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The oldest turritelline gastropods: from the Oxfordian (Upper Jurassic) of Kutch, India

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Abstract.—Turritellid gastropods are important components of many Cretaceous–Recent fossil marine faunas worldwide. Their shell is morphologically simple, making homoplasy widespread and phylogenetic analysis difficult, but fossil and living species can be recognized based on shell characters. For many decades, it has been the consensus that the oldest definite representatives of Turritellidae are from the Lower Cretaceous, and that pre-Cretaceous forms are homeomorphs. Some morphological characters of the present turritelline species resemble those of mathildoids, but many diagnostic characters clearly separate these two groups. We here describe and/or redescribe—based on examination of more than 2600 near complete specimens—four species from the Upper Jurassic Dhosa Oolite Member of the Chari Formation in Kutch, western India, and demonstrate that they are members of Turritellidae, subfamily Turritellinae, on the basis of diagnostic characters including apical sculptural ontogeny (obtained from SEM study), spiral sculpture, and growth line patterns. The four species are in order of abundance, *Turritella jadavpuriensis* Mitra and Ghosh, 1979; *Turritella amitava* new species; *Turritella jhuraensis* Mitra and Ghosh, 1979, and *Turritella dhosaensis* new species. The turritelline assemblages occur only on the northeastern flank of the Jhura dome (23°24’47.57”N, 69°36’09.26”E). Age of the Dhosa Oolite has recently been confirmed based on multiple ammonite species. All these points indicate that these fossils are the oldest record of the family Turritellidae—by almost 30 million years—in the world.

Introduction

The gastropod family Turritellidae is widely regarded as a monophyletic group within basal caenogastropods commonly known as “cerithioids” (Cerithioidea, sensu Strong et al., 2011; Cerithimorpha, sensu Golikov and Starobogatov, 1975; also see Lydeard et al., 2002; Ponder et al., 2008). Turritellids can be extremely abundant in assemblages in which they occur, from Lower Cretaceous to Recent (Allmon, 2007), including several fossil assemblages in India (Malarkodi et al., 2009; Mallick et al., 2013; Bardhan et al., 2014). The group has also been the subject of numerous studies of predation intensity in the fossil and Recent records (e.g., Allmon et al., 1990; Mallick et al., 2013, 2014; Paul et al., 2013).

The recent consensus has been that the oldest definite representatives of the subfamily Turritellinae (and perhaps the family Turritellidae, as well) are from the Lower Cretaceous (Valanginian Stage) of Poland (*Turritella polonica* Schröder, 1995; see Bandel, 1993; Tracey et al., 1993; Schröder, 1995; Kaim, 2004; Allmon, 2011) (ca. 133.9–139.4 Myr; Gradstein et al., 2012), and the group is moderately diverse and abundant by later in the Early Cretaceous (Ellisor, 1918; Abbass, 1962; Allmon and Cohen, 2008). Turritellidae was, however, long reported to have originated in the late Paleozoic (e.g., Knight et al., 1960, p. I316; Sepkoski, 1982, p. 28), and the genus *Turritella* sensu lato has occasionally been cited (although never with much detailed analysis) from the Jurassic and even Triassic (e.g., Hudleston, 1892, p. 227–235; Dacque, 1905; Edwards, 1980; Fürsich, 1984; Meier and Meiers, 1988; Tekin, 1999; Bandel, 2006). Many 19th and early-20th century workers considered any high-spired gastropod lacking a selenizone and with a U-shaped apertural sinus as “*Turritella*,” but many of the early Mesozoic examples so assigned have since been placed in other groups, especially Mathildoidea (Bandel, 1991, 1995; Hikuroda and Kaim, 2007; Gründel and Nützel, 2013).

Within Turritellidae, details of shell form, including apical angle, whorl profile, and especially spiral sculpture, usually allow relatively unambiguous recognition of species in fossils, and the group has long provided important guide fossils in Cretaceous and Cenozoic biostratigraphy (e.g., Woodring, 1930, 1931; Gardner, 1935; Stenzel, 1940; Wheeler, 1958; Kauffman, 1977; Sohl, 1977; Saul, 1983; Squires, 1988). These characters, however, are also clearly homeomorphic across the family (Merriam, 1941; Marwick, 1957; Kotaka, 1978; MacNeil and Dockery, 1984; Allmon, 1994, 1996). Thus, while detailed morphological examination (e.g., with SEM of protoconch and early apical ontogeny) allows for testing of phylogenetic hypotheses on a limited geographic scale, broader phylogenetic analysis—and reliable assignment to supraspecific taxa—based solely on shell characters remains problematic (Allmon, 1996, 2011; Beu, 2010, p. 89).

In this paper, we report four species assignable to the genus *Turritella* sensu lato, from the Late Jurassic (Oxfordian) Chari Formation of Kutch, western India, and argue that these represent the oldest turritellid species known. The age of the *Turritella*-bearing horizons is well constrained by the coeval ammonites and belemnites. Two of these species of *Turritella* were previously described from these deposits (Mitra and Ghosh, 1979). Unfortunately, however, they went unnoticed by the paleontological community, and the specimens were lost. We therefore here redescribe them, based on new data obtained from numerous additional specimens and SEM analysis, and describe two more species as new. We compare the Indian species with diverse species across many geological periods and continents to show the extent of homeomorphism, but we explicitly note that nothing phylogenetic is intended by these comparisons.

Turritellidae versus Mathildoidea

Within gastropods, mathildoids are phylogenetically distant from turritellids. They are sometimes referred to as "lower heterogastropods," more closely related to pulmonates and opisthobranchs than to cerithioids. Yet the shells of many mathildoids are superficially similar to turritellids in being high-spired, with relatively small apertures. The group was also apparently more diverse in the Mesozoic, especially the Jurassic, than it is today (see Bandel, 1995; Bieler, 1995; Gründel and Nützel, 2013), posing an additional potential difficulty in distinguishing its species from early representatives of Turritellidae.

The family Turritellidae is characterized by an elongate, high-spired shell of many whorls, ending in an aperture that is relatively small, simple, and entire, lacking any elaboration of its margin (Marwick, 1957). The subfamily Turritellinae is characterized by external teleoconch sculpture of spiral threads, sometimes beaded, and curved growth lines; the aperture is rounded or quadrate and not large; the inner wall of the aperture is smooth and concave (Marwick, 1957; Bandel, 2006).

Mathildoid species superficially resemble turritellids in shell shape and spiral ornamentation, but the former are usually more slender (Bandel, 1995). Many species of mathildoids have strong carination similar to one of the species discussed here. Strong carination is also found in turritellids, such as *Zaria angulata* (Sowerby, 1840) from the Miocene of the Indian sub-continent (see Harzhauser et al., 2009, fig. 3a–d), and "*Turritella*" *mortoni* from the Paleocene of the U.S. Gulf and Atlantic coastal plains (Allmon, 1994, 1996).

Shells of mathildoids, however, show a number of clear differences compared to turritellids, most conspicuously their heterostrophic (sinistral) protoconch, which shows an abrupt boundary with the dextral teleoconch. High-spired mathildoids are also smaller than most turritellids; their aperture frequently bears a short anterior canal; and their earliest teleoconch whorls almost always bear axial (vertical) ribs in addition to spiral sculpture.

None of our specimens has preserved protoconchs; our identification of them as turritellids is therefore based on other characters. For example, all our studied specimens lack axial sculpture and an apertural anterior canal, and all of our four species are relatively large (> 2 cm) compared to known Jurassic mathildoids. A broader analysis of shell characters of our Jurassic species, compared to a number of Cretaceous turritellines and Mesozoic mathildioid species originally identified as *Turritella* (Tables 1–3), further supports our assignment by demonstrating that our species are more similar to Cretaceous turritellids than to Mesozoic mathildoids. Growth-line data are poorly known from fossil mathildoids, but extant species show mostly irregular and opysthocyrt growth lines (Bieler, 1995). The species considered here, however, have prosocline growth lines. Ecologically, the modern family Mathildidae is a mostly deep-water group (Bieler, 1995), with many Recent species inhabiting 550–600 m depths within coral bank communities (Smriglio et al., 2007). The depositional environment of the Dhosa Oolite Member, from which the present species were obtained, in contrast, was an offshore setting below the fair-weather wave base (Singh, 1989; Fürsich et al., 1992), and no corals have been described from the Dhosa Oolite Member.

Geologic setting

Geologic time units.—During the Middle Jurassic (Bajocian–Bathonian), the Kutch Basin developed due to the fragmentation of Gondwana (Biswas, 1982, 1991). Mesozoic strata in Kutch

Table 1. Coded morphology of turritelline species described in this text (A–D), Cretaceous turritellines (E–I) and some mathildidoid species (J–N). The coded characters and their different states are given in Appendix 1.

