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A taxonomic and phylogenetic study of *Kutchithyris* – A Jurassic terebratulide from Kutch, India

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Abstract

Kutchithyris, the dominant terebratulide genus of the Jurassic sequence of Kutch, India made its first appearance in the Middle Bathonian continuing till the Oxfordian–Kimmeridgian boundary. The genus has been sporadically reported from the Upper Bathonian of Pamir, England and New Zealand and the Callovian of Madagascar and Israel, but its oldest and most diverse record is from Kutch. *Kutchithyris* systematics have been in a state of flux with most earlier works resorting to subjective splitting or lumping. The genus consists of 12 species; the present study deals with the taxonomy of nine species including one new species, *Kutchithyris mitra*. This revisionary work is undertaken on the basis of a large number of specimens that have been collected with precise stratigraphic data as well the type materials collected by earlier workers. A parsimony analysis of the genus indicate that the evolution was governed by heterochrony particularly paedomorphosis.

Keywords: Brachiopods; Systematics; Morphology; Evolution

1. Introduction

Arkell (1956), in his compendious work, drew attention to the classic area of Kutch in western India noting its extensively developed marine Jurassic rocks and the wealth of ammonite fossils contained in them. The Kutch Jurassic is a vast repository of diverse faunas of which brachiopods are a major group; the terebratulides and rhynchonellides that constitute this group have been the subject of much research effort (Kitchin, 1900; Buckman, 1918; Mitra and Ghosh, 1973; Mitra, 1978; Mukherjee et al., 2000, 2002a,b, 2003). Among the brachiopods the most dominant member is a terebratulide genus, *Kutchithyris* Buckman, which has a long stratigraphic range spanning the Middle Bathonian to the Oxfordian and exhibits much interspecific diversity. Besides Kutch, the genus has also been recorded in the Pamir area, England, New Zealand, Madagascar and Israel – all from the Middle Jurassic. The purpose of this paper is to review and redescribe the *Kutchithyris* species and to provide a phylogenetic analysis of the genus.

The invertebrate groups contributing to the richness and diversity of Kutch Jurassic fossil assemblages, viz., corals (Gregory, 1900; Pandey and Fürsich, 1993; Fürsich et al., 1994), gastropods (Jaitly et al., 2000; Das et al., 1999), nautiloids (Halder, 2000), bivalves (Kitchin, 1903) and ammonites (Bardhan et al., 1994; Callomon, 1993; Jana et al., 2005; Kayal and Bardhan, 1998) exhibit remarkable similarity at generic level with their counterparts of the European Tethys; however, a majority of species of these faunal groups are endemic to Kutch or at the most to the Indo-Madagascan faunal province of which Kutch basin was a constituent part. Kutch appears to be the centre of origin of *Kutchithyris*, for the genus exhibits maximum diversity here and the earliest record of each of its species is from this area. *Kutchithyris*, after appearing in Kutch, apparently underwent speciation and migrated to other areas.

Kitchin (1900) described the terebratulides for the first time recognizing 20 species which he placed in the comprehensive genus *Terebratula* Muller 1776. Subsequently,

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Buckman (1918) reclassified Kitchin's species placing them in five genera; four of these including *Kutchithyris* were new. In his classification Buckman gave more importance to certain characters such as muscle impressions and overall shell outline, basing his classification on these shell parameters, and so the classification do not fully reflect the nature of variation of the assemblages. Mitra (1960, 1974, 1978), from his studies of the terebratulides from the Jhura dome, concluded that they consisted of only three species belonging to two genera, *Kutchithyris* and *Lophrothyris* (Buckman, 1918). However, Mitra's biometric studies were based on only three shell parameters (length, width and thickness), which are not sufficient to describe brachiopod morphology. These works thus appear now as cases of subjective splitting or excessive lumping necessitating a through taxonomic revision. The present work is based on a large number of specimens collected from different sections with precise stratigraphic data together with the type specimens of Kitchin (1900) and Buckman (1918) housed in the Geological Survey of India's fossil repository. The study of *Kutchithyris* reveals that the genus is represented by 12 species in Kutch. Two of these species, *K. acutiplicata* and *K. euryptycha*, along with some transitional forms, have been reported from Pamir where they constitute an evolutionary lineage and have been cited as one of the classical examples of rapid evolution (Raup and Stanley, 1985). The transitional forms have also been found in Kutch and described as *K. propinqua* because of their distinctive attributes, abundance and longer vertical occurrence in the sequence (Mukherjee et al., 2003). The present study includes the taxonomy of the nine endemic species of *Kutchithyris*, of which one is a new species; the remaining three species were described earlier (Mukherjee et al., 2003). A canonical variate analysis of the genus has been done to understand their morphologic groupings. The phylogenetic relationships have been discussed with the help of cladistic analysis (Monks and Owen, 2000; Smith, 1994).

2. Stratigraphical and palaeontological background

The Kutch basin, located at the north-western margin of the Indian plate, developed through rifting of South Africa and India in the Late Triassic during fragmentation of the Gondwana superplate. As an east-west aligned pericratonic embayment the basin became a receptacle of a thick pile of sediments deposited during repeated episodes of marine transgression and regression in the Middle Jurassic–Early Cretaceous (Biswas, 1991). The Mesozoic sequence is disposed in two broad belt – one in the southern 'Mainland' where it is best exposed in three parallel anticlinal ridges (NW–SE) and the other in the northern salt marshes of the Rann (Mitra et al., 1979; Datta, 1992). The Mesozoic sediments are grouped into four formations, viz., Patcham, Chari, Katrol and Bhuj in ascending order (Rajnath, 1932; Poddar, 1959; Mitra et al., 1979). The Patcham and Chari formations are the main fossil-bearing units. A complete lithostratigraphic classification of the two formations has been worked out on the basis of facies analysis of the Patcham and Chari exposed at the localities of Jhura, Keera, Jumara and Jara (Datta, 1992; Mukherjee et al., 2003; Figs. 1 and 2).

At Jhura, the Patcham and Chari formations together consist of 15 beds having repeated alternations of limestones, shales, oolitic bands, sandstones and occasional intercalations of conglomerates. Deposition of both the formations initiated with carbonate platform environment that was subsequently followed by fluctuating marine conditions (Mukherjee et al., 2003). Three orders of sea-level changes indicating gradual deepening punctuated by a few shallowing trends have been noted in the sedimentary regime (Fursich and Oschman, 1993). The whole Jurassic succession of Kutch has been calibrated by reference to a

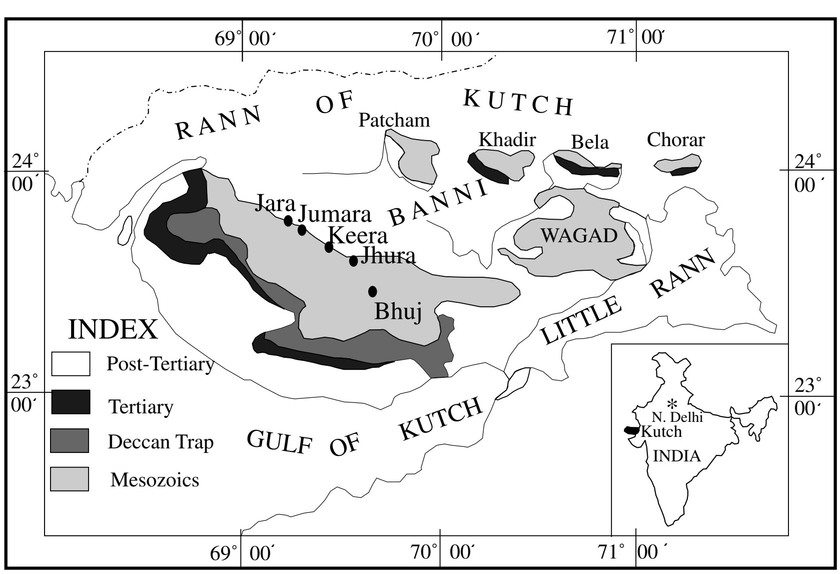

Fig. 1. Studied area, geographical localities and distribution of Jurassic rocks of Kutch, India.

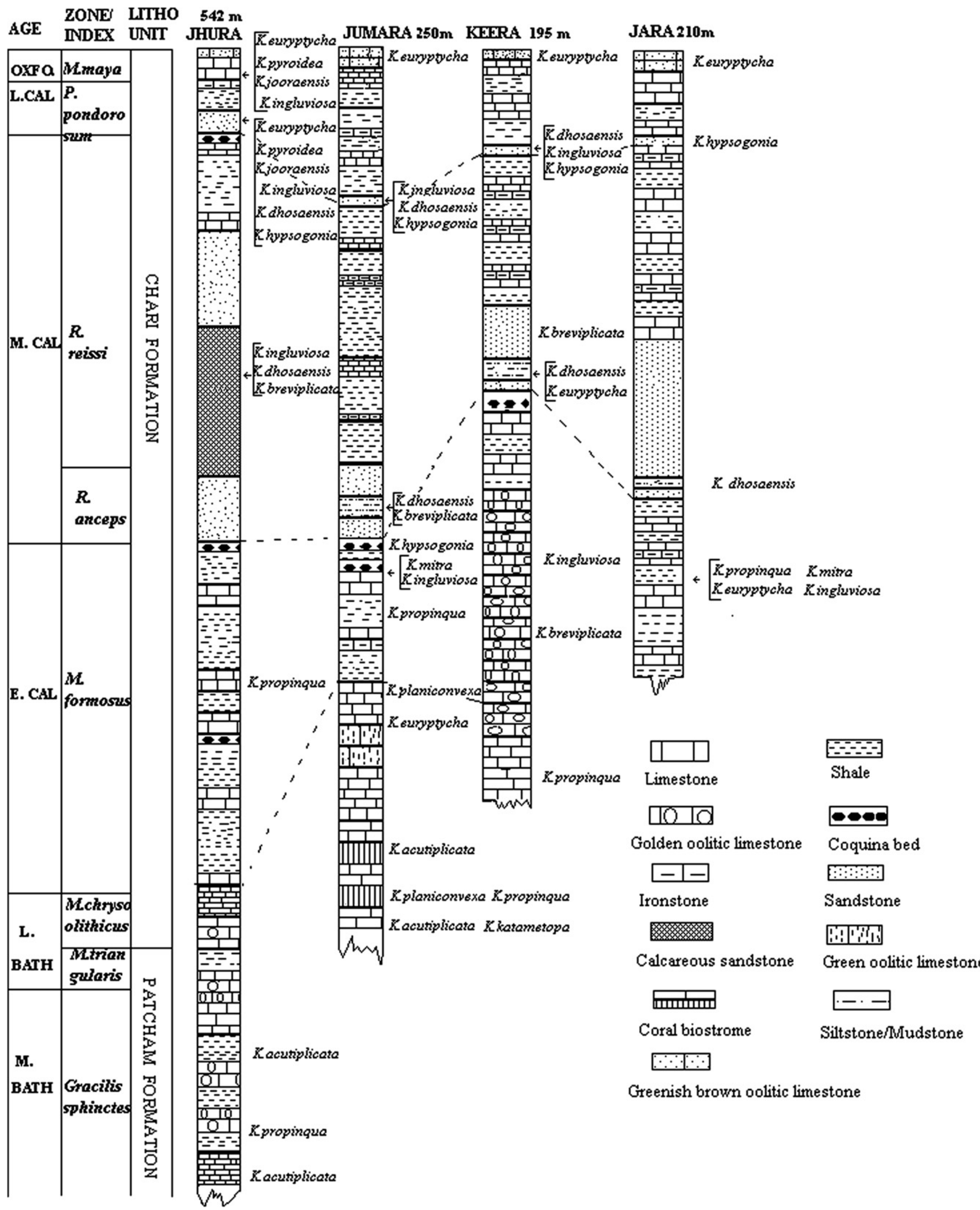

Fig. 2. Stratigraphical sections and ammonite zonation with the first appearances and last appearances of the *Kutchithyris* species at Jhura, Jumara, Keera and Jara. Zonations after Bardhan et al. (2002) and Jain et al. (1996).

standard biostratigraphy based on ammonites (Datta, 1992; Bardhan et al., 2001).

Brachiopods, especially terebratulides, apparently thrived nearly throughout, though their numbers varied widely depending on the lithofacies. In general, brachiopod shells occur in large numbers in limestones and in calcareous and fine grained sandstones in contrast to the coarse grained sandstones and shales in which occasional shells may occur. Their state of preservation varies accordingly, being well-preserved in the former lithotypes, and much abraded in the latter. In ferruginous shale-ironstone units the shells are highly fragmented or disarticulated, indicating perhaps much post-mortem transport and unsuitable conditions for proper preservation. When present in large numbers in a particular horizon the mode of occurrence of the brachiopods suggests they form a life assemblage, though the shells might have been removed from their original position of life and re-sorted locally. In such cases the shells display random orientation without any size sorting, complete preservation with external morpho-characters remaining undamaged and finally, frequent occurrence of gerontic individuals and juveniles of the same species in close proximity.

3. Systematic descriptions

Twelve terebratulide species described here belong to the genus *Kutchithyris* (Buckman, 1918). In the revised Treatise, *Kutchithyris* is placed in Superfamily Loboidothyridoidea, Family Postepithyrididae (Daphne Lee, personal communication, 2003).

When erecting 11 *Kutchithyris* species, which have been redescribed here (along with a new species), Kitchin (1900) specified several "types" for each species without nominating any particular one as the most representative and as such Kitchin's types are syntypes of the modern typological nomenclature. Thus, when redescribing these forms it is necessary to designate a lectotype. Besides Kitchin's material, many specimens from new collections have been used in the present study, all materials are housed at the Geological Survey of India.

Abbreviations used: L – shell length; W – shell width; T – shell thickness; Ll – length of loop, LD – length of dorsal valve; Ll/LD – ratio of length of loop to length of dorsal valve. All measurements are in cm unless mentioned.

Genus *Kutchithyris* (Buckman, 1918).

Type species: *K. acutiplicata* (Kitchin, 1900).

Lectotype, GSI type number 6601 is figured here for comparative purposes (Fig. 3A), its shell dimensions are L – 2.9, W – 3.09, T – 2.13 (pl. 1, Fig. 6a–c, Kitchin, 1900).

Occurrence: Middle Bathonian (Beds 1 and 2 of Patcham Formation) of Jhura and Upper Bathonian (Bed 1, Patcham Formation) of Jumara.

K. katametopa (Kitchin, 1900) Figs. 3D–E; 4A–C; 5.

1900 *Terebratula katametopa*; Kitchin, pp. 11–13, pl. 2, Figs. 5–8.

1918 *Sphaeroidothyris katametopa*; Buckman, pp. 115–117.

Type material. Kitchin's type specimens are numbered 6608–6611. GSI type number 6608 has been selected as the lectotype (Fig. 3E) L – 2.75, W – 2.7, T – 1.75 (pl. 2, Fig. 5a–d, Kitchin, 1900). Kitchin reported the species from 'upper Putchum beds' of Jumara.

Additional material. Specimen numbers Ju1/1-5 are from Bed 1, Jumara.

Occurrence. The present material is from the Upper Bathonian (Bed 1 of Patcham Formation) at Jumara, Kutch.

Diagnosis. Almost spherical shell with thickened anterior margin. Biplicate anterior commissure with fimbriation. Dorsal valve with median furrow and lateral ridges varying from 3 to 4.

