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FEATURED ARTICLE

A SELACHIAN FRESHWATER FAUNA FROM THE TRIASSIC OF KYRGYZSTAN AND ITS IMPLICATION FOR MESOZOIC SHARK NURSERIES

JAN FISCHER,*,[1] SEBASTIAN VOIGT,[1] JÖRG W. SCHNEIDER,[1] MICHAEL BUCHWITZ,[1] and SILKE VOIGT[2]
[1]Geologisches Institut, TU Bergakademie Freiberg, Bernhard-von-Cotta Strasse 2, 09599 Freiberg, Germany, j.fischer1@yahoo.de;
[2]Goethe Universität Frankfurt am Main, Institut für Geowissenschaften, Altenhöferallee 1, 60438 Frankfurt, Germany

ABSTRACT—Habitat partitioning and site fidelity of spawning grounds are well-documented phenomena in extant selachians, but little is known about the reproductive strategies of their fossil relatives. Here we describe the selachian fauna of the Middle to Late Triassic Madygen Formation in southwestern Kyrgyzstan, Central Asia, based on several dozen tooth crowns and egg capsules. The material is assigned to three new taxa: *Lonchidion ferganensis*, sp. nov., and *Palaeoxyris alterna*, sp. nov., being teeth and egg capsules of hybodontid sharks, and *Fayolia sharovi*, sp. nov., being egg capsules of probable xenacanthids. Teeth of *L. ferganensis*, sp. nov., were almost exclusively found in pelecypod-rich shallow lacustrine mudstones and belong to juvenile individuals. Oxygen and strontium isotope data of tooth enameloid indicate freshwater conditions of the ambient water at the time of tooth mineralization. The egg capsules are common findings in near-shore lake deposits as well. Considering the mass co-occurrence of juvenile teeth and egg capsules in the study area, we propose that hybodontid/xenacanthid sharks recurrently occupied littoral zones of the Madygen lake for spawning. The small number of full-grown individuals points to habitat partitioning of juveniles and adults wherefore the study site is interpreted as a shark nursery. The oviposition strategies inferred from this fossil example are remarkably similar to those of modern sharks, suggesting that the reproductive patterns seen in extant sharks originated well before the Cenozoic.

INTRODUCTION

Unlike extant selachians, which represent only a small proportion of some Recent tropical to subtropical freshwater ichthyofaunas (Compagno, 1990; Compagno and Cook, 1995), their extinct relatives are abundant, diverse, and widespread elements in nonmarine deposits (e.g., Schneider and Zajíc, 1994; Cuny et al., 2004; Heckert, 2004; Fischer, 2008; Prasad et al., 2008; Klug et al., 2010). This imbalance raises questions about the ecology of certain fossil sharks inasmuch as these animals were either (1) obligate freshwater fishes sensu Compagno and Cook (1995) (Schneider and Zajíc, 1994; Fischer et al., 2010b); (2) euryhaline fishes of coastal marine environments that frequently penetrated freshwater habitats for foraging and spawning (Schultze and Soler-Gijón, 2004); or (3) inhabitants of marine-influenced inland biotopes such as estuaries (Schultze and Soler-Gijón, 2004; Schultze, 2009). Besides teeth, scales and fin spines are the only mineralized skeletal remains of fossil sharks; their egg capsules are being increasingly reported from Paleozoic and Mesozoic brackish to fluvio-lacustrine deposits (Böttcher, 2010; Fischer et al., 2010a). Because all modern freshwater selachians are viviparous (live-bearing), and ovipary (egg-laying) is restricted to marine forms (Compagno, 1990; Compagno and Cook, 1995), it is sometimes concluded that fossil egg capsules exclusively indicate spawning in marginal marine environments (Schultze and Soler-Gijón, 2004). This, however, is in contrast to the habitat partitioning with freshwater nurseries proposed for Late Paleozoic xenacanthid and hybodontid sharks (Maisey, 1989; Schneider and Reichel, 1989; Schneider, 1996; Schneider et al., 2005).

Here we present the first comprehensive description of the selachian fauna from lacustrine deposits of the Middle to Late Triassic (Ladinian–Carnian) Madygen Formation, southwestern Kyrgyzstan, Central Asia. Sharks are recorded from these beds in the form of hybodontid teeth and two types of egg capsule collected during annual expeditions to Kyrgyzstan carried out from 2006 to 2009. Isotopic data for the shark tooth enameloid were obtained in order to test the interpretation of the Triassic Madygen lake as a freshwater hydrological system. On the basis of the distribution of teeth and egg capsules within the several-hundred-meter-thick succession of sedimentary rocks, we discuss the potential role of Madygen as a freshwater nursery for oviparous Mesozoic sharks. The present paper introduces this important fauna of freshwater selachians in more detail and evaluates these findings in the context of the controversies surrounding habitat requirements and reproductive strategies of fossil sharks.

LOCALITY AND GEOLOGICAL SETTING

The Madygen fossil site at the stratotype area of the Madygen Formation is situated about 50 km to the west of the provincial capital of Batken in southwestern Kyrgyzstan, Central Asia (Fig. 1A). By the number, diversity, and quality of its fossils, including plants, aquatic invertebrates, insects, fishes, and tetrapods with soft tissue preservation, the Madygen Formation has been classified as a conservation/concentration lagerstätte (Voigt et al., 2006; Shcherbakov, 2008). Macrofloral and insect remains suggest a Middle to Late Triassic (Ladinian–Carnian) age for the succession (Dobruskina, 1995; Shcherbakov, 2008). The Madygen Formation comprises an up to 600 m thick succession of interbedded conglomerates, sandstones, and mudstones that are interpreted as alluvio-fluvial to lacustrine deposits in a tectonically active, predominantly overfilled lake basin (Voigt et al., 2006; Berner et al., 2009; Voigt and Hoppe, 2010). The most complete section of the Madygen Formation is in the southwestern outcrop area (Urochishche Madygen) and records three intervals of lacustrine deposits, which range in thickness from 40 to 190 m (Fig. 1B). At the current state of knowledge, it is unclear whether the lacustrine sequences 1–3 represent successive lake stages with

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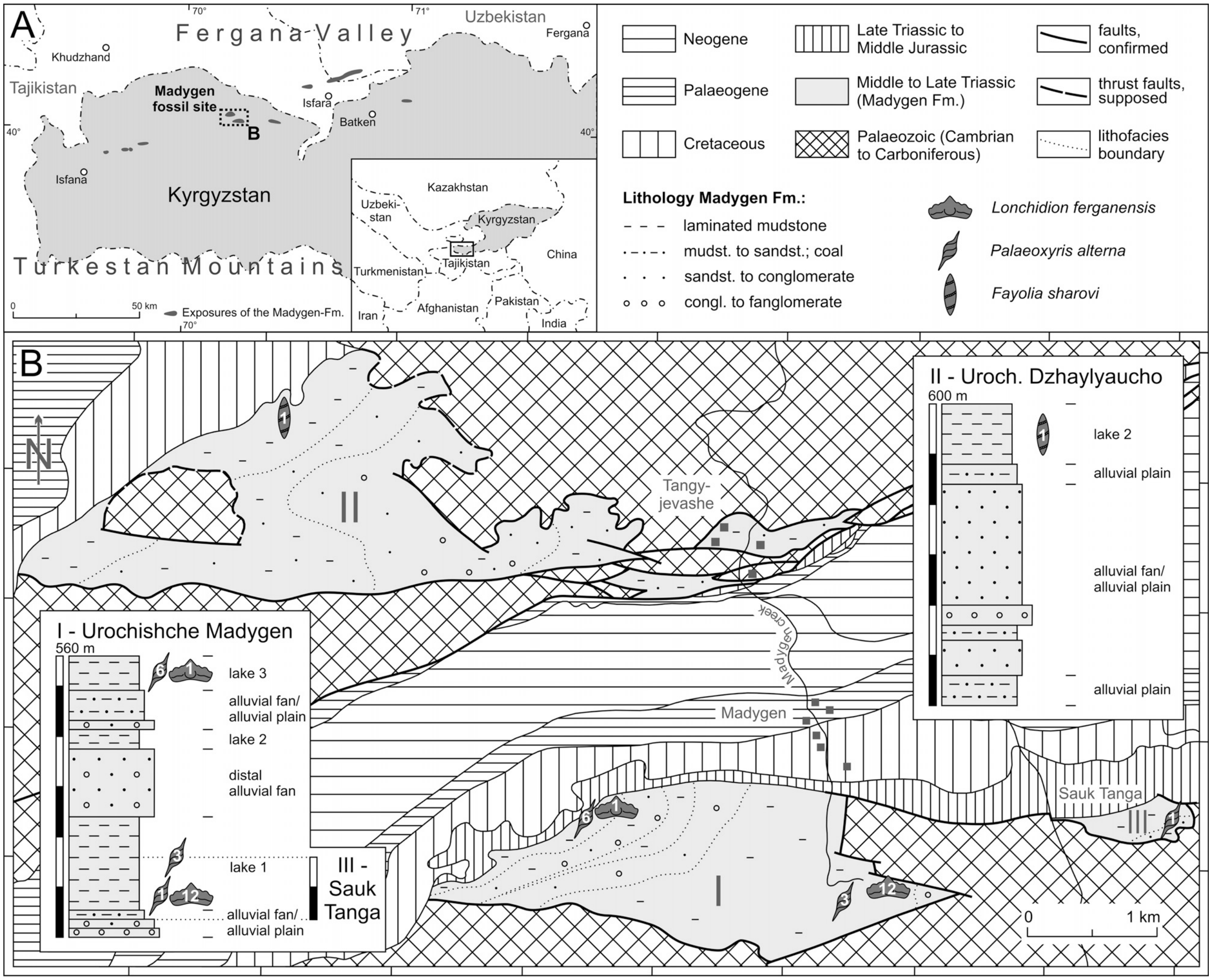

FIGURE 1. **A**, Diagrammatic map showing exposures of the Madygen Formation in southwestern Kyrgyzstan and neighboring territories in Central Asia. **B**, Simplified geological map of the Madygen area with generalized sections of the two most extended outcrop areas of the Madygen Formation (I, Urochishche Madygen; II, Urochishche Dzhaylyaucho; III, Sauk Tanga) showing the geographic and stratigraphic position of the shark remains (modified from Voigt and Hoppe, 2010). Numbers in the fossil symbols refer to the locality numbers in Table 1.

significantly fluctuating shorelines or three individually evolved lakes. The minimum lateral extent of the Triassic lake environment at Urochishche Madygen accounts for about 1.7 km. Paleogeographic reconstructions (Federenko and Militenko, 2002) suggest that during the Early Mesozoic most of the area forming the present day Fergana Valley was an upland denuded plain that might have been occupied by an extended lake ranging tens of kilometers in length. If this scenario is correct, Madygen could represent just a remnant of the margin of such a huge lake.

