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Cretaceous Research 27 (2006) 611–628

CRETACEOUS RESEARCH

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Status of "*Trigonia ventricosa*" (Bivalvia) from the Upper Jurassic–Lower Cretaceous of Kutch, western India: Kitchin's unfinished synthesis

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Received 9 January 2004; accepted in revised form 19 September 2005
Available online 20 July 2006

Abstract

Kitchin first reported *Trigonia ventricosa* (Krauss) from Kutch in 1903. The populations he studied came from different localities and stratigraphic horizons, but erroneous information on Kutch geology initially led him to believe that all his material was obtained only from Late Tithonian strata. He noted, however, that populations of different areas had distinct morphological characters and biofacies associations and later expressed uncertainties about the homogeneity of the Kutch species. *Trigonia ventricosa* was later included in *Pisotrigonia* van Hoepen (subfamily Pterotrigoniinae). Our field investigation and study of numerous specimens collected from different localities as well as the material examined by previous workers (Kitchin and Cox) reveal that populations of "*T. ventricosa*" are, in fact, found at four distinct stratigraphic levels ranging from Late Tithonian to Aptian in age; they differ both morphologically and morphometrically, allowing the recognition of four distinct species, some of which are temporally separated by as much as seven million years. The species, in ascending stratigraphical order, are *Pisotrigonia kitchini* sp. nov., *P. umiensis* sp. nov., *P. ventricosa* (Krauss) and *P. ghuneriensis* sp. nov. The Pterotrigoniinae are apparently polyphyletic since *Pterotrigonia* has myophorellian ancestry while *Pisotrigonia* has megatrigonian affinities; they are stratigraphically heterochronous and evolved initially in two different palaeobiogeographic provinces. During the Valanginian, *Pterotrigonia* and *Pisotrigonia* shared the same biogeographic area and showed character displacement. *Pisotrigonia* species in Kutch evolved anagenetically with initial increase in body size followed finally by size decrease. The mode of evolution is punctuational and was induced by heterochrony.

Keywords: *Pisotrigonia ventricosa*; Late Jurassic; Early Cretaceous; Kutch; Evolution

"Taxonomy is often undervalued as a glorified form of filing – with each species in its folder, like a stamp in its prescribed place in an album; but taxonomy is a fundamental and dynamic science, dedicated to exploring the causes of relationships and similarities among organisms, classifications are theories about the basis of natural order, not dull categories compiled only to avoid chaos. The best monographs are works of genius…" (Gould, 1989)

1. Introduction

Krauss (1843) first described "*Lyriodon*" *ventricosa* specimens from strata exposed below the "Uitenhage beds" on the left bank of the Zwatkopf River in South Africa, indicating them to be a "Lower Greensand" horizon (Kitchin, 1913). Kitchin (1903, 1913) expressed doubts about the homogeneity of Kutch populations of *Trigonia ventricosa* Krauss. He regarded it as a species characterised by contemporaneous intraspecific variability, close to the modern biological species concept, but not much in vogue in his day. Believing that all of the material at his disposal came from a single, Late Tithonian, stratigraphic level, he grouped them in a catch-all species, *T. ventricosa*. However, morphological differences of

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0195-6671/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.cretres.2005.09.002

specimens collected from different localities, their distinct "lamellibranch facies" associations and, moreover, his deep biological perspective on species, prompted him to express doubts about their homogeneity. Finally, setting aside the stratigraphic considerations, he was convinced that the Kutch material not only represented two different species, but differed from *T. ventricosa* sensu stricto from South Africa. He communicated his revised opinion to others and intended to revise Kutch trigoniids, but could not do so because of his untimely death. When Kitchin (1903) described the trigoniid bivalves of Kutch, the analytical approach to taxonomy held sway and species were described on the basis of single or a few morphological characters and specimens; morphological variations were considered as having no value (the typological species concept) and stratigraphic data were rarely used for species discrimination. Species and genera were thus morphospecies and morphogenera respectively. Nowadays, workers take a synthetic approach to taxonomy: species are seen as dynamic, showing intraspecific variability, and stratigraphical data are essential. In a rare insight, Kitchin wanted to view the species of Kutch trigoniids in the light of population dynamics, where coeval assemblages would show morphological gradation. Thus he virtually adopted a classificatory scheme that is close to today's concept of biospecies (cf. Callomon, 1985).