Description. Medium size spherical shell (maximum length 2.75, maximum width 2.7, maximum thickness 1.9), with outline rounded pentagonal in adult and sub circular in young which are also considerably less spherical. Length equal or slightly greater than width in adult. Shell ventribiconvex with ventral valve convexity increasing during ontogeny. Positions of maximum width at the middle and thickness slightly posterior to the middle in adult and at the middle during early ontogeny. Anterior margin variably thickened and biplicated with minor fimbriation at two sides in adult stage. Dorsal valve convex and develops a median furrow with variable depth which is bounded on both sides by two more or less sharp ridges just past mid valve; height of the ridge variable. Lateral furrows of lesser depth are also developed on both sides, with corresponding less conspicuous ridges. Three prominent ridges and sinuses develop in the ventral valve after mid point. Laterally fine ridges and furrows develop whose number varies from 3 to 4. Beak small, with a broad base and not strongly incurved. Foramen circular, truncates the beak obliquely. Pedicle collar present, cardinal process well developed. Ll/LD 0.4; crural plates curved, crest of transverse band broad and semicircular in plan.

Remarks. This species was described by Kitchin (1900) as *Terebratula katametopa* but Buckman (1918) assigned it to *Sphaeroidothyris* Buckman which has a rectimarginate – uniplicate anterior commissure, and an incurved umbo whereas *katametopa* is strongly biplicate with slightly incurved to sub-erect umbo. Moreover Buckman's genus is characterised by Ll-LD 0.5 or greater but *T. katametopa* has Ll/LD 0.4, which is characteristic of the genus *Kutchithyris*. These are clear indications that the species belongs to *Kutchithyris* and not to *Sphaeroidothyris*. The adult specimens of *K. katametopa* have highly inflated shells, and thickened anterior commissures with sharp ridges and long ventral valve median ridge resembling pre-adult *K. acutiplicata*. But the lateral fimbriation and high shell thickness distinguishes it from the adult *K. acutiplicata* (Fig. 3A, D and E).

It occurs only at the core (Bed 1, Fig. 2) at Jumara along with *K. acutiplicata* (Fig. 3A), *K. propinqua* (Fig. 3B) and *K. planiconvexa* (Figs. 3F, G and 4D, E) and is restricted to this bed. It occurs in small numbers compared to the other *Kutchithyris* species.

K. planiconvexa (Kitchin, 1900) Figs. 3F, G; 4D, E and 6.

1900 *Terebratula planiconvexa*; Kitchin pp. 15–16, pl. 3, Figs. 4 and 5.

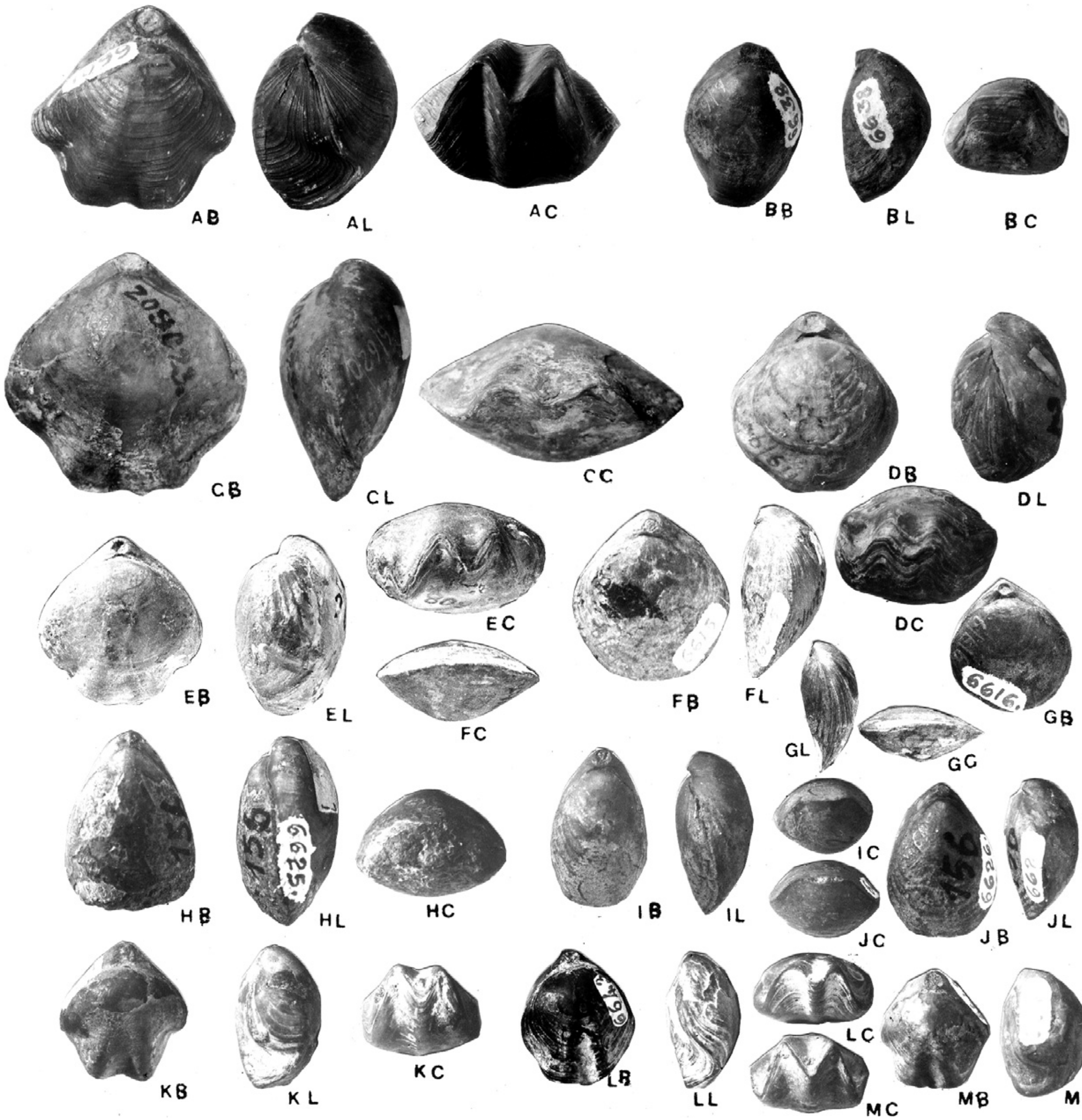

Fig. 3. *Kutchithyris* from Patcham and Chari formations of Kutch. All X 1. (A) *K. acutiplicata*, GSI Type No. 6601, lectotype, dorsal (AB), side (AL) and anterior (AC) views. (B) *K. euryptycha*, lectotype, GSI Type No. 6638, dorsal (BB), side (BL) and anterior (BC) views. (C) *K. propinqua*, GSI Type No. 6620, lectotype, dorsal (CB) side (CL) and anterior (CC) views. (D) *K. katametopa*, GSI type No. 6611, paralectotype, dorsal (DB), side (DL) and anterior (DC) views. (E) *K. katametopa*, GSI type No. 6608, lectotype, dorsal (EB), side (EL) and anterior (EC) views. (F) *K. planiconvexa*, GSI type No. 6615, lectotype, dorsal (FB), side (FL) and anterior (FC) views. (G) *K. planiconvexa*, GSI type No. 6616, paralectotype, dorsal (GB), side (GL) and anterior (GC) views. (H) *K. breviplicata* GSI type No. 6625, paralectotype, dorsal (HB), side (HL) and anterior (HC) views. (I) *K. breviplicata* GSI type No. 6629, lectotype, dorsal (IB), side (IL) and anterior (IC) views. (J) *K. breviplicata* GSI type No. 6626, paralectotype, dorsal (JB), side (JL) and anterior (JC) views. (K) *K. hypsogonia*, GSI type No. 6641, lectotype, dorsal (KB), side (KL) and anterior (KC) views. (L) *K. hypsogonia*, GSI type No. 6643, paralectotype, dorsal (LB), side (LL) and anterior (LC) views. (M) *K. hypsogonia*, GSI type No. 6642, paralectotype, dorsal (MB), side (ML) and anterior (MC) views.

1918 *Heimia planiconvexa*; Buckman pp. 103–104.

Type material. Kitchin's type specimens are numbered 6615–6616. GSI type number 6615 has been selected as the lectotype (Fig. 3F), L – 2.85, W – 2.6, T – 1.3, (pl. 3, Fig. 4, Kitchin, 1900). Kitchin worked on material of other workers and did not mention any particular bed number in his descriptions but merely said 'upper Putchum beds' of Jumara.

Additional material. Specimen numbers Ju1/1-4, Ju4/5-19 are from Jumara.

Occurrence. The present collection is from the Upper Bathonian (Bed 1 of Patcham Formation and 4 of Chari Formation) at Jumara, Kutch.

Diagnosis. Planoconvex, circular to subcircular shell with rectimarginate anterior commissure.

Description. Shell medium sized characteristically planoconvex (maximum length 2.7 cm, maximum width 2.5 cm,

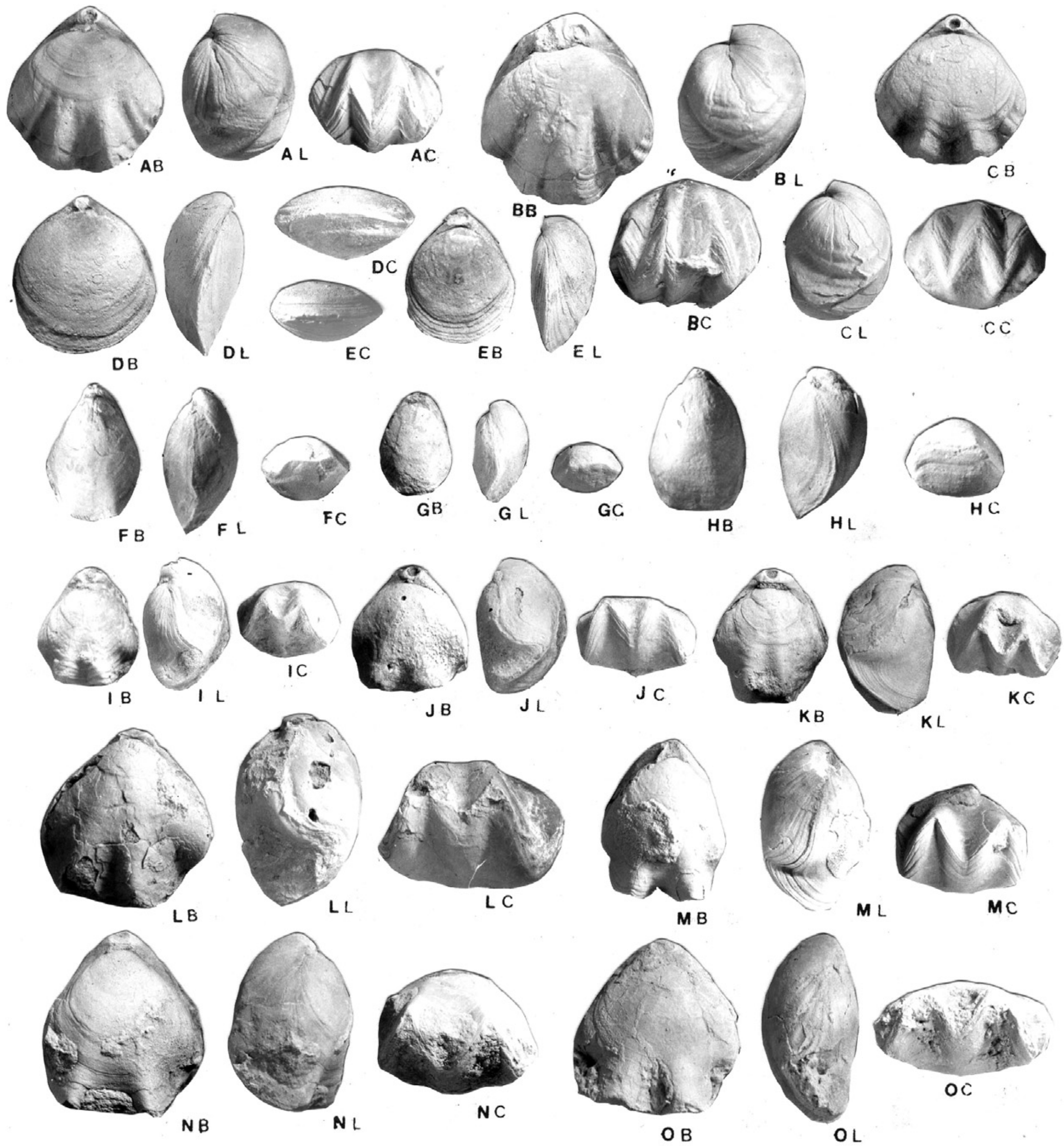

Fig. 4. *Kutchithyris* from Patcham and Chari formations of Kutch. All X 1. (A) *K. katametopa*, from Bed 1, Jumara, Ju1/1, dorsal (AB), side (AL) and anterior (AC) views. (B) *K. katametopa* from Bed 1, Jumara, Ju1/2, dorsal (BB), side (BL) and anterior (BC) views. (C) *K. katametopa*, from Bed 1, Jumara Ju1/4, dorsal (CB), side (CL) and anterior (CC) views. (D) *K. planiconvexa*, from Bed 4, Jumara, Ju4/1, dorsal (DB), side (DL) and anterior (DC) views. (E) *K. planiconvexa*, from Bed 4, Jumara, Ju4/18, dorsal (EB), side (EL) and anterior (EC) views. (F) *K. breviplicata* from Bed 9, Jumara, Ju9/8 dorsal (FB), side (FL) and anterior (FC) views. (G) *K. breviplicata* from Bed 8, Jhura, Jh8/12 dorsal (GB), side (GL) and anterior (GC) views. (H) *K. breviplicata* from Bed 7, Keera, K7/33 dorsal (HB), side (HL) and anterior (HC) views. (I) *K. hypsogonia* from Bed 8, Jhura, Jh8/3, dorsal (IB), side (IL) and anterior (IC) views. (J) *K. hypsogonia* from Bed 12, Jhura, Jh12/1 dorsal (JB), side (JL) and anterior (JC) views. (K) *K. hypsogonia* from Bed 8, Jumara, Ju8/1 dorsal (KB), side (KL) and anterior (KC) views. (L) *K. mitra* from Bed 1, holotype, Jara, Ja1/1, dorsal (LB), side (LL) and anterior (LC) views. (M) *K. mitra* from Bed 8, Jumara, Ju8/30, dorsal (MB), side (ML) and anterior (MC) views. (N) *K. mitra* from Bed 8, Jhura, Jh8/2, dorsal (NB), side (NL) and anterior (NC) views. (O) *K. mitra* from Bed 8, Jumara, Ju8/35, dorsal (OB), side (OL) and anterior (OC) views.

maximum thickness 1.48 cm), roughly circular to subcircular in outline – remaining unchanged during ontogeny (Fig. 3F and G). Position of maximum width at the middle in young and adult shells and maximum thickness slightly posterior to the middle.