	Species Name	Strat. Range	1	2	3	4	5	6	7	8	9	10	11
A	*Turritella jadavpuriensis*	Oxfordian	0	3	1	1	2	2	1	0	1	0	1
B	*Turritella jhuraensis*	Oxfordian	1	0-3	1	1	2	1	2	0	1	0	1
C	*Turritella amitava* n. sp.	Oxfordian	1	1-4	1	2	1	1	1	0	?	0	1
D	*Turritella dhosaensis* n. sp.	Oxfordian	1	5	?	2	?	1	2	0	1	0	1
E	*Turritella encina* Squires and Saul, 2006 (Squires and Saul, 2006)	Santonian	1	0	?	1	?	?	1	0	?	0	1
F	*Turritella iota* Popenoe, 1937 (Squires and Saul, 2006)	late Turonian	1	4	?	1	?	?	2	0	?	0	1
G	*Turritella hearni* Merriam, 1941 (Squires and Saul, 2006)	Turonian	1	1	?	0	?	?	2	0	?	0	1
H	*Turritella petersoni* Merriam, 1941 (Squires and Saul, 2006)	Cenomanian to early Turonian	1	0	?	1	?	?	?	0	?	0	1
I	*Turritella xylina* Squires and Saul, 2006 (Squires and Saul, 2006)	Cenomanian	1	0	?	1	?	?	1	?	?	0	1
J	*Mathilda bolina* (Bandel, 1995)	Late Triassic	2	3	?	2	?	1	1	1	1	1	0
K	*Promathilda decorta* (Bandel, 1995)	Late Triassic	2	3	1	1	2	1	2	1	1	1	0
L	*Tofanella decussata* (Bandel, 1995)	Late Triassic	2	3	0	1	2	2	1	1	1	1	0
M	*Cristalloella cassiana* (Bandel, 1995)	Late Triassic	2	3	0	0	2	1	2	1	0	1	0
N	*Mathilda* cf. *euglypha* Laube (Hudleston, 1892)	Early Jurassic	2	3	1	?	?	0	1	1	?	1	0

Table 2. Similarity matrix showing clusters of the Jurassic species discussed in this paper and selected Cretaceous turritelline species (based on data from Table 1). Methods based on Raup and Stanley (1978, p. 144–145).

	A	B	C	D	E	F	G	H	I
A		72	54	36	45	36	27	36	36
B			64	64	54	54	45	54	45
C				54	45	45	45	36	36
D					36	45	45	36	27
E						45	36	54	54
F							45	45	36
G								36	27
H									45
I									

Table 3 . Similarity matrix showing clusters of the Jurassic species discussed in this paper and selected Mesozoic mathildidoid species (based on data from Table 1).

	A	B	C	D	J	K	L	M	N
A		72	54	36	27	45	54	18	27
B			64	64	27	64	36	36	18
C				54	36	27	18	18	27
D					27	18	9	18	0
J						64	64	54	54
K							64	72	54
L								64	54
M									45
N									

are divided into several formations (Mitra et al., 1979). The major fossil-bearing units are the Patcham (Bathonian) and Chari (Callovian to Oxfordian) formations of the mainland of Kutch (Biswas, 1977). The fossils discussed here were collected from the Dhosa Oolite Member (Oxfordian) of the Chari Formation (23°24’47.57”N, 69°36’09.26”E) (Fig. 1).

Stratigraphic information.—Rocks of both the Patcham and Chari formations were the products of continental shelf margin sedimentation (Datta, 1992; Fürsich et al., 2001). The Dhosa Oolite Member is a condensed, time-averaged unit (Singh, 1989; Fürsich et al., 1992; Pandey et al., 2009; Roy et al., 2012). In sequence stratigraphic terms, it represents a Transgressive System Tract (TST; Fürsich et al., 2001) and Maximum Flooding Zone (MFZ; Fürsich and Pandey, 2003). The top part of the Dhosa Oolite is hard, conglomeratic, highly fossiliferous, and contains ferruginous oolite. The lower part contains shale and sandstone with sparse oolite (Fürsich et al., 2001; Roy et al., 2012) (Fig. 2). The present turritelline species were found in the lower part of the unit, mostly in shale, or occurring loosely, free of matrix.

Mitra and Ghosh (1979) reported two ammonite species, *Peltoceras kumagunense* Spath, 1931 and *Paryphoceras rugosum* Spath, 1928, in association with the *Turritella* specimens they described. According to them, these two species belonged to the Oxfordian and were found only in the Dhosa Oolite Member, which was overlain by layers of Kimmeridgian age. We also collected a single belemnite specimen tentatively assigned to *Belemnopsis tanganensis* (Futterer, 1894) (see Spath, 1927, p. 9, pl. 1, figs. 3a, b, 4) from one *Turritella*-bearing horizon.

Despite the previous discovery of these cephalopod fossils, determination of the precise age of the *Turritella*-bearing horizons remained unclear. Recently, however, Roy et al. (2012) demonstrated that the Dhosa Oolite Member spans the entire Oxfordian. *Peltoceras kumagunense* ranges from upper Callovian to lower Oxfordian (Spath, 1931; A. Roy, personal communication, 2016). Spath, on the other hand, described all species of *Paryphoceras* from the Dhosa Oolite Member without specifying from which part of the unit the species came. Alberti et al. (2015) revised the species of *Paryphoceras* of Kutch, and concluded that the majority of the species are found in the middle Oxfordian (*Cardioceras cordatum* to *Gregoryceras transversarium* zones; ca. 159.4–161.4 Myr; Gradstein et al., 2012). The only species described by Alberti et al. (2015) come from the lower Oxfordian part of the Dhosa Oolite. From these faunal occurrences, it appears that the *Turritella*-bearing horizons are either early Oxfordian or middle Oxfordian in age. From the lithological point of view, *Turritella*-yielding horizons are mostly shale and sandstone, occasionally within limestone with sparse ooids (Fig. 3). This facies association is typical of the upper part of the lower Oxfordian part of the Dhosa Oolite Member.

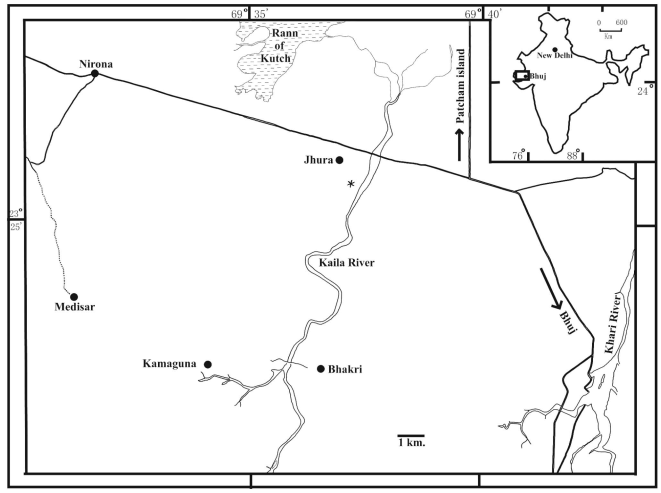

Figure 1. Geographic locations (solid circles) of the Dhosa Oolite Member. Present fossil collection has been made from a pond section near Jhura (*). Modified after Bardhan et al. (2012).

Locality information.—The Dhosa Oolite Member is widely distributed in the mainland of Kutch as well as in the Jhura dome. The *Turritella*-bearing assemblages, however, are restricted to a pond section (23°24’47.57”N, 69°36’09.26”E) near the village of Jhura, which is 45 km northwest of Bhuj, the district town of Kutch (Fig. 1).

Materials and methods

The samples were collected following both bulk sampling (see Kowalewski, 2002) and random surface-sampling protocols (see Mallick et al., 2013). Eleven bulk samples were collected in four separate field trips (2012, 2013, 2014, and 2016). The turritelline gastropods were separated in the laboratory. At several stratigraphic horizons, we collected all specimens encountered, including those small and large, broken, and intact. Turritelline specimens were identified at supraspecific levels following criteria and morphological terms used in the previous literature (e.g., Allison, 1965; Allmon, 1996; DeVries, 2007; Allmon and