Kitchin never visited Kutch and the trigoniid bivalves were passed on to him by a number of workers. Although his "*Trigonia*" *ventricosa* specimens were collected from various localities and lithologies, Kitchin was led to believe that they were contemporaneous and of Tithonian age. He doubted the homogeneity of the specimens and even in the appendix of his monograph (Kitchin, 1903, p.121) he hesitated to include all the Kutch material in one species. In 1913, while revising the South African trigoniids, Kitchin inspected *T. ventricosa* sensu stricto, and again expressed reservations about the homogeneity of the so-called *T. ventricosa* of Kutch. Finally, his great insight about species distinctiveness triumphed over stratigraphic inadequacies when, in a later manuscript note (see Cox, 1952, p. 119), he mentioned that the Kutch species were not only distinct from the South African *T. ventricosa* but also belonged to two different species.

Our study has revealed that the *T. ventricosa* population, which spans an age range of Late Tithonian–Aptian, includes four separate species, which now belong to *Pisotrigonia* van Hoepen. They are morphologically and morphometrically distinct, and are separated from each other by stratigraphic gaps of millions of years. The Tithonian species *Pisotrigonia kitchini* is the oldest previously undescribed pisotrigoniid species in Kutch as well as in the world.

2. Material and methods

Our study is based on more than 80 specimens, including the type material described by Kitchin (1903) and Cox (1952), which was collected from different sections in the western part of the mainland of Kutch (Fig. 1). Matrix was removed using various tools including chisels, vibrotools and needles. The specimens are of varying preservational quality; many are fragmented, especially near the posterior margin, and retrieval of intact specimens was further hindered by the indurated nature of the enclosing rocks. The state of preservation is, nevertheless, quite satisfactory, the majority of specimens retaining the original shell. Occasionally, for example, in *Pisotrigonia ghuneriensis*, mineralised ligaments have also been preserved.

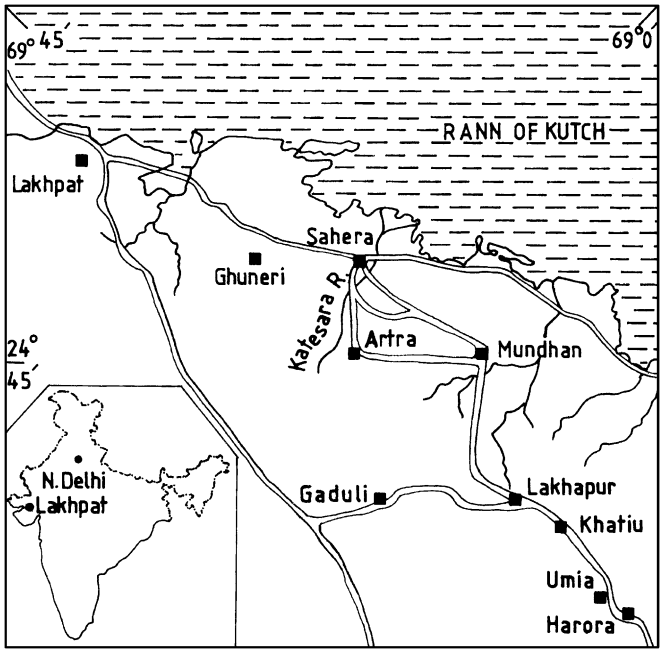

Fig. 1. Map of western Kutch showing all fossiliferous localities.

The type specimens of Kitchin and Cox are kept in the Repository Section of the Geological Survey of India, Kolkata. Their numbers are indicated either as GSI type nos. or are prefixed by the letter K. New specimens have been deposited in the Museum of the Geological Sciences Department of Jadavpur University and are prefixed by JUM/B/T/P.

The dimensions of *Pisotrigonia* described in the text and used for bivariate analysis are shown in Fig. 2. Measurements were taken using electronic calipers. Specimens were photographed after being whitened with magnesium oxide dust, which accentuates the finer details of ornamental features, essential for discriminating species. Type specimens, however, could not be coated with magnesium oxide owing to a restriction imposed by the Geological Survey of India.

3. Historical background

3.1. Stratigraphy is data

In his preface to the last volume on Kutch cephalopods, Spath (1933) realized how stratigraphic misinformation "causes a spurious homogeneity of the fauna" (p. vi) and he regretted that "…it took a long time to unlearn everything that the masters had taught us" (p. iii). He was especially critical of Waagen's (1875) attempt to blatantly correlate Kutch