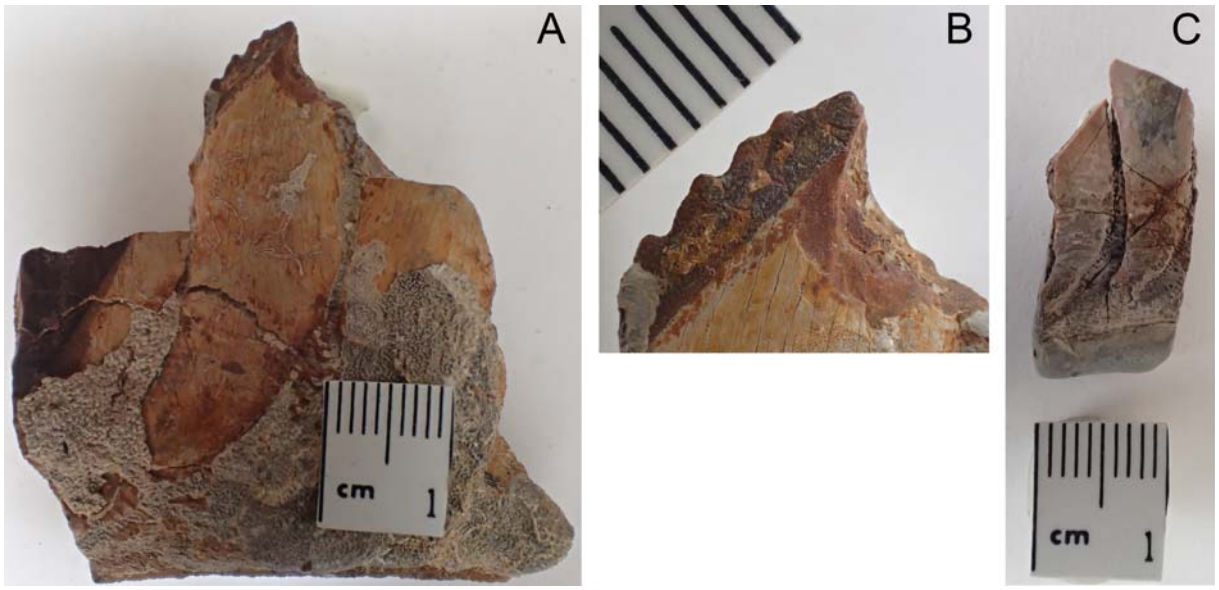
REMARKS ON TEXAS SPECIMENS FROM JACKSBORO LIMESTONE: USNM PAL330003 (Text-fig. 6) and USNM PAL330004 (Text-figs. 16A, B) are small tooth whorls that are similar to each other. They were previously catalogued as *Edestus* sp. They were found 3 miles (5 km) northeast of Jacksboro, Texas, USA, in the Jacksboro Limestone Member of the Graham Formation. The Jacksboro Limestone directly overlies the Finis Shale, so it is early Virgilian (early Gzhelian) in age (Buzas-Stephens and Kocurko 1993). There is no way to determine whether the two tooth whorls belong to juveniles or to mature individuals of a small species. The value of h/w is approximately 1.2, which is more similar to the value for *C. annectans* than to that for *C. ivanovi*. The edges are serrated. The serrations are better exposed on USNM PAL330004 (Text-fig. 16B) than on USNM PAL330003. On USNM PAL330004, ss is approximately 0.3 mm on a crown with w equal to approximately 4 mm, and sd/ss is equal to approximately 0.37. Little or no imbrication of adjacent crowns is observable on either specimen. There is insufficient evidence to assign the specimens to any particular species of *Campyloprion*, especially as we have no knowledge of early ontogenetic stages in either *C. annectans* or *C. ivanovi*.

Campyloprion sp.
(Text-figs 17A–C)

2003. *Edestus* sp.; McKinzie, pp. 115, 116, fig. 5.8.

REMARKS ON TEXAS SPECIMENS FROM FINIS SHALE: UCM 109521 (Text-fig. 17A, B) and UCM 109522 (Text-fig. 17C) are fragments of tooth whorls that were found at the same locality, in the Finis Shale Member of the Graham Formation. It is not known whether the two fragments are from the same individual, but that would be likely, given that they were found "within inches (i.e., a few centimeters) of each other" (M. McKinzie, pers. comm. 2015). The age is early Virgilian (basal Gzhelian). The crowns of UCM 109521 are incomplete, but a few, irregularly spaced serrations are preserved on the labial edge of one crown (Text-fig. 17B). There is no sufficient evidence to refer either specimen to any particular species of *Campyloprion*. Photographs of

Text-fig. 16. *Campyloprion* sp., USNM PAL330004, from the Jacksboro Limestone Member of the Graham Formation, early Virgilian (= early Gzhelian) Stage. A – Entire specimen. Anterior end to left. Scale in cm; B – View of six crowns, showing serrated edges. Scale divisions are in mm.