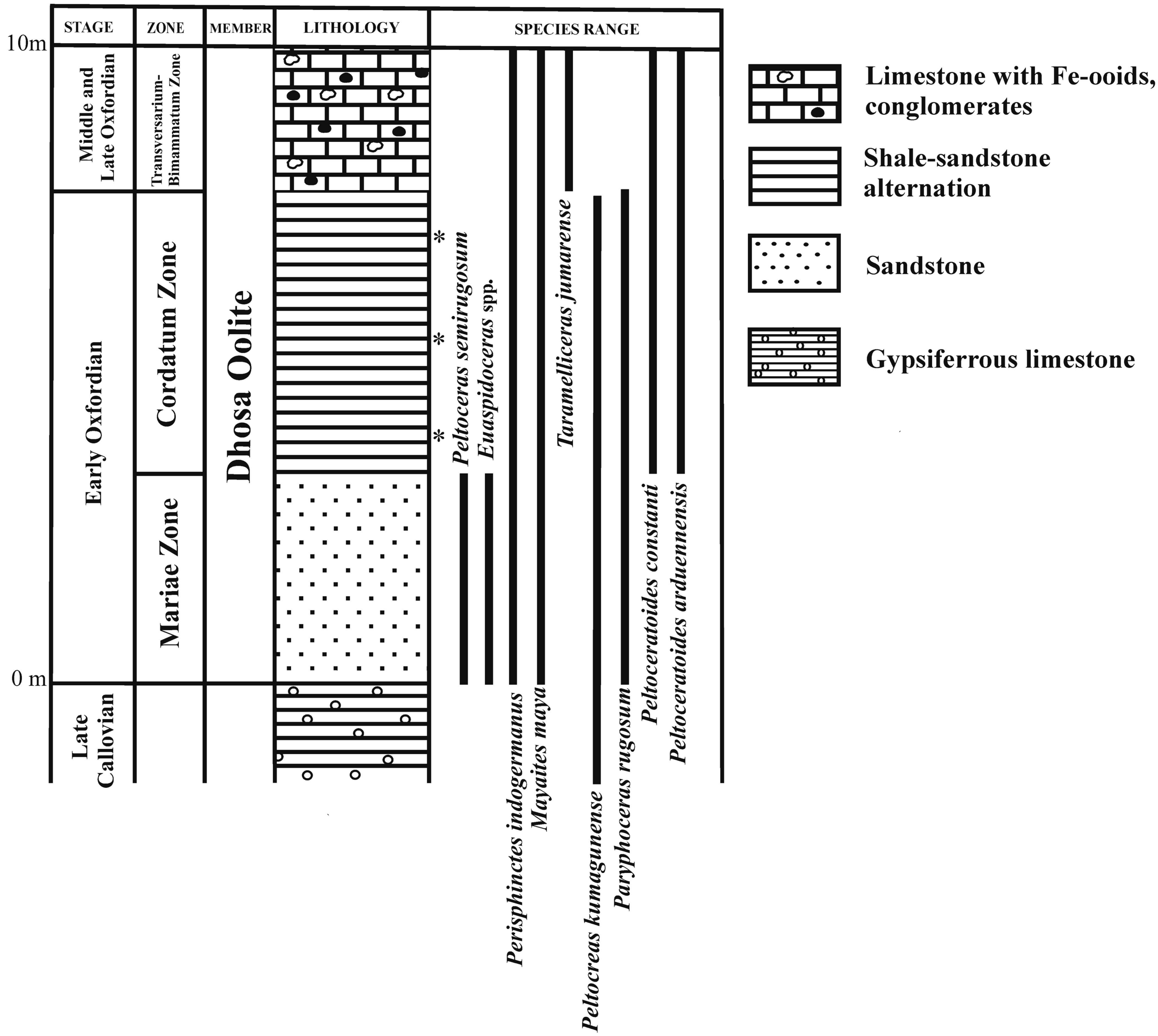

Figure 2. Stratigraphic distribution of a few time-diagnostic ammonite species from the Dhosa Oolite of mainland of Kutch. Asterisk (*) marks the sampling points. Modified after Roy et al. (2012), based on Waagen (1875); Spath (1928, 1931); Fürsich and Heinze (1998); Fürsich et al. (2001); Roy et al. (2012); and Alberti et al. (2015).

Harris, 2008). Turritellines comprise 85% of the total macrofossil assemblage, which satisfies the criteria of "turritelline-dominated assemblage" (TDA) (Allmon, 2007). Our collections included a total of 13,705 turritelline specimens, of which 2686 specimens are nearly complete. We assigned the turritellines to four species: *Turritella jadavpuriensis* (about 74.8% of all specimens), *Turritella jhuraensis* (about 9.2%), *Turritella amitava* new species (about 15.6%), and *Turritella dhosaensis* new species (about 0.003%).

In spite of good preservation of many specimens, no protoconchs were preserved, and early teleoconch whorls were preserved in only three specimens of *T. jadavpuriensis* and one specimen of *T. amitava* n sp. All measurements were made by digital caliper to the nearest 0.1 mm.

Repositories and institutional abbreviations.—All specimens, including the types, are archived in the museum of Geological Studies Unit, Indian Statistical Institute, Kolkata, India. Specimens are numbered following the institutional abbreviation ISI/g/Jur/T.

Systematic paleontology

Class Gastropoda Cuvier, 1797
Subclass Caenogastropoda Cox, 1960
Order Sorbeoconcha Ponder and Lindberg, 1997
Superfamily Cerithioidea Fleming, 1822
Family Turritellidae Lovén, 1847
Genus *Turritella* Lamarck, 1799

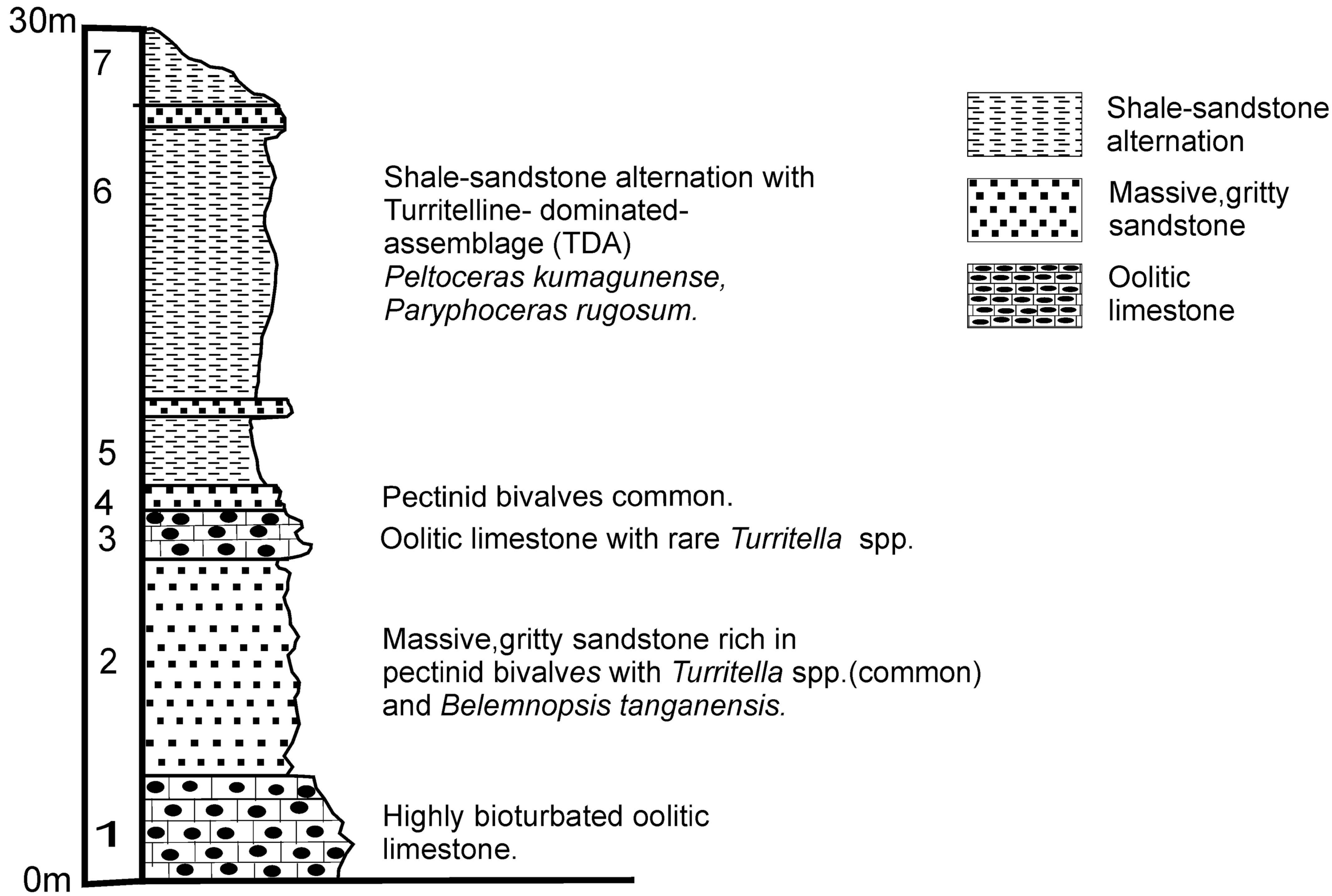

Figure 3. Schematic stratigraphic section of the pond section from where *Turritella* spp. were collected. Associated cephalopod taxa indicate the late early Callovian age.

Type species.—*Turbo terebra* Linnaeus, 1758 (original designation), Recent, Indo-Pacific.

Turritella jadavpuriensis Mitra and Ghosh, 1979
Figures 4.1–4.4, 5.1, 5.2, 6, 7.1–7.6, 8.1–8.4

Type.—Neotype: specimen no. ISI/g/Jur/T 1.

Occurrence.—This species is known only from the Oxfordian horizons near a pond ~ 1 km southeast of the village of Jhura, Kutch (23°24’47.57”N, 69°36’09.26”E).

Description.—Shell medium to large in size with 15–16 whorls. Maximum observed whorl diameter 23.5 mm and maximum observed height 64.5 mm. Apical angle 19–29°; apical angle and pleural angles not equal, pleural angle slightly less than apical angle. Suture moderately to deeply incised; incision increasing with ontogeny. Protoconch unknown (Figs. 4, 5). Apical sculpture formula $A_1B_1C_1d_2$. Primary spirals A, B, and C develop simultaneously; spiral A appears in the upper 1/3 of the first teleoconch whorl, spiral B in the middle of the whorl and spiral C in the lower 1/3 of the whorl. Spiral C quickly becoming prominent in the later whorls and forming an angulation near the anterior part of whorls. In inflated variant, spiral C changes during ontogeny from having a rounded edge to a well-marked, blade-like angulation. Spiral A becomes prominent in later whorls, but less strong with respect to C and B spirals. In second teleoconch whorl, a prominent D spiral appears between spiral C and suture. Strength of all spirals (A, B, C, and D) increases during ontogeny. Order of relative strength is C, D, B, and A, which remains unchanged on adult whorls. Secondary spirals appear between all primary spirals. Spiral A and spiral B separated by one or two secondary spirals. Spiral C and spiral D also separated by two fine secondary spirals. One secondary spiral developed between spiral A and posterior suture, between spiral B and spiral C, and between spiral D and anterior suture (Fig. 6). Shell basally bicarinate, with carinae thinner toward its peripheral (outer) part. Shape ranges from forms with high apical angle ~ 29° (i.e., “inflated” variants) to elongated forms with apical angle ~ 19° (i.e., “slender” variants). These two extreme variants are connected by intermediate forms forming overlapping morphotypes (Fig. 7.3, 7.4). All of them occur side-by-side in the same horizons. Shape of whorls in slender variants is imbricate and campanulate in robust variants. Spiral ornament in inflated variant forms a prominent keel-like angulation at whorl periphery. Both variants with convex early teleoconch whorls. Lateral aspect of growth line trace prosocline; lateral sinus is moderately deep (Fig. 8). Sinus with apex below mid-whorl is common while rarely occurring above mid-whorl. Single inflection point on top developed in some variants. Basal