Dorsal valve is slightly convex only near umbo and becomes flattened afterwards resulting in an almost planar valve without any fold or plication. Ventral valve is convex, convexity becoming less in the sides and near anterior margin. The valve is devoid of any ridge or depression. Lateral

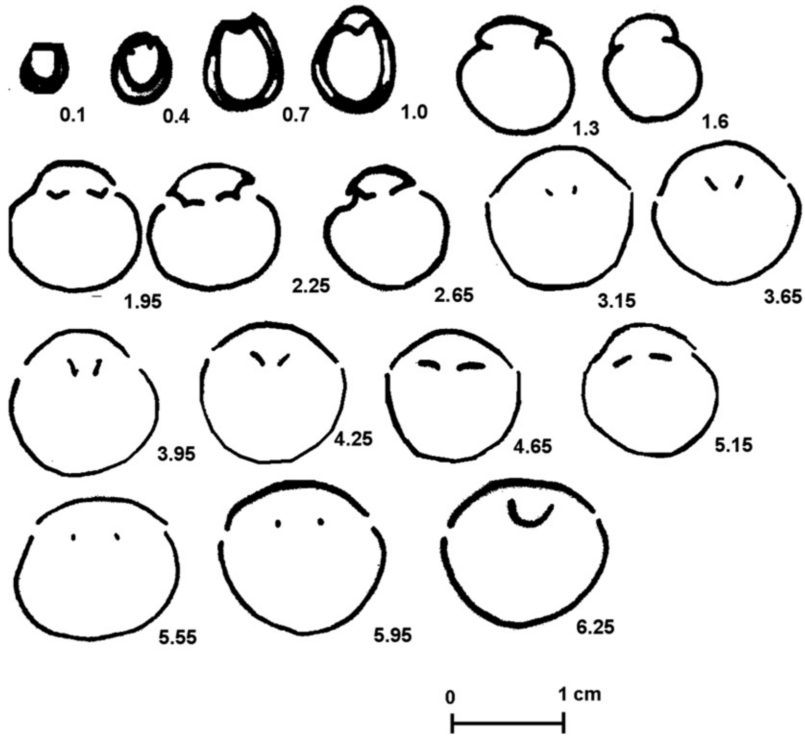

Fig. 5. Serial transverse section of *K. katametopa*. Original length of the specimen 20.0 mm; the loop disappears at 7.5 mm. Pedicle collar visible at 0.4 mm, cardinal process at 0.7 mm, concave hinge plate observed at 2.2 mm, transverse band almost semicircular in plan at 6.25 mm.

commissure uniformly circular and anterior commissure rectimarginate. Beak short, well incurved and with a broad base. Foramen circular, medium sized, vertically truncates the beak. Beak is erect to sub-erect in younger shells and exposes deltidial plates (Fig. 3G). No beak ridges are present. Surface with radial striations. Pedicle collar well developed. Ll/LD 0.4; crural plate concave, crest of transverse band broad, flat.

Remarks. Kitchin (1900) originally described *Terebratula planiconvexa* from the Upper Patcham beds of Jumara. Buckman (1918) revised Kitchin's specimens and assigned *T. planiconvexa* to *Heimia* Hass. Though the plano-convex character of *T. planiconvexa* is similar to *Heimia*, the latter is characterized by a sulcate to paraplicate anterior commissure and numerous growth lines or lamellae and it is anteriorly thickened whereas the former has a rectimarginate anterior commissure with very fine growth lines and anterior thickening is absent. Interestingly, the young specimens of *K. acutiplicata*, *K. propinqua* from the Middle-Upper Bathonian, *K. ingluviosa*, *K. dhosaensis* from the Middle Callovian, *K. jooraensis*, *K. pyroidea* from the Oxfordian, are all characterized by planoconvex shells and rectimarginate anterior commissures (Mitra, 1960 and personal observation). The crowding of growth lines which is a sign of maturity, is restricted to a very narrow portion near the anterior commissure of *K. planiconvexa* perhaps indicating prolonged juvenile growth period. The young shells of *K. acutiplicata* and *K. planiconvexa* are difficult to distinguish except for the erect beak and the vertical truncation of it by the foramen in *K. planiconvexa* (Fig. 4E) Adult *K. planiconvexa* also has similar features and differs only in size parameters.

K. breviplicata (Kitchin, 1900) Figs. 3H–J, 4F–H and 7.

1900 *Terebratula breviplicata*; Kitchin, pp. 24–25, pl. 4, Figs. 7–8, pl. 5, Figs. 1–2.
1918 *Lobothyris breviplicata*; Buckman, pp. 107–109.

Type material. Kitchin's syntype specimen numbers 6625–6626, 6628–6629. GSI Type number 6629 has been selected as the lectotype (Fig. 3I) L – 2.5, W – 1.55, T – 1.2 (pl. 5, Fig. 2, Kitchin, 1900). Kitchin described the species from 'Golden Oolite' Keera.

Additional material. Specimen number Ju 8/1-4 are collected from Bed 8, Jumara, Ju 9/5-25 from Bed 9, Jumara, K2/26-29 from Bed 2 Keera and K6/30-34 from Bed 6 Keera.

Occurrence. The present collection is from the Lower–Middle Callovian of (Beds 8 and 9 of Jumara and Beds 2 and 6 of Keera from Chari Formation) Kutch.

Diagnosis. Subelliptical elongated to subtriangular, shells, posteriorly tapering, anterior commissure uniplicate to slightly biplicate.

Description. Shell medium size (maximum length 3.0, maximum width 2.2, maximum thickness 2.0), inflated, subelliptical to suboval outline, juvenile shells elliptical; elongated, posteriorly narrow or tapering (Fig. 4G). Position of maximum width slightly anterior to the middle and position of maximum thickness slightly posterior. Plano-convex in juvenile shells, ventribiconvex in adults.

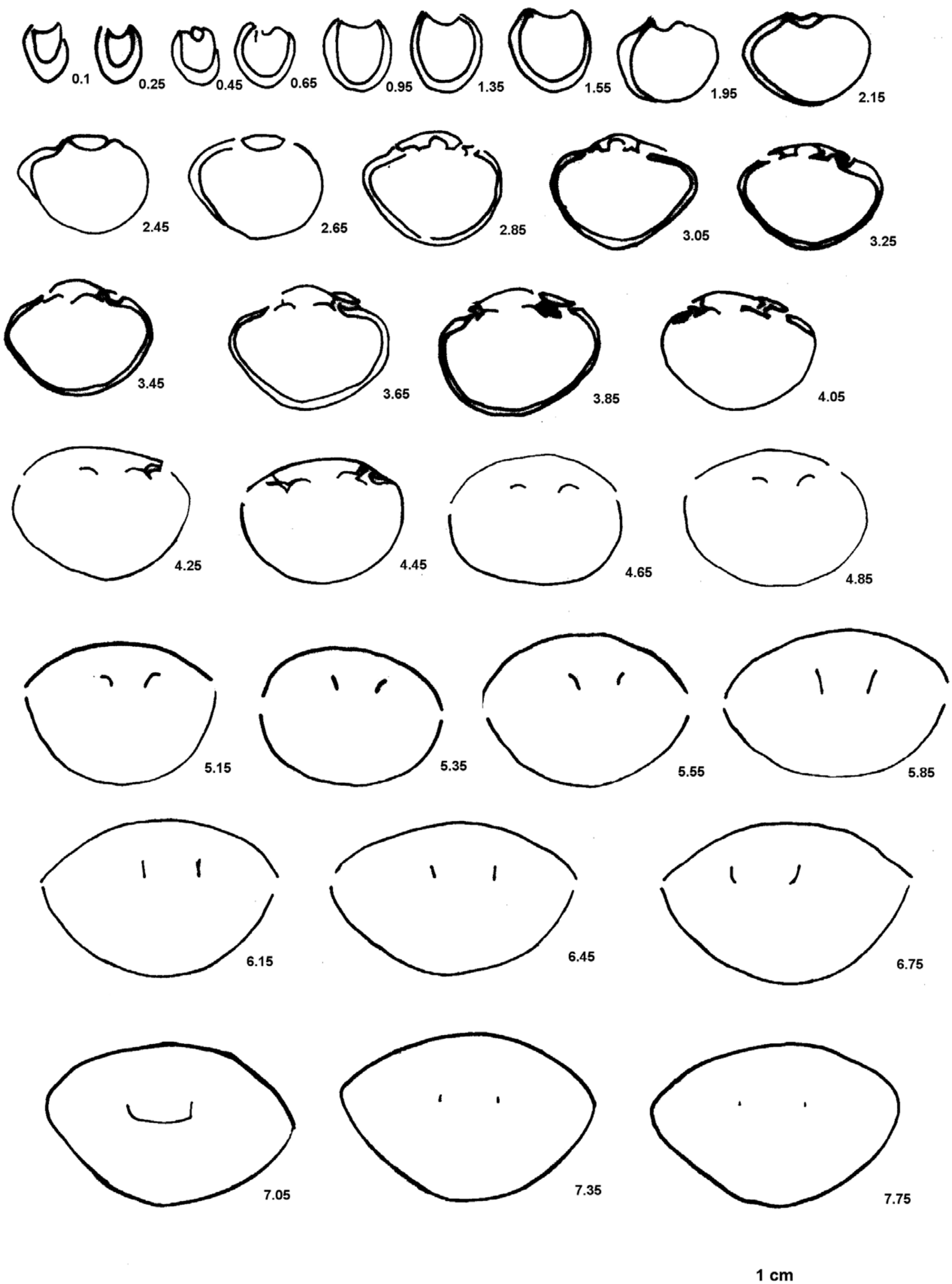

Fig. 6. Serial transverse section of *K. planiconvexa*. Original length of the specimen 23.5 mm; the loop disappears at 8.75 mm. Pedicle collar can be seen partly at 0.65 mm, cardinal process is visible at 2.15 mm, broad, flat transverse band visible at 7.05 mm.

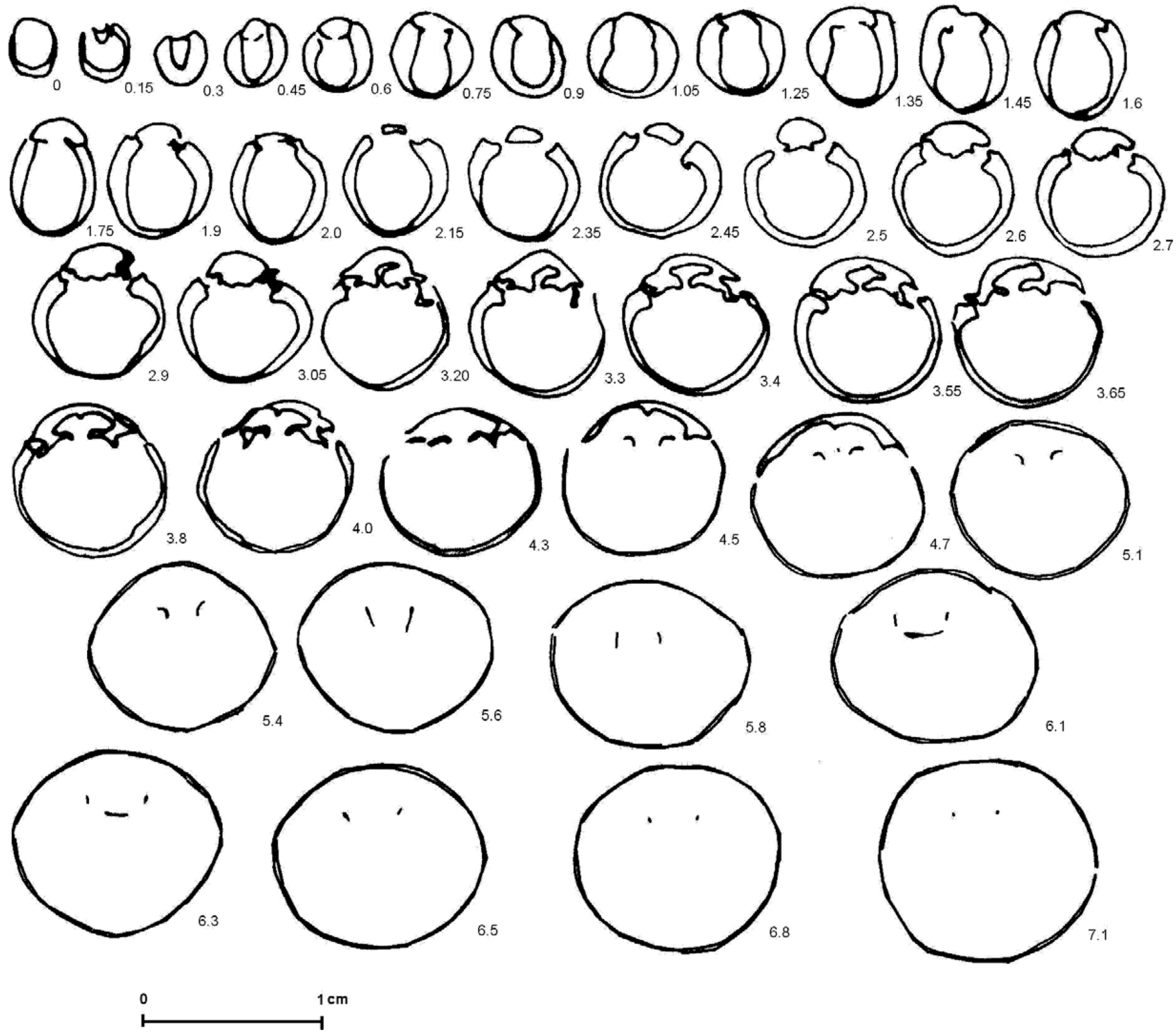

Fig. 7. Serial transverse section of *K. breviplicata*. Original length of the specimen 20.5 mm; the loop disappears at 7.8 mm. Teeth and socket can be observed from 2.6 mm, straight crest of transverse band visible at 6.1 mm.

From slightly anterior to middle part dorsal valve is raised into a flattened median fold, sides of which slope down gradually forming a shallow bay on either side. Near anterior commissure at a late stage a shallow sinus appears at median part of the fold and commissure is weakly biplicate (Figs. 3JC). Ventral valve is more inflated and near the anterior a median ridge separates depressions on two sides. In some cases this is absent and an uniplicate anterior commissure results. Lateral commissure with a wide curve that takes a slight bend towards ventral valve at about one third shell length from anterior. Beak suberect, narrow; beak ridges absent. Foramen small to medium and circular in shape. Foramen truncates the beak plane vertically. Surface marked by radial striations faintly visible in some specimens. Pedicle collar present. Teeth well inserted into sockets, denticulum weakly developed. Crural plates thick, curved, converging. Ll/LD 0.45; crural process posterior to mid valve. Transverse band slightly broad with flattened crest.

Remarks. Buckman (1918) placed *T. breviplicata* (Kitchin, 1900) in the genus *Lobothyris* Buckman. Many European species that were included by Buckman (1918) in *Lobothyris* were externally quite different (Muirwood, 1934) and they were reassigned to different genera by later workers (e.g. Mitra, 1960, 1974, 1978; Cooper, 1983). *T. breviplicata* is a small, narrow, elongated, moderately biconvex, uniplicate to weakly biplicate form, with the characteristic radial striae of *Kutchithyris*. Internally, the crural processes are posterior to mid-valve and the species has a moderately long loop with medium terminal points. The external and internal characters both support its designation under *Kutchithyris*.

K. hypsogonia (Kitchin, 1900) Figs. 3K–M, 4I–K, and 8A.

1900 *Terebratula hypsogonia*; Kitchin, pp. 28–30, pl. 6, Figs. 1–4.

1900 *Terebratula longicarinata*; Kitchin, pp. 30–32, pl. 6, Figs. 5 and 6.