Shark remains are known from six localities in three different outcrop areas of the Madygen Formation (Table 1). Hybodontid egg capsules (*Palaeoxyris alterna*, sp. nov.) were recovered in the lacustrine sequence 1 of the Sauk Tanga area and in the lacustrine sequences 1 and 3 of the southwestern outcrop area (Urochishche Madygen; Fig. 1B, Table 1). A 5 m thick horizon of dark-grey, carbonaceous bivalve-rich mudstones at the base of the lacustrine sequence 1 at Urochishche Madygen has yielded several dozen hybodontid teeth (*Lonchidion ferganensis*, sp. nov.). A second type of egg capsule (*Fayolia sharovi*, sp. nov.) comes from lake deposits at the top of the succession in the northwestern outcrop area (Urochishche Dzhaylyaucho) (Fig. 1B, Table 1). In accordance with Dobruskina (1995), we correlate these lake deposits with the lacustrine sequence 2 of the type section at Urochishche Madygen. Accordingly, selachians are present in all three lacustrine sequences of the Madygen Formation in the study area.

MATERIALS AND METHODS

Shark microfossils have been gained by processing about 70 kg of a bivalve shell bed with light petrol according to the method of Layne (1950). The loosened rock matrix was dissolved in 10% formic acid. Specimens were coated with graphite and photographed with a scanning electron microscope (JEOL JSM6400). Several egg capsule specimens have been prepared. The surfaces were sealed by a thin layer of PVAC (Polyvinylacetat), and photographed with a reflex camera. The descriptive terminology of the teeth is modified from Duffin (1985)

TABLE 1. Locality specification of the recovered tooth crowns and egg capsules from the Madygen Formation.

Locality	Horizon	Interpretation	Taxon	Specimen no.
LI/1: Urochishche Madygen, R 0604559/H 4432577	Lacustrine sequence 3; Brown-Grey Member (T5)	Lacustrine, Sublittoral (prodelta)	*Lonchidion ferganensis*	FG 596/III/42
LI/3: Urochishche Madygen, R 0606721/H 4431875	Lacustrine sequence 1; Lower Grey Member (T2)	Lacustrine, Littoral to sublittoral	*Palaeoxyris alterna*	FG 596/III/46–47
LI/6: Urochishche Madygen, R 0604424/H 4432548	Lacustrine sequence 3; Brown-Grey Member (T5)	Lacustrine, Sublittoral (prodelta)	*Palaeoxyris alterna*	FG 596/III/1, 12–17, 22–41
LI/12: Urochishche Madygen, R 0606897/H 4431953	Lacustrine sequence 1; Dark Member (T1)/Lower Grey Member (T2)	Lacustrine, Littoral to sublittoral	*Lonchidion ferganensis*	FG 596/III/49–70, 92–94
LII/1: Urochishche Dzhaylyaucho, R 0602032/H 4435521	Lacustrine sequence 2; Upper Grey Member (T4)	Lacustrine, Littoral to sublittoral (delta-front)	*Fayolia sharovi*	FG 596/III/2, 18–21, 71–72
LIII/1: Sauk Tanga, R 0608814/H 4432590	Lacustrine sequence 1; Dark Member (T1)/Lower Grey Member (T2)	Lacustrine, Littoral to sublittoral	*Palaeoxyris alterna*	FG 596/III/48

(Fig. 2A–D); the scale terms are modified from Thies (1995) and Johns et al. (1997) (Fig. 2E–F); and the egg capsule terminology follows Crookall (1928a), Fischer et al. (2010a), and Böttcher (2010) (Fig. 2G–H).

Due to the very small size of fish teeth, the oxygen isotope composition ($\delta^{18}O_P$) was measured for several bulk tooth samples, each comprising three to six individual crown fragments. About 0.7–1.0 mg of tooth enameloid or enameloid-rich parts was dissolved in dilute nitric acid and the isolated phosphate group chemically converted into Ag_3PO_4 and weighted into silver capsules according to the method of Joachimski et al. (2009). Oxygen isotope analyses were performed in triplicate on CO generated by reducing trisilverphosphate at 1450°C using a high-temperature conversion elemental analyzer (TC-EA) connected to a ThermoFinnigan Delta Plus mass spectrometer at the Geological Institute of the University of Erlangen, Germany. All values are expressed in ‰ in δ-notation relative to VSMOW (Vienna Standard Mean Ocean Water), with reproducibility better than ±0.2‰ (1σ). The mean $\delta^{18}O_P$ value of the international laboratory standard NBS 120c (Miocene phosphorite) is 22.4‰ VSMOW.

Strontium isotope analyses were performed on several bulk tooth samples. About 0.7–0.9 mg of tooth material was decomposed in dilute hydrochloric acid, processed, passed through preconditioned cation-exchange micro-columns, and loaded onto wolfram filaments similar to the method described by Schmitz et al. (1991). The $^{87}Sr/^{86}Sr$ ratios were determined on a Finnigan MAT 262 mass spectrometer at the Mineralogical Institute of the Technical University Freiberg, Germany. Samples were measured in 20 blocks, with mean analytical uncertainty (σ) for the measured $^{87}Sr/^{86}Sr$ ratios of $\pm16^{-5}$.

Institutional Abbreviations—All fossil specimens are housed at the Department of Paleontology, Geological Institute, Technical University Bergakademie Freiberg, Germany, and catalogued as FG 589/III/1 to 94 (Table 1).

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Cohort EUSELACHII Hay, 1902
Superfamily HYBODONTOIDEA Owen, 1846
Family LONCHIDIIDAE Herman, 1977
Genus *LONCHIDION* Estes, 1964

Type Species—*Lonchidion selachos* Estes, 1964, latest Cretaceous (Maastrichtian) Lance Formation of eastern Wyoming, U.S.A.

Diagnosis—See Rees and Underwood (2002).

Record—Middle Triassic (?Ladinian) (Rees and Underwood, 2002) to Late Cretaceous (Maastrichtian) (Estes, 1964), from Europe, Asia, North America, and Africa.

LONCHIDION FERGANENSIS, sp. nov.
(Fig. 3)

2009 *Lissodus* sp. Kogan et al., 2009:145, fig. 5g.

Etymology—Named after the type locality situated at the southern margin of the Fergana Valley, Central Asia.

Holotype—FG 596/III/58, a mesial tooth crown of morphotype III (Fig. 3A).

Type Locality—SW Madygen outcrop area (Urochishe Madygen) south of Madygen village, Batken District (Oblast), SW Kyrgyzstan (Madygen locality LI/12; Fig. 1, Table 1).

Type Horizon—Base of the lacustrine sequence 1 ('Dark-coloured Member' sensu Dobrsukina, 1995), Madygen Formation (Ladinian–Carnian, Middle to Late Triassic).

Paratypes—FG 596/III/49, a lateral to posterolateral tooth crown of morphotype I; FG 596/III/54, an anterolateral tooth crown of morphotype II; FG 596/III/62, a mesial tooth crown of morphotype III; FG 596/III/42, a tooth crown of a supposed adult specimen (Fig. 3B–E).

Referred Material—17 tooth crowns; three of morphotype I (FG 596/III/50–51; FG 596/III/56), two of morphotype II (FG 596/III/52; FG 596/III/55), 12 of morphotype III (FG 596/III/53; FG 596/III/57; FG 596/III/59–61; FG 596/III/63–69).

Diagnosis—Tiny, heterodont tooth crowns of *Lonchidion* measuring from 0.88 to 2.04 mm mesiodistally, 0.44 to 0.87 mm labiolingually, and 0.32 to 0.77 mm apicobasally. Central cusp low or prominent, becoming slightly inclined labially in mesial teeth; flanked by up to three pairs of lower lateral cusplets. In occlusal view, distal parts slightly inclined lingually in mesial teeth, teeth symmetrical to slightly asymmetrical triangular. Crown faces triangular-shaped and smooth except for several randomly distributed nodules labially, lacking vertical striations or accessory cusplets on the crown shoulders; a strong longitudinal, partly interrupted ridge surmounts the crown shoulders, is occasionally crenulated, and may be continuous around the crown. Occlusal crest moderate to strong with occasional crenulations; expanding mesiodistally through cusplet apices, and also descending from the central cusp to the labial peg. Labial peg well developed, triangular in occlusal view, narrow to broad; up to two accessory cusplets on the labial ridge. Lingual peg moderate, wider than labial peg, faint extension of occlusal crest may descend. Crown/root junction is moderate to strongly incised around the whole crown. Root unknown in any specimen.

Description—Three morphotypes can be distinguished among the tooth crowns (Table 2):*Morphotype I* (Fig. 3B) is the most

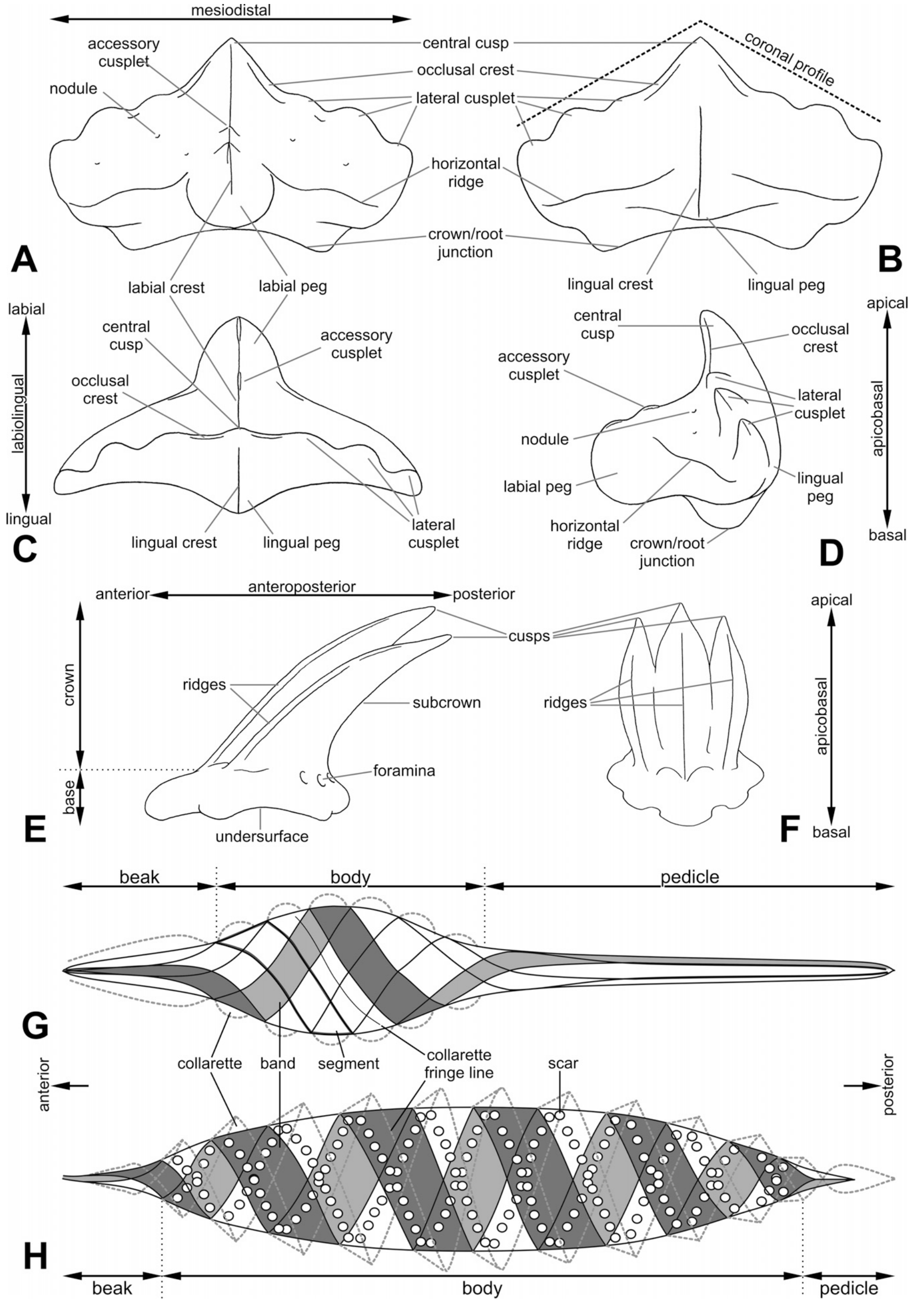

FIGURE 2. Descriptive terminology of teeth, denticles, and egg capsules used in this study. **A–D**, tooth crowns following Duffin (1985) in **A**, labial; **B**, lingual; **C**, occlusal; and **D**, lateral views. **E–F**, dermal denticle modified from Thies (1995) and Johns et al. (1997) in **E**, lateral and **F**, oblique anterior views. **G**, egg capsule terminology of *Palaeoxyris* after Fischer et al. (2010a) and Böttcher (2010). **H**, egg capsule terminology of *Fayolia* after Crookall (1928a). The course of one band in both capsule types is shaded with grey to emphasize its course around the capsule.