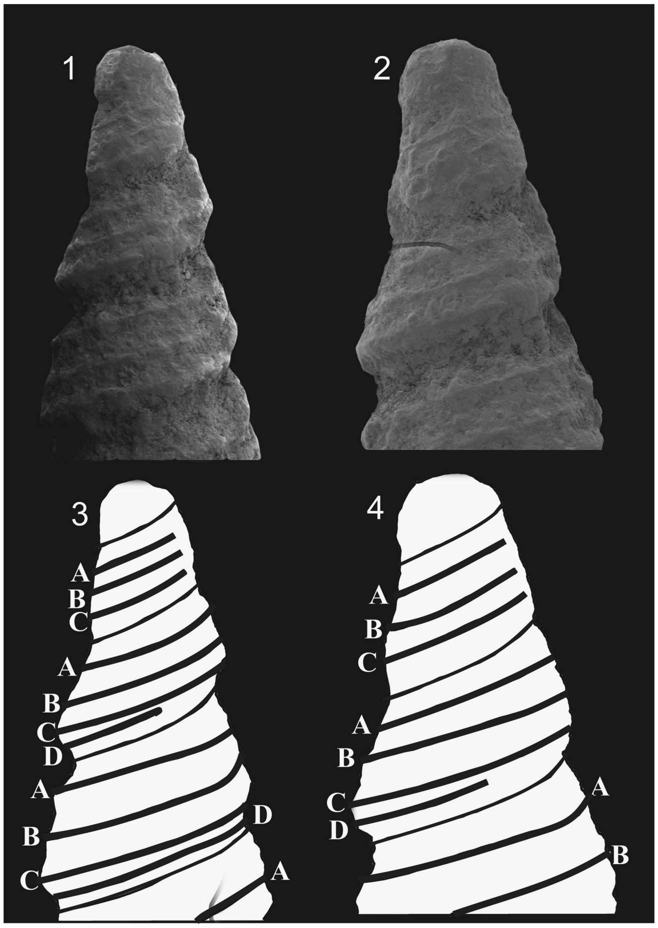

Figure 4. Scanning electron micrographs of apices of two specimens of *Turritella jadavpuriensis* Mitra and Ghosh, 1979. (**1**) Paraneotype (no. ISI/g/Jur/T 1) showing early teleoconch part and well-developed apical sculpture (×105); (**2**) paraneotype (no. ISI/g/Jur/T 2) with completely preserved early teleoconch (×105); (**3**) sketch of **1**, showing primary spiral ribs (notation after Allmon, 1996); note A, B, C spirals appear simultaneously and apical sculpture formula is therefore, $A_1B_1C_1d_2$; (**4**) sketch made from **2**, showing similar appearance of primary spiral ribs.

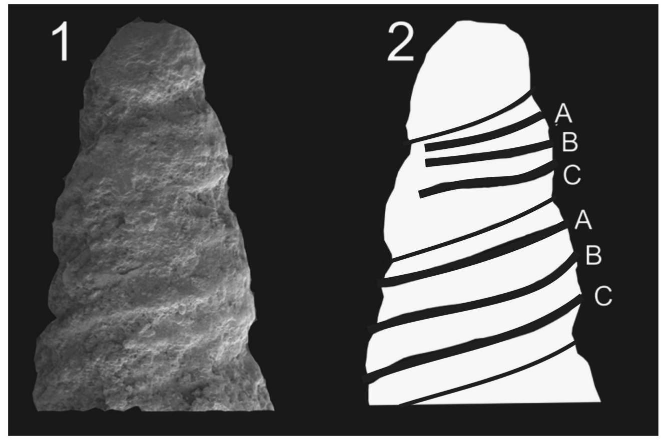

Figure 5. Scanning electron micrograph of apex of one specimen of *Turritella jadavpuriensis* Mitra and Ghosh, 1979. (**1**) Paraneotype (no. ISI/g/Jur/T 101) showing completely preserved early teleoconch (×105); (**2**) sketch of **1**, showing primary spiral ribs.

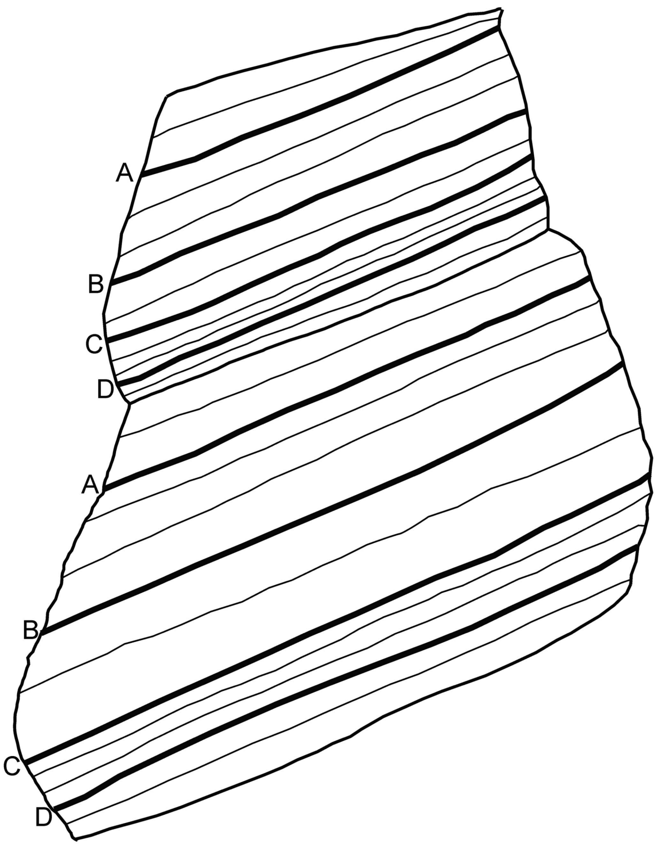

Figure 6. Sketch of the adult whorls of a paraneotype (no. ISI/g/Jur/T 9) of *Turritella jadavpuriensis* Mitra and Ghosh, 1979, showing all secondary spiral ribs within the primary spirals (maximum diameter 18.3 mm).

sinus mostly not discernible; in some cases, it appears to be shallow. Growth line formula 3-3-M-A/C-P. Aperture subquadrate, higher than wide. Columellar lip distinct, outer lip very thin and fragile, in most specimens not preserved.

Materials.—Four syntypes originally selected by Mitra and Ghosh (1979) were declared lost by the Repository Section, Geological Survey of India (G.S.I), Kolkata. Neotype specimen no. ISI/g/Jur/T 1; 41 paraneotype specimens, nos. ISI/g/Jur/T 2-30 and 101-112.

Remarks.—*Turritella jadavpuriensis* Mitra and Ghosh, 1979 is the most abundant species in the studied assemblages. The angular whorl profile and large size of *T. jadavpuriensis* distinguish it from the other two species described from the same Oxfordian horizons of Kutch.

Turritella jadavpuriensis and *Mathilda* cf. *euglypha* Laube, 1867 from the Lower Jurassic of England (see Hudleston, 1892, p. 235, pl. 17, fig. 10) have a similar angular teleoconch whorl profile, but they differ in many respects. *Turritella jadavpuriensis* has exclusively spiral sculpture and a holostomatous aperture. On the other hand, *M*. cf. *euglypha* has dominantly axial sculpture and a siphonastomatous aperture. Moreover, *T. jadavpuriensis* has a larger size (maximum observed height 64.5 mm) compared to *M*. cf. *euglypha* (height ~ 3 mm).