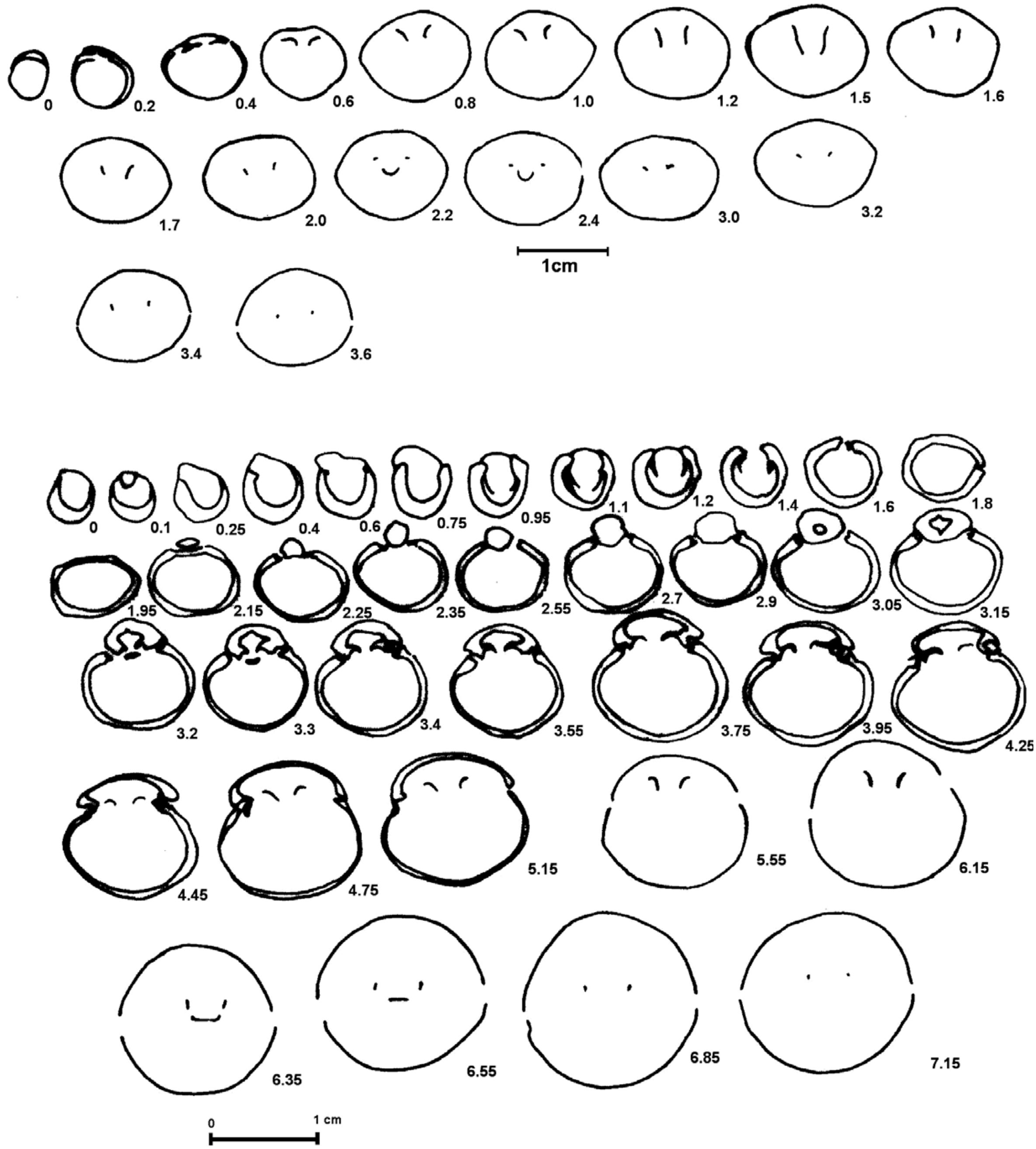

Fig. 8. (A) Serial transverse section of *K. hypsogonia*. Original length of the specimen 18 mm; the loop disappears at 4.85 mm. Hinge plate tapering at 0.4 mm, curved crest of transverse band at 2.2 mm; (B) Serial transverse section of *K. mitra*. Original length of the specimen 25.0 mm; the loop disappears at 8.05 mm. Pedicle collar at 1.4 mm, cardinal process visible at 2.15 mm, transverse band flat crested seen at 6.35 mm.

1918 *Kutchithyris hypsogonia*, Buckman, p. 113.
1918 *Kutchithyris longicarinata*; Buckman, p. 113.
1960 *Kutchithyris hypsogonia*; Mitra, pp. 83–87, pl. 13 and 14.

Type material. Kitchin's type specimen numbers 6639–6644. GSI Type number 6641 has been selected as the lectotype. Fig. 3K, L – 2.05, W – 2.0, T – 1.25 (pl. 6, Fig. 3, Kitchin, 1900). Kitchin did not specify any horizon but merely said that they came from 'Upper Charee beds, north of Suddera Bela'.

Additional material. Specimen numbers Ju8/1-2, Ju 9/1-3, Ju 12/1-14 are from Jumara, Jh 12/1-59 from Jhura and Ja6/1-8 from Jara.

Occurrence. The present collection is from the Middle to Upper Callovian of Kutch (Beds 8, 9, 12 at Jumara, Bed 9 Keera, Bed 6 Jara and Bed 12 Jhura).

Diagnosis. Small sized subtriangular shells with two diverging, sharp crested ridges in dorsal valve; strongly biplicate anterior commissure.

Description. Shell small (maximum length 2.8 cm, maximum width 2.0 cm, maximum thickness 1.6 cm), subtriangular in shape. Maximum width and thickness anterior to middle and at about the middle respectively in adult and lies near the middle in young shells. Shell weakly ventribiconvex, convexity of shell increases during ontogeny. Length generally greater than width. Thickness variable but never high. Dorsal valve convexity varies from posteriorly flattened to convex in most spherical variants. Two diverging, narrow, sharp crested plicae, start at about the middle and continue to anterior margin; divergence of plicae variable; a median sinus with variable depth that broadens anteriorly present; laterally, two depressions present that diverge widely. Ventral valve shows greater convexity; anterior portion projected a little backward. Median longitudinal fold with variable height runs from anterior margin to the middle of shell or beyond – to the umbo in a few shell. Hinge line short, curved. Lateral commissure straight at first but after approaching the middle of shell it forms an angle directed to ventral valve, which may be sharp or rounded. Anterior commissure strongly biplicate. Beak short and narrow, slightly incurved and ill-defined. Foramen circular and relatively large and the foramen – beak intersection plane variable being nearly vertical to slightly inclined. Surface smooth showing concentric growth lines and radial growth striations. Ll/LD 0.4; crural plates slightly curved, converging towards each other, crural process elongated. Descending branches of loop forming broad plates converging towards each other. Transverse band with rounded crest in cross-section, extended terminal points.

Remarks. *K. hypsogonia* was originally described by Kitchin (1900) from the beds of “upper Charee age” occurring north of Suddera Bela, Kutch and *Terebratula longicarinata* “from beds just overlying those containing *K. hypsogonia*”. Buckman (1918) included both *T. hypsogonia* and *T. longicarinata* within *Kutchithyris* but placed *K. hypsogonia* in ‘Bathian’ and *K. longicarinata* in Callovian without any stratigraphic details. But the present study and previous works of Mitra (1960, 1974, 1978) show that it is a Callovian form and both the species occur together. Mitra combined *T. hypsogonia* and *T. longicarinata* into *K. hypsogonia* because characters used by Kitchin (1900) to distinguish the two species (*T. longicarinata* is a flatter form with less prominent plication) show continuous variation. L,W,T measurements of Kitchin’s type specimens and other collection show that they represent the same homogeneous population (Mitra, 1960, Figs. 12–14). Hence, the present worker agrees with Mitra (1960, 1974, 1978) that *K. longicarinata* should be synonomised with *K. hypsogonia* and the latter retained because of page priority. Mitra (1974, 1978) reported *K. hypsogonia* only from “Bed 14 of Jhura *Montlivaltia* – Terebratulidae subzone” (Mitra, 1960) (Bed 12, Jhura, Fig. 2) but the present collection show that *K. hypsogonia* occurs at the *Reineckeia anceps* zone and continues till the *Peltoceras pondorosum* zone at Jumara, Jhura, Keera and Jara.

Kutchithyris mitra sp. nov. Figs. 4L–O and 8B.

Type material. Forty specimens; Ja 1/1 is designated holotype L –, W –, T –, (Fig. 4L). The specimen has been collected from Bed 1, Jara. L, W, T. Paratypes are Ju 7/1-5, Ju 8/1-23; K 5/1-2; Ja 1/1-4, Jh8/1-6.

Repository. The specimens are in the GSI repository.

Occurrence. The collection is from Early to Middle Callovian of Kutch. The fossil horizons are in the middle part of Chari Formation, Beds 7 and 8 Jumara Bed 5, Keera, Bed 1 Jara and Bed 8 Jhura.

Diagnosis. Subtriangular shells with sharp plications that start at the middle of dorsal valve and diverge. Ventral valve with prominent, long mid-ridge and two furrows on either side and weak lateral ridges; anterior portion extended slightly backward. Foramen at the tip of the ventral umbo and cuts the beak plane obliquely.

Description. Shell medium sized (maximum length 3.56, maximum width 2.97, maximum thickness 2.19) with subtriangular outline which is subcircular in early ontogeny. Length greater than width. Shell ventribiconvex. Position of maximum width slightly anterior to midvalve and maximum thickness at the middle. From the middle of dorsal valve two sharp, subparallel to slightly diverging plicae start and continue to the anterior border. From near the plica a little posterior to midvalve lateral depressions are present on both sides; anterior commissure biplicate, plication strength increasing during ontogeny. Pedicle valve convexity increases anteriorly, a median ridge with rounded crest develops at times near the umbo but generally just posteriorly to mid-valve. Two smaller lateral ridges start near the middle. In between the ridges a furrow develops at each side of the median ridge, starting near middle part and continuing to the anterior margin. The anterior portion of ventral valve narrows and extends slightly towards the dorsal valve. Beak rises from a broad base, erect to suberect, foramen cuts the beak plane vertically. Foramen circular, medium sized and at tip of the dorsal valve. Surface with radial growth striae, characteristic of all kutchithyrids. Pedicle collar present, cardinal process simple. Teeth deeply inserted, denticulum weakly developed. Crural plates concave, crural process short. Ll/LD 0.4; transverse band broad forming a flattened crest in cross-section.

Remarks. Though this species bears some resemblance to *K. acutiplicata* of the Middle Bathonian because of their similarities in thickness, presence of sharp ridges in both valves, biplicate anterior commissure and sharp angle made by lateral commissure, a careful inspection shows significant differences. The shell outline in the new species is subtriangular, while it is pentagonal in *K. acutiplicata.* The average length of the new species is higher than *K. acutiplicata*; in the new species the convexity of the dorsal valve is less and the position of maximum width is at the middle while in adult *K. acutiplicata* it is at one-third the length from anterior. Though the lateral commissure in the new species bends at an angle similar to that of *acutiplicata*, it is just anterior to mid-length in the latter whereas it is more anteriorly in the former.

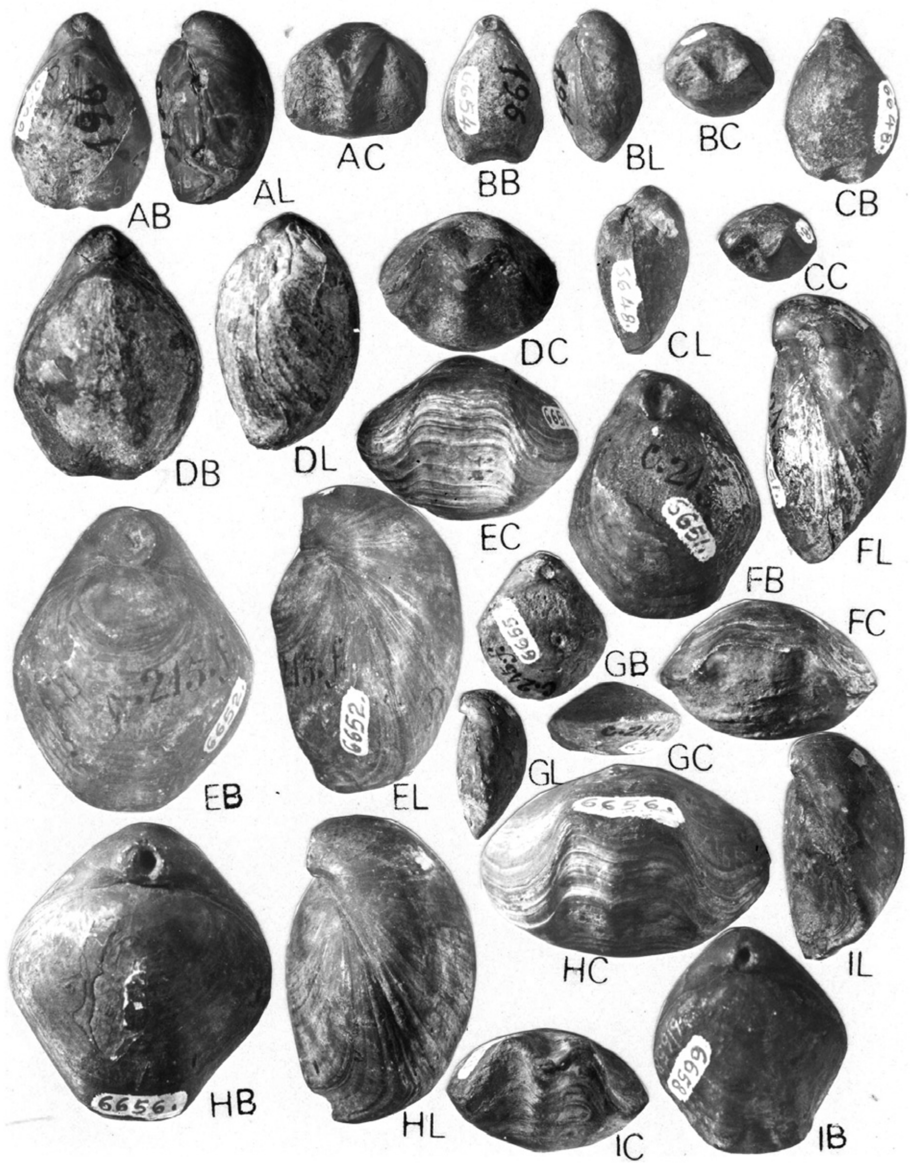

Fig. 9. *Kutchithyris* from Chari Formation of Kutch. All X 1. (A) *K. ingluviosa*, GSI Type No. 6650, lectotype, dorsal (AB), side (AL) and anterior (AC) views. (B) *K. ingluviosa*, GSI Type No. 6654, paralectotype, dorsal (BB), side (BL) and anterior (BC) views. (C) *K. dhosaensis*, GSI Type No. 6648, paralectotype, dorsal (CB), side (CL) and anterior (CC) views of an young individual. (D) *K. dhosaensis*, GSI Type No. 6647, lectotype, dorsal (DB), side (DL) and anterior (DC) views. (E) *K. pyroidea*, GSI Type No. 6652, lectotype, dorsal (EB), side (EL) and anterior (EC) views. (F) *K. pyroidea*, GSI Type No. 6651, paralectotype, dorsal (FB), side (FL) and anterior (FC) views. (G) *K. pyroidea*, GSI Type No. 6655, paralectotype, dorsal (GB), side (GL) and anterior (GC) views of an young individual. (H) *K. jooraensis*, GSI Type No. 6656, lectotype, dorsal (HB), side (HL) and anterior (HC) views. (I) *K. jooraensis*, GSI Type No. 6658, paralectotype, dorsal (IB), side (IL) and anterior (IC) views.

The new species shows some significant similarities with a younger species *K. hypsogonia* of the Middle–Upper Callovian. Though the latter is small, its shape, shell outline, anterior commissure and foramen make it appear as a miniaturized version of the former. Apart from size, the two can be distinguished by the more angular plication and the sharper ventral valve median ridge in *K. hypsogonia*; further the shells of *K. mitra* have greater convexity and thickness. Also internally the crural process is relatively short and transverse band have a flattened crest in *K. mitra*, that being rounded in *K. hypsogonia* (Fig. 8A–B).

Etymology. It is named after the late Prof. K.C. Mitra who had made important contributions on the Kutch brachiopods.

K. ingluviosa (Kitchin, 1900) Figs. AB;A–C;9–11.

1900 *Terebratula ingluviosa*; Kitchin, pp. 34–35, pl. 7, Figs. 1–3.
1918 *Lobothyris ingluviosa*; Buckman, p. 108.
1978 *Kutchithyris ingluviosa*; Mitra (parts), Figs. 5A–C.