Text-fig. 17. Two fragments of tooth whorls of *Campyloprion* sp. from the Finis Shale Member, Graham Formation, early Virgilian (= early Gzhelian), near Jacksboro, Texas, USA. A – specimen UCM 109521 in lateral view. Anterior to left. Scale in cm; B – Detail of UCM 109521, showing serrated edge of crown. Scale in mm; C – specimen UCM 109522. Anterior to left. Scale in cm

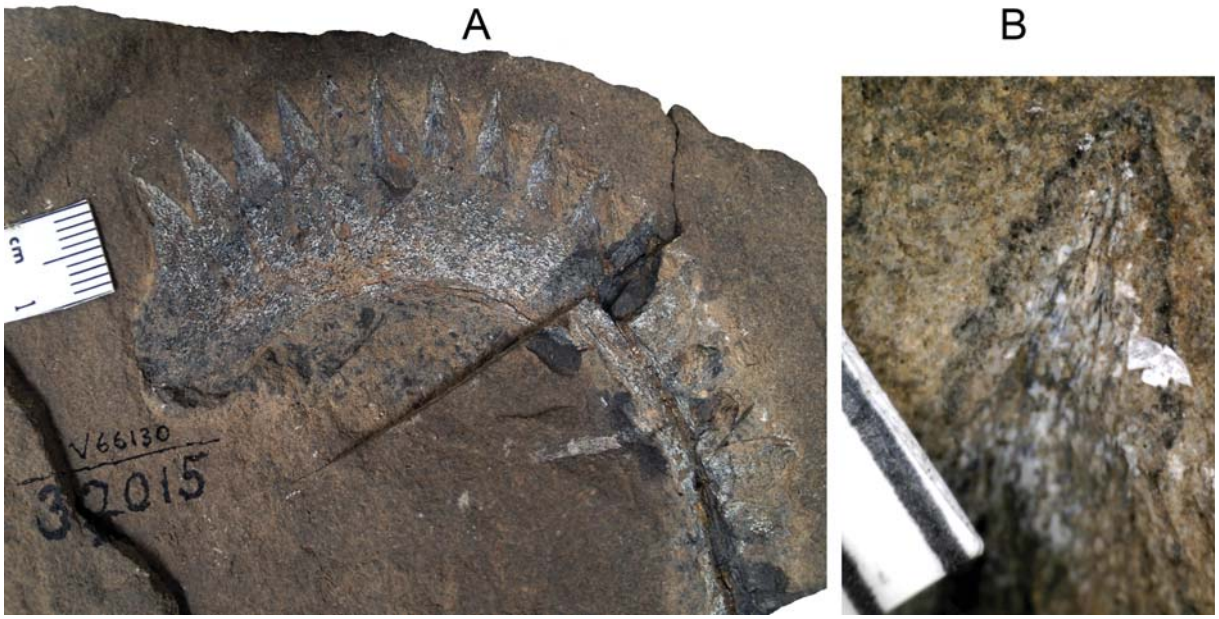
UCM 109521 were published prior to its donation to the UCM (McKinzie 2003, fig. 5.8). In that publication, it was identified as *Edestus* sp. Itano *et al.* (2012, p. 401) remarked that the morphology was inconsistent with *Edestus* and that it might be *Campyloprion.*

REMARKS ON *TOXOPRION LECONTEI* (DEAN, 1898)