An angular whorl profile like that of *T. jadavpuriensis* is also present in *Mathilda bollina* (Münster, 1841) from Late Triassic St. Cassian Formation (see Bandel, 1995, p. 6, pl. 2, figs. 1–4, 6), but the latter's very small size, axial

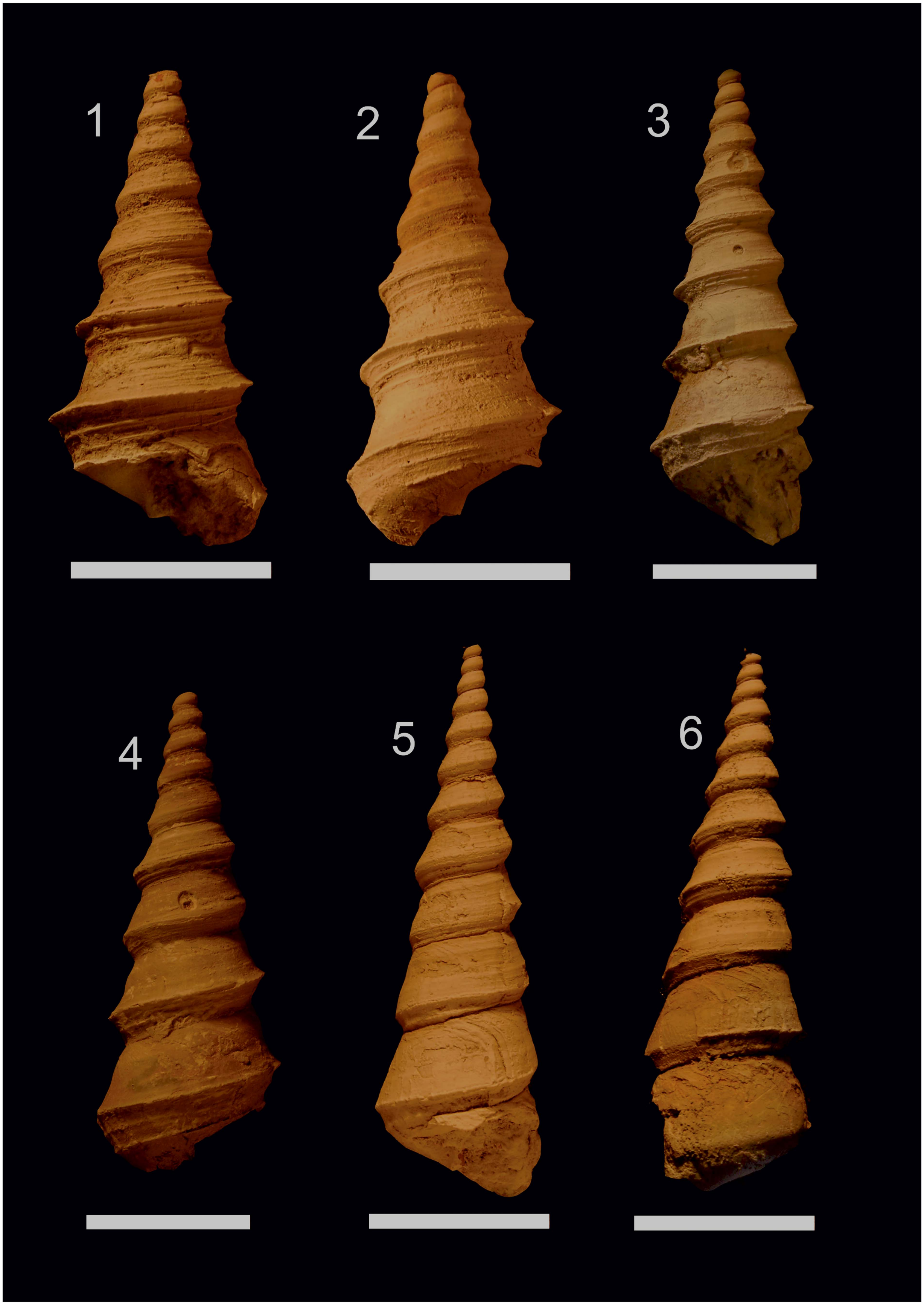

Figure 7. *Turritella jadavpuriensis* Mitra and Ghosh, 1979. (**1, 2**) Apertural and abapertural views of robust variant (paraneotype no. ISI/g/Jur/T 5); (**3, 4**) apertural and abapertural views of intermediate variant (paraneotype no. ISI/g/Jur/T 7); (**5, 6**) apertural and abpertural views of slender variant (paraneotype no. ISI/g/Jur/T 6). All specimens are coated with magnesium oxide. Scale bars = 1 cm.

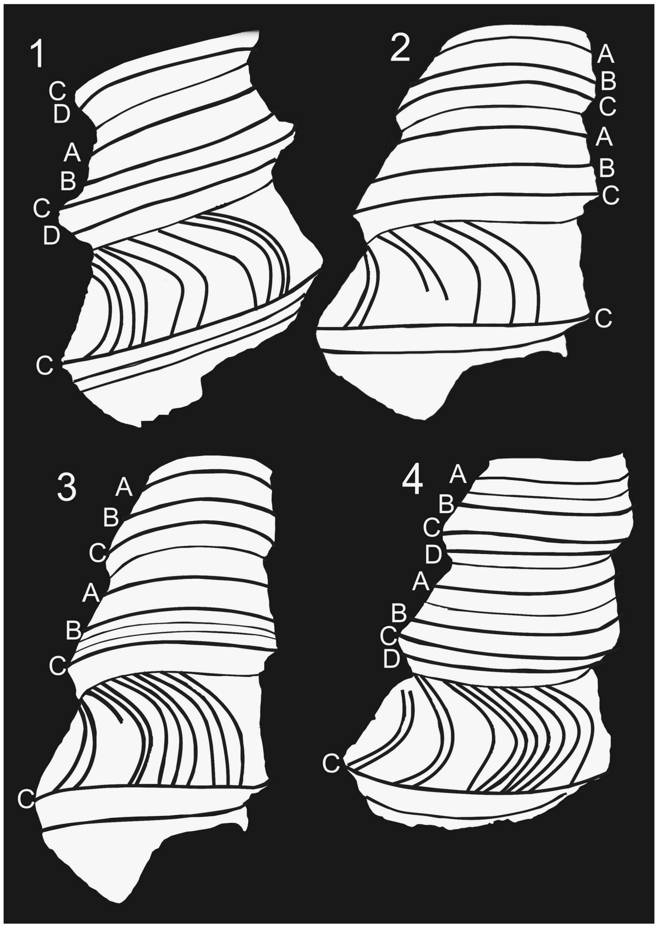

Figure 8. Sketch of growth line patterns in *Turritella jadavpuriensis* Mitra and Ghosh, 1979. Note wide intraspecific variability of growth line traces. For full description of the patterns see text. (**1–4**) Abapertural views (maximum diameters: (**1**) 16.1 mm, (**2**) 14.5 mm, (**3**) 15.1 mm, (**4**) 15.3 mm) with broken aperture.

sculpture, and siphonotomatous aperture clearly differentiate it from *T. jadavpuriensis.*

Turritella jadavpuriensis might be compared with *Turritella woodsi* Lisson, 1925 from the Oligocene to Miocene of southern Peru (DeVries, 2007, p. 341, fig. 6.8–6.14) in having keeled ornamentation. However, the position of the keel differs in these two species. In *T. jadavpuriensis*, the keel is anteriorly (abapically) placed while in *T. woodsi* the keel is located posteriorly (adapically). Moreover, the Peruvian species attains very large size (up to 110 mm) and has more whorls. *Turritella jadavpuriensis* is also distinguished from *T. woodsi* in growth line pattern: growth line formula 3-3-M-A/C-P in *T. jadavpuriensis* versus 5/4-1/2-D-B-P/OR in the Peruvian species.

Eames (1952) identified *Turritella imbricataria* Lamarck, 1804 from the Eocene of Pakistan, based on a single fragmentary specimen whose apical part was, however, well preserved, and he placed it within the genus (or subgenus) *Haustator*. This species resembles *T. jadavpuriensis* in being basally (abapically) carinate. Eames (1952) provided a detailed description of the apical ornamentation (which was very rare in those days). According to him, the Pakistani *T. imbricataria* is characterized by a smooth, rounded protoconch with one convex whorl. Apical ornamentation, he said, is characterized by "unicarinate" spiral ornamentation, but he did not specify the primary spirals (i.e., the apical ontogenetic formula). In *T. jadavpuriensis*, however, all three primary spirals appear simultaneously (formula $A_1B_1C_1d_2$).

Zaria angulata (Sowerby, 1840) from the Miocene sediments of Kutch (Vredenburg, 1928; Harzhauser et al., 2009, p. 343, fig. 3A–D; Kulkarni et al., 2010, p. 314, fig. 2g) is similar to the slender variant of *T. jadavpuriensis*. Both have a similar imbricate whorl profile, basally bicarinate shell and relatively less-strong keel in comparison with the inflated variant of the present species. Growth line patterns, however, differ in these two species: *Z. angulata* is characterized by opisthocline growth lines, while *T. jadavpuriensis* has prosocline growth lines. Moreover, *T. jadavpuriensis* is larger than *Z. angulata* and has a more acute apical angle compared to *Z. angulata*. Unfortunately, the nature of apical ornamentation is not known for *Z. angulata*.

Turritella jhuraensis Mitra and Ghosh, 1979
Figures 9.1–9.3, 10.1–10.3

Type.—Neotype: specimen no. ISI/g/Jur/T 31.

Occurrence.—This species is known only from the Oxfordian horizons ~ 1 km south-east of the village of Jhura near a pond, Kutch (23°24’47.57”N, 69°36’09.26”E).

Description.—Shell small to medium in size with five to eight whorls. Maximum observed whorl diameter 8.5 mm; maximum observed height 28.2 mm. Apical angle 22–26°; apical angle and pleural angle not equal; pleural angle slightly smaller. Suture moderately to deeply incised. Protoconch and early teleoconch whorls unknown. Earliest known whorl ~ 0.6 mm in diameter; A, B, and C spirals prominent, but C spiral stronger and B spiral weak. Space between A and B spirals wider than space between B and C. In later whorls (~4.3 mm diameter), D spiral developed between C spiral and suture, its strength remaining much weaker than other three spirals (Fig. 9). Primary spiral C remains strong throughout ontogeny. Spiral C rounded in profile on early whorls, but becomes sharp, keel-like in adult whorls. One secondary spiral between A and B spirals in later whorls (whorl diameter = 6.4 mm) (Fig. 9). Shell basally carinate; carina thin and sharp at peripheral (outer) margin. Between inner carina and outer carina, a feeble thread developed. Whorl profile convex to frustrate. Lateral growth lines not well preserved, but probably straight and slightly prosocline (Fig. 9). Aperture subrounded, higher than wide. Columellar lip distinct and outer lip very thin.