Type material. Kitchin's type specimen numbers 6649–6650, 6654. GSI type number 6650 has been selected as the

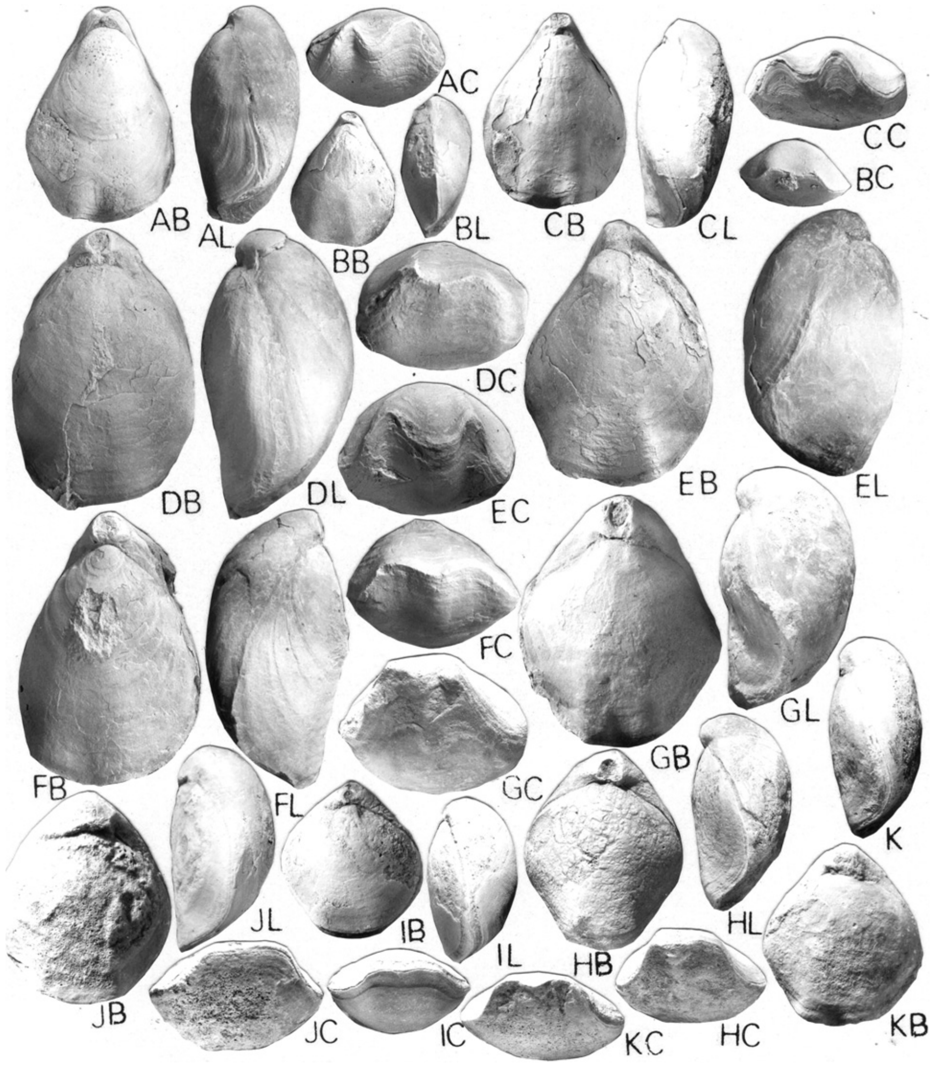

Fig. 10. *Kutchithyris* from Chari Formation of Kutch. All X 1. (A) *K. ingluviosa*, from Bed 9, Keera, K9/29, dorsal (AB), side (AL) and anterior (AC) views. (B) *K. ingluviosa*, from Bed 14, Jhura, Jh14/39, dorsal (BB), side (BL) and anterior (BC) views of an young individual. (C) *K. ingluviosa*, from Bed 9, Keera, K9/3, dorsal (CB), side (CL) and anterior (CC) views. (D) *K. dhosaensis* from Bed 9, Jumara, Ju9/1, dorsal (DB), side (DL) and anterior (DC) views. (E) *K. dhosaensis* from Bed 6, Keera, K6/2, dorsal (EB), side (EL) and anterior (EC) views. (F) *K. dhosaensis* from Bed 6, Keera, K6/1, dorsal (FB), side (FL) and anterior (FC) views. (G) *K. pyroidea* from Bed 14, Jhura, Jh14/11, dorsal (GB), side (GL) and anterior (GC) views. (H) *K. pyroidea* from Bed 14, Jhura, Jh14/27, dorsal (HB), side (HL) and anterior (HC) views. (I) *K. pyroidea* from Bed 14, Jhura, Jh14/42, dorsal (IB), side (IL) and anterior (IC) views. (J) *K. jooraensis* from Bed 14, Jhura, Jh14/3, dorsal (JB), side (JL) and anterior (JC) views. (K) *K. jooraensis* from Bed 14, Jhura, Jh14/30, dorsal (KB), side (KL) and anterior (KC) views.

lectotype (Fig. 9A), L – 3.2, W – 2.3, T – 1.95, (pl. 7, Fig. 2, Kitchin, 1900). Kitchin's collection is from Dhosa oolite, north of Suddera Bela.

Additional material. Specimen numbers Ju 7/36-37, Ju 8/39-40, Ju 9/3-7, Ju 12/1-25 are from Jumara, K 2/1-28 from Keera, Jh8/1-2, Jh15/28-30 from Jhura, Ja1/1-3, Ja3/1-5 from Jara.

Occurrence. The species has been found from the top of Early Callovian to Oxfordian. The present material is from Beds 7, 8, 9 and 12 of Jumara; Bed 2 Keera; Beds 8, 14 Jhura; Beds 1, 3 Jara of Chari Formation, Kutch.

Diagnosis. Shells subtriangular, weakly inflated, dorsal valve relatively more convex than other *Kutchithyris* species. Lateral commissure angular near the anterior margin. Anterior commissure biplicate with angular plication.

Description. Shell moderately large (maximum length 4.3, maximum width 3.3, maximum thickness 2.1), biconvex always longer than wide, weakly inflated, roughly triangular in outline, tapering posteriorly. The maximum width is attained at about one third of shell length from the anterior margin. Just after mid dorsal valve a shallow lateral depression broadens anteriorly (Fig. 10BB) which is sometimes inconspicuous posteriorly becoming prominent anteriorly (Fig. 10AB). Two sharp ridges bounded at the sides by lateral depressions begin about 1/3 of shell length (from anterior margin) in adults, and continue to

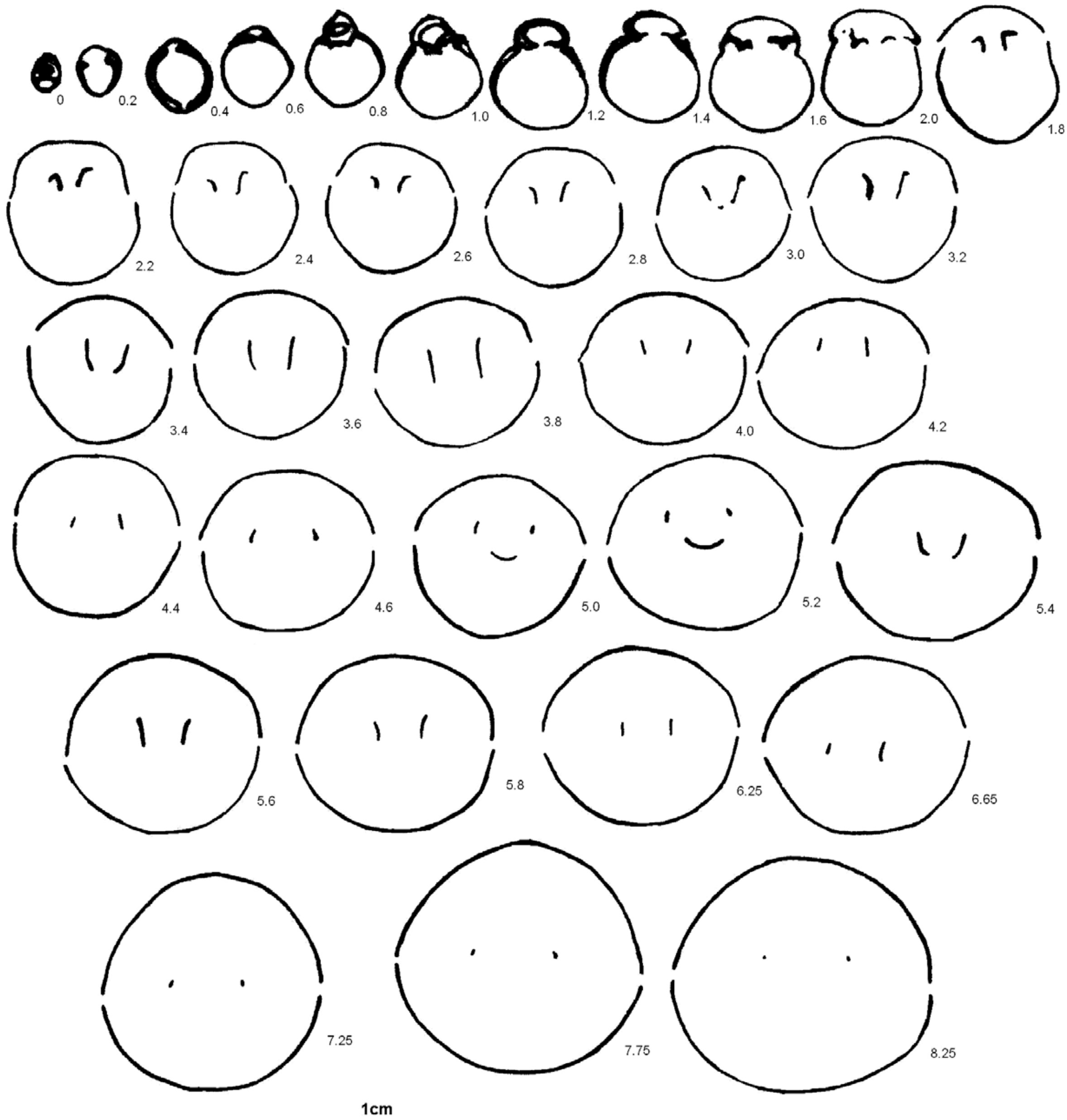

Fig. 11. Serial transverse section of *K. ingluviosa*. Original length of the specimen 36 mm; the loop disappears at 14.0 mm. Concave hinge plate at 1.6 mm, transverse band visible at 5.0 mm.

the anterior and are separated by a deep and short median sinus, the strength increasing during ontogeny. Ventral valve is more convex and tapering at the posterior and broadens at the anterior. A median plica/ridge gently rounded at the hinge appears at 1/3 length from anterior margin corresponding to the median sinus in dorsal valve. Hinge line curved and very short. Lateral commissure straight in the major portion of shell from umbo but at a point approximately 1/5 of length from anterior margin it curves suddenly towards ventral side turning again at a sharp angle to dorsal valve (e.g. Fig. 10BB). The angularity is a characteristic of adult stage of species, the younger forms being more rounded. Anterior commissure biplicate; hinge of the plica shows considerable variation in tightness and height, but the young stage shows more rounded plicae. Beak narrow, thick and slightly incurved, foramen medium to large, rounded or oval. The foramen cuts the beak in an inclined plane. Shell surface smooth except some growth striae and occasionally radial striations. Pedicle collar well developed, cardinal process simple. Teeth deeply inserted into sockets. Crural plates curved, converging towards each other, crural base elongated and passing into high, thin crural process. Ll/LD 0.4; crest of transverse band slightly curved in plan.

Remarks. Kitchin (1900) described the species from beds stratigraphically equivalent to the Dhosa Oolite from the north of Suddera Bela, Kutch, and placed it in the genus *Terebratula*. Later, Buckman (1918) placed it under

Lobothyris. But the studies by Mitra (1960, 1978); Mitra and Ghosh (1973) and the present study reveal that it belongs to the genus *Kutchithyris*. *Lobothyris* has a rectimarginate anterior commissure whereas *K. ingluviosa* is characterised by a strongly biplicate anterior margin. The lateral commissure of *Lobothyris* is a simple curve but in *ingluviosa* it is initially straight but takes a sharp, nearly angular turn towards the ventral valve close to the anterior margin. Mitra (1974) and Mitra and Ghosh (1973) combined *K. ingluviosa*, *K. pyroidea*, *K. jooraensis* into a single species *K. ingluviosa* based on only three shell parameters – length, width, and thickness. As can be observed from the type specimens as well as from new collections, the size ratios of the three species are not much different, hence bivariate scatter plots are not helpful in separating them. When other shell parameters, such as umbonal length–width, plica width, foramen diameter, distance of foramen from beak, are considered and multivariate statistical analyses are employed the species show considerable differences (Mukherjee et al., 2002b). Apart from this, *K. ingluviosa* has a triangular shell outline whereas *K. pyroidea* has a pentagonal to subcircular-elliptical outline and *K. jooraensis* has a subcircular-polygonal shell. The lateral commissure takes a sharp angular ventral convexity at almost 1/4 length from the anterior in *K. ingluviosa* but the curve is much rounded and is almost at the middle or slightly towards the anterior in *K. pyroidea* and *K. jooraensis*.

K. ingluviosa resembles *K. dhosaensis* in shell shape, posterior tapering and posterior inflation in the younger specimens (Fig. 10B and E), but the adult specimens of the two markedly differ in size, nature of biplication, nature of shell compression etc. (Fig. 10A, C–F).

K. dhosaensis (Kitchin, 1900) Figs. 7; 9C–F; 10D–F.

1900 *Terebratula dhosaensis*; Kitchin, pp. 32–34, pl. 6, Figs. 7–10.
1918 *Lobothyris dhosaensis*; Buckman, p. 108.

Type material. Kitchin's type specimen numbers 6645–6648. GSI type number 6647 has been selected as the lectotype (Fig. 9D) L – 4.2, W – 3.0, T – 2.55. Kitchin's material came from Upper Chari, at Dhosa village.

Additional material. Specimen numbers Ju9/1-2, Ju 12/1-5 are from Jumara, K6/1-4 from Keera, K10/1-21 from Keera, Jh 8/1-8, Jh15/1-5 from Jhura, Ja3/1 from Jara.

Occurrence. The species is found in Middle Callovian to Oxfordian in Kutch. The present collection is from the middle to upper part of Chari Formation; Beds 9, 12 Jumara; Beds 6, 10 Keera; Beds 8, 15 Jhura and Bed 3 Jara.

Diagnosis. Large, biconvex, elongated, highly inflated shells with subpentagonal outline. Thickness of ventral valve highest among *Kutchithyris* species. Lateral commissure bends to form a broad angle near the anterior margin. Anterior commissure biplicate with short rounded plication.

Description. Shell large in size (maximum length 5.0, maximum width 3.55, maximum thickness 2.8). Elongated oval to subpentagonal in outline, younger shells are mostly oval to subtriangular. Shell length much greater than width, maximum width always anterior to the middle. Shell thickness considerably high, because ventral valve is much inflated. Shell width and thickness increases allometrically with growth. Strongly ventribiconvex shell, convexity increasing with age. Anterior commissure is strongly biplicate – the plications varying from rounded to moderately angular. Ventral valve develops a median ridge at about 1/3rd length from the anterior and short and shallow depression on either side. Dorsal valve, considerably flatter, develops shallow lateral depressions from about the middle which broaden near anterior margin. A shallow median sinus starts from mid-valve and increases slightly in depth near anterior margin. Hinge line short and curved. Lateral commissure straight at the beginning but forms a ventrally directed curve at 1/4 length from the anterior. The development of ventral valve ridge coincides with the angle made by the lateral commissure in most specimens. The bend of the lateral commissure shows variability, being gently rounded in most cases but moderately angular in a few (Figs. 9DL, 10E–F). Beak thick, massive, rounded and moderately incurved. Foramen circular, moderately large and truncates beak vertically. Shell surface shows growth lines and occasionally fine radial striae. Pedicle collar present, cardinal process simple. Teeth deeply inserted into sockets, denticulum weakly developed. Crural plates curved. Ll/LD 0.35; transverse band forming a broad U in cross-section, crest flat.

