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The terebratulid *Kutchithyris* (Brachiopoda) from the Jurassic sequence of Kutch, western India—revisited

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Abstract. The Kutch basin developed due to the fragmentation of Gondwana during the Middle Jurassic and hosted diverse endemic fauna, of which brachiopods are one of the chief constituents. The dominant brachiopod faunal element is the terebratulid genus *Kutchithyris* Buckman. The genus is represented throughout the exposed Middle Bathonian to Oxfordian sequence in Kutch and is also reported sporadically from outside Kutch. The systematics of this small but distinct clade is in a state of flux. The present paper focuses on revising the systematics of the genus and its three dominant species, namely, *K. acutiplicata*, *K. propinqua* and *K. euryptycha*, based on numerous specimens collected from the field with precise stratigraphical and sedimentological background and the type materials. They constitute an evolving lineage, and have been known from the Upper Bathonian rocks of the Pamirs, where they are cited as one of the celebrated examples of rapid speciation. A detailed comparison of the specimens from these two areas reveals that the speciation took place in Kutch and involved cladogenesis. Thus, it provides a good example of the punctuational model of evolution.

Key words: brachiopods, Jurassic, *Kutchithyris*, systematics, western India

Introduction

The Mesozoic sequence of Kutch in western India, known for its fossil treasures, has often been a favourite hunting ground for palaeontologists in the past and present. The Kutch basin emerged as a result of intense tectonic activities associated with the fragmentation of Gondwana during the Bajocian to Bathonian (Biswas, 1991; Singh *et al.*, 1982). This newly opened-up basin provided a virgin area for faunal invasion, thereby prompting speciation events in diverse groups. *Kutchithyris* Buckman, 1918, a terebratulid brachiopod genus represented by *K. acutiplicata* as the type species, made a sudden appearance in the Middle Bathonian of Kutch with no obvious ancestor and is in fact a fleeting fossil (cf. Ager, 1984; Mukherjee *et al.*, 2000). The genus *Kutchithyris* is represented by 12 species in Kutch and spans a time interval of about 13 million years from the Middle Bathonian to Oxfordian (unpublished).

Taxonomic study of *Kutchithyris* of the Kutch sequence has a long history starting with Kitchin (1900) and Buckman (1918). The genus constitutes an important faunal element of the Indo-Madagascan brachiopod assemblage from evolutionary as well as biogeographic standpoints. However, its taxonomy, though having had a tortuous history (see Mitra, 1974, 1978; Mitra and Ghosh, 1973), still remains in a state of flux and needs major revision. In the present study we try to rationalize the systematic position of different species described under *Kutchithyris*. It now becomes clear that the inadequate sample size used in the previous studies precluded a proper understanding of intraspecific variability; further, imprecise stratigraphical and sedimentological data lay behind their classification, involving much subjective splitting. Besides, internal morphological study, a powerful tool for generic discrimination, was not adequately applied (see also Cooper, 1983). We here redefine the genus *Kutchithyris* and provide an emended diagnosis. Three species,

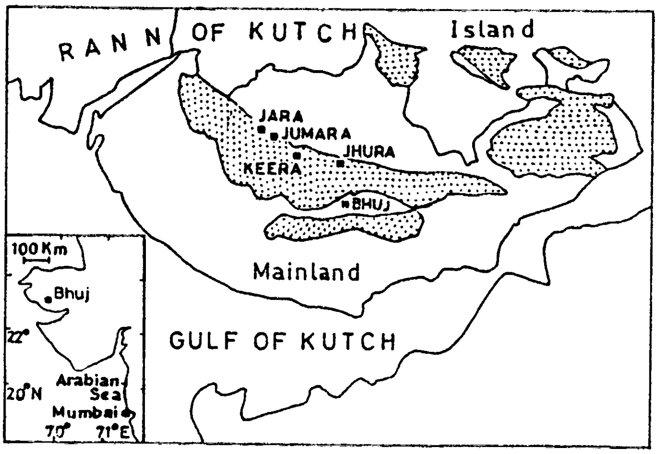

Figure 1. Studied area, geographical localities and distribution of Jurassic rocks (stippled) in Kutch, India.

viz., *K. acutiplicata*, *K. propinqua*, and *K. euryptycha* are redescribed. They are not only dominant elements in the *Kutchithyris* lineage of the study areas and stratigraphically important, but they have also wider biogeographical distribution across different faunal provinces. In the Pamirs, these three species constituting an important evolutionary lineage have been cited as one of the classical examples of rapid evolution (Raup and Stanley, 1985). Naturally, they deserve special attention and are discussed here in detail.

The *Kutchithyris* species have not previously been regarded in the context of facies distribution in Kutch. A detailed facies analysis reveals varying lithological associations of the different species. Their temporal distribution patterns indicate an environmental gradient from carbonate ramp to argillaceous mid-shelf. While the two older species, *K. acutiplicata* and *K. propinqua*, had a strong calcareous facies association, *K. euryptycha* had a heterolithic association.

Geological setting

The Mesozoic sediments of Kutch were deposited during repeated marine transgressions in a pericratonic rift basin developed by the fragmentation of Gondwana (Biswas, 1977, 1991). The rocks, ranging in age from the Bathonian to Aptian are subdivided into four major divisions, namely, the Patcham, Chari, Katrol and Bhuj formations in ascending order (Mitra *et al.*, 1979; Krishna, 1984). The Patcham and Chari formations are the principal brachiopod fossil-bearing units and are of interest in the present study. In the mainland, the Patcham Formation is exposed at Jumara, Keera and Jhura, while the Chari Formation, besides being exposed at these sections, also crops out at the other remaining domes (Figure 1).

A detailed lithological succession of the Patcham and

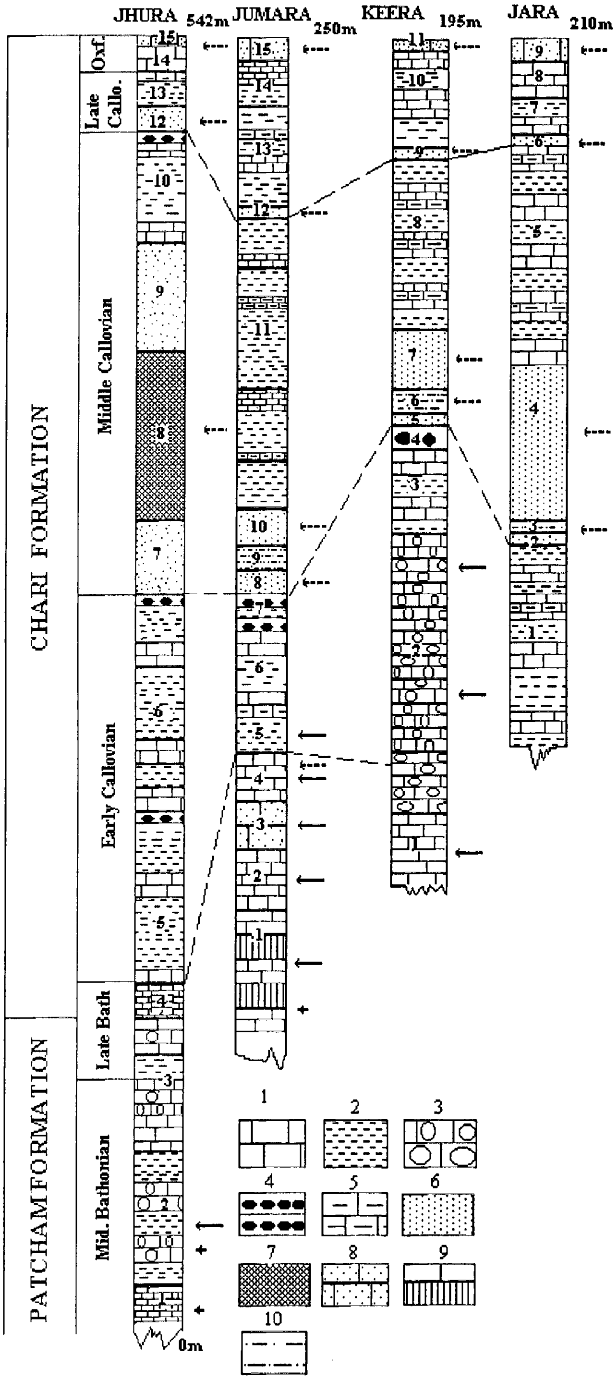

Figure 2. Stratigraphical sections at Jhura, Jumara, Keera and Jara (modified after Bardhan *et al.*, 1994). Numbers inside sections indicate bed numbers. Dotted lines indicate age boundaries. Arrowheads indicate horizons of *Kutchithyris acutiplicata* (Kitchin), solid arrows indicate horizons of *Kutchithyris propinqua* (Kitchin) and broken arrows indicate horizons of *Kutchithyris euryptycha* (Kitchin). Keys: 1, limestone; 2, shale; 3, Golden Oolitic limestone; 4, coquina bed; 5, ironstone; 6, sandstone; 7, calcareous sandstone; 8, oolitic limestone; 9, coral biostrome; 10, siltstone/mudstone.