Materials.—Four syntypes originally selected by Mitra and Ghosh (1979) and deposited in the Repository Section, Geological Survey of India (G.S.I), Kolkata were lost. One neotype (specimen no. ISI/g/Jur/T 31) and nine paraneotypes (specimen nos. ISI/g/Jur/T 32-40) have been assigned here.

Remarks.—*Turritella jhuraensis* lacks the highly angulated C spiral, which forms a very sharp, blade-like ridge in *T. jadavpuriensis*. In *T. jadavpuriensis*, the distances between

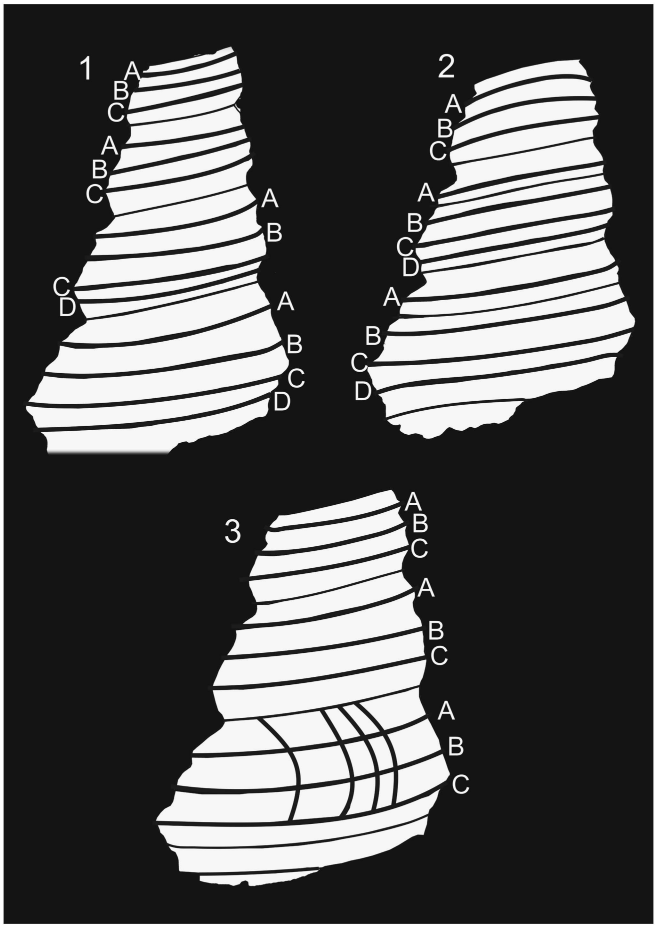

Figure 9. Sketch of *Turritella jhuraiensis* Mitra and Ghosh, 1979. (**1**) Diagram showing all the primary spirals present in the adult whorls (maximum diameter 9.3 mm); (**2**) diagram showing all the primary spirals and one secondary spiral present within the A and B spiral (maximum diameter 6.2 mm); (**3**) diagram showing the growth line patterns of the species, i.e., straight and faint prosocline (maximum diameter 3.9 mm).

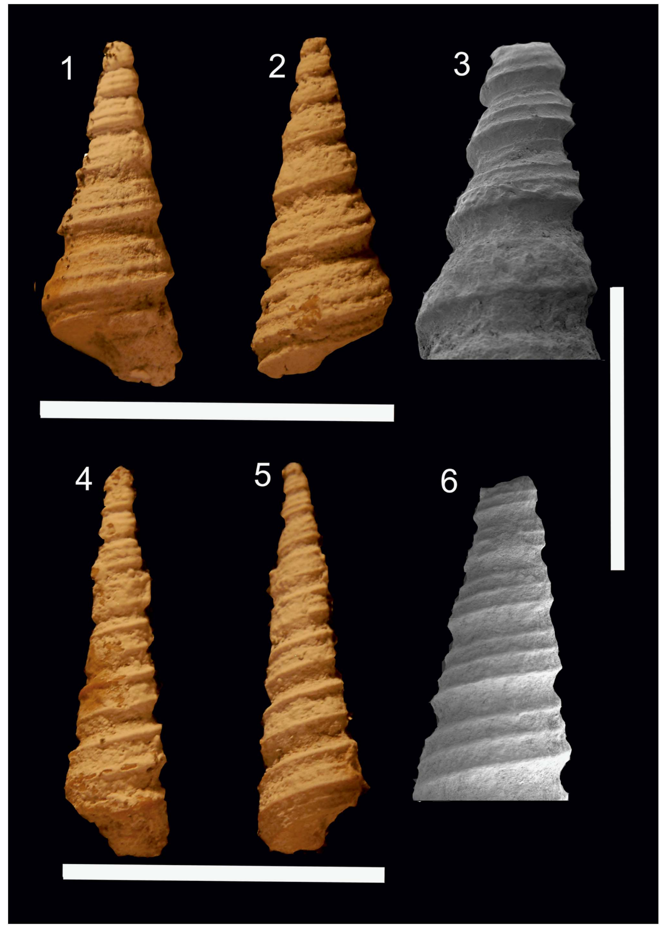

Figure 10. (**1–3**) *Turritella jhuraensis* Mitra and Ghosh, 1979. (**1, 2**) Apertural and abapertural views (paraneotype no. ISI/g/Jur/T 32). Specimens are coated with magnesium oxide; (**3**) SEM image of early teleoconch whorls of the same species (paraneotype no. ISI/g/Jur/T 33) showing three primary spirals of varying strength (see systematic description for details). Scale bars = 1 cm; (**4–6**) *Turritella amitava* new species. (**4, 5**) Apertural and abapertural views (paratype no. ISI/g/Jur/T 45). Specimen is coated with magnesium oxide; (**6**) SEM image of early teleoconch whorls of the same species (paratype no. ISI/g/Jur/T 46) showing three spirals of equal strength (see systematic description for details). Scale bars = 1 cm.

primary spirals are equal, but in *T. jhuraensis*, spirals B and C are closer than spirals B and A. Moreover, number of secondary spirals is greater in *T. jadavpuriensis*, while in *T. jhuraensis* only a single faint secondary spiral is present. These two species also differ in their growth lines. *Turritella jadavpuriensis* is characterized by a curved, prosocline lateral growth line (growth line formula is 3-3-M-A/C-P), while it is straight (albeit faint) in *T. jhuraensis*. *Turritella jadavpuriensis* is basally bicarinate, while *T. jhuraensis* has three basal cords; the middle one is weakly developed. The aperture in *T. jadavpuriensis* is subquadrate, while in *T. jhuraensis* it is subrounded.

Turritella jhuraensis resembles *T. pelusae*, described by Von der Osten (1957, p. 586, pl. 65, fig. 15) from the Lower Cretaceous of Venezuela, in having similar shell size and whorl profile. *Turritella jhuraensis*, however, differs from the South American species in having a higher apical angle (22–26° versus 13° in *T. pelusae*). Von der Osten mentioned the presence of five ribs on early whorls and one additional rib on later whorls, but he did not specify which spiral he was referring to. In contrast, *T. jhuraensis* has three primary spirals and two secondaries up to the last whorls, and these and spiral elements have varying strength, whereas in Venezuelan species they are of equal strength.

Turritella jhuraensis is also comparable to “*Turritella*” *toulmini* described by Allmon (1996, p. 90, pl. 12, figs. 6, 7) from the lower Paleocene Clayton Formation of Alabama in having a similarly convex whorl profile. *Turritella jhuraensis*, however, differs from the American species in having a smaller and less slender shell (apical angle in *T. toulmini* 10° versus 22–26° in *T. jhuraensis*). Although both species have same number of spiral threads, the strength of spirals in *T. toulmini* is about equal. In *T. jhuraensis* they are of varying strength.

Turritella jhuraensis is very similar to *T. narica,* described from the Miocene Khari Nadi Formation of Kutch (Vredenburg, 1928, p. 375, pl. 18, figs. 13–17, 21, pl. 19, figs. 2, 6; Kulkarni et al., 2010, p. 312, fig. 2d, e) in having a similar apical angle and whorl profile. But *T. narica* is larger (maximum observed height 37.0 mm compared to 28.2 mm in *T. jhuraensis*). Moreover, sculpture in *T. jhuraensis* consists of five spiral threads of unequal strength while *T. narica* has six spirals, of which five are of equal strength and the basal thread is stronger.

Another Miocene species from Kutch, *Turritella assimilis* Sowerby, 1840 (see Harzhauser et al., 2009, p. 341, fig. 3j–n), strongly resembles *T. jhuraensis* in many characters, including shell size, shell outline, whorl profile (flat to convex), and moderately impressed suture. Harzhauser et al. (2009) provide a detailed account of the ontogeny of spiral sculpture in *T. assimilis*. In both species, the early teleoconch whorls possess three primary spirals, but in *T. assimilis* many secondaries develop later. One of them, located near the anterior suture, becomes equal in strength with the primaries. Two additional secondaries occur between the anterior-most primary spiral and the anterior suture, and the posterior-most primary spiral and the posterior suture. Such development of secondaries is not observed in *T. jhuraensis*, where the total number of spiral elements including secondaries remains the same (five) all through the later part of the teleoconch.

Turritella amitava new species
Figures 10.4–10.6, 11.1, 11.2, 12.1, 12.2

Holotype.—Holotype: specimen no. ISI/g/Jur/T 41.

Diagnosis.—Shell small, with subquadrate whorls; primary teleoconch spirals equidistant; spiral B weak to obsolete; secondary spirals faint and discontinuous; growth line formula 4-4-S-P.