Remarks. *Terebratula dhosaensis* Kitchin was placed by Buckman (1918) in *Lobothyris*. *T. dhosaensis* is a highly elongated form and resemble *K. ingluviosa*, which was also placed by Buckman (1918) in *Lobothyris*. Muirwood (1934), while studying *Terebratula punctata*, the type species of *Lobothyris* remarked that many of the species included by Buckman as *Lobothyris* can be distinguished from *L. punctata* by marked differences in external characters. *Lobothyris* is a form having subcircular to subelliptical outline, plano-convex to moderately biconvex lateral profile and rectimarginate to incipiently sulciplicate anterior commissure (Muirwood, 1934, 1965; Cooper, 1983) *T. dhosaensis* is a highly elongated, and inflated, biconvex, biplicate form with a thick, moderately incurved beak unlike *Lobothyris*. The radial striations characteristic of *Kutchithyris* is also visible in *T. dhosaensis*. The shell shape, convexity, commissure, beak and foramen, presence of ridge and sinus in ventral and dorsal valve respectively show similarities with other *Kutchithyris* species; thus it is included in *Kutchithyris*.

Among the other Kutch forms of the Middle Callovian it shares some similarities with the stratigraphically older *K. ingluviosa*, in shell shape, and moderately incurved beak. Interestingly, the moderately biplicate anterior commissure, median ridge at the anterior 1/3rd of ventral valve, gentle bend of the lateral commissure are reminiscent of the young stage of *K. ingluviosa* (Fig. 10B and F). But there are distinct differences between the adult shells of the two species,

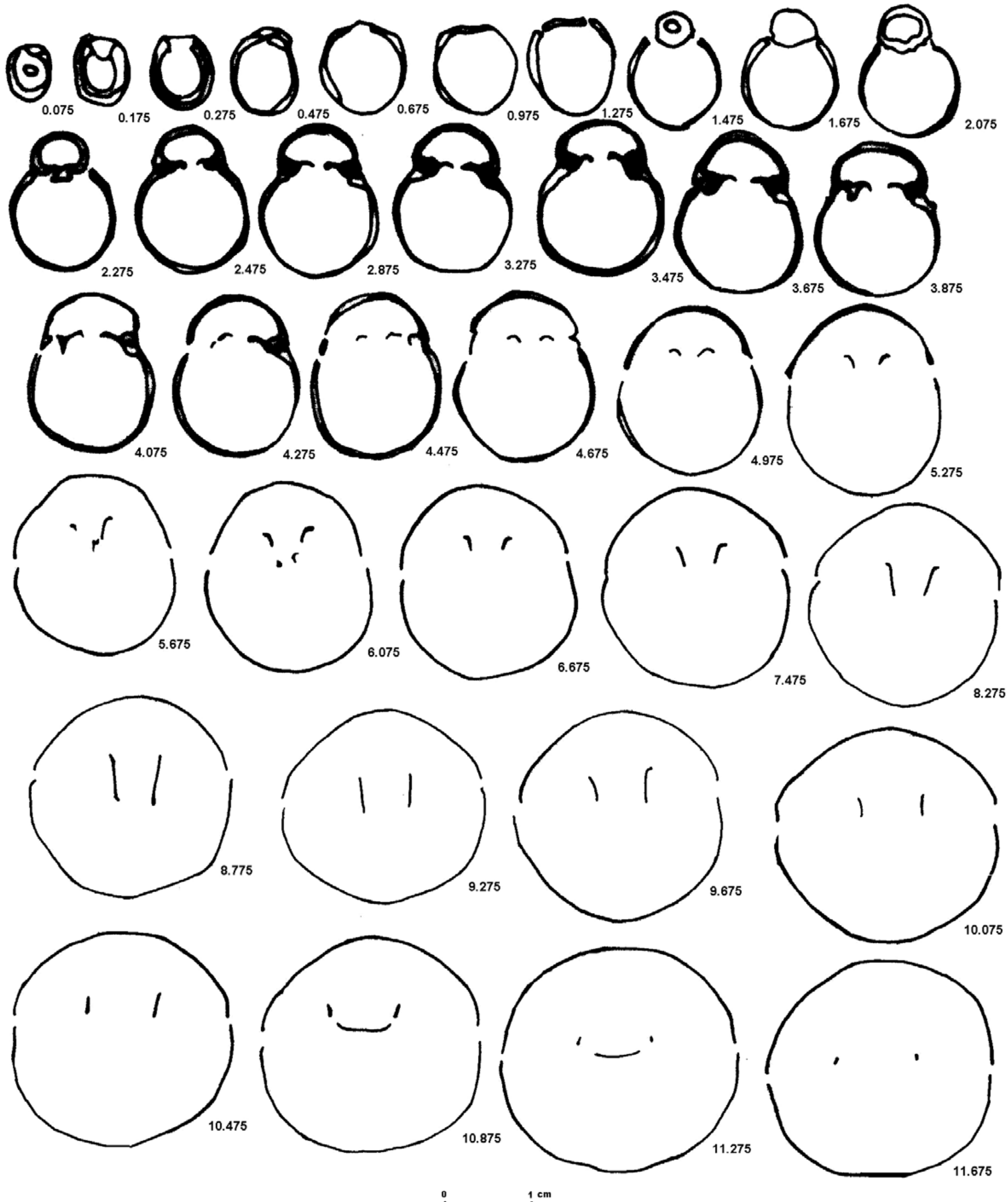

Fig. 12. Serial transverse section of *K. dhosaensis*. Original length of the specimen 41 mm; the loop disappears at 13.05 mm. Concave tapering hinge plate 2.875–3.875 mm, broad, flat transverse band visible at 10.875 mm.

the most notable of which is the highly inflated ventral valve in *K. dhosaensis* imparting to it a strong ventriconvex aspect, whereas *K. ingluviosa* is a much compressed form with its ventral valve being slightly more convex than the dorsal valve. *K. ingluviosa* is also much smaller in size and its biplication is much more pronounced with the two plicae being more raised and sharp, while *K. dhosaensis* has a gently curved biplication with extremely weak plicae strength. Further, the ventral valve median ridge of *K. dhosaensis* is flatter and broader compared to that of *K. ingluviosa* and the foramen – beak intersection is vertical in the former and inclined in the latter. Internally *K. dhosaensis* has a much shorter loop than *K. ingluviosa*. Statistical comparison between the two in multivariate space reveal two distinct clusters (Mukherjee et al., 2002b) Fig. 12.

Kutchithyris pyroidea (Kitchin, 1900) Figs. 9E–G; 10G–I; 13.

1900 *Terebratula pyroidea*; Kitchin, pp. 35–37, pl. 7, Figs. 4–7.

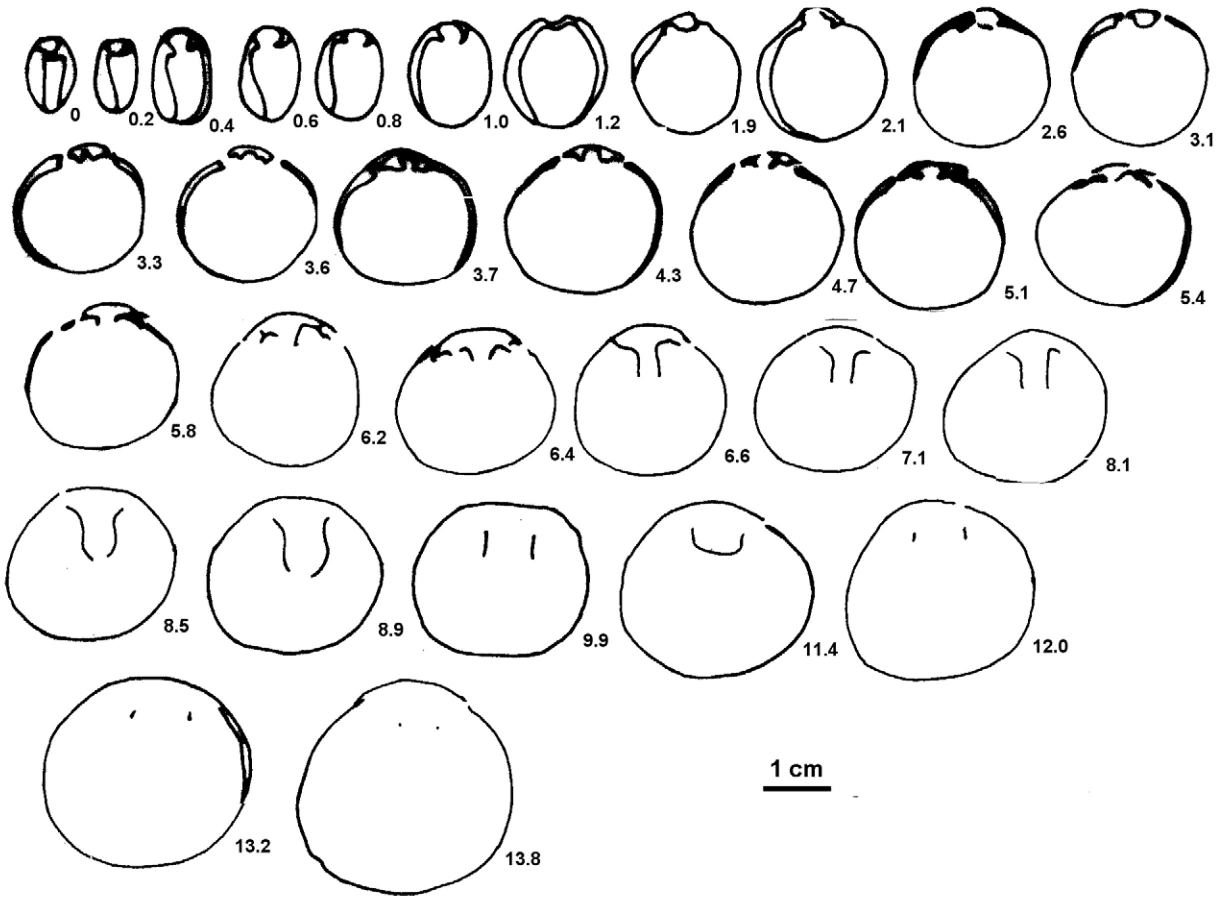

Fig. 13. Serial transverse section of *K. pyroidea*. Original length of the specimen 40 mm; the loop disappears at 14.2 mm. Pedicle collar at 0.8 mm, cardinal process at 1.9 mm, concave hinge plate at 5.8 mm.

1918 *Heimia pyroidea*; Buckman, pp. 103–105.
1978 *Kutchithyris ingluviosa*; Mitra (part), Figs. 5D–F.
2001 *Kutchithyris landeri*; Feldman, Owen and Hirsch, pp. 646–647, pl. 1, Figs. 24–26.

Type material. Kitchin's type specimen numbers 6652–6655, GSI type number 6652 has been selected as the lectotype (Fig. 9E) L – 4.7, W – 3.9, T – 3.0. Kitchin described the species from Dhosa Oolite of Jooria and Lodai.

Additional material. Specimen numbers Jh 12/1-2, Jh14/1-26 are from Bhakria.

Occurrence. The species is found in Upper Callovian to Oxfordian of Kutch and Israel. The present collection is from uppermost part of Chari Formation, Beds 12, 14 Jhura and Bhakria.

Diagnosis. Large weakly biconvex shells with high thickness.. Anterior commissure biplicate with occasionally asymmetric plication; ventral valve shows linguiform projection. Foramen large, irregularly elongated with thick margin.

Description. Shell large in size (maximum length 4.8, maximum width 4.0, maximum thickness 2.8), elliptical to subpentagonal in outline, young shells being mostly circular in outline (Fig. 9G); slightly longer than broad, width increasing allometrically. Maximum thickness at the middle and maximum width anterior to middle. Shell roughly planoconvex, ventral valve being more convex, with convexity increasing during ontogeny. Dorsal valve has a centrally raised low fold bounded by two lateral shallow depressions, the fold has a shallow median sinus between two short plicae in the anterior quarter. Anterior commissure weakly biplicate. Ventral valve has a median ridge variable in length but mainly in the anterior. The ridge is prominent and well defined in adult shells (Figs. 10GC, HC) but low in young ones (Fig. 10IC). The anterior part of ventral valve is extended as a linguliform projection. Hinge line a gentle, wide curve. Lateral commissure gently curved with ventral convexity but as it approaches the anterior, forms a broad curve and rises to form biplicate anterior commissure with moderately strong to weak plications. The plications are occasionally asymmetric (Figs. 9EC, FC). Distance of the plica from the posterior margin increases allometrically during ontogeny. Beak is large, massive, and strongly incurved concealing deltidial plates; beak angle acute. Beak ridges absent. Foramen irregularly elongated with thick margins, the walls have undergone somewhat internal thickening. Foramen truncates beak vertically. Surface has radial growth striations. Pedicle collar present, cardinal process simple. Denticulum well developed, teeth deeply inserted into sockets. Crural plates curved, converging towards each other, crural base appears at 5.8 mm from posterior and elongates rapidly to form high, thin crural process. Ll/LD 0.4; transverse band forms a broad U in cross-section.

Remarks. *Terebratula pyroidea* described by Kitchin (1900) was reassigned to *Heimia* by Buckman (1918). *Heimia* is a small, subtriangular, biconvex genus with a long beak, medium sized foramen and smooth shells from the Bajocian of England, France and Switzerland. *K. pyroidea* is restricted to the Upper Callovian to Oxfordian of Kutch and is large in size, oval to subpentagonal in shape and biconvex, weakly biplicate and with short, incurved beak and a large circular to elliptical foramen. The young specimens have a characteristic circular shell with rectimarginate commissure and suberect beak common to all *Kutchithyris* species. Thus *T. pyroidea* cannot be assigned to *Heimia* and it should belong to *Kutchithyris*.

This species along with *K. ingluviosa* (Kitchin), *K. jooraensis* (Kitchin) and *K. dhosaensis* (Kitchin) have been combined as *K. ingluviosa* by Mitra (1978), although no detailed justification was provided for this. When only length, width and thickness of the shells are considered in bivariate plots the scatter diagrams shows some overlap between the species but when other parameters such as position of maximum width and plica width are taken into account and multivariate statistical method like discriminant analysis and principal components analysis are applied, species fall into separate clusters (Mukherjee et al., 2002b).

K. pyroidea and *K. jooraensis* are found together – in the same localities of Bhakri, Lodai and in the same stratigraphic horizon, Dhosa oolite, and rarely in a sandstone horizon (Bed 12).

Recently, Feldman et al. (2002) described *Kutchithyris landeri* from the Upper Callovian Matamor Formation of Israel; it bears strong similarity with the present form in its subpentagonal outline, incipient biplication, short massive umbo, beak angle acute and large circular foramen. With these common features and an overall similarity between the two, *K. landeri* is considered here to be conspecific with *K. pyroidea*.

K. jooraensis (Kitchin, 1900) Figs. 9H and I; 10J and K; 14.

1900 *Terebratula jooraensis*; Kitchin, p. 37, pl. 8, Figs. 1–4.
1918 *Kutchithyris jooraensis*; Buckman, p. 113.
1978 *Kutchithyris ingluviosa*; Mitra (in part), Figs. 5D–F.

Material. Kitchin's type specimens are 6655–6659, 15586. GSI type number 6656 has been selected as the lectotype (Fig. 9H) L – 4.65, W – 4.25, T – 2.9. The material was collected from Dhosa Oolite (present Bed 15) of Jooria.

Additional material. Specimen numbers Jh 12/1-4, Jh14/1-42 are from Jhura and Bhakria.

Occurrence. The species is found in the Upper Callovian to Oxfordian horizon of Kutch. The present collection is from uppermost part of Chari Formation; Bed 12, 14 at Jhura and Bhakria.

Diagnosis. Moderately large, thickness low, weakly biconvex shells. Ventral valve shows linguiform projection, anterior commissure uniplicate to weakly biplicate.