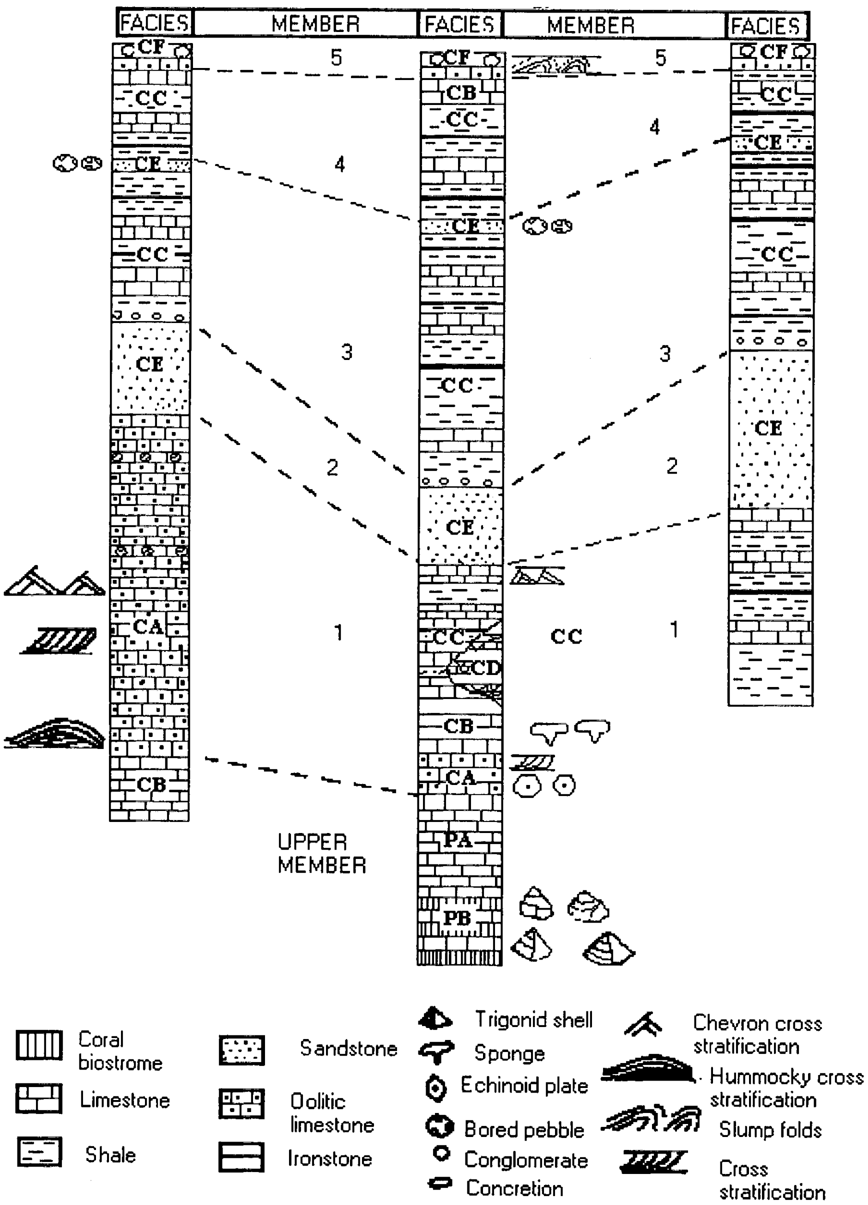

Figure 3. Characteristic facies assemblage within beds comprising different members of Patcham and Chari formations. Numbers indicate members.

Chari formations found in the four major sections is shown in Figure 2 (modified after Bardhan *et al.*, 1994), in which the distribution of the species studied is indicated.

Facies and fauna

A high resolution facies analysis and systematic recording of vertical facies transitions have resulted in building up a comprehensive stratigraphical framework (Figure 3) with requisite details in standard sedimentological terms, which helps in delineating the important events of palaeogeographical shifts in the course of sequence building. It reveals that fluctuating sea levels not only brought about changes in the lithofacies associations but also influenced temporal changes in the faunal compositions, especially in the case of the species of *Kutchithyris*.

Revisionary work at Jhura is still going on and preliminary investigation reveals that all major facies associations are traceable and the major part of the Patcham Formation is exposed here. A brief description of the facies associations and faunal distribution is given below.

Patcham Formation

This formation exposed in Jumara is considered as a single unit (informal Upper Member) in view of its general monotony. However, detailed facies analysis reveals two distinct facies.

Facies PA.—This facies consists of limestone-marl alternation. The limestone is wackestone/floatstone. It is massive and has tabular geometry, and the average thickness is about 9 cm. A parallel-sided bioclastic packstone (1–3 cm thick) is locally intercalated (also see Fürsich and Oschmann, 1993). Their basal contact is sharp, whereas the upper contact is slightly diffused. Bivalve shells within them show a dominantly concave-up attitude. The marl is 15 cm in average thickness, darker in colour than the limestone and is laterally persistent, but with broadly undulated boundaries. This facies is dominated by diverse genera of corals and sponges and also by brachiopods including four species of *Kutchithyris*, *viz.*, *K. acutiplicata*, *K. propinqua*, *K. katametopa* and *K. planiconvexa*.

Facies PB.—This facies (Figure 3) is made up of rudstone layers (average thickness is 6 cm) which are parallel-sided and contain fossils largely preserved intact. Some beds are dominated by corals, others by sponges and brachiopods. Ripped up mud clasts are common. This facies is mainly present in Bed 1 of the lower part of the Patcham Formation at Jumara, alternated with facies PA and is a coralline limestone (Figure 2). It hosts different species of brachiopods, *i.e.*, *Kutchithyris acutiplicata, K. propinqua, K. katametopa, K. planiconvexa.* The next unit, Bed 2 at Jumara, represented solely by facies PA, is marked by the disappearance of *K. acutiplicata* and the continuation of *K. propinqua*. The depositional environment of these two facies has been interpreted as warm, agitated and fully marine and the fauna grew near the fair-weather wave base (Datta, 1992; Fürsich *et al.*, 1994, Mukherjee *et al.*, 2002).

Our preliminary investigation has found *K. acutiplicata* right from Bed 1, the oldest exposed carbonate facies in Jhura, which is a white limestone with shale and grayish-yellow slabby limestone alternations (Figure 2). The next unit, Bed 2, in the lower part of the Patcham Formation at Jhura is massive Golden Oolite and shale alternation (Figure 2). The Golden Oolite is thick and characterized by symmetrical wave-ripples of large wave-length. It sparsely yields specimens of *K. acutiplicata. K. propinqua* suddenly appears in Bed 2 and is represented by a few specimens quite distinct from *K. acutiplicata*.

Chari Formation

The Chari Formation can be divided into five informal members (Figure 3) which are broadly correlatable not only across the mainland; some of them can even be traced up to Patcham island. However, some degree of lateral variation within individual members exists. Detailed description of the members in each section and their formalization will be dealt in a later communication. The lowest member (Member 1) has the interformational demarcation plane at its base. It can be traced in all the four domes. The lower beds consist of oolitic limestone, sometimes overlain by slabby limestone and shale, limestone, ironstone alternation horizon. Its upper boundary lies at the base of a sandstone layer forming the next member. Member 2 consists of a massive ridge forming sandstone layers that can be traced easily in Jumara, Jara, Keera and Jhura. The next member, Member 3, has a shale, limestone, ironstone alternation horizon in its lower part overlain by a sandstone bed which is a marker horizon in all the four domes. The upper boundary is defined by the top of the sandstone bed. Member 4 consists of shale-wackestone alternation sometimes interrupted by ironstone beds. The upper boundary lies at the base of an oolitic limestone unit (Member 5) which has bored limemudstone pebbles at its lower part, indicating an omission surface (Datta, 1992; Fürsich *et al.*, 1992). The oolitic limestone is highly fossiliferous and a marker horizon in all the four domes. The upper boundary of Member 5 is defined by the Katrol Formation.

The facies changes are very rapid vertically as well as laterally. The faunal characters, especially the brachiopod associations, vary markedly with the facies changes. Brachiopods, particularly terebratulids including *Kutchithyris*, are generally rare in argillaceous facies, but they are ubiquitous in calcareous and arenaceous sandstone and more so in fine-grained varieties where clusters of *K. breviplicata* have been found. The lithocharacters of the six facies (CA to CF) are summarized below (modified after Datta, 1992).

Facies CA.—This facies is multistoreyed cross-stratified (both chevron and hummocky) bioclastic limestone (packstone/grainstone) with local presence of ooids. There are at least three levels where bored pebbles (wackestone) are sporadically strewn. At Jumara and Keera the facies has an erosive contact with the underlying marly limestone of the Patcham Formation. *K. propinqua* is found in this facies and appears abundantly in Bed 2 of the lower levels of the formation at Keera (Figures 2, 3). The facies can be divided into two distinct subfacies on the basis of abundance of the ooids. Brachiopods are prolific in the ooid-poor part and considerably decrease in number in the ooid-rich part. This facies is also a product of a high-energy milieu, the deposition taking place within the wave zone and it possibly acted as a barrier bar (Biswas, 1981; Datta, 1992).

Facies CB. — This facies is a white limestone (wackestone) with a few corals and diverse sponges preserved in live attitudes (Figure 3). The environment has been interpreted as a sponge meadow in shallow water, but below the wave base. The facies is found in Bed 4 exposed in Jumara and in Bed 4 at Jhura (Figure 2). In Jumara the first appearance of CB is also marked by the first appearance of *K. euryptycha*. It also hosts other brachiopod species, especially *K. propinqua*.

Facies CC.—This facies is marked by repeated alternation of shale, white limestone (wackestone) and reddish or brownish limestone (packstone/grainstone) and also occurs more than once in the stratigraphical sequence (Figure 3). Chevron cross-stratification is occasionally present in the grainstone but the packstone and wackestone are relatively massive. The facies, representing a shoaling up parasequence, was possibly deposited in a restricted lagoon near the wave base and is well developed in all the four sections (e.g., Bed 5 at Jumara, Bed 5 at Jhura, Bed 8 at Keera, Bed 1 at Jara; Figure 2). Brachiopods, especially terebratulids, are rare and mostly broken.

Facies CD.—This facies is represented by lenticular beds of thick shale interbedded with thin, parallel-sided, dark brown, ferruginous limestone. This facies is present only in Bed 6 at Jumara (Figure 2) amidst the shale-limestone alternation background. It was formed possibly due to ponding within a swale. Terebratulids are almost absent.

Facies CE.—This facies is yellowish-grey sandstone present in all the four sections (Figure 3), and occurs more than once in the stratigraphical sequence and increases in thickness towards the landward side, *i.e.*, towards Jhura (e.g., Beds 7, 9 at Jhura, Beds 8, 10 at Jumara, Beds 5, 7 at Keera, Beds 2, 4 at Jara; Figure 2). It is commonly multistoreyed, massive with an upward-coarsening sequence and devoid of bioturbation, and it also contains large-scale cross-beds. The sandstone represents a shoaling-upward phase, followed by renewed deposition of fine-grained siliciclastics (Fürsich and Oschmann, 1993). Terebratulids present include *K. euryptycha* and are very common. The sandstone facies is repeated as reworked concretions and bored pebbles (protected shelf of Fürsich and Oschmann, 1993) in the late Callovian (Bed 12 at Jumara, Bed 12 at Keera, Bed 9 at Keera; Figure 2) and thus points to fluctuating sea-level and nonsequence with erosive phases (Fürsich *et al.*, 1992).