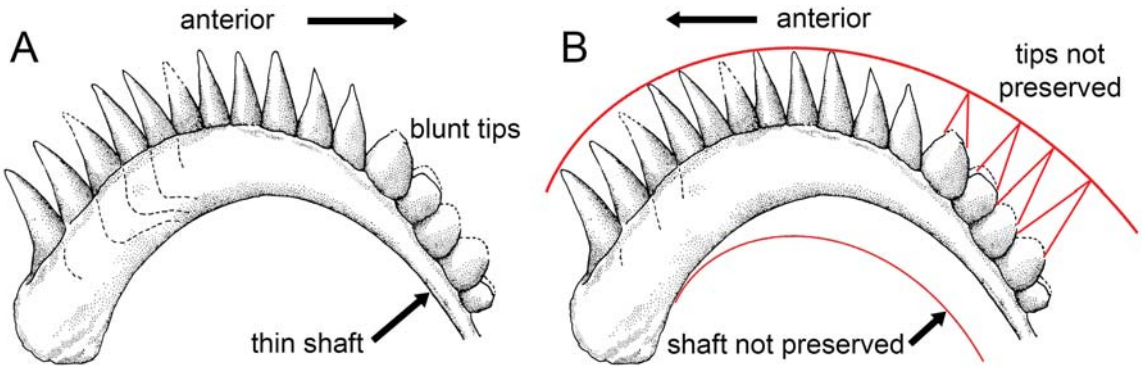
The locality of the holotype of *Toxoprion lecontei* (UCMP 32015) is poorly known. It was found within 1 mi (i.e., 1.6 km) of Eureka, Nevada, USA (Dean 1898). When it was found, its age was presumed to be Devonian or Carboniferous, since the fossiliferous deposits in that area were thought to be of those ages. The museum label still states that the locality is Devonian or Carboniferous, with a handwritten notation "Mississippian" (WMI, pers. obs. 2014). Recent references give the age as Upper Carboniferous (Obruchev 1964), ?Carboniferous (Zangerl 1981), and Carboniferous, ?Pennsylvanian (Ginter *et al.* 2010). However, there are no Devonian or Carboniferous deposits within 1.6 km of Eureka. The specimen must have come from the lower Permian Carbon Ridge Formation (Nolan *et al.* 1971, 1974), which has been dated to the Wolfcampian through Leonardian Stages by foraminiferal biostratigraphy (Stevens *et al*. 1979; Strawson 1981; Davydov *et al.* 1997). This interval corresponds to the entire Cisuralian Epoch and probably cannot be refined without more field work. However, the early Permian age is still an important correction to the previous, incorrect Carboniferous age assigned to the specimen.

UCMP 32015 (Text-fig. 18A) is incomplete. The counterpart is missing, and with it, much of the specimen. According to the conventional interpretation (Zangerl 1981), the older part of the tooth whorl is to the right in Text-fig. 19A. As new material is added to the left (lingual) end, the shaft broadens, while the crowns change shape. The change in shape of crowns, from low and blunt older crowns to high and pointed younger crowns, has been taken to be an ontogenetic change. Dean (1898) stated that the edges of UCMP 32015 are not serrated, but some of the crowns do show serrations (Text-fig. 18B). Most crowns do not show serrations, but this is likely an artifact of imperfect preservation, including the fact that the matrix might have broken along a plane not containing the crown edges.

An alternative interpretation is shown in Text-fig. 19B. The best-preserved crown apices were found to fit to a logarithmic spiral characterized by $\alpha = 62^{\circ}$, with the spiral expanding as the polar angle increases clockwise. If the spiral is then extended clockwise, a possible interpretation that obviates the need to posit an ontogenetic crown-shape change is that the "blunt-tipped" crowns are incomplete, with the apices miss-



Text-fig. 18. Holotype of *Toxoprion lecontei* (Dean, 1898), UCMP 32015 from the Carbon Ridge Formation, lower Permian (Cisuralian) near Eureka, Nevada, USA. A − View of entire specimen. Scale in cm; B − Seventh tooth from the left of the view of the tooth whorl in A, showing serrated edges. Scale in mm



Text-fig. 19. *Toxoprion lecontei* (Dean, 1898). A − Previous interpretation; B − Alternative interpretation, reversing orientation and reinterpreting incomplete parts. Curved lines are logarithmic spirals characterized by α = 62º. The polar angles increases as the spirals expand clockwise. The base (black and white) drawings in both A and B are modified from Ginter *et al.* (2010, fig. 120B) with permission from the publisher. The additions (red) to B are original with this work

ing. If a second spiral characterized by α = 62º, is fitted to the base, a possible interpretation is that the shaft broadens to the right, but most of the material is not preserved. With the alternative interpretation, anterior and posterior are reversed, and there is no drastic ontogenetic change in crown shape with age, only a gradual increase in size. The opposite anterior-posterior orientation would imply that the tooth whorl contracts, rather than expands, with age.

To the best of our knowledge, photographs of UCMP 32015 have not been published previously, forcing most workers to rely on the drawings of Dean (1898). The drawings perhaps give an unwarranted sense of clarity, given the imperfect state of preservation that can be seen in Text-fig. 18A. In particular, the dotted lines meant to show the outlines of the basal parts of the teeth are not as clear on the original as in Dean's drawings (Text-fig. 19A). For that reason, the dotted lines are truncated in Text-fig. 19B where the basal outlines are not clear on the specimen. Dean's interpretation of the specimen was likely influenced by his belief that it belonged to the genus *Edestus*.