Description. Shell moderately large (maximum length 4.3 cm, maximum width 3.9 cm, maximum thickness 2.4 cm), younger shells subcircular, approaching a polygonal outline during later stage of ontogeny; length slightly greater than width; thickness low, shell relatively flat. Shell plano-convex in lateral profile, ventral valve being convex, plano-convex character increases during ontogeny. Maximum width and thickness anterior to middle and at middle respectively. Dorsal valve is slightly depressed along its two sides so that middle part appears raised up as a flattened arch. The arch may be depressed centrally near anterior margin to form a shallow median sulcus which separates two low plicae. Anterior commissure is rectimarginate in young shells to uniplicate to weakly biplicate in adults. The more convex ventral valve is narrowed anteriorly to form a linguiform projection, which becomes prominent during growth. On each side of this valve there develops a weak lateral fold. The central part is slightly depressed and a very low median ridge is present. The ridge is also very inconspicuous in some shells and it has a variable length never exceeding the mid-point of ventral valve. Lateral commissure gently curved at the posterior but convexity increases from mid- point till anterior margin. Hinge line curved. Beak arises from a broad base with obtuse beak angle, massive, and strongly incurved concealing deltidial plates. Beak suberect and deltidial plates more freely exposed in young shells. Beak ridges generally absent but present in a few cases. Foramen moderate sized, circular, truncates beak vertically. The surface bears radial striations apart from growth lines. Cardinal process simple. Teeth linguiform, weakly inserted into sockets. Crural plates incurved. Ll/LD 0.3. Transverse band broad, crest flattened.

Remarks. *Terebratula jooraensis* described by Kitchin (1900) from 'Dhosa Oolite' of Kutch was placed by Buckman (1918) in *Kutchithyris* Buckman along with five other Kutch species; Mitra (1960, 1974, 1978) clubbed *T. jooraensis* and *K. pyroidea* with *K. ingluviosa* on the basis of bivariate statistics using length, width and thickness.

Compared to *K. jooraensis*, the older *K. ingluviosa* is slightly smaller in size, elongated, subtriangular, position of maximum width shifted towards anterior end; lateral commissure is a broad curve in *K. jooraensis* but is angular in *K. ingluviosa*. The anterior commissure is uniplicate to slightly biplicate in *K. jooraensis* but sharply biplicate in *K. ingluviosa*.

Though there is some resemblance to the nearly contemporaneous *K. pyroidea* (also noted by Kitchin, 1900), *K. jooraensis* is relatively broader, plano-convex with a near polygonal outline; but the linguiform extension of the anterior commissure is stronger in *K. pyroidea* than in *K. jooraensis*. *K. pyroidea* is also much more inflated than *K. jooraensis*. The beak is more massive and suberect to

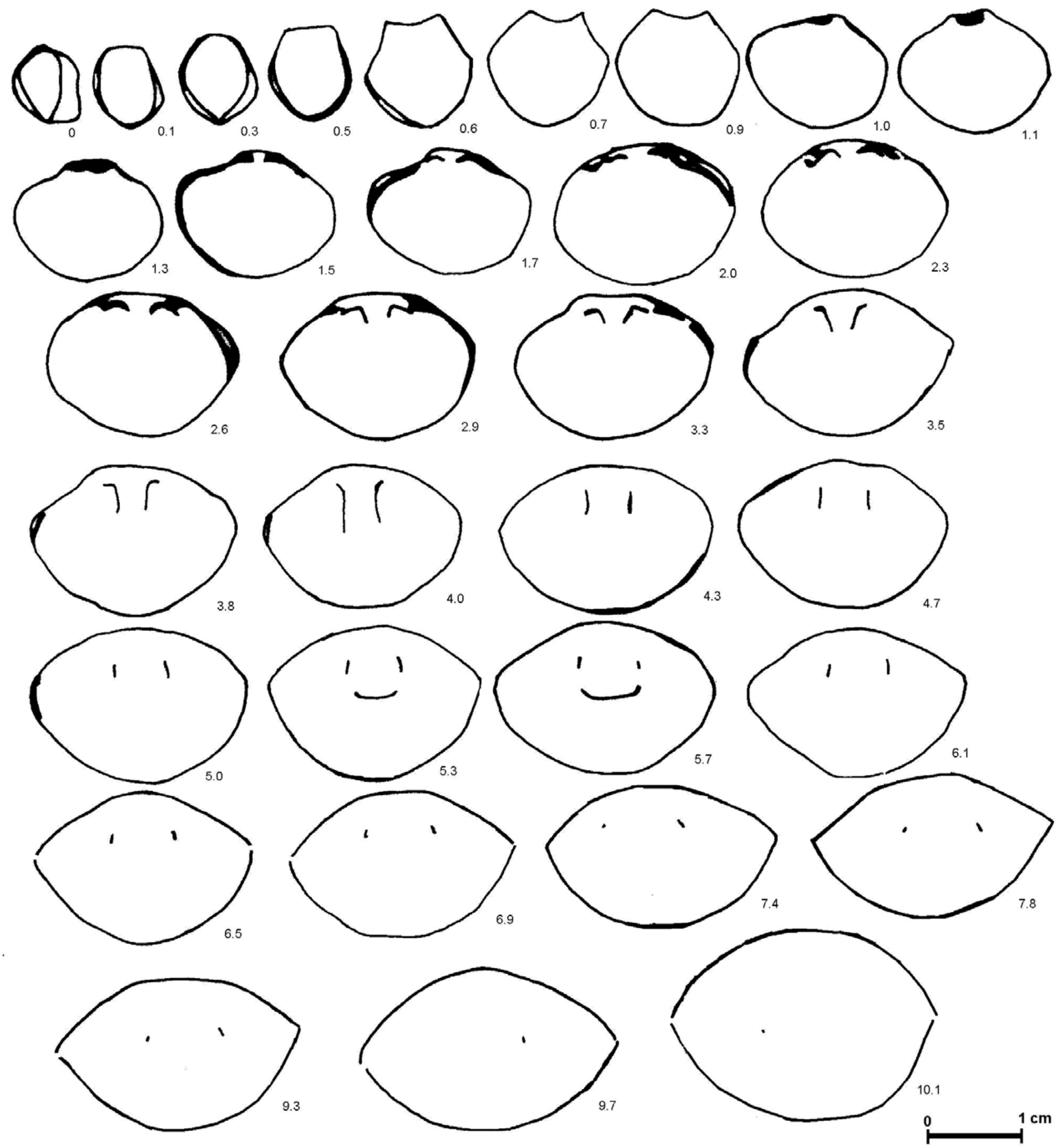

Fig. 14. Serial transverse section of *K. jooraensis*. Original length of the specimen 35 mm; the loop disappears at 10.5 mm. Cardinal process prominent at 1.1 mm, hinge plate concave, tip extended up 2.6–2.9 mm.

weakly incurved in *K. pyroidea* but strongly incurved in *K. jooraensis*, the beak angle is acute in the former and obtuse in the latter. The foramen is smaller in *K. jooraensis* and the walls are not thickened or protruding as in *K. pyroidea*. However, the young specimens of *K. pyroidea* and *K. jooraensis* are characterized by a subcircular shell outline, rectimarginate anterior margin, suberect beak and exposed deltidial plates differing only in shell thickness which is greater in *K. pyroidea*.

The different species are separated by discriminant analysis and principal components analysis using shell parameters such as foramen diameter, umbonal length, umbonal width, plica width and distance of plica from posterior margin apart from length, width and thickness (Mukherjee et al., 2002b).

4. Statistical analysis

Cannonical variate analysis is used in the present study to understand the interrelationships between the different *Kutchithyris* species. About 800 specimens of *Kutchithyris* have been subjected to canonical variate analysis. Based on Kitchin's conventional taxonomic classification and the present study, 198 specimens belong to *K. acutiplicata*, 94 to

K. propinqua, 370 to *K. euryptycha*, 46 to *K. dhosaensis*, 74 to *K. ingluviosa*, 38 to *K. jooraensis*, 26 to *K. pyroidea*, 56 to *K. hypsogonia*, 34 to *K. breviplicata*, 40 to *K. mitra* and 5 to *K. katametopa*. The data used here are based on 8 shell dimensions, measured with digital calipers. The shell parameters represent significant external characters of the genus. These are shell length (L), width (W), thickness (T), foramen diameter (F), position of maximum width (PMW), curved length (CL), plica width (PW), plica distance from posterior margon (PD) and plica height (PH). In this statistical study 11 species were subjected to multivariate analysis leaving out the species *K. planiconvexa* which is a distinct nonplicate form and also without the parameters related to plication, the form does not lend itself to the specified multicharacter clustering.

The eigenvalues, percentage of variance and canonical correlations for the functions and the group means are shown in Table 1. The first three functions account for 97.4% of the variance so the rest are not shown. A strong correlation exists between the discriminant scores and the groups. The Wilk's lambda ranges from 0.037 to 0.565 for the first three functions and the χ^2 statistic has a significance of zero indicating that the group means differ widely. The canonical variate scores have been plotted taking Functions 1 and 2 as the axes (Fig. 15A). Function 1 gives maximum weightage to length, width and the starting point of plication and Function 2 to height of plication. The plots show considerable overlap though their separate specific identity is established from the external and internal morphology as discussed in the previous section. Next a separate CVA is done excluding the Bathonian species *K. acutiplicata*, *K. propinqua* and *K. euryptycha* and the results are shown in Table 2 and Fig. 15B. Interestingly, the species show low overlap and have distinct clusters. Function 1 gives the maximum weightage to the same shell parameters as in the previous analysis but Function 2 gives maximum weight to position of maximum width of the shell.

In the newly opened up Kutch basin *K. acutiplicata* suddenly appeared in the Middle Bathonian beds of Jhura without any obvious ancestor. The instability of the environment and the stiff competition for occupying more space in the newly formed basin may have prompted a burst of speciation that gave rise to the other Bathonian species. Among them *K. propinqua* and *K. euryptycha* were the most successful in terms of number and longevity. They crossed the Bathonian–Callovian boundary and gave rise to the Callovian–Oxfordian forms. The phylogenetic analysis of the *Kutchithyris* species discussed in the next section

Table 1
CVA of the *Kutchithyris* species

Function	Eigen value	% of variance	Cumulative %	Cannonical correlation	Functions at group centroid										
					1	2	3	4	5	6	7	8	9	10	11
1	4.91	68.8	68.8	.912	−0.092	2.71	−2.05	−0.557	−1.26	−2.35	2.11	3.69	3.50	5.02	0.767
2	1.565	21.9	90.7	.781	1.90	0.309	−0.658	1.144	−2.66	0.059	−1.63	−1.17	−0.741	−0.654	0.607
3	0.475	6.7	97.4	.568	−0.015	0.063	−0.403	−0.078	0.300	1.185	0.769	1.510	−1.72	−0.874	1.23

Table 2
CVA of the Callovian–Oxfordian *Kutchithyris* species

Function	Eigen value	% of variance	Cumulative %	Cannonical correlation	Functions at group centroid							
					4	5	6	7	8	9	10	11
1	7.961	78.7	78.7	.943	−1.549	−2.699	−3.612	.577	2.003	3.242	4.291	−.654
2	.971	9.6	88.3	.702	−1.783	.769	−.604	.786	1.678	−1.329	−.571	−.325
3	.779	7.7	96.0	.662	.603	−1.817	.377	−.199	.976	−.621	−.040	1.664

Table 3
Data matrix

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Lobothyris	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Holcothyris	1	0	2	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
K. acutiplicata	1	1	0	0	0	1	1	0	0	0	0	0	2	1	1	0	2	0	0	0	0	0	1
K. katametopa	1	1	0	0	1	1	1	0	0	1	0	0	2	1	1	0	2	0	0	1	0	1	1
K. planiconvexa	1	1	0	0	0	2	2	0	0	1	0	0	1	1	1	0	1	0	0	0	0	0	2
K. propinqua	1	1	0	0	0	0	1	1	0	1	1	0	1	1	1	0	2	0	0	0	0	0	2
K. breviplicata	1	1	2	1	1	1	1	0	0	1	1	0	1	2	1	0	3	0	1	0	0	1	2
K. mitra	1	1	2	0	1	0	1	1	0	1	1	0	1	2	2	1	2	0	1	0	0	0	2
K. hypsogonia	1	1	2	0	1	1	1	1	0	1	1	0	1	2	2	1	2	0	2	0	0	1	1
K. euryptycha	1	1	0	1	1	0	0	1	1	1	1	1	1	1	3	0	1	1	1	0	1	0	1
K. ingluviosa	1	1	2	1	1	0	1	1	1	2	1	1	2	2	3	0	3	0	1	0	0	1	1
K. dhosaensis	1	1	2	1	1	1	1	1	1	2	1	1	2	2	3	0	3	0	2	0	0	1	2
K. pyroidea	1	1	1	0	1	1	1	1	1	1	1	1	2	2	3	0	3	1	1	0	0	1	2
K. jooraensis	1	1	3	0	1	0	1	1	1	1	1	1	2	2	3	0	3	1	0	0	0	1	2

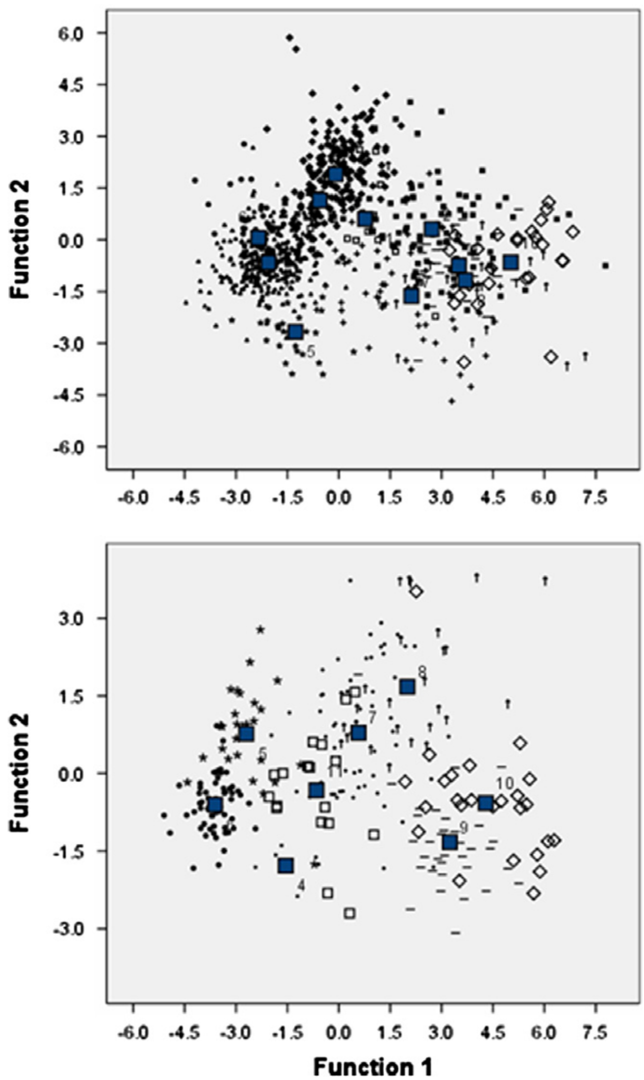

Fig. 15. Scatter plot of cannonical variate scores of *Kutchithyris* species in Function 1–Function 2 axes. (A) CVA done with all the *Kutchithyris* species. The first canonical axis (Function 1) is specified by the relationship $z_1 = 0.851L + 0.810W + 0.710T + 0.640CL + 0.23F + 0.697PMW + 0.249PMT + 0.336PW + 0.225PH + 0.810PD$, this has mainly contributions from the shell length, width and the point at which plication appears; and the second canonical axis Function 2 by $z_2 = 0.026L + 0.426W + 0.189T + 0.197CL + 0.190F - 0.174PMW + 0.035PMT + 0.282PW + 0.646PH - 0.10PD$ which has main contributions from plication height. (B) CVA done excluding the species *K. acutiplicata*, *K. propinqua* and *K. euryptycha*. $z_1 = 0.788L + 0.834W + 0.591T + 0.665CL + 0.352F + 0.515PMW + 0.173PMT + 0.458PW + 0.063PH + 0.711PD$ and $z_2 = 0.450L - 0.084W + 0.238T + 0.078CL - 0.164F - 0.629PMW + 0.088PMT + 0.268PW + 0.058PH - 0.376PD$. Keys: solid diamond – *K. acutiplicata*, solid square – *K. propinqua*, solid triangle – *K. euryptycha*, cross – *K. katametopa*, star – *K. mitra*, solid circle – *K. hypsogonia*, plus – *K. breviplicata*, arrow – *K. ingluviosa*, long dash – *K. dhosaensis*, open diamond – *K. pyroidea*, open square – *K. jooraensis*.

reveals this genealogical relationships from the character distribution. Therefore the morphologic relationships of the Callovian–Oxfordian forms is reflected in the strong regions of overlap when plotted with the Bathonian species – *K. acutiplicata–K.propinqua–K.euryptycha*.