massive crown morphotype containing the largest of all recovered crowns from Madygen locality LI/12 (Fig. 3F); *Morphotype II* (Fig. 3C) represents the smallest specimens of the crown bulk (Fig. 3F), strongly resembling morphotype I in its low coronal profile but it is less massive with a narrower labial peg than the latter; *Morphotype III* (Fig. 3A, D) represents the most common crown type in the tooth assemblage. A single large crown (Fig. 3E, Table 2) from Madygen locality LI/1 (Fig. 1, Table 1) exhibits a somewhat different morphology. In spite of the missing lateral and accessory cusplets, whose existence can only be assumed from abraded areas in corresponding parts, and the noticeable bifurcation of the horizontal ridge, the preserved suite of characters strongly resembles morphotype III (Table 2), despite the size difference of about 40% (Fig. 3F).

Tooth crowns sectioned for histological investigations reveal a thick layer of enameloid (up to 40 μm), especially well developed on apical side (Fig. 3H). Beneath the enameloid, an orthodentine core is developed containing long, subparallel dentine tubules radiating in a fan-shaped pattern in direction of the enveloping enameloid layer (Fig. 3G). Osteodont structures are not developed in any of the tooth crowns of *L. ferganensis*, sp. nov., examined histologically.

Comparison—The reconstruction of heterodont shark dentition based on disarticulated, root-less teeth is difficult (Duffin, 1985). Assuming that the tooth morphotypes constituted the dentition of a single species, the main characteristics allow some determination of relative position on the jaw (e.g., Duffin, 1985; Duncan, 2004; Heckert et al., 2007; Cuny et al., 2009). Morphotype I is hypothesized to represent teeth of lateral to posterolateral position because it is massive, with a broad and relatively obtuse labial peg. Morphotype II is regarded as anterolateral as a result of its prominent narrow labial peg but the low coronal

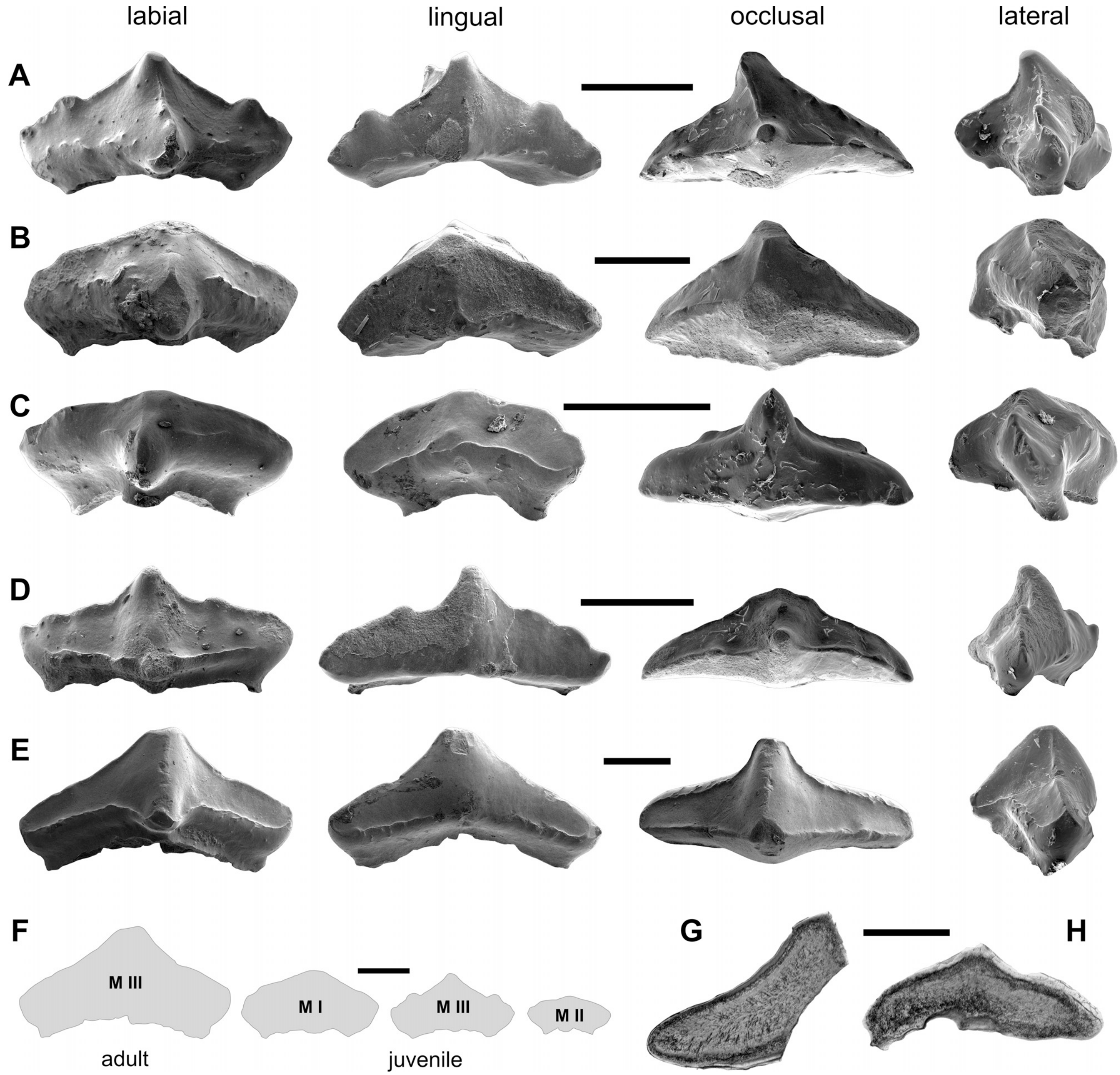

FIGURE 3. Tooth crowns of the hybodontid *Lonchidion ferganensis*, sp. nov., in labial, lingual, occlusal, and lateral views. **A**, holotype FG 589/III/58, (morphotype I); **B**, paratype FG 589/III/49, (morphotype I); **C**, paratype FG 589/III/54, (morphotype II); **D**, paratype FG 589/III/62, (morphotype III); **E**, paratype FG589/III/42, adult tooth crown (morphotype III). Thin sections of crowns of *Lonchidion ferganensis*, sp. nov., shown under ordinary light in **G**, FG 589/III/70, occlusal view; and **H**, FG 589/III/92, lateral view. **F**, outline comparison of the general size of juvenile morphotypes I–III with adult morphotype III (FG 589/III/42). Scale bars for **A**–**E**, **F** equal 0.5 mm and for **G**–**H** equal 0.3 mm.

profile. Morphotype III most likely occupied a mesial position due to the high coronal profile and the prominent labial peg, which is in accordance with the mesial position of '*Lonchidion*-like' tooth forms in the dentition of *Lissodus nodosus* (Seilacher, 1943) as reconstructed by Duffin (1985). Morphological variation of teeth in heterodont dentitions is of functional significance, for example, clutching in mesial positions and crushing in anterolateral to posterolateral positions (Duffin, 1985; Cappetta, 1987; Heckert et al., 2007). Continuous anterior occlusal pressure could explain the abrasion pattern seen in all tooth morphotypes.

Several characteristics (e.g., crowns are mesiodistally wider than high, labial peg is well developed, cusps prominent to low) argue for an assignation of the Madygen crowns to the hybodontid family Lonchidiidae (Rees and Underwood, 2002), which contains the genera *Lonchidion* Estes, 1964, *Vectiselachos* Rees and Underwood, 2002, *Parvodus* Rees and Underwood, 2002, and *Hylaeobatis* Woodward, 1916, or to the genus *Lissodus* Brough, 1935, which is currently left without family assignment (Rees, 2008). The presence of distinct central cusp and lateral cusplets, the pronounced labial peg in all three morphotypes, and

TABLE 2. List of characters available to distinguish the different crown morphotypes and the single specimen FG 596/III/42 of *Lonchidion ferganensis*, sp. nov.

Character	Morphotype I	Morphotype II	Morphotype III	FG 596/III/42
Mesiodistal length	1.38–1.48 mm	0.88–0.98 mm	0.91–1.27 mm	2.04 mm
Labiolingual length	0.70–0.79 mm	0.44–0.52 mm	0.44–0.66 mm	0.87 mm
Apicobasal length	0.50–0.67 mm	0.32–0.40 mm	0.39–0.59 mm	0.77 mm
Coronal profile	Low	Low	High	High
Central cusp	Obtuse	Obtuse	Prominent, pointed, slightly labially inclined	Prominent
Lateral cusplets	Abraded to absent	Up to 2 pairs, obtuse	Up to 3 pairs, moderate, slightly labially inclined	?
Crown face	Several randomly distributed nodules labially	Smooth	Several randomly distributed nodules labially	Smooth
Horizontal ridge	Strong	Strong	Strong, casually crenulated	Strong, crenluated and bifurcated
Labial peg	Broad, triangular, moderate occlusal crest	Narrow, moderat occlusal crest	Narrow, elongated, bent in ?mesial direction, strong occlusal crest, 2 accessory cusplets	Narrow, occlusal crest and accessory cusplets indicated but abraded
Lingual peg	Faint, broader than labial peg, weak occlusal crest	Faint, weak occlusal crest	Moderate, as broad as labial peg, weak occlusal crest	Moderate
Occlusal shape	Symmetrical	Symmetrical, lateral extremities slightly bent lingually	Mesiodistally elongated, asymmetrical, lateral extremities slightly bent lingually	Mesiodistally elongated, symmetrical
Occlusal crest	Moderate, occasionally slightly crenulated	Moderate	Strong	Strong
Crown/root junction	Moderate incised	Strong incised	Moderate incised	Moderate incised
Assumed jaw position	Lateral to posterolateral	Anterolateral	Mesial	?Mesial

the lack of distinct surface striations or reticulate folds separate the Madygen specimens from *Hylaeobatis* or *Vectiselachos* even if nodules (= granulae) on the labial crown faces are rarely existent. Well-developed crown shoulders and the assymmetric occlusal shape of *L. ferganensis*, sp. nov., are in contrast to *Parvodus*. The discrimination between *Lissodus* and *Lonchidion* is more difficult. Morphotypes I and II of *L. ferganensis*, sp. nov., appear more *Lissodus*-like sensu Rees and Underwood (2002) considering the massive, triangular crown, the low coronal profile, the minute to absent lateral cusplets, and an altogether slightly enlargement of the lateral teeth compared to the mesials. The gracile morphotype III with its narrow labial peg, strong occlusal crest, and three pairs of lateral cusplets, on the other hand, is more typical for *Lonchidion* crowns sensu Rees and Underwood (2002). However, because none of the Madygen crowns exhibit *Lissodus*-type ornamenting folds on the face but have nodules characteristic among Lonchidiidae, a moderate occlusal crest is present even in lateral teeth, and the histological structure is in accordance with those described for several teeth of *Lonchidion* (fan-shaped radiation of dentinal tubles, the lack of an osteodentine core; Estes, 1964; Patterson, 1966; Heckert et al., 2007) we prefer the interpretation that all crowns of the Madygen assemblage belong to a single species of *Lonchidion*. Nevertheless, this example underlines the necessity of more quantifiable criteria to differentiate disarticulated remains of heterodont dentitions of sharks such as *Lissodus* or *Lonchidion* (Heckert, 2004).