Facies CF.—This facies is present throughout the mainland of Kutch with its characteristic lithological and faunal associations and found in Bed 15 at Jhura, Bed 15 at Jumara, Bed 11 at Keera and Bed 9 at Jara. It is a heterolithic facies represented by repeated alternation of oolitic limestone and gray shale. The top is characterised by a distinct conglomeratic sub-facies. At its basal part, bored limestone pebbles are found in various concentrations. Small-scale synsedimentary deformation structures like fault and slump folds are fairly common within the conglomeratic sub-facies (Figure 3). Deposition of this facies took place in a deeper offshore setting but during high energy episodes such as storms, induced by a major transgressive event (Singh, 1989; Fürsich *et al.*, 1992). Numerous species of terebratulids including *K. euryptycha* are found in it.

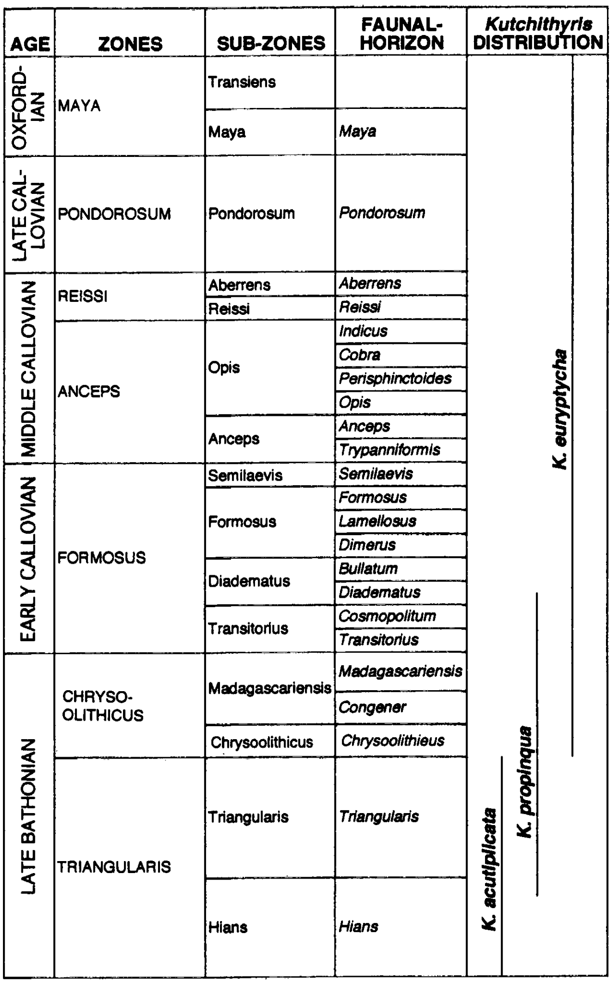

Figure 4. Range chart of *Kutchithyris acutiplicata* (Kitchin), *Kutchithyris propinqua* (Kitchin) and *Kutchithyris euryptycha* (Kitchin) as documented in Western Kutch. Zones and subzones are modified from Datta (1992) and Bardhan *et al.* (2001).

Stratigraphical distribution of the three *Kutchithyris* species is shown on the standard chronostratigraphical zonation based on endemic ammonite species (Figure 4).

From the above discussion, it is revealed that the depositional milieus of the Patcham and Chari formations are different although both are the products of initial carbonate platform deposition. The transition from the storm-dominated shallow environment of the Patcham Formation to the overlying low-energy mid-shelf environment of the Chari Formation also reflects the compositional change of

Table 1. Ontogenetical growth patterns of three *Kutchithyris* species.

Reduced major axis	Correlation coefficient	Growth pattern
Kutchithyris acutiplicata		
logW = 1.14logL + .8045	r = 0.64	positive allometry
logT = 1.45logL + .3624	r = 0.49	positive allometry
logCL = 1.37logL + 1.0904	r = 0.80	positive allometry
logF = 1.92logL + .048	r = 0.27	positive allometry
logPMW = 1.68logL + .3221	r = 0.48	positive allometry
logPMT = 1.77logL + .2046	r = 0.38	positive allometry
logPLD = 1.96logL + .2793	r = 0.67	positive allometry
Kutchithyris propinqua		
logW = .99logL + .8621	r = 0.78	negative allometry
logT = .99logL + .566	r = 0.73	negative allometry
logCL=1.59log L + .6728	r = 0.62	positive allometry
logF =1.77log L + .037	r = 0.23	positive allometry
logPMW = 1.16logL + .505	r = 0.81	positive allometry
logPMT = 1.35logL + .3	r = 0.55	positive allometry
logPLW = 1.12logL + .547	r = 0.71	positive allometry
logPLD = 1.31logL + .552	r = 0.08	no correlation
Kutchithyris euryptycha		
logW = 1.01logL + .8157	r = 0.79	positive allometry
logT = 1.23logL + .4425	r = 0.82	positive allometry
logCL = 1.209logL + 1.2684	r = 0.85	positive allometry
logF = 2.34logL + .0407	r = 0.48	positive allometry
logPMW = 1.14logL + .5631	r = 059	positive allometry
logPMT = 1.28logL + .3682	r = 0.47	positive allometry
logPLW = 1.12logL + .6	r = 0.60	positive allometry
logPLD = .96logL + .8479	r = 0.80	negative allometry

the *Kutchithyris* community. The two older species *K. acutiplicata* and *K. propinqua* became extinct stepwise in "palaeontological relay fashion" as the basin became progressively shallower during the Patcham time. *K. propinqua* appeared immediately before the Bathonian-Callovian transition which marks a global sea-transgression (Haq *et al.*, 1987) and this is also evident in the regional scenario. Fürsich and Oschmann (1993) showed that three orders of sea-level changes indicate gradual deepening, punctuated occasionally by shallowing trends within the Patcham-Chari Formations. *K. euryptycha* occurs only in the Chari Formation and is poorly represented or totally absent in the facies, indicating a deeper bathymetry (Facies CC), while it is abundant in Facies CE and CF, which are the products of a shallower environment. *Kutchithyris* finally disappears from Kutch during the Oxfordian-Kimmeridgian transition that heralded a sharp rise in global sea level (Datta, 1992; Haq *et al.*, 1987; Fürsich and Oschmann, 1993).

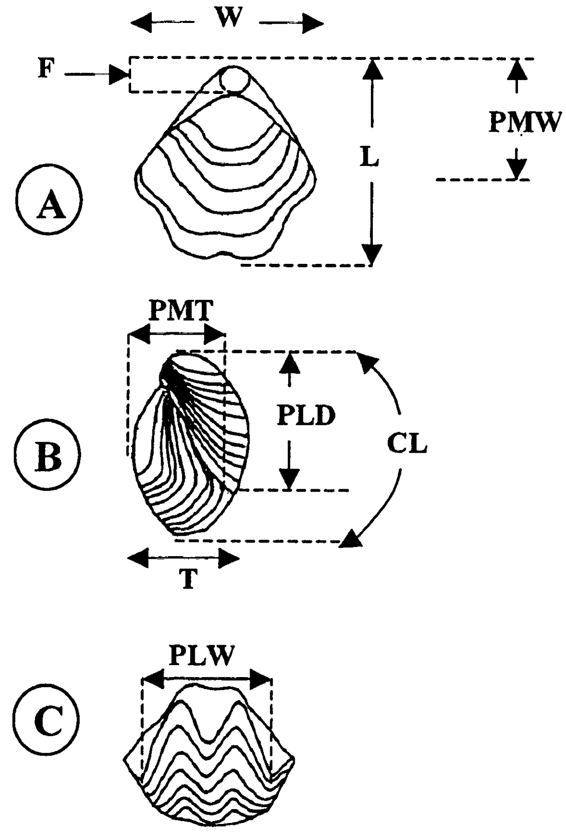

Figure 5. Major morphological characters for measurements used in statistical analyses. **A.** Dorsal view. **B.** Side view. **C.** Commissural view. Keys: L, distance from anterior to posterior; W, total width of shell; PMW, position of maximum width from posterior margin; F, foramen diameter; PMT, position of maximum thickness; PLD, distance of origination of plica from posterior margin; T, thickness of valves; CL, curved length along pedicle valve; PLW, width of plica.

Systematic palaeontology

The major morphological characters considered here for bivariate analyses (Table 1) are shown in Figure 5. The dimensions however are not provided since specimens are plentiful. They will be available upon request.

Superfamily Terebratuloidea Gray, 1840
Family Terebratulidae Gray, 1840
Genus ***Kutchithyris*** Buckman, 1918

Type species.—Kutchithyris acutiplicata (Kitchin, 1900).

Generic diagnosis.—Small to large, unequally biconvex valves. Anterior commissure highly variable both ontogenetically and interspecifically, rectimarginate, uniplicate to sulciplicate. Adult lateral commissure simple, straight, with a ventral convexity anteriorly. Umbo short, incurved, permesothyrid. Foramen small to large, oval to circular. Radial capillation present on shell surface. Loop long, almost half of dorsal valve length. Crural process posterior to midloop and long terminal points. Transverse band narrow.

Discussion.—Kitchin (1900) described altogether 20 species of terebratulids from Kutch and placed all under the comprehensive genus *Terebratula.* Later, Buckman (1918) assigned Kitchin's species to *Kutchithyris*, which comprised 10 species. Of these, six were reported from Kutch and the remaining four from England (see Buckman, 1918). Buckman's description of *Kutchithyris* was based mainly on the external shell characters. Mitra and Ghosh (1973) emended the generic diagnosis of *Kutchithyris* by including the internal characters of the shell. Ovcharenko (1969) reported *K. acutiplicata* and *K. euryptycha* from the Upper Bathonian deposits of the southeast Pamirs. He also showed the internal structure of the two species.

Middlemiss (1980) placed some species from the Lower Cretaceous of Morocco in *Kutchithyris*, but Cooper (1983) correctly showed that the external morphology of the Moroccan species differs considerably from that of *Kutchithyris*, the Moroccan species being spherical.