5. Phylogenetic study

Kutchithyris acutiplicata, the earliest representative of the genus which appears in the Middle Bathonian of Kutch, is distinguished by the presence of prominent radial striae and a transverse band with a gently curved crest. All the remaining 11 *Kutchithyris* species, occurring up to the Oxfordian, have these two characters in common. Thus, these shared derived characters are synapomorphies that unite the 12 species into a close nexus making *Kutchithyris* a monophyletic group. In order to understand the genealogical relationships among its members, the group was subjected to cladistic analysis. Two outgroups have been chosen, an Early to Middle Bathonian terebratulide genus, *Lobothyris*, known from Europe, Turkey and Somaliland, and a Bathonian – Callovian genus *Holcothyris* known from Burma, England and France. *Lobothyris* is ventriconvex, with loop length nearly half the dorsal valve length (Muirwood, 1934; Cooper, 1983). *Holcothyris* is unequally biconvex, anterior commissure paraplicate and shell surface radially capillate (Sahni, 1940; Cooper, 1983). Both *Lobothyris* and *Holcothyris* are characterized by position of crural processes posterior to mid-loop – a character that is also shared by *Kutchithyris*.

The source of characters are external shell morphology and also a few internal morphological characters which distinguish the *Kutchithyris* species. Appendix I lists 23 characters used in this analysis with the different states exhibited by the analysed taxa presented in a data matrix (Table 3). The analysis was carried out using the parsimony analysis program PAUP 4.0b10 version (Swofford, 1998). The optimality criterion used was that of maximum parsimony. All characters were unordered and initially given equal weight. After the first run the data set was reweighed using the rescaled consistency index. Searching was done by using the branch and bound option which guarantees to find the most parsimonious trees. The first run using equal character weighings produced seven trees, the strict consensus of which is shown in Fig. 16A. After the characters were reweighed by rescaled consistency index only a single tree was produced (Fig. 16B). Each node of the tree is labeled and a full character transformation list for each node is given in Appendix 2. The basis for the subsequent discussion of phylogeny is this tree and the strict consensus tree. Bootstrap values taken as an estimate of support of the nodes in a cladogram. In the present study, bootstrap was performed using PAUP on 100 replicates, and the values above 50% has been shown (Fig. 16B).

K. acutiplicata is the earliest one to appear in the Middle Bathonian of Jhura, marking the advent of the *Kutchithyris* clade and continues in the Upper Bathonian. In the strict consensus tree, (Fig. 16A) *K. katametopa* and *K. planiconvexa* both occurring in the Upper Bathonian, alongwith *K. acutiplicata*, forms a subclade. *K. acutiplicata*, apart from being statigraphically oldest, also has the maximum number of plesiomorphic characters and no unique apomorphy and therefore can be considered as the

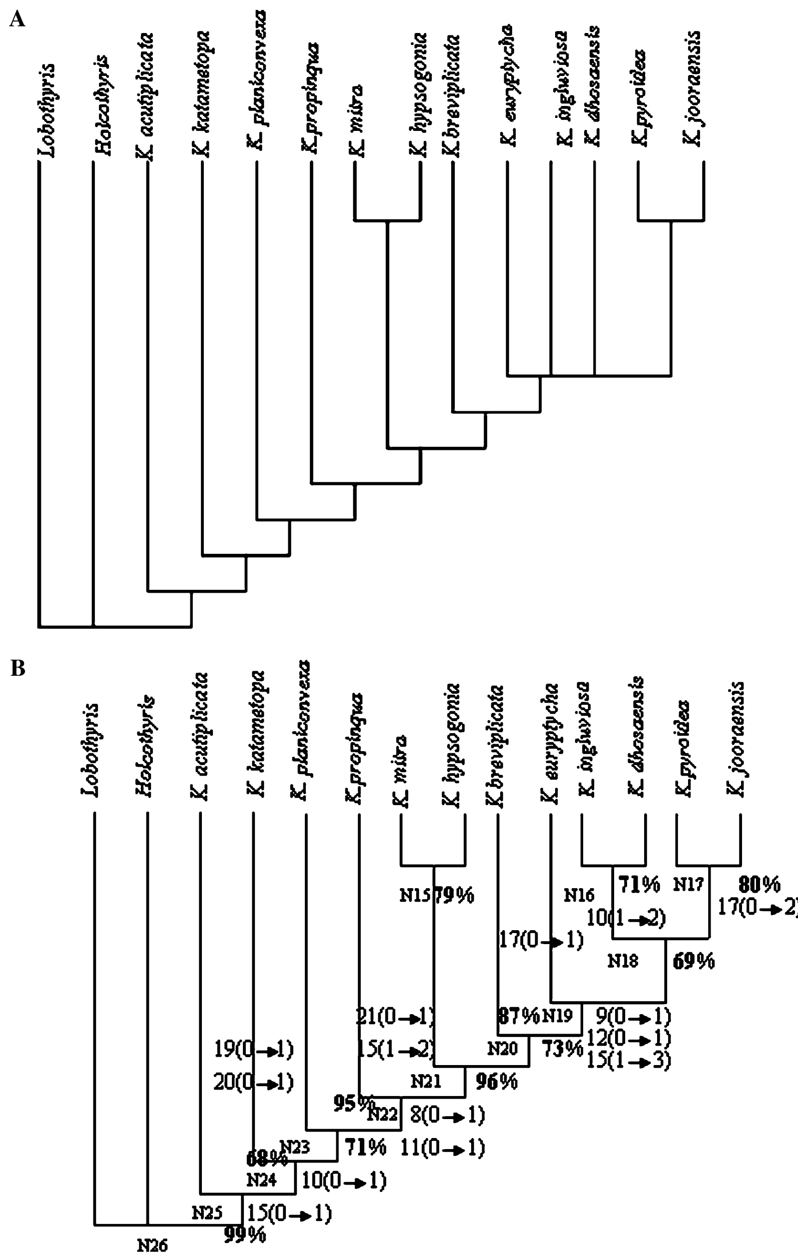

Fig. 16. Cladograms of the genus *Kutchithyris*. (A) Strict consensus of 7 trees. (B) Single tree produced after reweighing by rescaled C.I. Synapomorphies, Bootstrap values indicating the percentage of bootstrap trees within which that branch occurs and the node numbers (for reference in the apomorphy list in Appendix 3) are written at the nodes. Tree length 23.3, Consistency Index 0.81, Retention Index 0.88.

ancestral stock in the *Kutchithyris* clade. It is notable that when the ontogenetic changes of *K. acutiplicata* are considered, its juvenile stage and pre-adult advanced stage exhibit overall morphological similarity to the adult of *K. planiconvexa* and *K. katametopa* respectively (see Discussion of *K. katametopa* and *K.planiconvexa*). However, adult *K. planiconvexa* and *K. katametopa* has unique apomorphic states such as weakly inflated, rectimarginate commissure and subspheroidal, laterally fimbriated morphology, respectively.

In the *K. propinqua* subclade, *K. propinqua* appears as the sister taxon to the later species; the clade is distinguished by the shared derived character – presence of posteriorly raised dorsal valve and asymmetry of anterior margin and plication (Fig. 16B, Appendix 2). *K. propinqua*, among all the other taxa constituting this group, retains maximum number of primitive characters, the most notable being its shell outline and beak incurvature in common with the *K. acutiplicata* group and *Lobothyris.*

The Middle Bathonian to Early Callovian *K. propinqua* reaches a maximum length of 51 mm. Plicae develops later in ontogeny after shell attains about 23–25 mm in length and a short and shallow median sulcus is present between the two plicae. In *K. acutiplicata* plication develops earlier, at about 12–14 mm and is sharper than *propinqua* and also a long and deep sulcus is present in between the two plicae.

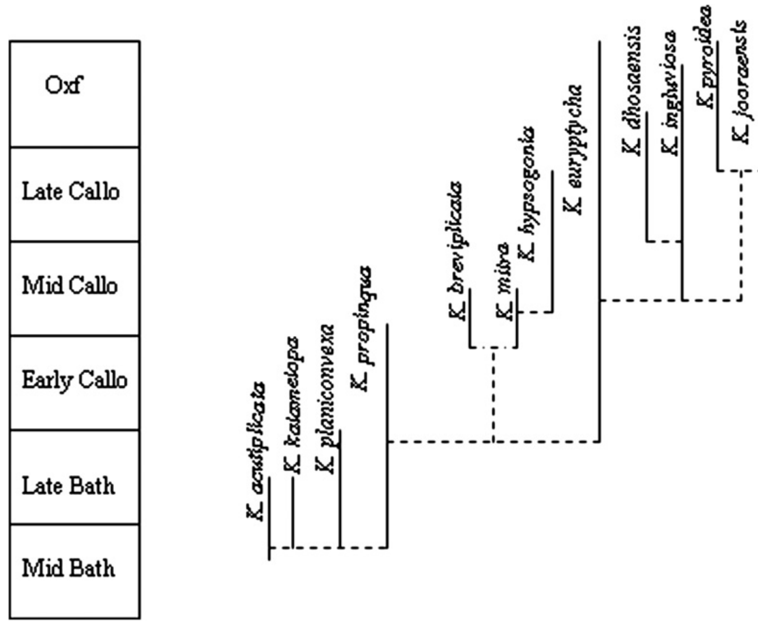

Fig. 17. Evolutionary tree of the genus *Kutchithyris* based on the analysis described in the text. The vertical lines shows the stratigraphic ranges and the dashed lines the phylogenetic relationship based on the cladogram.

The characteristic crowding of growth striae which is a signature of maturity, starts in the early growth stage in *K acutiplicata* whereas it is restricted only to the last part near the anterior margin in *K. propinqua*. Even though *K. propinqua* is larger in size it has a characteristically less developed plication, a less elevated beak with a distinctively smaller foramen and a less developed median ridge in the pedicle valve recalling the early growth stage of *K. acutiplicata*. The larger size of *K. propinqua* with shell characters of early growth stage of *K. acutiplicata* suggests slower growth rate which resulted in delayed onset of sexual maturity. A longer period was spent in the most rapid period of juvenile growth, resulting in a larger final adult size – the heterochronic process being neoteny (also see Mukherjee et al., 2003).

K. euryptycha ranging from Upper Bathonian to the Oxfordian show close resemblance to the juvenile forms of *K. propinqua*, having a nearly elliptical shell outline, broad and flattened dorsal valve and narrow, weakly incurved to erect beak (Mukherjee et al., 2003). Its adult shells are distinguished by the development of characters like maximum shell thickness at the middle, anterior lateral commissure bending close to the anterior margin and well developed linguiform extension of the ventral valve which are also the shared derived characters of the younger Callovian–Oxfordian species, *K. ingluviosa*, *K. dhosaensis*, *K. pyroidea* and *K. jooraensis*, which forms an ingroup. Therefore, *K. euryptycha* appears to be the ancestor to the Middle–Late Callovian *Kutchithyris* species.

The morphologic relationships depicted in the cladogram is evolutionary and not a ecophenotypic phenomenon because the ancestor-descendant pairs constituting the lineages have overlapping stratigraphic ranges and occur in the same beds in the same section, also, some species occur in more than one sediment type (Figs. 2 and 17).

The *Kutchithyris* species longevities are variable but 50% have a longivity of one ammonite zone of which *K. mitra* and *K. katametopa* are restricted to a subzone. Assuming that one ammonite zone lasted on average for 1 m.y. and average Jurassic brachiopod longevity 2 m.y. (Hallam, 1987), 50% of *Kutchithyris* species had shorter durations and the other half lived for more than 2 m.y. among which *K. propinqua* and *K. euryptycha* were long straddlers ranging about 5 m.y. and 11 m.y., respectively. The Kutch record shows that appearances of new species are sudden and restricted within a few zones (Fig. 2).

5.1. Role of heterochrony in Kutchithyris evolution

The *Kutchithyris* species exhibit a number of adult morphological characters which occur at earlier stages of shell development of the oldest species *K. acutiplicata*, indicating that evolution within the genus has proceeded by paedomorphosis. The juvenile forms are characterised by a subcircular to elliptical outline, rectimarginate to slightly uniplicate asymmetrical anterior margin, position of maximum width and thickness at the middle, bending of anterior lateral commissure to ventral side in a broad angle while the intermediate stage is characterized by elliptical to sub-pentagonal outline, weakly biplicate anterior commissure sometimes asymmetrical, position of maximum width and thickness shifted slightly anteriorly from the middle. The adult specimens have a pentagonal outline, strongly biplicate, symmetrical anterior commissure, position of maximum thickness slightly posterior to middle and position of maximum width at one-third length from anterior margin. The synapomorphies of the *propinqua* subclade (characters 8,11 see Fig. 16B) and the *euryptycha* subclade (characters 9,12,15 see Fig. 16B) are the intermediate or juvenile stage characters of *K. acutiplicata*. The morphological changes which occurred in the *Kutchithyris* clade follow the opposite direction to morphological changes which occurred during the ontogeny of *K. acutiplicata*. *K. acutiplicata*, after making its first appearance, in the Bathonian gave rise to *K. propinqua*, *K. katametopa* and *K. planiconvexa* emolying paedomorphic mechanisms. The only Middle Bathonian *Kutchithyris* species surviving into the Callovian, *K. propinqua*, proliferated with time serving as an ancestral stock to several Late Bathonian–Callovian forms. Of these new forms *K. euryptycha* was the most successful species in terms of abundance and longevity. It appeared in the Upper Bathonian and continued to the Oxfordian, a period of 11 m.y. In its long history of survival *K. euryptycha* did not undergo any gradual morphological change even though there is a change in the character of the sediment in which the species occur. The species therefore remained essentially morphologically static and acted as a potential ancestor to the Late Callovian and Oxfordian forms. In fact, paedomorphosis dominate the evolutionary processes within brachiopod phylogeny (Rudwick, 1970; Stehli, 1956; Williams and Wright, 1961). Jin and Chatterton (1996) has envisaged a progenetic origin of the order Terebratulida.

6. Conclusion

The Kutch basin, initiated during the Middle Jurassic fragmentation of Gondwana, was monopolized by many groups right from the Bathonian and the terebratulide *Kutchithyris* was one of them. It appeared in the fossil record in the Middle Bathonian, without any obvious ancestor and speciated to monopolize quickly the space in a newly emerging basin thereby creating an impressive fossil record of 12 species within a span of 13.5 m.yrs. (Middle Bathonian to Oxfordian). Burst of speciation took place in the Upper Bathonian, Mddle Callovian and Late Callovian, which were also the major transgressive phases. The systematic and cladistic analysis shows that *Kutchithyris* evolution was governed by paedomorphosis.

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