The tooth crowns of *L. ferganensis*, sp. nov., differ from most other *Lonchidion* species by the lack of vertical ornamentation, but parallels in this respect almost a dozen other species, including *L. humblei* Murry, 1981 (Late Triassic, Carnian–Rhaetian, North America), *L. incumbens* Prasad et al., 2008 (Late Triassic, Carnian–Norian, India), *L. delsatei* (Guennegues and Biddle, 1989) (Early Jurassic, Toarcian, France), *L. indicus* Yadagiri, 1986 (Early Jurassic, ?Toarcian, India), *L. reesunderwoodi* Cuny et al., 2009 (Middle Jurassic, Bathonian–Callovian, Thailand), *L. breve* Patterson, 1966 (Early Cretaceous, Berriasian–Aptian, NW Europe), *L. microselachos* Estes and Sanchíz, 1982 (Early Cretaceous, Barremian–Aptian, Spain), *L. anitae* (Thurmond, 1972) (Early Cretaceous, Aptian–Albian, North America), *L. griffisi* (Case, 1987) (Late Cretaceous, Campanian, North America), *L. babulski* Cappetta and Case, 1975 (Late Cretaceous, Campanian–Maastrichtian, North America), and *L. selachos* Estes, 1964 (Latest Cretaceous, Maastrichtian, North America).

Despite their overall similarity, all these species are distinguished from the crowns of the Madygen assemblage by at least one feature each. For example, *L. humblei*, *L. delsatei*, and *L. babulskii* differ in the lack of distinct lateral cusplets and the prominent horizontal ridge on the crown shoulders. The latter feature is also missing in *L. selachos*, *L. microselachos*, *L. indicus*, and *L. breve*, whereas the lack of a subterminal accessory cusplet on the labial crest excludes *L. indicus* and *L. breve*. In *L. incumbens* the central cusp is strongly inclined labially and at most one pair of lateral cusplets is developed. *L. griffisi* otherwise develops up to five pairs of lateral cusplets. Longitudinal ridges are only weakly developed labially and absent lingually in *L. anitae*. *L. reesunderwoodi*, as the most similar species including the same number of morphotypes, is different by showing up to three secondary ridge-like branches to the labial crest. In spite of many similarities with various types of *Lonchidion* teeth, the crowns from Madygen differ significantly from all other known taxa, affording its taxonomic distinction at species level.

Ontogenetic Heterodonty—Tooth crowns of Madygen locality LI/12 (Fig. 1, Table 1) are at least 40% smaller than the single specimen FG 596/III/42 from locality LI/1 (Figs. 1, 3E, Table 1). Despite its size and unique horizontal ridge pattern, the latter appears to represent a mesial tooth by virtue of its remaining suite of characters (Table 2). The noticeable differences to all smaller specimens of morphotype III (Fig. 3A, D) may be the result of ontogenetic heterodonty. Such a pattern is very common in extant sharks, but rarely documented in fossil forms due to the scarcity of cartilaginous skeletal remains (Klug, 2010). In isolated material, such as teeth, ontogenetic changes are difficult to identify, and are usually based on differences in size and/or ornamentation (Duffin, 1993; Rees and Underwood, 2008). Hence, the abundant tooth crowns of *L. ferganensis*, sp. nov., measuring ≤1.5 mm in size are here interpreted as belonging to immature individuals, whereas the larger crown, FG 596/III/42, is from a subadult to adult specimen (Fig. 3F).

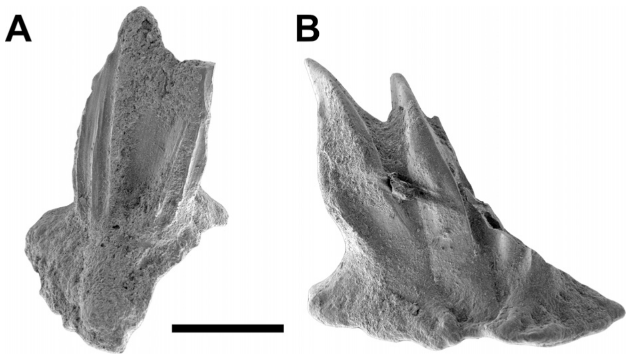

FIGURE 4. Dermal denticles of the hybodontid *Lonchidion ferganensis*, sp. nov., in **A**, FG 589/III/93, oblique lateral view; and **B**, FG 589/III/94, lateral view. Scale bar equals 0.2 mm.

DERMAL DENTICLES

Two morphologically identical fragments of dermal denticles have been found in the residues of the processed mudstone from Madygen locality LI/12 (Fig. 4A–B; Table 1). The denticle measures 0.50–0.60 mm apicobasally and 0.6 mm in maximum width. The base with its concave undersurface and cycloid outline is wider than the crown to all margins. The crown is slightly inclined posteriorly, laterally elongated, and compressed anterioposteriorly. The multicuspid crown is of rake-like appearance exhibiting several strong to moderate ridges on the convex anterior side, whereas the concave subcrown face is featureless posteriorly. These denticles resemble the hybodontoid scale morphotype of Reif (1978), hybodontiform scales described by Rees (2002), Fischer et al. (2010b), and Klug et al. (2010), as well as the *Duplisuggestus* scale morphotype of Johns et al. (1997). Given their hybodontiform shape and close association with teeth of *L. ferganensis*, sp. nov., it is likely that the scales belong to the same species of hybodontid shark as the teeth.

SHARK EGG CAPSULES

Remarks—Despite their ambiguous orthotaxonomic position (Pruvost, 1930), egg capsules of fossil sharks are conventionally treated in accordance with the rules of the International Code of Zoological Nomenclature (Zidek, 1976; Rössler and Schneider, 1997). We follow this example for practical reasons.

GENUS *PALAEOXYRIS* Brongniart, 1828

Type Species—*Palaeoxyris regularis* Brongniart, 1828, Middle Triassic (Anisian) of Sultz-les-Bains, Northern Vosges, France.

Emended Diagnosis—Chondrichthyan egg capsule; three-fold division into beak, body, and pedicle; body broadly fusiform, gradually tapering toward each end, composed of three or more parallel helicoidally twisted bands; anterior end gradually tapering into shorter pointed beak; posterior end tapering to long, slender pedicle marked by either spiral ribbing or parallel ribs; collarettes accompanying band margins; fine longitudinal striation on bands and collarettes; compressed specimens with transverse rhomboidal pattern.

Record—Late Mississippian (Visean) (Schneider et al., 2005) to Late Cretaceous (Vialov, 1984), from Europe, Asia, North America, and Australia.

PALAEOXYRIS ALTERNA, sp. nov.
(Fig. 5)

2007 *Palaeoxyris* sp. (type no. 1) Fischer et al., 2007:42, fig. 2a–g.

2009 *Palaeoxyris* sp. Kogan et al., 2009:145, fig. 5f.

Etymology—From *alternus*, Latin for alternate; in allusion to the alternating width of bands constituting the capsule.

Holotype—FG 596/III/39, compressed specimen of an almost complete capsule (Fig. 5A).

Type Locality—SW Madygen outcrop area (Urochishe Madygen) west of Madygen village, Batken District (Oblast), SW Kyrgyzstan (Madygen locality LI/1; Fig. 1, Table 1).

Type Horizon—Uppermost part of lacustrine sequence 3 ('Brown-Gray Member' sensu Dobruskina, 1995), Madygen Formation (Ladinian–Carnian, Middle to Late Triassic).

Paratypes—FG 596/III/12, essentially complete compressed capsule with beak, body, and long pedicle; FG 596/III/24 less compressed complete beak and body fragment; FG 596/III/29, compressed body fragment and long pedicle; FG 596/III/30, less compressed body; FG 596/III/35, compressed body and pedicle fragment; FG 596/III/40, compressed complete beak and body; FG 596/III/48, compressed beak and body fragment (Fig. 5B–H).

Referred Material—23 specimens with fragments of various completeness (FG 596/III/1; FG 596/III/13–17; FG 596/III/22–23; FG 596/III/25–28; FG 596/III/31–34; FG 596/III/36–38; FG 596/III/41; FG 596/III/46–48).

Diagnosis—Three-fold divided capsule; broadly fusiform body, up to 25 mm long, 14 mm maximum width in compressed specimens, 12 mm maximum width in least compressed specimens, with gradual tapering toward both ends; traversed by six helicoidally twisted bands each showing one and a half turns, forming up to 11 segments; bands with double rib line between them; bands show alternating breadth pattern (broad-broad-narrow-broad-broad-narrow), broad bands averaging 3 mm in width, narrow bands averaging 2 mm in width; pointed beak up to 24 mm long; pedicle with gradual constriction to the end, marked by parallel arranged ribbing structures, up to 55 mm long, 5–8 mm wide at transition point to body; band ribs on the pedicle arranged parallel to the body axis becoming narrower towards the tapering end; bands and pedicle lined with collarette, 1.5 mm in height, without ornamentation.

Description—*Palaeoxyris* from Madygen comprises 24 specimens with the typical transverse rhomboidal pattern of compressed fragments, and 6 specimens with the spiral ribbing structure of less compressed fragments. The consistently fusiform body (Fig. 5A) ranges from 22 to 25 mm in length, the maximum width varies between 11 and 14 mm in compressed specimens (Fig. 5C), and uniformly measures 12 mm in all less compressed remains (Fig. 5C). At the transition from the beak to the body, the orientation of the bands changes from medial to transversal position. With a length of up to 24 mm (Fig. 5F), the beak is almost as long as the body. At the pointed end of the beak in FG 596/III/40 (Fig. 5D), part of a tendril is preserved. The long and slender pedicle is most completely preserved in FG 596/III/29, measuring 55 mm (Fig. 5E), and is 39 mm long in FG 596/III/12 (Fig. 5B), resulting in minimum body/pedicle length ratios of 1.6. The maximum width of the pedicle ranges from 5 to 8 mm, which is about half the width of the body (Fig. 5E, H). The pedicle is characterized by axial ribs that converge at the posterior end of the structure (Fig. 5B, E, H). Each specimen consists of six spirally twisted bands that form up to 11 segments (Fig. 5I) and are united at their margins by raised, single or doubled ribs (Fig. 5E, H). The alternating breadth pattern of the bands is especially distinct in FG 596/III/48 (Fig. 5G). Preservation in less-compressed specimens shows the originally clockwise turning of the spiral bands (Fig. 5C, F). Conspicuous are the detailed remains of the up to 1.5 mm wide collarettes that accompany the band margins over the whole specimens, and form lateral triangular (Fig. 5A) or round (Figs. 5D, H) fragments on both sides of the body in compressed and uncompressed specimens (Fig. 5C). Moreover, the original width can be inferred from a fringe line parallel to the spiral trend in the middle of the bands in specimens FG 596/III/29 and FG 596/III/35 (Fig. 5E, H). Distinctive fragmentary collarettes are also present on the pedicle (Fig. 5H).