Cooper (1989) described two doubtful species of *Kutchithyris* ranging from the Upper Bathonian (Middle Dhruma Formation) to Middle Callovian (Tuwaiq Mountain Formation) of Saudi Arabia. The measurements of shell parameters show that they have much larger thicknesses compared to the Kutch species and hence do not belong to *Kutchithyris* (unpublished data).

Kutchithyris acutiplicata (Kitchin, 1900)

Figures 6, 7

Terebratula acutiplicata Kitchin,1900, p. 6–9, pl. 1, fig. 1–7.
Kutchithyris acutiplicata (Kitchin). Buckman, 1918, p. 113, pl. 20, fig. 17; Ovcharenko, 1969, figs. 1–3; Mitra and Ghosh, 1973, p. 185, fig. 3, 4K-R; Cooper, 1983, p. 96, pl. 63, fig. 3.
Terebratula (*Kutchithyris*) cf. *acutiplicata* (Kitchin). Trechman, 1923, p. 284, pl. 16, figs. 5–7.
Kutchithyris cf. *acutiplicata* (Kitchin). Allan, 1945, p. 1–22.
Kutchithyris hendersoni Marwick, 1953, p. 85, pl. 15, figs. 13, 14.

Types.—Kitchin (1900) selected a series of specimens to describe *Terebratula acutiplicata.* We here designate G. S. I. Type No. 6601 (Kitchin, 1900, fig. 1) as the lectotype (Figure 6.7a–d) and Nos. 6596–6600, 6602–6603 and 15588 as paralectotypes (Figure 6.8–6.10). The types are kept at the Repository of the Geological Survey of India, Kolkata.

Material.—223 specimens including the types. Ju 1a/1–208 from Bed 1, Jumara, Jh a/1–2 from Bed 1 and Jh 2 a/1–4 from Bed 2, Jhura. They are kept at the Jadavpur University Museum. G. S. I. Type nos. 6596–6603, 15588 from Upper Patcham Beds (Bed 1of Jumara in this paper).

Description.—Shell outline changes through growth, oval in juvenile stage (L > 15 mm), subpentagonal in middle stage (L = ca. 20 mm), pentagonal in adult stage (L = ca. 30 mm). Shell shape as seen in lateral profile also changes from lenticular to subglobose through growth and becomes more convex during shell growth. Maximum width lies at about 1/3 length from anterior margin and greatest thickness at about mid-length. Generally, convexity of brachial valve lies posteriorly (Figure 6.1b, 6.3b), but broader and flattened variants are less convex and narrower and globose forms strongly inflated (Figure 6.10b). In extreme variants, pedicle valve relatively more convex (Figure 6.9b). Anterior commissure strongly biplicate with two sharp and strong plicae at about mid-length. Distance of plica from posterior margin (PLDI) shifts allometrically (Table 1). Crest of plica rounded in younger stage but becomes angular in adults. In adult shell, ventral valve develops a sharply raised median ridge that starts about 2/3 length from posterior end, which is also end of early oval stage, flanked on both sides by two lateral elevations, separated from central ridge by a lateral depression. Central ridge with a flattened crest, gradually widens anteriorly; lateral ridges less elevated than central one.

Hinge line gently to strongly curved. Commissure simple until it reaches a point about 2/3 length from posterior end where it sharply turns to ventral side almost at a right angle. It forms two well-marked plicae with characteristic M-shape.

Beak with a broad base, incurved; lateral ridge absent. Foramen large, permesothyrid, circular to oval in outline and inclined. Foramen often bordered by a rim (Figure 6.1a, 6.4a). Cardinal margin terebratulid, but some specimens show submegathyrid cardinal margin in younger stage.

Shell occasionally shows distinct traces of weak and fine radial 'striping' usually in anterior part. Growth lines strongly approximated near anterior commissure.

Pedicle collar present; cardinal process simple, teeth mallet-shaped, inserted in socket, denticula very weakly developed. Hinge plates concave, crural bases recurved from hinge plates, loop 14.1 mm long and almost half length of dorsal valve, crural process posterior to mid loop, transverse band narrow arch, terminal points moderately long .

Discussion.—Upper Bathonian deposits of the southeastern Pamirs contain *K. acutiplicata* (Ovcharenko, 1969). The specimens from the Pamirs have a broad, biplicate shell and a well-developed furrow on the brachial valve. We concur with Ovcharenko's identification because the

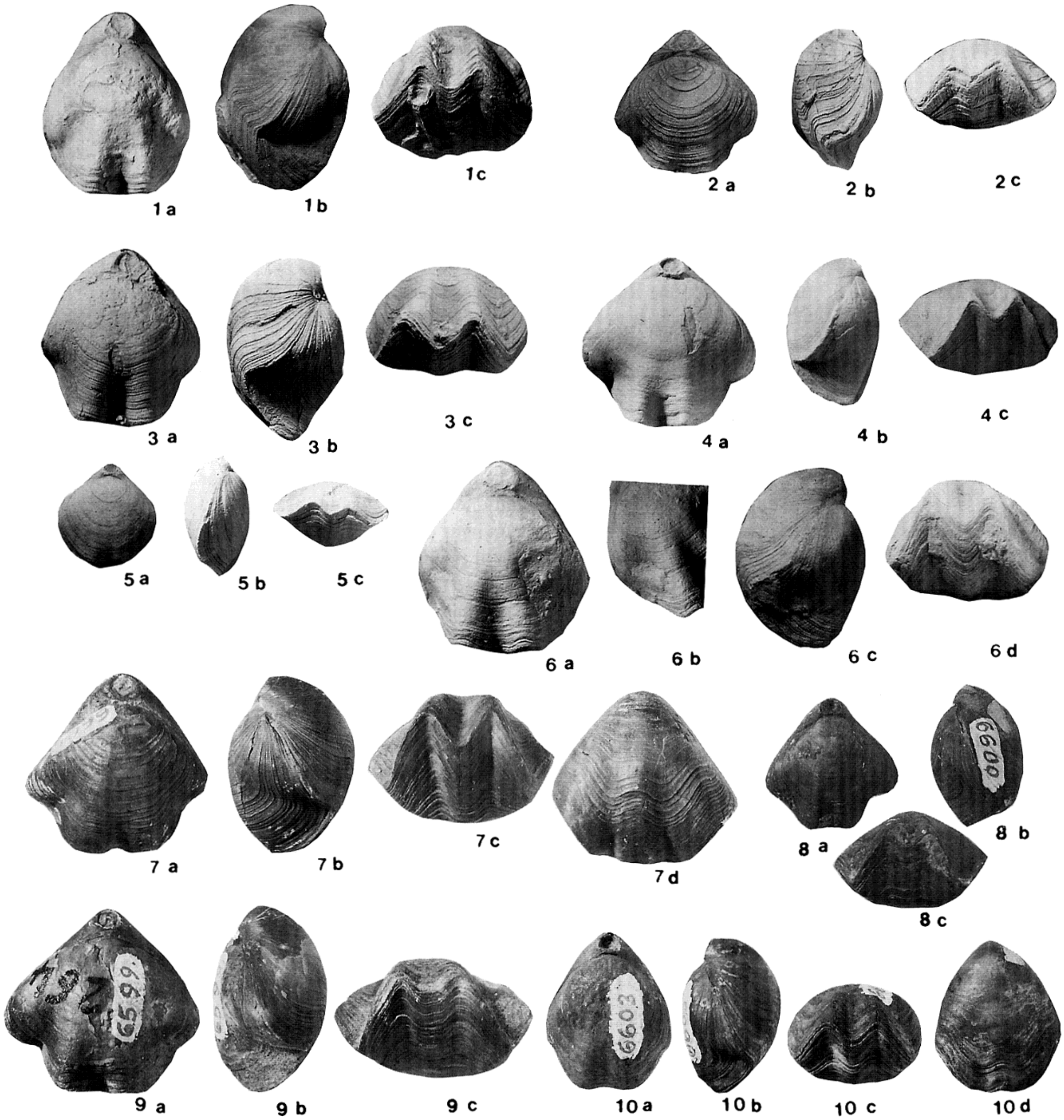

Figure 6. *Kutchithyris acutiplicata* (Kitchin) from Patcham Formation of Jumara. All ×1. **1a–c**. B/Jul/7 dorsal, side and anterior view. **2a–c**. B/Jul/3, dorsal, side and anterior views. Note radial stripes in anterior portion (a). **3a–c**. B/Ju1/114, dorsal, side and anterior views. **4a–c**. B/Ju1/170, dorsal, side and anterior views. **5a–c**. B/Jul/172, dorsal, side and anterior views of a young individual. Note gentle curve of lateral commissure and rounded plica. **6a–c**. B/Jul/73 dorsal, side and anterior views. Magnified view of left dorsal valve showing radial striations (d). **7a–d**. Lectotype, G.S.I. Type No. 6601, from "Upper Patcham Beds" (Bed 1, Jumara, Figure 2), dorsal, side, anterior and ventral views. **8a–c**. G.S.I. Type No. 6600, dorsal, side and anterior views. **9a–c**. G.S.I. Type No. 6599, dorsal, side and anterior views. **10a–d**. G.S.I. Type No. 6603, dorsal, side, anterior and ventral views.