Occurrence.—This species is known only from the Oxfordian horizons near a pond ~1 km south-east of the village of Jhura, Kutch (23°24’47.57”N, 69°36’09.26”E).

Description.—Shells small to medium in size with nine to ten whorls. Maximum observed whorl diameter 13.5 mm; maximum observed height 28.0 mm. Apical angle 20–24°; apical and pleural angles equal. Sutures weakly to moderately incised. Protoconch unknown. Apical sculpture formula $C_1B_2A_3$. C spiral in earliest teleoconch in lower 1/3 of whorl; B spiral in middle of that whorl. A spiral within upper 1/3 of third teleoconch whorl. A and C spirals in later whorls become more conspicuous, but B spiral remains relatively weak. Three primary spirals equidistant. Spiral A and spiral B separated by one secondary spiral that is weaker in strength compared to primary spiral. Spiral C and anterior suture also separated by one secondary spiral, which is very faint, discontinuous, and only preserved in two consecutive whorls at whorl diameter 6.13 mm (Fig. 12). Shell basally bicarinate and carinae restricted in peripheral outer part of the base. Upper carina stronger than lower carina. Whorl profiles subquadrate to slightly concave. Lateral aspect of growth line traces slightly prosocline, straight (Fig. 12). Basal sinus shallow. Growth line formula 4-4-S-P (Allmon, 1996, text-fig. 10). Aperture axially ovate. Columellar lip distinct, outer lip very thin and fragile, in most specimens not preserved.

Etymology.—The species is named in honor of the late Amitava Koyal, Geologist, Oil and Natural Gas Corporation Limited (ONGC), India.

Materials.—Holotype (ISI/g/Jur/T 41) and 10 paratypes specimens ISI/g/Jur/T 42-51.

Remarks.—*Turritella amitava* n. sp. is comparable to the American upper Eocene species *Haustator perdita* (Conrad, 1865), as described by Allmon (1996, p. 74, pl. 8, figs. 1–9). Both species are small to medium size, with moderately incised sutures, and similar maximum observed whorl diameter and whorl profile. The American species, however, is more slender and has more whorls. Apical ontogeny is similar in both species, but strength and relative position of primary spirals differ. *Turritella amitava* n. sp. is characterized by the presence of faint and discontinuous secondary spirals, whereas *H. perdita* has many fine secondaries developed in different growth stages.

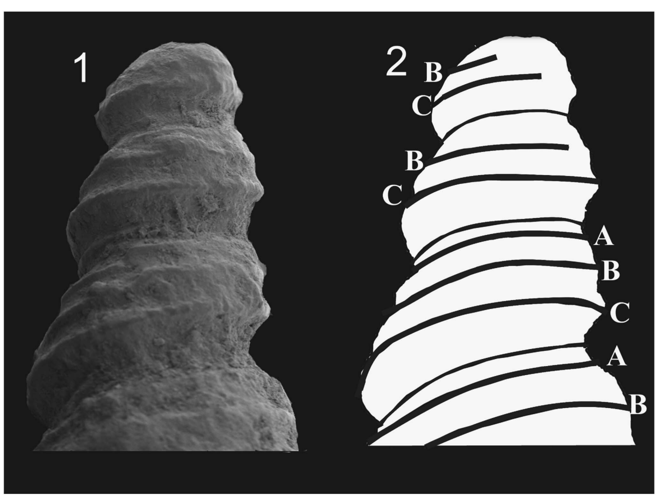

Figure 11. SEM image of apex of *Turritella amitava* n. sp. (**1**) Paratype (no. ISI/g/Jur/T 42) showing development of early teleoconch stage and well-developed apical sculpture (×105); (**2**) sketch of **1**, showing primary spiral ribs (notation after Allmon, 1996). Note order of appearance of spiral ribs in ontogeny: C spiral rib appears first, quickly followed by spiral rib B, with A coming later. Therefore, apical sculpture formula is $C_1B_2A_3$.

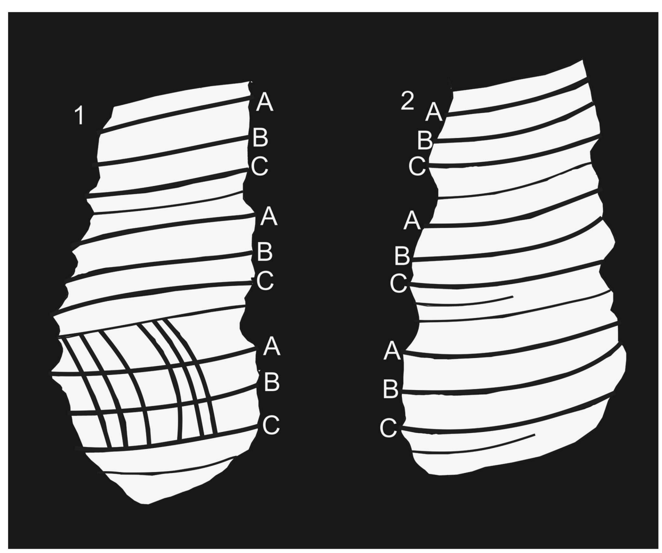

Figure 12. Sketches of late teleoconch of *Turritella amitava* n. sp. (**1**) Showing the growth line pattern, slightly prosocline and straight (maximum diameter 6.1 mm); (**2**) showing the spiral ornamentation, which illustrated three primary spiral ribs (A, B, C) and one secondary spiral present between spiral C and the anterior suture (maximum diameter 5.28 mm).

The two species also differ in the nature of growth line patterns. Growth line formula is 4-4-S-P for *T. amitava* n. sp., compared to 4-2-M-B/C-P/OR for *H. perdita*.

Turritella dhosaensis new species
Figures 13.1, 13.2, 14.1–14.5

Holotype.—Specimen no. ISI/g/Jur/T 52.

Occurrence.—This species is known only from the Oxfordian horizons ~ 1 km south-east of the village of Jhura near a pond, Kutch (23°24’47.57”N, 69°36’09.26”E).

Description.—Shell small to medium in size with eight to nine preserved whorls. Maximum observed whorl diameter 7.5 mm; maximum observed height 23.2 mm. Pleural angle 22°. Suture deeply grooved. Protoconch and early teleoconch whorls unknown. Earliest known whorl ~ 2.0 mm in diameter. A, B, and C spirals prominent; strength of spirals decreases from posterior suture to anterior suture. Primary spiral A remains strong throughout ontogeny. Space between A and B spirals wider than space between B and C. No secondary spirals between primary spirals (Fig. 13). Shell basally bicarinate, carina thin and sharp at its peripheral (outer) margin. Whorl profiles telescoped. Lateral aspect of growth line traces indistinct, slightly prosocline, convex with inflection point at or above mid-whorl. Basal aspect of growth line traces not discernible (Fig. 13). Aperture axially ovate. Columellar lip distinct, outer lip thin.

Etymology.—The species is named after the Dhosa Oolite Member of the Chari Formation in which it is found.

Materials.—Holotype (ISI/g/Jur/T 52) and 13 paratype specimens ISI/g/Jur/T 53-65.

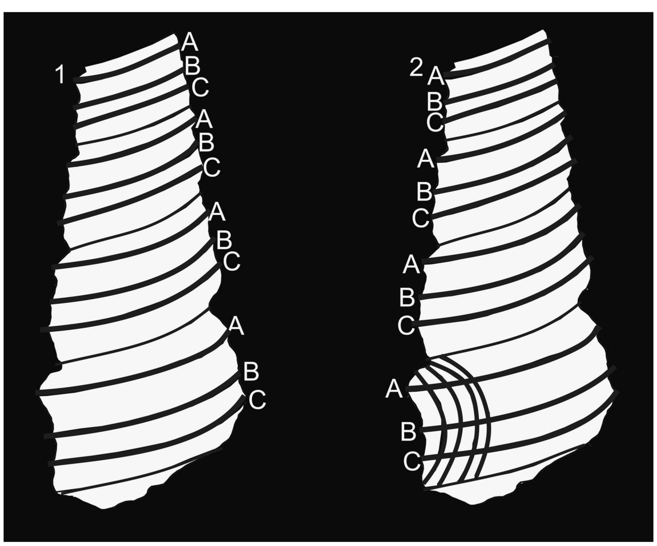

Figure 13. Sketches of adult whorl of *Turritella dhosaensis* n. sp. (**1**) Showing the spiral ornamentation that demonstrates three primary spiral ribs (A, B, C) throughout the late growth stage (maximum diameter 7.5 mm). Note the absence of secondary spiral within the primaries; (**2**) growth line patterns, slightly prosocline, convex with inflection point at or above the mid-whorl (maximum diameter 7.5 mm).

Remarks.—*Turritella dhosaensis* n. sp. has a telescoped whorl profile, whereas whorl profiles are subquadrate to slightly concave in *T. amitava* n. sp., described above. In *T. amitava* n. sp., the distances among primary spirals are equal, but in *T. dhosaensis* n. sp., spirals B and C are closer than spirals A and B. Moreover, *T. dhosaensis* n. sp. lacks secondary spirals, while in *T. amitava* n. sp., a number of secondary spirals are present. *Turritella dhosaensis* n. sp. is characterized by indistinct, slightly prosocline, convex lateral growth lines with the inflection point at or above the mid-whorl, while it is slightly prosocline or straight in *T. amitava* n. sp.