Helicoprion, to which it might be more closely related, was not known at the time. *Edestus* and *Helicoprion* have quite different tooth whorl morphologies (Zangerl 1981; Ginter *et al.* 2010). Further, we now know that the tooth whorls of both *Edestus* and *Helicoprion* are dental apparatuses located in the oral region (Hay 1912; Bendix-Almgreen 1966; Lebedev 2009; Tapanila *et al.* 2013). Dean (1898) believed that the fossils of *Edestus*, including the species represented by UCMP 32015, were defensive spines located in some other part of the body than the oral region. Such a spine would have different constraints on growth and morphology than a tooth whorl required to be part of a functional feeding apparatus. Our increased knowledge since Dean's work might justify a reexamination of the assumptions leading to his drawings.

If the alternative interpretation of the type specimen of *Toxoprion lecontei* is accepted, that species might prove to belong to *Campyloprion*. However, we refrain from reclassifying it at this time, pending more information. Lacking other specimens from the locality, a micro-CT (micro computed tomography) examination of the holotype might help to distinguish between the alternative interpretations.

HOW MANY SPECIES OF *CAMPYLOPRION* IN THE PENNSYLVANIAN?

At the present time, two species of *Campyloprion* are recognized in the Pennsylvanian – *C. annectans* and *C. ivanovi*. Identification of *Campyloprion* specimens to species is difficult, given the scarcity of specimens from any given locality and the incomplete nature of the type material. *Campyloprion* is defined by having symphyseal teeth like those of *Helicoprion*, but a tooth whorl having a more open spiral shape. *Campyloprion annectans*, the type species of the genus, has a tooth whorl, the shape of which is approximated by a logarithmic spiral with a spiral angle of approximately 60º. The holotype of *C. ivanovi* is not complete enough to determine the spiral angle. In the present work, the assignment of PIN 1655/1, which does display an open spiral shape, to *C. ivanovi* has been questioned, due to differences in crown morphology. Hence, it is possible that discovery of more complete remains definitely referable to *C. ivanovi* might result in that species being transferred to some other genus, if the shape of the complete tooth whorl of *C. ivanovi* turns out to be very different from that of *C. annectans*. In that case, *C. annectans* and *C. ivanovi* would remain distinct species, but *C. ivanovi* would have to be assigned to a genus other than *Campyloprion*. It is also possible that more than two species of *Campyloprion* are represented in the assemblage of known Pennsylvanian specimens. However, at the present time, defining new species would be unwarranted, given the lack of knowledge of intraspecific variability, possible sexual dimorphism, and ontogeny. Given the present state of knowledge, it is possible that all three of the Russian specimens – PIN 1655/132, PIN 1655/1, and PIN 1655/653, represent variation within a single species, *Campyloprion ivanovi*. It is also possible, given the present state of knowledge, that *C. ivanovi* is a junior synonym of *C. annectans*. Until more specimens are found, the situation cannot be resolved with any degree of certainty.

AGE RANGE OF *CAMPYLOPRION*

The oldest, well-documented occurrence of *Campyloprion* is that of the New Mexican specimen of *Campyloprion* cf. *C. ivanovi*, in the late Missourian (late Kasimovian). The Russian occurrences, in the early Gzhelian (Dobryatino Horizon), are younger. The latest known occurrences of *Edestus* are in the late Desmoinesian (earliest Kasimovian) of North America and Russia (Lebedev 2001; Itano *et al.* 2012). Thus, there is a temporal gap between the last known occurrence of *Edestus* and the first known occurrence of *Campyloprion*.

A poorly documented specimen of a partial tooth whorl from the Volga region of Russia is mentioned for completeness (Petukhov *et al.* 2011). Based on conodont biostratigraphy, it is dated to the Khamovnikian Substage of the Kasimovian Stage. A photograph has been published on the World Wide Web (https://www.museum-21.ru/Edestus_sp/E%20_sp.html). Although labeled as *Edestus* sp., it more resembles *Campyloprion*. If this specimen does belong to *Campyloprion*, then the temporal gap between the youngest *Edestus* and the oldest *Campyloprion* is narrowed but not closed. Given the apparent convergence in morphology of *Campyloprion* and *Edestus* tooth whorls, the temporal gap suggests that *Campyloprion* might have evolved to fill an ecological niche left vacant by the extinction of *Edestus*.

In the absence of any preserved cranial material of *Campyloprion* other than the tooth whorls, the position of the tooth whorls within the head is unknown. It is possible that the tooth whorl fits entirely inside the oral cavity, as is the case for *Sarcoprion* (Nielsen 1952). It is also possible that the labial end of the tooth whorl extended outside the oral cavity, as has been hypothesized for *Edestus* (Itano 2014, 2015, 2018).

Acknowledgments

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