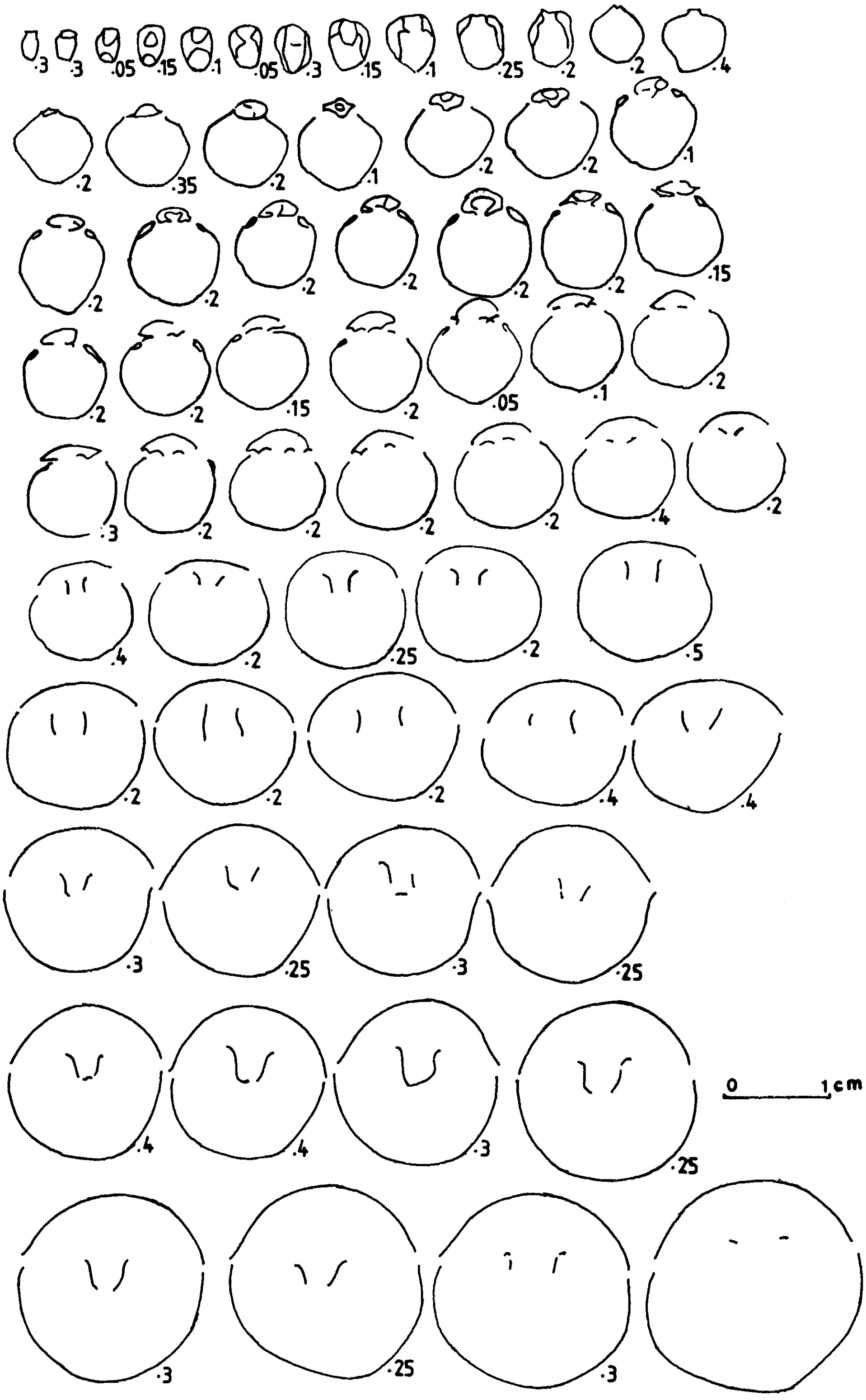

Figure 7. Serial transverse sections of *Kutchithyris acutiplicata* (Kitchin). Numbers indicate grinding increments in mm.

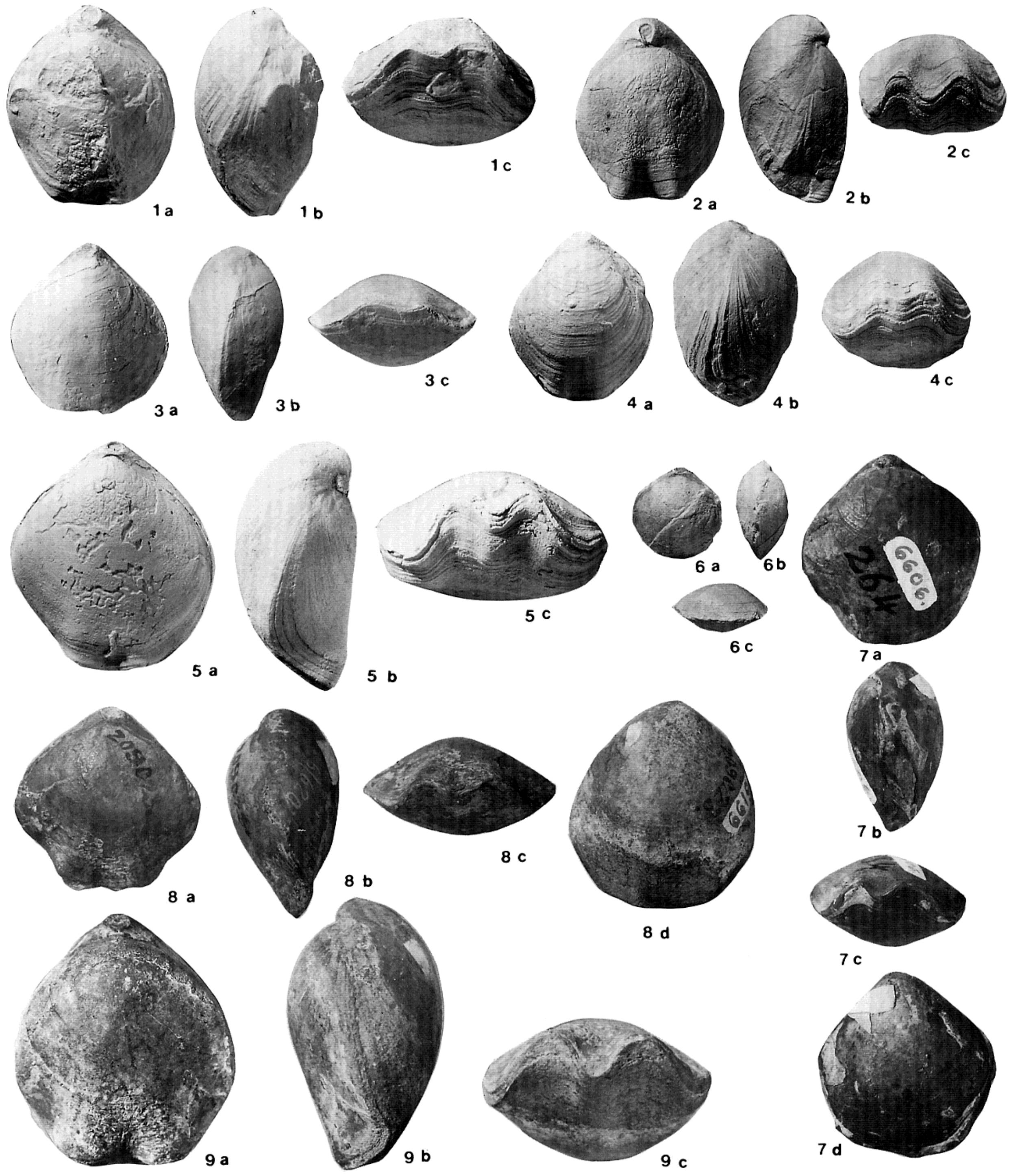

Figure 8. *Kutchithyris propinqua* (Kitchin) from Patcham and Chari formations of Kutch. All ×1. **1a–c**. B/Ju4/34, from Bed 4, Jumara, dorsal side and anterior views, respectively. **2a–c**. B/Ju2/29, from Bed 2 Jumara, dorsal side and anterior views. **3a–c**. B/Ju4/8, from Bed 4 Jumara, dorsal, side and anterior views. **4a–c**. B/Ju4/2, from Bed 4 Jumara, dorsal, side and anterior views. **5a–c**. B/Ju4/49, from Bed 4, dorsal, side and anterior views of a large individual. **6a–c**. B/Ju4/37, from Bed 4 Jumara, dorsal side and anterior views of a young individual. Note rounded anterior commissure and absence of ridge at 1.68 cm of length. **7a–d**. G.S.I. Type No. 6606 from "lower beds of Chari Group", Keera (Bed 2, Keera, Figure 3) dorsal, side anterior and ventral views, respectively. **8a–d**. G.S.I. Type No. 6620, lectotype, from "Upper Putchum Beds" of Jumara (Bed 1), dorsal, side, anterior and ventral views. **9a–c**. G.S.I. Type No. 6619, from "lower beds of Charee Group", Keera, (Bed 2, Keera, Figure 3), dorsal, side and anterior views.

Pamir specimens are difficult to distinguish from those of *K. acutiplicata* from Bed 1 in Jumara.

Trechman (1923) described a few specimens from the Upper Bathonian of Totara, Kawhia, New Zealand and identified them as *Tereburatula* (*Kutchithyris*) cf. *acutiplicata.* The shell dimensions and other valve characters of the New Zealand specimens are similar to those of *K. acutiplicata* from Kutch. Trechman (1923) also mentioned that most of his specimens bears resemblance to those figured by Kitchin (1900). In our view the New Zealand specimens are to be *K. acutiplicata.*

Marwick (1953) described *Kutchithyris hendersoni* from the Upper Temaikan Stage of the Kawahia Series in Totara Peninsula, New Zealand. He distinguished his species from *K. acutiplicata* by the uniformly less inflated shells and with strong anterior folding. In spite of the distortion, the shell shape and the characteristics of beak and plication are similar to those of *K. acutiplicata.* (Marwick, 1953, pl. 15, figs. 13, 14). We consider that *K. hendersoni* also to be identical to *K. acutiplicata.*

Sahni and Bhatnagar (1958) described *Kutchithyris jaisalmerensis* from an unspecified horizon in the Callovian sequence of Jaisalmir, western India. It resembles *K. acutiplicata* in the characters of beak and anterior plication. According to Sahni and Bhatnagar (1958), *K. jaisalmerensis* has dorsal muscle impressions similar to those of the genus *Selerithyris* and the anterior plication ranges from rectimarginate, uniplicate to strongly biplicate during ontogeny. However, our inspection of the type specimens revealed that *K. jaisalmerensis* has neither the rectimarginate nor uniplicate stage in the anterior commissure, and the uniplicate stage also does not appear in the specimens of *K. acutiplicata* from Kutch. The most remarkable difference between the two species, however, lies in the development of multiple narrow folds that produce fimbriation. This feature in *K. jaisalmerensis* is reminiscent of another coeval Kutch species, *K. katametopa* (Kitchin 1900).

Occurrence.—Kitchin (1900) worked on the material collected by others in the Geological Survey of India, and did not specify the horizons from where the fossils were collected. He merely described the fossils as coming from "Upper Putchum Beds" of his "Putchum Group". However, the state of preservation and the nature of the enclosing matrix definitely indicate that they came from Bed 1 of the Patcham Formation exposed in Jumara. Beside Bed 1 in Jumara this species occurs in Bed 1 and Bed 2 in Jhura.