Turritella dhosaensis n. sp. resembles *Haustator tennesseensis* (Gabb, 1860) of the lower Paleocene of the Gulf and Atlantic coastal plains, USA (Allmon, 1996, p. 79, pl. 7, figs. 6–9) in having a similar shell size, number of primary spirals (three), growth line pattern (both have slightly prosocline growth line traces), and absence of secondary spirals. However, the American species has more whorls. Both species also differ in their whorl profiles: *H. tennesseensis* is characterized by trapezoidal to concave whorl profiles, while it is telescoped in *T. dhosaensis* n. sp.

Turritella dhosaensis n. sp. is similar to another American species, *Haustator rina* (Palmer, 1937), described by Allmon (1996, p. 76, pl. 10, figs. 1, 4, 5) from the middle Eocene Lisbon Formation. Both species have similar number of primary spirals, suture (deeply incised), and growth line patterns (slightly prosocline growth line traces and inflection points above the mid-whorl). *Haustator rina*, however, is characterized by medium to large shell, straight-sided whorl profile, and presence of faint secondaries while *T. dhosaensis* is characterized by small- to medium-sized shell, telescoped whorl profiles and lack of secondaries.

Another American upper Eocene species, *Haustator perdita* (Conrad, 1865), described by Allmon (1996, p. 74, pl. 8, figs. 1–9), is also similar to the new species. Both species have similar shell size and similar number of primary spirals. The American species, however, has more whorls. Secondary spirals are present between primaries in *H. perdita*, while it is absent in *T. dhosaensis* n sp. Whorl profile and growth line patterns, however, also differ. In *H. perdita*, the whorl profile is subquadrate, while it is telescoped in *T. dhosaensis* n. sp. Lateral growth line traces is orthocline to slightly prosocline in *H. perdita*, whereas it is slightly prosocline in *T. dhosaensis* n. sp.

Turritella dhosaensis n. sp. can be compared with *Incatella cingulatiformis* Möricke in Möricke and Steinmann, 1896 from the Oligocene to Miocene of southern Peru (DeVries, 2007, p. 334, fig. 3.4–3.7, 3.20) in having similar number of primary spirals (three). *Incatella cingulatiformis*, however, has a number of secondary spirals, while they are absent in *T. dhosaensis* n. sp. Moreover, the Peruvian species attains a very large size (up to 70 mm) and has more whorls and a more acute pleural angle. These two species also differ in their whorl profiles and growth line traces. *Incatella cingulatiformis* is characterized by strongly subquadrate whorls and the growth line formula is 1/2-1-M-A-OR/OP, while *T. dhosaensis* n. sp. is characterized by telescoped whorl profiles and an indistinct, convex and slightly prosocline lateral growth line.

Another Cenozoic species from western Pacific Islands (Pliocene and Pleistocene), *Turritella* (*Kurosioia*) *fileola*

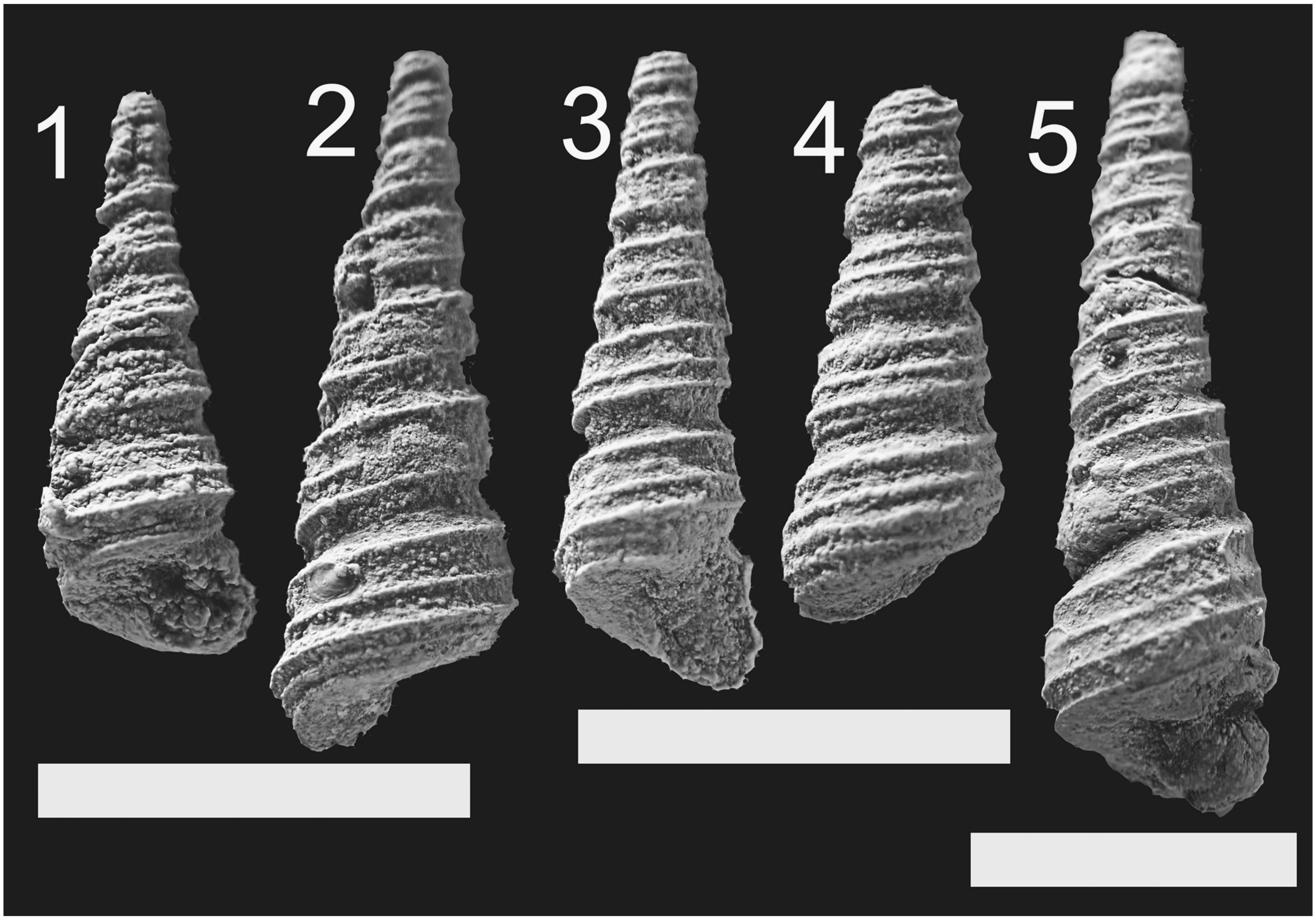

Figure 14. *Turritella dhosaensis* n. sp. (**1**) Apertural view (specimen no. ISI/g/Jur/T 54); (**2**) abapertural view (specimen no. ISI/g/Jur/T 58); (**3**) apertural view (specimen no. ISI/g/Jur/T 60); (**4**) abapertural view (specimen no. ISI/g/Jur/T 61); (**5**) apertural view (specimen no. ISI/g/Jur/T 52). Specimens are coated with magnesium oxide. Scale bars = 1 cm.

Yokoyama, 1928 (see Ladd, 1972, p. 16, pl. 1, figs. 8–14), strongly resembles *T. dhosaensis* n. sp. in shell size and number of primary spirals present. Ladd (1972) provided a brief description of the species. In both species, the early teleoconch whorls possess three primary spirals, but in *Turritella* (*Kurosioia*) *fileola* primaries are equidistant and have secondary spirals between them. Such development is not found in the new species. Moreover, *T.* (*Kurosioia*) *fileola* is characterized by flattened whorl profiles, while they are telescoped in *T. dhosaensis* n. sp. The aperture in *T.* (*Kurosioia*) *fileola* is subquadrate, while in *T. dhosaensis* n. sp. it is ovate.

Discussion

Even though the Permian-Triassic mass extinction severely affected caenogastropods, it is generally agreed that at least some cerithioids (or stem group cerithioids) were present in the late Palaeozoic (e.g., Nützel, 1998, 2002; Nützel and Bandel, 2000; Bandel et al., 2002; Nützel and Pan, 2005; Frýda et al., 2008; Ponder et al., 2008). The phylogenetic relationships and timing of appearance of various cerithioids in the Mesozoic, however, remain unclear. In the Triassic and Jurassic, at least some cerithioids appear to have been widely distributed and diverse (Nützel, 2002; Nützel and Erwin, 2002; Kaim, 2004; Bandel, 2006; Ferrari, 2012). Although numerous, previous reports of pre-Cretaceous *Turritella* sensu lato have remained poorly documented (see Allmon, 2011). The present report, therefore, appears to represent the oldest well-documented occurrence of at least this branch of the family Turritellidae, and thereby provides additional documentation of the timing of the radiation of post-Paleozoic cerithioids (e.g., Bandel, 1993, 2006; Bandel and Kowalke, 1997; Nützel, 2002; Nützel and Erwin, 2002).

It is noteworthy that the turritelline species described here are not markedly “primitive” compared to Lower Cretaceous species that were previously the oldest known representatives of the group, and these Cretaceous forms, furthermore, lack primitive characters that are not found in the Tertiary (see, e.g., Allmon, 1996). In other words, turritellines appear to have occupied approximately the same shell morphospace since the beginning of the group. It remains to be seen, however, whether this is a result of lineages continuously occupying an area of morphospace once it was attained, or extinction of forms followed by repeated (convergent) reoccupation of those areas of morphospace.

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Accessibility of supplemental data

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.mb14c

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