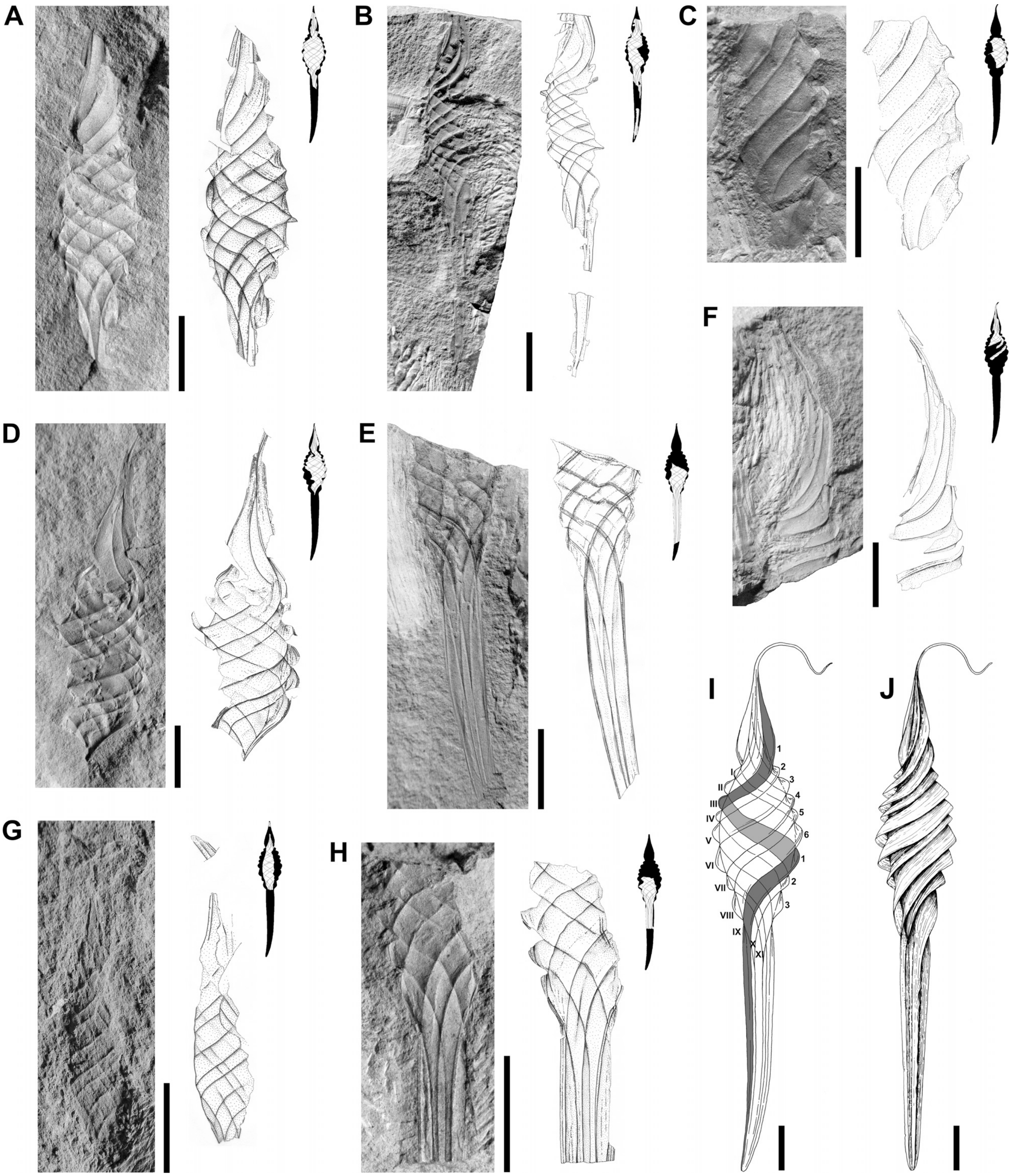

FIGURE 5. Photograph, sketch, and overview of the hybodontid egg capsule *Palaeoxyris alterna*, sp. nov. **A**, holotyoe FG 589/III/39; **B**, paratype FG 589/III/12; **C**, paratype FG 589/III/30; **D**, paratype FG 589/III/40; **E**, paratype FG 589/III/29; **F**, paratype FG 589/III/24; **G**, paratype FG 589/III/48; **H**, paratype FG 589/III/35. **I**, diagrammatic illustration of a complete *P. alterna*, sp. nov., capsule showing the principal division of the fossil and the arrangement of the bands on it. The visible segments are designated by Roman numerals and the true bands are designated by Arabic numerals. The course of band 1 is shaded with dark grey on exposed side and light grey on unexposed side. **J**, reconstruction of a living *P. alterna*. All scale bars equal 1 cm.

No clear fine striations are observable on any specimen surface except for some indistinct striae in FG 596/III/30 (Fig. 5C).

Discussion—All described specimens are generally uniform and meet the generically diagnostic features of *Palaeoxyris* Brongniart, 1828. The transverse rhomboidal pattern of many specimens is a taphonomic phenomenon resulting from the compression and superimposition of helicoidal twisted bands and is typical for this form genus (Crookall, 1928b; Zidek, 1976). The body of the Madygen specimens almost equals the length of the beak, which is in accordance with other species of *Palaeoxyris* (Müller, 1978). A body/pedicle length ratio of 1:2 up to 1:2.9 in complete *Palaeoxyris* (Müller, 1978) allows estimations of total pedicle lengths of 50–70 mm for the Madygen specimens, which is about the length of the beak and the body together (Fig. 5I). Based on this, the total length of the egg capsule can be calculated to 90–120 mm with the pedicle covering about 60%. The subparallel arrangement of the ribs on the pedicle is a typical character of Mesozoic *Palaeoxyris* (e.g., Brongniart, 1828; Ettingshausen, 1852; Crookall, 1930), whereas all Paleozoic specimens show spiral/rhomboidal ribbing over the entire length of the capsule (Fischer and Kogan, 2008, Fischer et al., 2010a).

Collarettes are membranous flanges that are attached to the anterior margins of the bands, resulting in the screw-like appearance of modern heterodont capsules (Fig. 6J). Principally, the same structure is assumed for *Palaeoxyris* (Fig. 5J). Distinct collarette fringe lines impressed on the underlaying bands were previously observed in *Fayolia moyseyi* from the Middle Pennsylvanian of England and northern France (Pruvost, 1919), but have never been recovered in *Palaeoxyris*. The fine striation running parallel to the ribs on the bands and on the collarettes is a poorly preserved phenomenon in the Madygen specimens but well known from other *Palaeoxyris* records (Lesquereux, 1870; Saporta, 1891; Böttcher, 2010; Fischer et al., 2010a), as well as modern shark egg capsules (Zidek, 1976).

Clutches of 2–14 capsules have been described from several other occurrences of *Palaeoxyris* (Ettingshausen, 1852; Frentzen, 1932; Schneider, 1986), but is not recorded for the Madygen specimens, suggesting clutch disintegration during transport to the place of deposition. The beak end of *Palaeoxyris* with its coiled tendril structures has been shown to be an attachment organ for anchoring capsules to each other and submerged structures (Crookall, 1932; Waterlot, 1934; Langford, 1958). Fragmentary tendrils are also preserved in some of the Madygen specimens (FG 596/III/24 and 40; Fig. 5C, G).

In summary, *P. alterna*, sp. nov., seems to be an approximately 120 mm long screw-like egg capsule similar to those of modern heterodontid sharks from which it is otherwise distinguished by the large number of collarettes and a long, slender, distally tapering pedicle (Figs. 5J, 6J).

The distinctive band pattern of *P. alterna*, sp. nov., is paralleled by only two other *Palaeoxyris* species: (1) *P. helicteroides* (Morris in Prestwich, 1840) from the Late Carboniferous (Middle to Late Pennsylvanian) of North America, England, France, Germany and Russia; and (2) *P. lewisi* Zidek, 1976, from the Late Carboniferous (Middle Pennsylvanian) of North America. Both species are different to the Madygen specimens by the transversally arranged ribs on the pedicle. Gall (1971:pl. 25, fig. 1) documented a bunch of *Palaeoxyris* specimens from the Middle Triassic (Anisian) of France that he attributed to *P. regularis* Brongniart, 1828. The holotype of *P. regularis* exhibits four bands, whereas the specimens collected by Gall (1971) have six bands and are significantly larger, suggesting a separate species (Böttcher, 2010). Most importantly, the material of Gall (1971) shows the same band pattern (broad-broad-narrow-broad-broad-narrow) as *P. alterna*, sp. nov., and differs only from Kyrgyz material by its larger size (180 mm in total length) and broader bands (4 mm of maximum width). Another similar form is described by Romanowski (1880) as *P. gilewii* from the Middle to Late Triassic (Ladinian–Carnian) Koldzhat Formation of the Ketmen Range, southeastern Kazakhstan. According to Romanowski's drawing, *P. gilewii* has 10–12 segments and bands that slightly alternate in their width (2–2.5 mm). For stratigraphic, palaeogeographic, and morphological reasons, it is not unlikely that *P. gilewii* and *P. alterna*, sp. nov., are homotaxial; however, the systematic pattern of alternating band width cannot be confirmed for *P. gilewii* on the basis of Romanowski's illustration and the type material could not be located, wherefore we introduce *P. alterna*, sp. nov., as a new species.

GENUS *FAYOLIA* Renault and Zeiller, 1884

Type Species—*Fayolia dentata* Renault and Zeiller, 1884, Latest Carboniferous (Gzhelian–Asselian) of Commentry, France.

Emended Diagnosis—Chondrichthyan egg capsule; body large, cylindrical fusiform, gradually tapering toward the ends, composed of two parallel helicoidally twisted bands; anterior end gradually tapering into smooth, narrow beak; posterior end tapering into short, single twisted pedicle; beneath the band margins a series of small circular or elliptical scars; broad collarettes parallel to band margins, overlapping scar lines, free-standing margin solid or denticulate; fine longitudinal striae on bands and collarettes; transverse rhomboidal pattern in compressed specimens.

Record—Latest Devonian (Famennian) (Stainier, 1894) to Middle to Late Triassic (Ladinian–Carnian) (this paper); from Europe, North America, and Asia.

FAYOLIA SHAROVI, sp. nov.
(Fig. 6)

2007 Egg capsule indet. (type no. 2) Fischer et al., 2007:42, fig. 2h–j.

2009 Egg capsule indet. Kogan et al., 2009:145, fig. 5e.

Etymology—After the Russian paleoentomologist Alexander G. Sharov in honor of his research efforts on the Madygen fossil biota (Shcherbakov, 2008).