Kutchithyris propinqua (Kitchin, 1900)

Figures 8, 9

Terebratula propinqua Kitchin, 1900, p. 10, pl. 2, figs. 2–4
Terebratula aurata Kitchin, 1900, p.18, pl. 14, figs. 1-4.
Terebratula cf. *acutiplicata* Kitchin, 1900, p. 9, pl. 2, fig. 1.
Terebratula sp. indet. Kitchin, 1900, p. 16, pl. 3, figs. 1, 2.
Terebratula cf. *aurata* Kitchin,1900, p. 21, pl. 4, figs. 5, 6.
Kutchithyris propinqua (Kitchin). Buckman, 1918, p.113, pl. 19, fig. 18.
Kutchithyris aurata (Kitchin). Buckman, 1918, p.113, pl. 19, fig. 19.

Types.—Kitchin (1900) used a series of specimens to describe *Terebratula propinqua* and *Terebratula aurata.* We here designate G. S. I. Type No. 6620 (Figure 8.8a–d) as the lectotype of *K. propinqua* and Nos. 6605–6606, 6619, 6621–6624 as paralectotypes (Figure 8.7, 8.9).

Material.—118 specimens. Ju1 p/1–9, Ju2 p/1–23, Ju4 p/1–54 were collected from Beds 1, 2 and 4 in Jumara; K2p/1-19 from the uppermost Golden Oolite (Bed 2 in Figure 3a), Keera; Jh 2 p/1–3, Jh 3 p/1 from Beds 2 and 3 at Jhura. G. S. I. Type numbers 6605–6606 from "Upper Putchum beds" in Jumara, (= Beds 1–4 in Figure 2b), 6619–6624, 15587 from Golden Oolite limestone, "lower beds of Charee Group" (= Bed 2 in Figure 3a), Keera and are kept at the Repository of the Geological Survey of India, Kolkata.

Description.—Shell large (maximum length 51 mm), highly variable in form from rounded pentagonal to subpentagonal or subcircular both ontogenetically and individually. Length always greater than width and thickness, maximum width lies at middle, position of maximum thickness lies at one-third length from posterior end. Shell biconvex, pedicle valve more convex, curvature (CL) increases allometrically with growth (log CL = 1.59 log L + 0.6728). Dorsal valve with two weak, blunt, broadly rounded plicae, starting at about one-third length from anterior margin, with plicae highly variable in width and height. Plicae develop later in ontogeny after shell attains ca. 23 mm in length and widens with growth (Table 1). A short and shallow median sulcus present between two plicae. Ventral valve more convex than dorsal and in some specimens (Figure 8.7d) tends to form a posterior median carination, which becomes flatter and narrower anteriorly forming a median ridge; median ridge inconspicuous or scarce in some variants.

Lateral commissure forms a wide curve towards ventral valve, and anterior commissure biplicate with low and rounded plicae. Beak weakly developed, slightly incurved. Foramen circular, medium in size, inclined. Lateral ridges present in some variants (Figure 8.9a).

Surface devoid of any ornamentation except growth striae, represented by series of constrictions in anterior end of adult specimens; in some specimens radial striping similar to *K. acutiplicata* present near anterior end (Figure 8.3a).

Young specimens, according to Kitchin (1900), almost

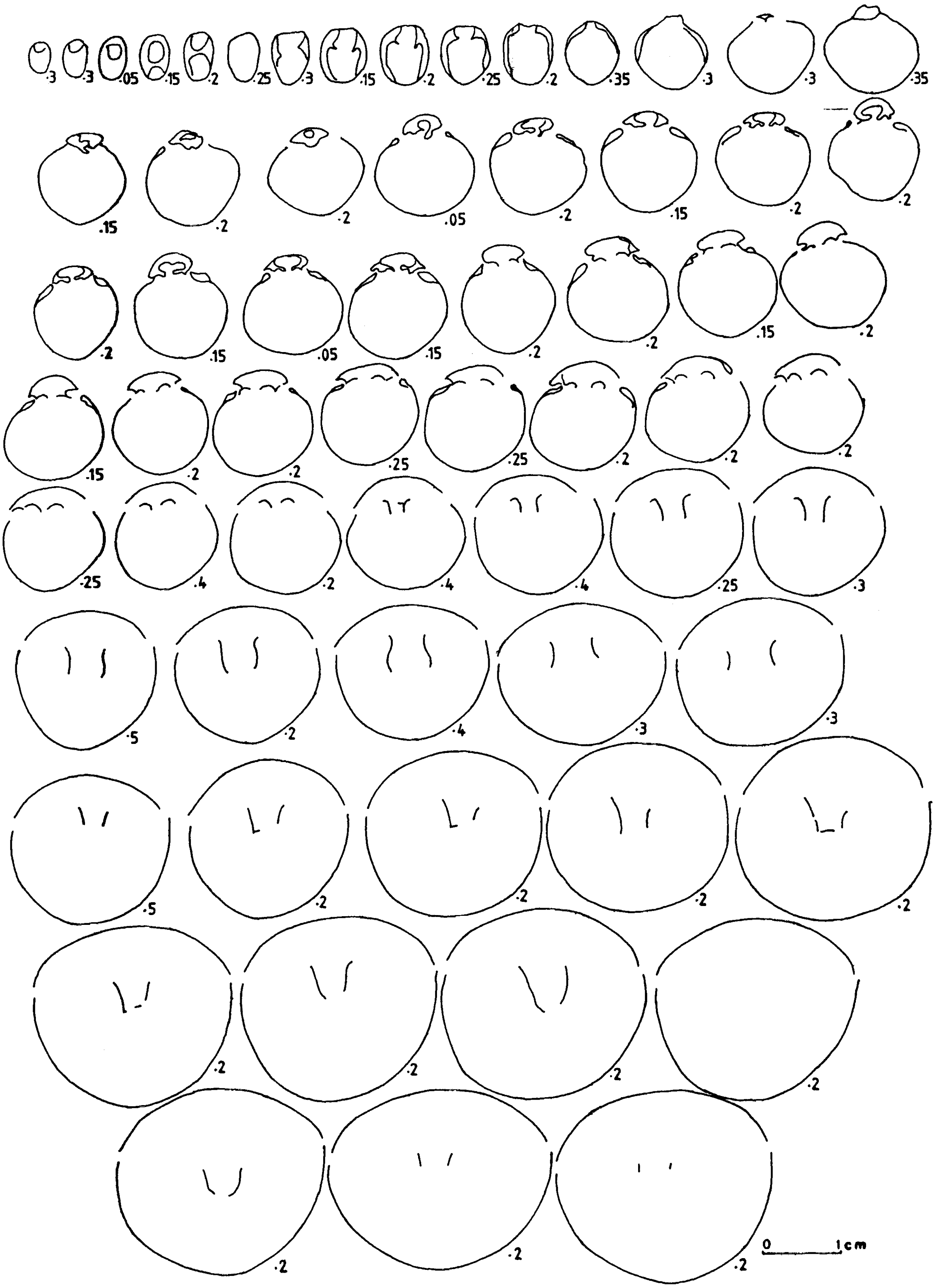

Figure 9. Serial transverse sections of *Kutchithyris propinqua* (Kitchin). Numbers indicate grinding increments in mm.

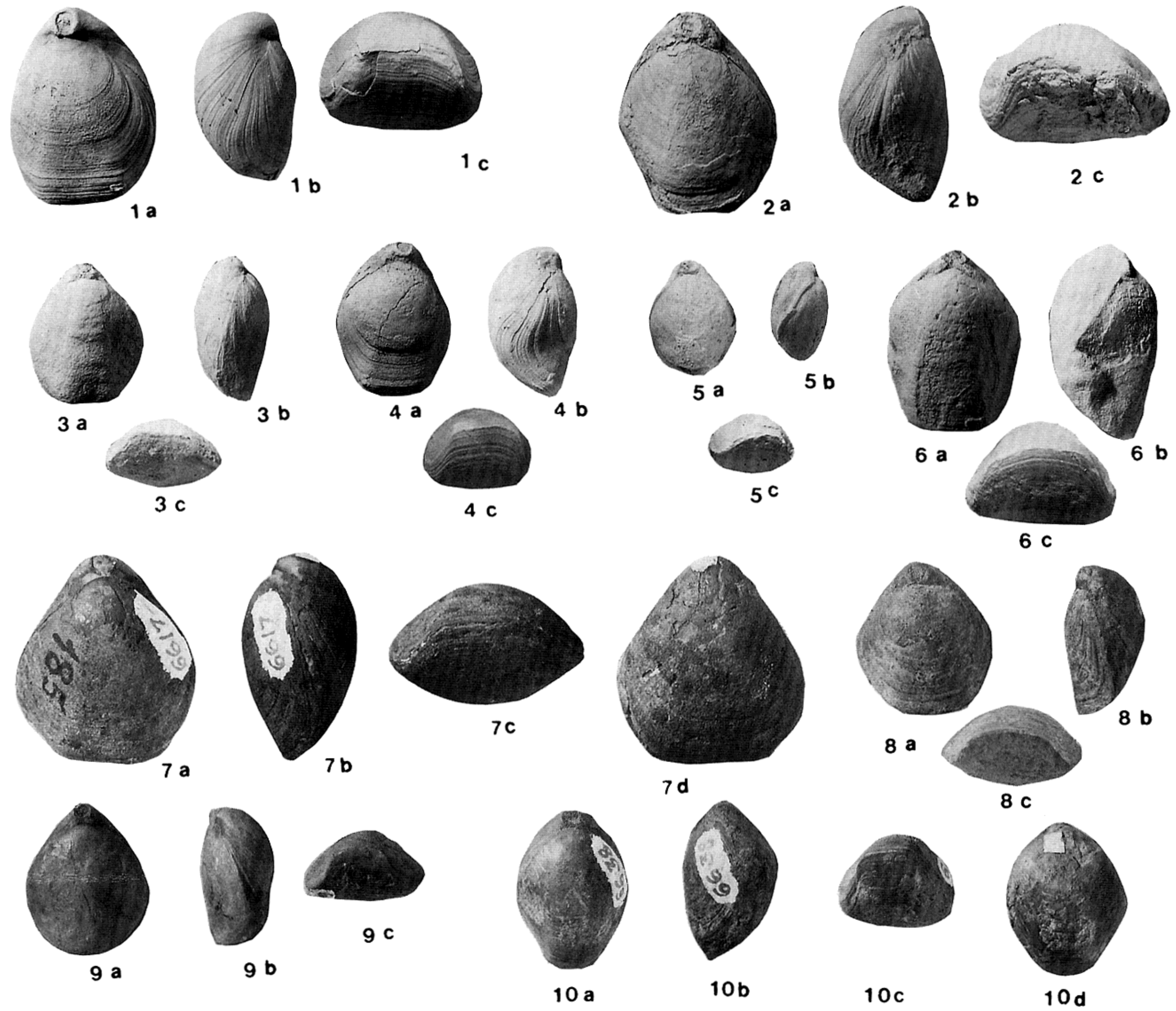

Figure 10. *Kutchithyris euryptycha* (Kitchin) from Chari Formation of Kutch. All ×1. **1a–c**. B/Ju4/25, from Bed 4 Jumara, dorsal, side and anterior views, mark radial stripes (b). **2a–c**. B/Ja6/18, from Bed 6, Jara, dorsal, side and anterior views. **3a–c**. B/Ja6/6, from Bed 6 Jara, dorsal, side and anterior views. **4a–c**. B/Ja4/37, from Bed 4 Jara, dorsal, side and anterior views. **5a–c**. B/Jh9/4,from Bed 4 Jhura, dorsal, side and anterior views, note development of uniplicate commissure at L = 1.6 cm. **6a–c**. B/Jh15/20, from Bed 15, Jhura, dorsal side and anterior views. **7a–d**. G.S.I. Type No. 6617, dorsal, side, anterior and ventral views. **8a–c**. G.S.I. Type No. 6635, dorsal side and anterior views. **9a-c**. G.S.I. Type No. 6634, dorsal, side and anterior views. **10a–d**. G.S.I. Type No. 6658, dorsal, side, anterior and ventral views.

circular in outline with equal length and width. Maximum width lies at middle, which shifts towards anterior margin during later ontogeny. Shell margins very sharp with a narrow beak. Ventral valve with a low posterior carina in some variants, which dies out anteriorly. Biplication of anterior commissure appears between 18 and 23 mm length from posterior end.

Pedicle collar present, and deltidial plates broad and shallow. Cardinal process low, and hinge plates slender or bladelike in shape and dorsally inclined. Loop 14.55 mm long, about half of brachial valve length. Crural process posterior of mid-loop. Transverse band slightly broader than that in *K. acutiplicata*.

Discussion.—The present species shows strong allometric growth in many respects during ontogeny. The shell outline varies from circular to subpentagonal, the beak is narrower in the early growth stage, and the position of maximum thickness migrates from the middle to the anterior. The anterior commissure is rectimarginate in the juvenile while weaker and shorter plications are present in the adult.

The adult specimens of *K. propinqua* are similar to those of *K. acutiplicata* at the intermediate stage (see Figures 6.5a–c, 8.1a–c). The plica widens in a positively allometric manner both in *K. propinqua* and *K. acutiplicata* (Table 1). The central ridge on the pedicle valve is less strongly developed in *K. propinqua* than in *K. acutiplicata* and appears only in the later growth stage of the former species (see Figures 6.2c, 6.7d and 8.5c). Also, the shell outline is subpentagonal and the shell curvature is relatively low in *K. propinqua*, therefore approximating those features of the immature specimens of *K. acutiplicata* (see Figures 6.5a, 8.5a). Additionally, the beak rises from the broad base, is less elevated and has a distinctively smaller foramen in *K. propinqua*, recalling the early ontogeny of *K. acutiplicata* (see Figures 6.5a–b, 8.3a–b). Finally, the characteristic crowding of growth striae starts in the early growth stage in *K. acutiplicata,* whereas it is narrowly restricted only to the last third of the length from the anterior end in *K. propinqua* (see Figures 6.2, 6.5, 8.2 and 8.5). These imply that *K. propinqua* is a paedomorphic offshoot of *K. acutiplicata*, possibly through neoteny. However, the adult specimens of *K.propinqua* differ from *K. acutiplicata* in their larger size, weaker and shorter plication, lateral commissure with a broad curvature, and less shell curvature.

Terebratula aurata Kitchin (1900) from the Golden Oolite of Keera exhibits ontogenetical shell transformation and has shell features which are the same as *K. propinqua.* Kitchin (1900) mentioned that these two forms were closely related. Detailed morphometrical analyses based on a large number of specimens as well as the type specimens reveal that these two species are difficult to distinguish. Moreover, our systematic sampling in Kutch also shows that the two species occur in the same stratigraphical interval and *T. aurata* does not occur in beds younger than those bearing *K. propinqua*, as stated by Kitchin. Many specimens from the Golden Oolite of Keera, the type strata of *T. aurata*, are identical to those found in Bed 4 of Jumara. Thus we conclude that *T. aurata* is a junior synonym of *K. propinqua*.

Kitchin (1900) found several specimens different from *T. acutiplicata* and tentatively identified them as *Terebratula* cf. *acutiplicata.* They are characterized by a more rounded and less angular fold and broad and shallow dorsal lateral depression with rounded troughs. Thus, these shell characters evidently indicate that *T.* cf. *acutiplicata* should be referred to the coeval species *K. propinqua.*

Occurrence. — Kitchin (1900) reported *T. propinqua* from the "Upper Putchum Beds" and "*T*". *aurata* from the Golden Oolite in Keera. Our specimens are from Beds 1-5 in Jumara, Bed 2 of Jhura and Beds 1-2 in Keera.

Kutchithyris euryptycha (Kitchin, 1900)

Figures 10, 11

Terebratula sella var. Sowerby, 1840, p. 328, pl. 22, fig. 12.
Terebratula sella Sowerby. Wynne, 1880, p. 88.
Terebratula jumarensis Kitchin, 1900, p.13, pl. 3. figs. 3, 6.
Terebratula euryptycha Kitchin, 1900, p. 25, pl. 5, figs. 3–11; Barrabé, 1929, p. 25, pl. 21, fig 16.
Lophrothyris euryptycha (Kitchin). Buckman, 1918, p. 114, pl. 21, fig. 13a; Mitra, 1960, p. 89, pls. 15–20.
Kutchithyris euryptycha (Kitchin). Ovcharenko, 1969, figs. 4–6.

Types.—Kitchin (1900) did not select the holotype of *T. euryptycha.* We here designate one of his specimens, G. S. I. Type No. 6638, as the lectotype.

Material.—290 specimens including the types. Ju4 e/1–55 from Bed 4, Ju 10 e/1–46 from Bed 10, Ju 12 e/1–11 from Bed 12, Ju15 e/59–72 from Bed 15 in Jumara; Jh 9 e/1–62 from Bed 9, Jh 15 e/1–50 from Bed 15 in Jhura; K7 e/1–2, 40–57 from Bed 7 in Keera; Ja1 e/1–13 from Bed 1, Ja9 e/51–58 from Bed 9 Jara; G.S.I Type no, 6614, 6617 from Upper Patcham Beds of northwest Jumara, 6630–6638 from above the *Macrocephalus* beds to the top of the Charee Group in Jhura.

Description.—Shell small, 31.2 mm in maximum shell length, consistently longer than wide. Shell highly variable, circular in young, oval to subpentagonal in middle and elliptical in adult. Shell convexity variable, increasing allometrically during ontogeny (log CL = 1.209 log L + 1.2684; Table 1). Maximum width and thickness of shell at middle. Dorsal valve with a more or less marked longitudinal dorsal plica or fold. Some variants with a plica very low in height, giving a flattened appearance, with an anterior commissure almost rectimarginate. Plica variable in width, narrow to broad. Ventral valve more convex than brachial, with a sulcus variable in strength, corresponding to dorsal plica; sulcus broader and shallower in relatively wider and thinner shells than in narrower and thicker shells. In some cases ventral valve forms an anterior linguiform projection (Figure 10.2, 10.4, 10.9 and 10.10). Shell surface bears fine radial striae as in *K. acutiplicata* and *K. propinqua,* and growth lines become crowded near anterior margin in adult.

Lateral commissure near posterior end curves towards ventral side, then proceeding anteriorly with a wide curve, giving rise to form anteriorly a single central arch, broadly or narrowly rounded and even straight in some variants (Figure 10.3c). Anterior commissure rectimarginate to uniplicate.

Beak broad to narrow, suberect to slightly incurved. Lateral ridges absent. Foramen circular, moderate in size, truncating beak in vertical plane. Deltidial margin sometimes slightly thickened. Pedicle collar present and cardi-