Holotype—FG 596/III/2 an essentially complete, compressed capsule (Fig. 6A).

Type Locality—NW Madygen outcrop area (Urochishe Dzhaylyaucho) west of Tangyjevashe village, Batken District (Oblast), SW Kyrgyzstan (Madygen locality LII/1; Fig. 1, Table 1).

Type Horizon—Lacustrine sequence 2 ('Upper Gray-coloured Member' sensu Dobruskina, 1995), Madygen Formation (Ladinian–Carnian, Middle to Late Triassic).

Paratypes—FG 596/III/19, less compressed body with fragmentary beak; FG 596/III/20, less compressed capsule with body and pedicle; FG 596/III/21, compressed body with collarette; FG 596/III/72 two less compressed capsules, agglutinated by their beaks (Fig. 6B–G).

Referred Material—FG 596/III/18; FG 596/III/71.

Diagnosis—Body oval to fusiform, up to 44 mm long; 18 mm wide in compressed specimens, 11 mm in least compressed specimen, gradually tapering toward both ends; traversed by two helicoidally twisted bands, averaging 10 mm in width, each band with two complete turns over the capsule's length; band margins paralleled by a 1.5 mm wide line of fusiform scars, two to three scars per mm lateral distance, closely arranged scars producing a fence-like appearance; long, slender beak, up to 2 mm in width and 23 mm in maximum length, composed of tightly twisted bands; pedicle obscured; bands with collarettes up to 5 mm in width, collarette fringe line in the middle of each band, band margins solid; fine longitudinal striae on bands and collarettes.

Description—*Fayolia* from Madygen comprises five compressed fragmentary specimens with a transverse rhomboidal pattern and three less compressed specimens with spiral ribbing. Flattened specimens 34–44 mm long, 13–18 mm in maximum

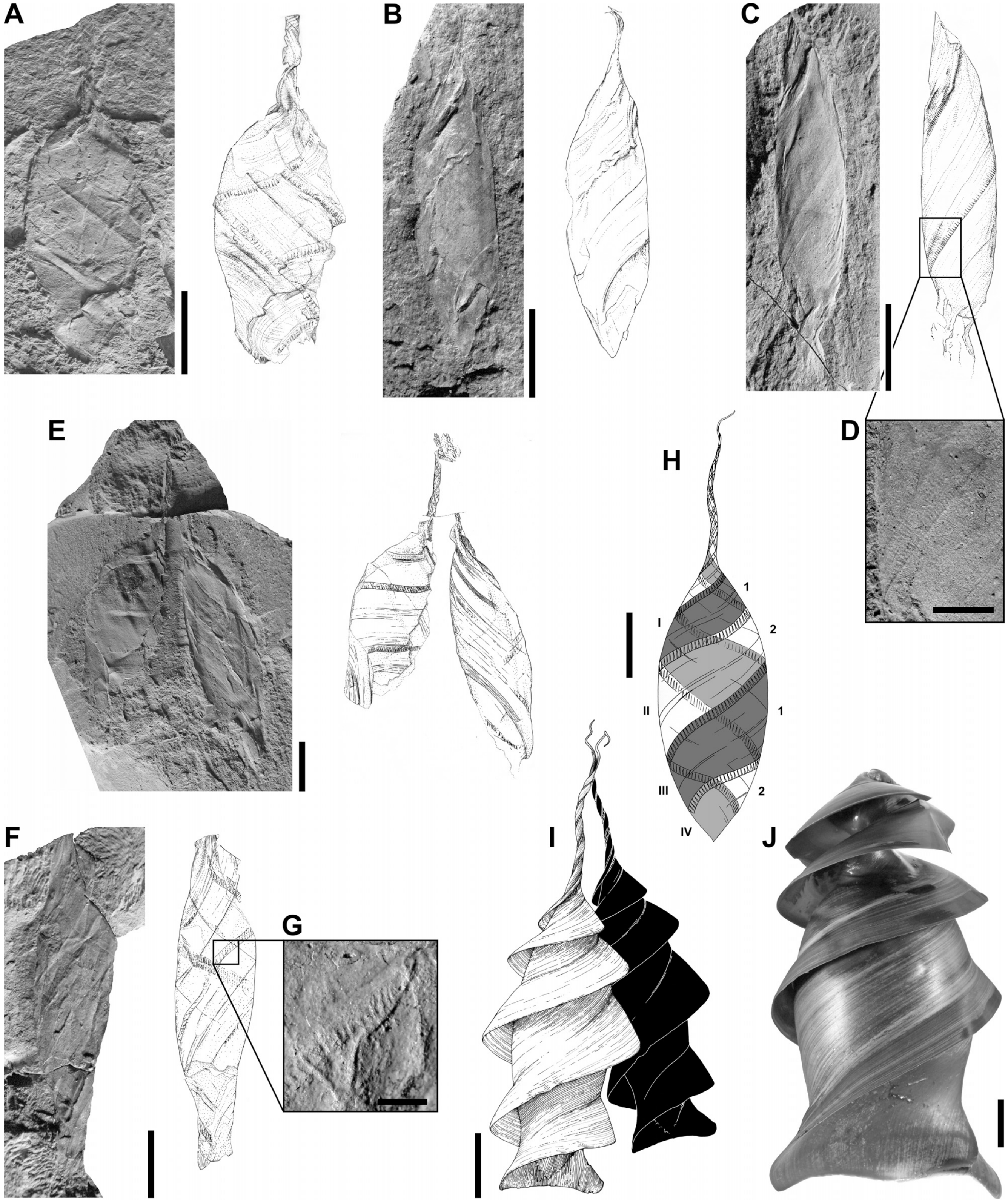

FIGURE 6. Photograph and sketch of the presumed xenacanthid egg capsule *Fayolia sharovi*, sp. nov. **A**, holotype FG 589/III/2; **B**, paratype FG 589/III/20; **C**, paratype FG 589/III/19; **D**, enlargement of the zipper-like disintegration of the scar line of FG 589/III/21; **E**, paratype FG 589/III/72 with two capsules agglutinated by the most distal ends of their pedicles; **F**, paratype FG 589/III/21; **G**, enlargement of a part of the fence-like scar line of FG 589/III/21; **H**, diagrammatic illustration of a complete *F. sharovi*, sp. nov., capsule showing the principal division of the fossil and the arrangement of the bands on it. The visible segments are designated by Roman numerals and the true bands are designated by Arabic numerals. The course of band 1 is shaded with dark grey on exposed side and light grey on unexposed side. **I**, reconstruction of a pair of living *F. sharovi*, sp. nov. **J**, egg capsule of the extant heterodontid *Heterodontus francisci* (Girard, 1855). Scale bars in **A**–**D**, **F**–**I** equal 1 cm and that in **E** equals 3 mm.

width, with oval body (Fig. 6A, E); less compressed specimens 8–11 mm of maximum width (Fig. 6B). The body gradually tapers toward the ends (Fig. 6C). The pedicle is short and indistinct (Fig. 6B), often broken off (Fig. 6A) or obscured (Fig. 6C, E). The beak at the opposite termination is longer and more slender than the pedicle, best preserved in the holotype (FG 596/III/2) and in FG 596/III/72 with its stalk-like appearance of tightly twisted bands (Fig. 6A, E). In less compressed specimens the beak forms a tendril-like structure (Fig. 6B). The beak is up to 23 mm long and 2 mm wide (Fig. 6E). As visible in FG 596/III/2 both bands manage two complete turns in the spirals of the species (Fig. 6A, H). The scar line appears as a separate small band of 1.5 mm width accompanying the proximal margin of every of the two capsule-forming broad bands (Fig. 6A, E, F). It is clearly recognizable by its narrow, drawn-out spindle-like scars, which form a fence-like surface structure by virtue of the dense occurrence with two to three per mm in parallel (Fig. 6G). In FG 596/III/19 the scar line shows signs of disintegration into two separate scar lines (Fig. 6C, D), whereas in FG 596/III/20 most of the scar lines are covered by the other band or may be deformed (Fig. 6B). A triangular structure protruding beyond the margin of the body anteriorly in FG 596/III/21 (Fig. 6F) indicates collarette width and fits well with the characteristic, longitudinally suture-like fringe line in the middle of every band (Fig. 6A–F). A fine longitudinal striation is present on the band and the collarettes running parallel to the turning direction (Fig. 6A–E). On the basis of the less compressed specimens, the original band turning direction is clockwise (Fig. 6B, C). Specimen FG 596/III/72 consisting of two egg capsules agglutinated by their beaks (Fig. 6F).

Discussion—Transitional stages of preservation facilitate the reconstruction of the Madygen *Fayolia*. Distortion of individual scars suggests that the scar line was a three-dimensional structure in life. The scar line was likely overlapped by the broad collarette. Preservation of a collarette in FG 596/III/21 proves the distinct line in the middle of each band to be the impression of the posterior fringe of the collarettes. In a preliminary description, the collarette was misidentified consisting of the narrow scar line only (Fischer et al., 2007:fig. 2j). Additional material now supports the interpretation as a broad flange that covers the scar line well (Fig. 6I).

The Madygen specimens FG 596/III/19 (Fig. 6C) yield intriguing data approaching the construction and function of scars in *Fayolia*. Renault and Zeiller (1884) assumed that scars are the base of tiny spines. Their so-called 'spine scar' theory was further developed by subsequent authors (Moysey, 1910; Pruvost, 1919; Brown, 1950), although nobody has ever been able to confirm the presence of spines in *Fayolia*. Sections of *F. sharovi*, sp. nov., show slightly diverging scar lines (Fig. 6D), suggesting that there are actually two scar lines with one on each margin of adjacent bands. This observation could support the idea of zipper-like interlocked scar lines introduced by Pruvost (1919).

Clustering is a well-documented phenomenon in *Fayolia*. Renault and Zeiller (1888) illustrated four agglutinated capsules of *F. dentata* from the Late Pennsylvanian of Commentry, France; paired capsules are known of *F. bohemica* from the Middle Pennsylvanian of Nyrany, Czech Republic (Prantl, 1933), and Schneider et al. (2005) reported on clutches of up to six capsules of *Fayolia* sp. from the Visean of the Erzgebirge Basin, Germany. Clutches of at least two capsules agglutinated by their beaks are recorded in *F. sharovi* (FG 596/III/72; Fig. 6E).

With respect to the broad collarettes, the fine surface striation, and the clockwise twisted bands *F. sharovi*, sp. nov., seems to be similar to modern heterodontid egg capsules (Fig. 6I, J). According to our reconstruction the scar line of *F. sharovi* was hidden by the broad collarettes, and the capsule reached a total length of up to 70 mm. Judging from the long twisted beak, these capsules were probably attached to submerged plants.

Fayolia is hitherto known only from Paleozoic strata with the youngest record from the Asselian of the Saar-Nahe Basin, Germany (Poschmann and Schindler, 1997). All Paleozoic species of *Fayolia* (reviews in Crookall, 1928a; Poschmann and Schindler, 1997) are significantly larger than the Madygen specimens. Our assignment is based upon major characteristics, including the construction of the bodies from only two bands, scar lines paralleling the band margins, the presence of broad collarettes, indistinct posterior ends, and slender beaks. Unique features of *F. sharovi* such as the small size, the low number of spiral turns, and the elongated fusiform shape of the scars justify the erection of a new species. It is the youngest record of *Fayolia*, and extends its stratigraphic range to the Early Mesozoic.