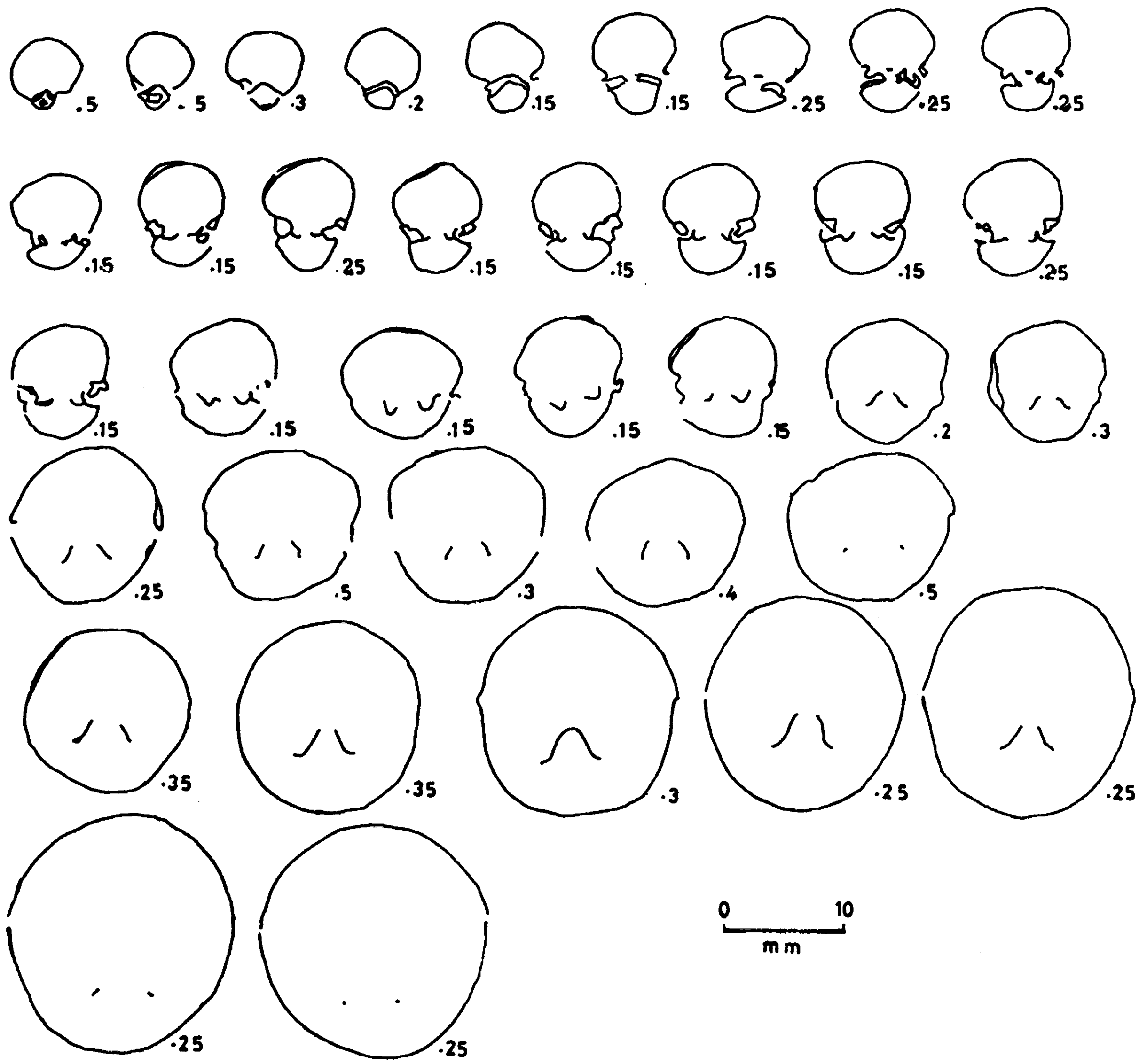

Figure 11. Serial transverse sections of *Kutchithyris euryptycha* (Kitchin). Numbers indicate grinding increments in mm.

nal process without lobe. Teeth linguiform in shape and denticula weakly developed. Hinge plates thin, highly concave; crural bases sharply recurved from hinge plates, crural plates distinctly converging. Loop 9.3 mm long, about half of brachial valve, and transverse band short and narrow.

Discussion. — Kitchin (1900) described *Terebratula euryptycha* based on a specimen which Grant (1840) previously identified as *Terebratula sella* var. from the beds immediately overlying the "*Macrocephalus* beds" of Waagen (1875). Kitchin (1900) also mentioned that it ranges right up to the top of his Charee Group. Buckman (1918) placed the species in his new genus *Lophrothyris* based on the external shell characters such as strong development of uniplica, short and obliquely truncated beak close to the umbo and slightly divergent muscle tracks. He selected *Lophrothyris lophus* Buckman as the type species of the genus but gave no description either of the muscle scars or of the internal structure for this species. Later, Mitra (1960, 1978) also allocated *T. euryptycha* to *Lophrothyris* following Buckman (1918), but did not compare the internal structure between the two species. When Muir-Wood (1937) reported two specimens of *L. euryptycha* from Jhaler in Attock district, Pakistan, she was sceptical about the inclusion of *T. euryptycha* within *Lophrothyris*, as no detailed investigation had been made of the internal characters of these two species. Almeras and Moulan (1988) were also uncertain of the inclusion of *T. euryptycha* within

Lophrothyris.

We examined shell character and internal structure of *K. euryptycha* in detail based on 290 specimens from Kutch. *K. euryptycha* has an internal structure which is the same as that of the type species of the genus, *K. acutiplicata* (Figures 7, 11). Moreover, *K. euryptycha* has a shell outline very similar to that of the smaller specimens of *K. acutiplicata* less than 15 mm in length. To sum up these similarities, *K. euryptycha* can be safely assigned to *Kutchithyris*.

Terebratula jumarensis Kitchin (1900) from Bed 4 in Jumara is similar to *K. euryptycha* in overall shell morphology. Our detailed morphometrical analysis shows that the two species are conspecific. Kitchin (1900) found *K. euryptycha* from horizons (Beds 10–15) much higher than that of *T. jumarensis* and this stratigraphical hiatus may have prompted him to assign it to a different species. Our systematic collecting reveals that this species sustained stasis for about 11 million years. Both *T. jumarensis* and *T. euryptycha* appeared in the same volume of Kitchin (1900) and T. *jumarensis* has page priority. However, we prefer to select *K. euryptycha* as the valid name since this name is more familiar and deeply entrenched in the literature.

The adult specimens of *K. euryptycha* in turn are closely comparable with the medium-sized specimens of *K. propinqua* as they have very incipient (Figure 10.1a–c) or no plications (Figure 10.3, 10.7) in the anterior commissure. The young individuals of *K. propinqua* (Figure 8.6a–c) and the adult individuals of *K. euryptycha* are hardly distinguishable since they have a nearly elliptical shell outline, broad and rather flattened dorsal valve, and narrow and weakly incurved to erected beak. However, the adult individuals of *K. euryptycha* have a well-marked longitudinal dorsal arch and a gently rounded curve in the lateral commissure at the middle. Furthermore, the sharpness of the angular bend decreases markedly in *K. propinqua* while the position of the angular bend shifts posteriorly until it becomes completely rounded at the midpoint of the shell length in *K. euryptycha*. Since *K. euryptycha* is stratigraphically younger, with a slight overlapping with *K. propinqua* in Bed 4, and it resembles the younger specimens of *K. propinqua*, we suggest that *K. euryptycha* is a paedomorphic derivative of *K. propinqua*, as *K. propinqua* was paedomorphically derived from *K. acutiplicata*. Consequently, they constitute an evolutionary lineage.

Ovcharenko (1969) recorded specimens of *K. euryptycha* from the Upper Bathonian deposits of the southeastern Pamirs. His specimens are represented by distended uniplicate shells without the median furrow. He observed that *K. euryptycha* has a brachial loop shorter than that of *K. acutiplicata*. They resemble the coeval specimens of *K. euryptycha* from Bed 4 of Jumara.

Barrabé (1929) reported a specimen of *Terebratula euryptycha* from the Callovian in the west of Ankidave, Madagascar, which Muir-Wood (1937) regarded as a broader form of *T. euryptycha* with a less incurved umbo. Such a variant is also seen in the specimens from Kutch and is particularly similar to those from Bed 7 (Jara) and Bed 9 (Jumara).

Wynne (1880) identified a specimen from the Jurassic of Shekh Budin Hills, Trans-Indus extension of the Salt Range as *Terebratula sella*. It is most probably referable to *Kutchithyris euryptycha*.

Occurrence.—Beds 4–5 in Jumara, Beds 9–15 in Jhura, Beds 1–9 in Jara and Beds 7–11 in Keera. Kitchin (1900) did not mention the specific horizon from which '*T*'. *jumarensis* was collected but merely mentioned "Upper Putchum Beds of north west Jumara" as the locality. He found *T. euryptycha* from "above the macrocephalus beds to top of Chari Group". From his description, it is inferred that his specimens come from Bed 10 to 15 of Jumara (Figure 2).

Discussion

Interestingly, the present three species form an evolutionary lineage with a long geological history from the Middle Bathonian to Oxfordian and have also been recorded from contemporaneous sequences in the Pamirs, where the lineage is cited as a classical example of the punctuational model of evolution (Ovcharenko, 1969; Raup and Stanley, 1985). Ovcharenko (1969) described two species of *Kutchithyris*, namely, *K. acutiplicata* and *K. euryptycha* from the Upper Bathonian of the southeastern Pamirs, where *K. acutiplicata* and *K. eurytpycha* were reported to occur in the lower and the upper parts of a 1–1.5 m thick marl bed, respectively. Between these two parts of the layer, there is an only 10 cm-thick interval that contains both species along with some transitional forms. According to Ovcharenko (1969), the transitional forms appeared in extremely small numbers (hybridization of two species, sensu Geary, 1992) and were not found elsewhere—a rare insight at that time, when the punctuational model of evolution (Eldredge and Gould, 1972) was not in vogue. Ovcharenko claimed to document a rapid mode of speciation in a small, isolated population. Generally, the forms depicting such a speciation event elude preservation due to the brief time intervals and small areas involved and also to the smallness of the sample size. Consequently, the apparent discontinuity in the fossil record of a lineage is taken as the absence of the intermediate forms. Thus, the Pamir appears to be a rare site preserving the record of an allopatric speciation event with the transitional forms having survived the vagaries of fossilization. In Kutch, the same ancestor-descendant lineage *K. acutiplicata-K. euryptycha* has been found along with the transitional forms and all of them are represented by plenty of individuals, enabling us to comment on their population structures. Detailed taxonomical treatment in the present study reveals that the so-called transitional forms are not only present within the Kutch brachiopods, but also that they appeared much earlier (Middle Bathonian) and occupy an intermediate stratigraphical interval. They were recognised much earlier by Kitchin (1900) and Buckman (1918) as a distinct species and named *Kutchithyris propinqua* (Kitchin). It evolved rapidly from *K. acutiplicata.* The species occurs in profusion in Kutch and spans a considerable geological range. In the Pamirs, the specimens are fewer in number and the lineage occupies a much lesser thickness, about 10 cm, thus perhaps indicating a stratigraphical condensation. In fact, it is also observed that *K. propinqua* has stratigraphical distributions overlapping with both the ancestral species *K. acutiplicata* and the descendant species *K. euryptycha* and the evolving lineage follows cladogenesis (sensu Gould and Eldredge, 1993), involving branching speciation rather than phyletic transformation as suggested by Ovcharenko (1969).

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