ISOTOPIC ANALYSES

Biogenic fluor-apatite of shark tooth enameloid represents a reliable geochemical archive of the ambient water chemistry at the time of tooth mineralization because of the formation near the thermodynamic equilibrium and its resistance to diagenetic alteration (Vennemann et al., 2001; Zacke et al., 2009). Thus, δ^{18}O data of shark teeth may discriminate between marine and freshwater paleoenvironmental conditions (Kolodny and Luz, 1991). The enameloid $\delta^{18}O_P$ values obtained from six crown bulk samples of *L. ferganensis*, sp. nov., range from 10.1‰ to 10.9‰ VSMOW (Table 3), with a mean $\delta^{18}O_P$ value of 10.5‰ ± 0.3‰ VSMOW for Madygen. These values coincide with two $\delta^{18}O_P$ measurements gained from closely associated *Saurichthys* teeth (Table 3). All $\delta^{18}O_P$ values are fractionated by 8–11‰ relative to the seawater δ^{18}O signal derived from fully marine organisms of Ladinian (19.4–20.7‰ VSMOW; Sharp et al., 2000), and Carnian–Norian (18.7–20.8‰ VSMOW; Rigo and Joachimski, 2010) age from the Tethyan Southern Alps. The numerical distance of the $\delta^{18}O_P$ is too large to be explained by different water temperatures, suggesting instead a significantly different hydrochemistry with mineralization of the Madygen teeth in a freshwater environment. Similar low values in shark tooth enameloid, which are likewise interpreted as unequivocal freshwater signatures, are described from the Late Jurassic (Oxfordian) Junggar Basin of China (9.7‰ ± 0.4‰; Klug et al., 2010), and from the Lower Miocene of the Swiss Molasse Basin (10.3‰ and 11.3‰; Kocsis et al., 2007).

Ranging from 0.7096 to 0.7099 (Table 3), the ^{87}Sr/^{86}Sr ratios of two samples of *Lonchidion* and one sample of *Saurichthys* are notably higher than the proposed seawater ratios of around

TABLE 3. Oxygen isotope composition and strontium ratios of bioapatite of *Lonchidion ferganensis*, sp. nov., and *Saurichthys orientalis* Sytchevskaya, 1999, from lake phase 1 of the Madygen Formation.

Sample	Taxon	No. of crown fragments	$\delta^{18}O_P$ VSMOW (‰)	^{87}Sr/^{86}Sr
MLM 1	*Lonchidion ferganensis*	4	10.6	
MLM 2	*Lonchidion ferganensis*	4	10.1	
MLM 3	*Lonchidion ferganensis*	6	10.5	
MLM 4	*Lonchidion ferganensis*	4	10.5	
MLM 5	*Lonchidion ferganensis*	6	10.4	
MLM 6	*Lonchidion ferganensis*	3	10.9	
MLM 7	*Lonchidion ferganensis*	8		0.70965 ± 10
MLM 8	*Lonchidion ferganensis*	7		0.70991 ± 19
MS 1	*Saurichthys orientalis*	4	10.7	
MS 2	*Saurichthys orientalis*	4	10.2	
MS 3	*Saurichthys orientalis*	1		0.70976 ± 19

Coeval Middle to Late Triassic marine $\delta^{18}O_P$ signals range from 18.7‰ to 20.8‰ VSMOW (Rigo and Joachimski, 2010), whereas marine ^{87}Sr/^{86}Sr ratios are between 0.7075 and 0.7081 (Korte et al., 2003).

0.7075–0.7081 for the Middle to Late Triassic (Ladinian–Norian; Korte et al., 2003). Given that freshwater environments generally show higher isotopic ratios than contemporaneous seawater (Schmitz et al., 1991), the Sr ratios from Madygen support the freshwater interpretation based on $\delta^{18}O_P$ values.

PALEOBIOLOGICAL IMPLICATIONS

Affinities of the Egg Capsules—Assignment of fossil egg capsules to potential producers has been controversial since their animal origin was first proposed (e.g., Renault and Zeiller, 1888; Moysey, 1910; Pruvost, 1919; Zidek, 1976; Schneider and Reichel, 1989; Fischer and Kogan, 2008). Reliable data, such as the co-occurrence of egg capsules and shark skeletal remains in the same horizon, is scarce (Saporta, 1891; Schneider and Reichel, 1989; Schneider et al., 2005), wherefore assignments are mainly based on the coincident stratigraphical range of these two types of fossils (Zidek, 1976; Fischer et al., 2010a). A good example is the record of hybodontiform sharks (Middle Devonian–Late Cretaceous; Rees, 2008) and *Palaeoxyris* egg capsules (Early Carboniferous–Late Cretaceous; Fischer et al., 2010a). This assignment was introduced by Crookall (1932), revived by Zidek (1976) and Müller (1978), and substantially supported by Schneider (1986) who reported an association of *Palaeoxyris* and skeletal remains of hybodontid sharks from Late Carboniferous (Late Pennsylvanian) lake deposits of the Saale Basin, Germany. This is in agreement with *Palaeoxyris* and hybodontid teeth discoveries in Late Triassic (Norian) strata of the Chinle Formation, Arizona, U.S.A. (Fischer et al., 2010a), and the record from the Madygen Formation as described herein.

Schneider and Reichel (1989) and Schneider et al. (2005) argued substantially for the assignment of *Fayolia* egg capsules to xenacanthiform sharks, a hypothesis that was proposed earlier (Renault and Zeiller, 1888; Pruvost, 1919, 1930). This correlation is mainly based on the occurrence of related egg capsules and shark remains in Paleozoic nonmarine deposits. Xenacanthids were most diverse during the Late Paleozoic (Turner et al., 2008), but a few taxa such as *Mooreodontus* Hampe and Schneider in Ginter et al. (2010) (= xenacanthid "*moorei*" group sensu Schneider, 1996) are common elements of Middle–Late Triassic nonmarine ichthyofaunas in England, Germany, North America, Australia, and India (Ginter et al., 2010), partially dominating the shark assemblage by the number of individuals (Heckert, 2004). Xenacanthids apparently became extinct during the Late Triassic (Norian) (Schneider, 1996) and *Fayolia*-type egg capsules are not known from deposits younger than Middle–Late Triassic in age.

Considering the co-occurrence of hybodontid teeth and hybodontid egg capsules in the Madygen Formation and the absence of other hybodontiforms in these beds, we regard *Lonchidion ferganensis*, sp. nov., as the producer of *Palaeoxyris alterna*, sp. nov. Even though related skeletal remains have not been found so far from the Madygen Formation, the record of *Fayolia sharovi*, sp. nov., is an argument for xenacanthids being present in the Triassic Madygen lake basin. The co-occurrence of xenacanthid and hybodontid sharks would not be exceptional in Triassic freshwater deposits (Seilacher, 1943; Heckert, 2004; Prasad et al., 2008; Turner et al., 2008).

Paleoecological Implications—Sharks are among the apex predators in marine and freshwater habitats, even if they just form a minor component of the ichthyofauna (Compagno, 1990) or are represented solely by juveniles in estuaries (Lowe, 2002). Extant sharks with heterodont dentition prefer benthic invertebrates (crustaceans, mollusks, sea urchins, polychaete worms) and rarely small fishes for food (Compagno, 1990). By analogy, a durophagous lifestyle is assumed for the hybodontid *L. ferganensis*, sp. nov., with its heterodont crushing-grinding-type dentition. Potential prey so far recorded for the Madygen lake includes large branchiopods (kazacharthrans), gastropods, bivalves, and infaunal oligochaetes or insect larvae (Voigt and Hoppe, 2010). As modern durophagous and/or oviparous chondrichthyans are bottom-dwelling organisms (Compagno, 1990; White and Sommerville, 2010), a habitus also suggested for several hybodontid species from their dermal denticles (Hampe, 1996; Fischer et al., 2010b), we suppose a necto-benthic lifestyle for *L. ferganensis*, sp. nov., as well. The typical tricuspid teeth of xenacanthid sharks and fossilized food residues indicate a variety of prey including fish and semiaquatic vertebrates (Hampe, 1989; Soler-Gijón, 1995; Schneider, 1996; Kriwet et al., 2007; Whitenack and Motta, 2010). If there was really a xenacanthid in the Madygen lake, it may have preyed on the abundant small- to medium-sized actinopterygians (Kogan et al., 2009), probably in competition with large piscivorous actinopterygians (e.g., *Saurichthys orientalis* Sytchevskaya, 1999) and semiaquatic reptiliomorphs (*Madygenerpeton pustulatus* Schoch et al., 2010).

Oviparity—Extant sharks possess a k-strategy of reproduction with around 43% of all species being oviparous (Compagno, 1990). Although, oviparity is generally considered to be the ancestral reproductive mode (Dulvy and Reynolds, 1997; Rodda and Seymor, 2008), there are still ambiguities regarding pre-Mesozoic forms (Kohring, 1995; Grogan and Lund, 2004, 2011). Oviparity is a lecithotrophic (yolk-based embryonic feeding) mode of reproduction (Hamlett et al., 2005b) where the fertilized eggs are enclosed in large leathery, yet flexible capsules composed of multilamellar collagenous material (Hamlett et al., 2005a; Rodda and Seymor, 2008) and deposited externally. Two types of oviparity are distinguished (Compagno, 1990; Wyffels, 2009). In single (extended) oviparity, which is the most common type, a continuous oviposition at a time from each oviduct occurs where the embryo develops mostly externally to the mother. In multiple (retained) oviparity, several egg capsules are retained in the females oviduct during most of their incubation but are deposited before hatching. Multiple oviparity constrains the number of eggs per reproduction cycle in comparison with single oviparity, but it reduces the predation risk on deposited egg capsules (White and Sommerville, 2010). Horns or coiled tendrils are attachment tools for fixing the egg capsules onto bottom structures, that is, mostly submerged plants (Wyffels, 2009). Incubation is significantly affected by temperature (Rodda and Seymor, 2008), and may last a few months to more than 1 year (Compagno, 1990) in the absence of maternal care. Despite mechanical protection of the embryo by the tough, horny capsule, they offer an abundant food supply for a variety of organisms (Cox and Koob, 1993), resulting in partially high mortality rates (Powter and Gladstone, 2008).

Morphological similarities between *Palaeoxyris*-*Fayolia* and extant egg capsules as well as details from the three-dimensional preservation suggest a similar collagen-like composition and functional role (protection, filtering) for fossil and modern shark egg cases. Tendril remains in both Madygen capsule types prove anchorage to subaqueous objects, as is the case in extant sharks. The length of the incubation period is difficult to evaluate for fossil eggs from freshwater environments. The relatively unstable physicochemical conditions in those settings (Compagno and Cook, 1995), however, suggest a rather short incubation. Additionally, some kind of retained oviparity may have buffered fluctuations in habitat conditions. The relatively large size of extant and fossil shark egg capsules in relation to the body size of mature females is a reason to assume that only a smaller number of eggs were produced by each individual per breeding season (normally <20 eggs in extant forms; Compagno, 1990; Rodda and Seymor, 2008; largest known fossil clutch with 14 eggs; Frentzen, 1932). The record of 27 specimens of *P. alterna*, sp. nov., from a single locality (LI/1; Fig. 1C, Table 1) indicates egg-laying activity of more than one individual.

Nursery Pattern—The co-occurrence of egg capsules and almost exclusively small teeth of sharks in lacustrine near-shore deposits of the Madygen Formation can be interpreted in terms of a reproductive strategy and in analogy to recent elasmobranchs. Several groups of recent marine and freshwater elasmobranchs show an ontogenetic shift in habitat use. Gravid females of these taxa migrate inshore of the usual species range to deposit their eggs or give birth to young in specific nursery areas (Castro, 1993; Grubbs, 2010). Persistence through time of nurseries is due to strong natal philopatry (site fidelity to the nursery) by the females (Hueter et al., 2005). Nurseries are characterized by providing ample food resources and low predation risk by conspecific and/or other sharks (Compagno, 1990; Castro, 1993; Lowe, 2002; Heupel et al., 2007). The offspring remain in these protected habitats for an extended period (months to years) until they reach a size allowing them to join the adult stock (Castro, 1993). In this respect nurseries are essential for the survival of certain groups of sharks.

Habitat partitioning and nursery pattern have been discussed for Carboniferous xenacanthid and hybodontid sharks from Middle Europe and Kansas (Maisey, 1989; Schneider and Reichel, 1989; Schneider, 1996; Schneider et al., 2005), for lamnoid taxa from the Paleocene and Late Oligocene of South Carolina (Purdy, 1996, 1998), for scyliorhinids from the Late Eocene of Washington (S. Kiel, pers. comm., May 2011), and for *Carcharocles megalodon* (Agassiz, 1843) from the Late Miocene of Panama (Pimiento et al., 2010).

Heupel et al. (2007) proposed three primary criteria to identify extant nursery areas: (1) sharks are more commonly encountered there than in other areas; (2) sharks remain or return for extended periods; and (3) the nursery is repeatedly used over a number of years. Considering Madygen, the majority of recovered teeth are linked to littoral facies and composed of juvenile remains. The continuous occurrence of *Palaeoxyris* remains in the Madygen profile (Fig. 1) suggests persistent use of the nursery through time and therefore probably natal philopatry, at least, by *L. ferganensis*, sp. nov. Therefore, the findings from Madygen fulfill criteria 1 and 3, whereas an assessment of criterion 2 is impossible. The available data indicate use of the Madygen nursery area by different shark species, probably with some degree of temporal partitioning, as is seen in several recent species coexisting in the same geographic area (Castro, 1993).

Palaeoxyris and *Fayolia* prove spawning of hybodontid and xenacanthid sharks in the Triassic Madygen lake system. The egg fossils from different parts of the profile (Fig. 1C) appear as allochthonous elements within massive greyish mudstones that represent prodeltaic fluvial input into the nearby lake. The turbulent vegetated shallow water zones along the shorelines of the Madygen lake and/or feeder rivers are assumed to represent the original spawning grounds based on comparable finds from Paleozoic and Mesozoic strata (Schneider and Reichel, 1989; Fischer et al., 2010a). The juvenile *L. ferganensis*, sp. nov., teeth occur as probable autochthonous elements in sediments of the pelecypod-rich littoral zone. Moreover, it is noticeable that apart from teeth and several dermal denticles, fin spine elements are absent from the fossil assemblage. This may to some degree be artificial, representing the effect of sampling or preservation bias. Otherwise, according to Heupel et al. (2007), the protection of the offspring

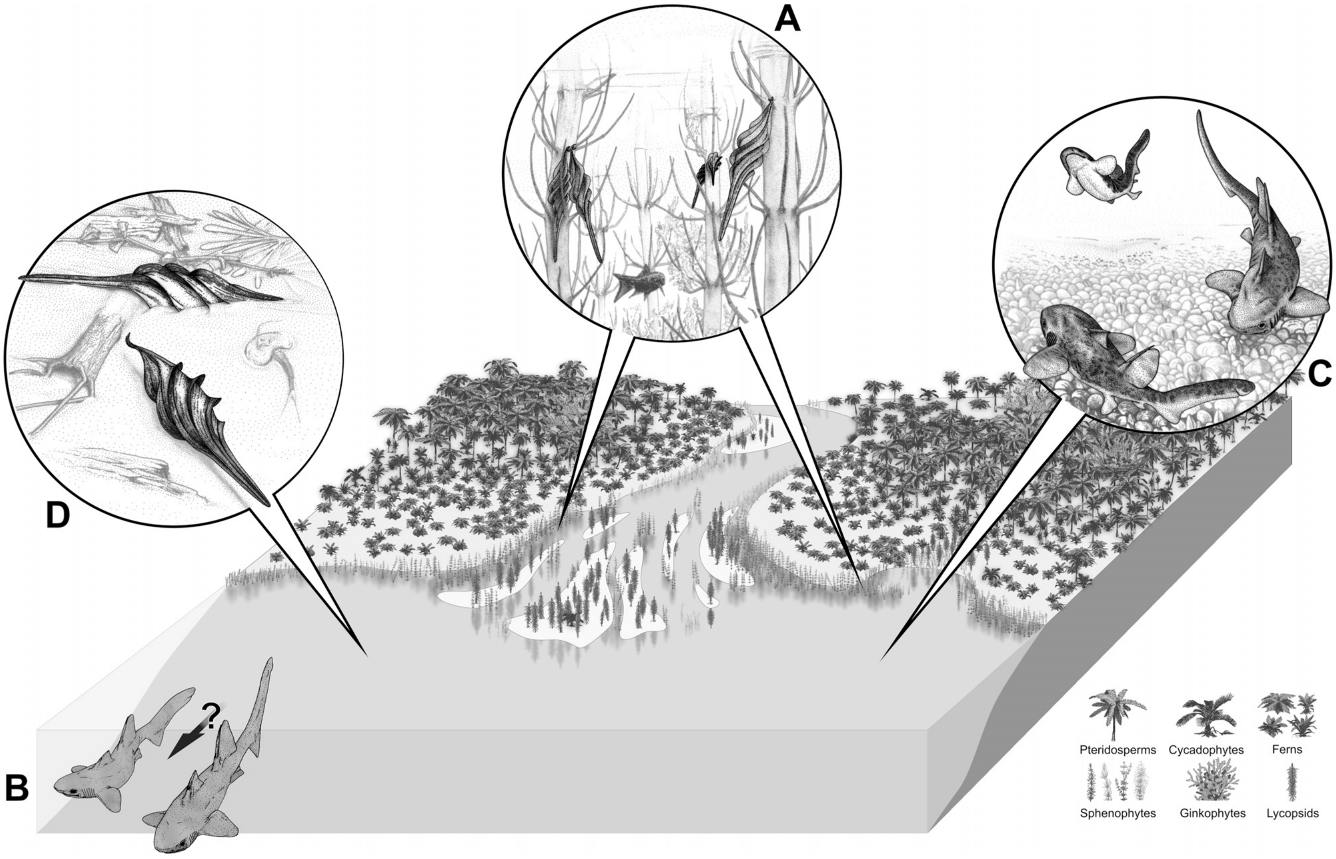

FIGURE 7. Diagrammatic model of the nursery area of *Lonchidion ferganensis*, sp. nov., within the Madygen lake system. **A**, *Palaeoxyris alterna*, sp. nov., capsules attached to submersed plants inshore the lake or alongside feeder rivers; **B**, adults migrated after oviposition to their life habitat, which is more distant from the nursery; **C**, juveniles of *Lonchidion* in the protected shallow pelecypod-rich littoral; **D**, drifted and allochthonously buried *Palaeoxyris* capsules after hatching. See text for more details.

in nurseries results in lower natural mortality rates compared to non-nursery areas. Therefore, only replacement structures such as teeth and denticles are normally shed here. In the course of the migration of larger juveniles to the adult stocks, the spines, which grow throughout life, are not preserved in the nurseries.

Altogether, we propose the following model for the Madygen nursery of *L. ferganensis*, sp. nov.: Females seasonally migrated to the vegetated shallower inshore water zones of the Madygen lake and/or alongside feeder rivers. Here the capsules were attached to submerged objects (Fig. 7A). Subsequent to oviposition the adults returned to their normal life habitats more distantly from the nursery (Fig. 7B). The offspring tended to stay in the shallow pelecypod-rich littoral zone. The availability of hard-shelled benthos and oligochaetes served as an abundant food resource (Fig. 7C) until the juveniles matured sufficiently to join the adult stock. Remaining capsules, empty after hatching, drifted and were buried as allochthonous components in low-energy zones of the Madygen lake environment (Fig. 7D).

Adult Habitats—The oxygen and strontium isotopic analyses of *Lonchidion* teeth indicate freshwater conditions for the Madygen lake, although all geochemically investigated fragments came from juveniles that are considered growing up in the Madygen area. Therefore, nothing can be said for certain about the adult habitats. Whereas most of the associated Madygen fishes are apparently endemic actinopterygians and a dipnoan (Sytchevskaya, 1999), the saurichthyid *Saurichthys* and both sharks, by contrast, are ubiquitous forms in marine and nonmarine strata (Fischer, 2008; Kogan et al., 2009; Ginter et al., 2010). Both contradict the hypothesis of an internally drained upland basin, indicating connection to other freshwater basins, or even directly to the Paleo-Tethys (Voigt et al., 2006; Fischer et al., 2007; Kogan et al., 2009). The general connection of the lake to a large-scale drainage pattern, however, does not presuppose long-distance migration of the gravid sharks or even euryhaline lifestyle. As seen in nursery behavior of recent potamotrygonid freshwater stingrays of South America, the offspring remained in shallow shore areas, whereas the adults generally remained in deeper waters nearby (Rosa et al., 2010). Referring to the Madygen nursery, the adult sharks might have simply come from the deeper waters of the Madygen lake and not necessarily from distant freshwater environments or even a marine stock.

CONCLUSION

A new freshwater selachian fauna is described from the Middle to Late Triassic Madygen Formation of Kyrgyzstan, Central Asia, on the basis of teeth and egg capsules. The main conclusions drawn from this study are (1) the small hybodontid *Lonchidion ferganensis*, sp. nov., is represented by juvenile teeth of different tooth morphotypes, and is regarded as the producer of the egg capsules *Palaeoxyris alterna*, sp. nov.; (2) a second egg capsule *Fayolia sharovi*, sp. nov., implies the presence of an yet unknown xenacanthid shark as the most probable producer; (3) the new species of *Fayolia* is the youngest record of this capsule form genus extending its stratigraphical range to the Middle–Late Triassic, and also represents its first record in Asia; (4) the co-occurrence of *Lonchidion* teeth and *Palaeoxyris* egg capsules is in agreement with the earlier assignment of *Palaeoxyris* capsules to hybodontid sharks; (5) the spatial and temporal distribution of teeth and capsules together with the faunistic context allows the interpretation of the Madygen environment as a nursery area for different ancient sharks by analogy with extant forms; and (6) low enameloid $\delta^{18}O_P$ values of around 10‰ and high $^{87}Sr/^{86}Sr$ ratios of around 0.7098 reflect tooth formation in freshwater conditions in the Madygen environment.

The Madygen finds show that habitat partitioning and site fidelity of spawning grounds represent an ancient specific phylogenetic pattern of behavior of sharks long before the rise of neoselachians. Moreover, these finds demonstrate the potential of fossil shark egg capsules as indicators for the distribution area and migration patterns of the egg-laying sharks, especially in nonmarine environments.

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