Boraginaceae seeds from the Lameta Formation (Late Cretaceous) of Gujarat, India and possible evolutionary trends in fossil borages

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ABSTRACT

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Seeds assignable to the dicotyledonous family Boraginaceae are described, for the first time, from the dinosaur rich Lameta Formation. The seeds recovered from dinosaur egg and bone bearing limestone and marl beds near Balasinor, Kheda District, Gujarat, western India have been assigned to a new genus and species *Proboraginocarpus balasinorensis*. Further, a review of fossil and modern Indian borage seeds reveals that the characters of basal attachment scar, i.e. its shape, tapering anterior end, surface ornamentation are characters which indicate close lineage links of Late Cretaceous *Proboraginocarpus balasinorensis* with *Boraginocarpus lakhanpalii* Mathur from Tatrot Formation (Pliocene) of the Siwalik Group and the modern *Anchusa officinalis*. An American Pliocene borage seed *Cryptantha coroniformis* from Ogallala Formation also has characters which are close to *Boraginocarpus lakhanpalii* and appears to belong to the basic Late Cretaceous stock. Many genera of the Tribe Boragineae, family Boraginaceae are native to the Old World and are distributed in Asia, Africa and Europe. Studies on the origin and evolution of Tertiary relict floras have shown that these are distributed throughout large part of the Tertiary in Northern Hemisphere and are now restricted to south-eastern and western North America, East Asia and South-west Eurasia.

Key-words: Boraginaceae seeds, Lameta Formation, Late Cretaceous, Balasinor, Gujarat, evolutionary trends.

INTRODUCTION

The Lameta Formation is well known in Indian stratigraphy for its dinosaurian remains and is widely distributed in central and western India as thin outcrops (Text-figure 1). Besides Jabalpur (Madhya Pradesh), where they show the best development, the Lameta sediments are present in Kheda, Panchmahal (Gujarat), Chhindwara, Seoni, Narsingpur, Sagar (Madhya Pradesh) and Chanda, Nagpur (Maharashtra) (Sahni 1983). The discovery of dinosaurian eggs in Kheda (Gujarat) revived attention of palaeontologists in Lameta sediments (Mohabey 1983, 1984, Srivastava et al. 1986, Mathur & Pant 1986, Mathur & Srivastava 1987).

During the last two decades, a number of contributions on various aspects such as palaeobiogeography, palaeovegetation, terrestrial fauna, etc. of volcano-sedimentary sequences of the K-T boundary and especially on the Late Cretaceous events have been made (Sahni 1984, Sahni & Tripathi 1990 Bhatia et al. 1990, 1996, Ghosh et al. 1995, Mohabey 1996). Mathur and Mathur (1985) were the first to record angiospermous seeds assigned to the family Boraginaceae from the Lameta beds of Gujarat but



Text-Figure 1. Distribution of Lameta Formation (Late Cretaceous) in India

did not describe them in detail. Sahni et al. (1999) described three seed types, Seed Type Ia, Seed Type Ib and Seed Type II from Lameta Formation of Bara Simla Hill section near Jabalpur, Madhya Pradesh.

The Lameta Formation exposed in a quarry near Balasinor, Kheda District, Gujarat has yielded dinosaurian eggshells and seeds (Text-figure 2). The basal part of Lameta Formation here comprises gritty and pebbly calcareous/ferruginous sandstone followed upwards by yellow calcareous claystone and brown marl lenses. The eggshells as well as seeds have been found in the marl in upper part.

MATERIAL AND METHOD

The marls from Lameta Formation are hard, compact and well indurated. To separate microfossils from these, small pieces, 2-3 cm in size, were boiled with sodium thiosulphate (Na₂S₂O₇ known as hypo in photographic material) for about $1\frac{1}{2}$ hour and then transferred to a dish and placed in oven at 180° to 200°C. In this way, sodium thiosulphate was recrystalised which helped in breaking down the marls and release fossil seeds after repeated processing. The material was washed through 20, 60, 100 ASTM mesh sieves and dried in oven at 60°C. The dried material was examined under Leica stereozoom MZ 12 microscope. The fossil seeds were picked and studied. Selected seeds were placed over stub and further studied and photographed under Scanning Electron



Text-figure 2. Geological map of Balasinor – Rahioli area, Kheda district, Gujarat, India (after Mohabey 1984), showing fossil seed locality.

Microscope LEO 440. The specimens described in this work are deposited with Curator, Geological Survey of India, Kolkata under catalogue nos. 20360 to 20362.

SYSTEMATIC DESCRIPTION

Family: Boraginaceae Genus: *Proboraginocarpus* A. K. Mathur & U. B. Mathur, gen. nov.

Type Species: *Proboraginocarpus balasinorensis* A. K. Mathur & U. B. Mathur, sp. nov.

Diagnosis: Seed small, bilaterally symmetrical, ovoid trigonal, scar of attachment basal (posterior), circular with raised collar. Ventral side with knotty keel running from collar of attachment scar to apical end. Apically narrowed, basally inflated. Surface with varying degree of irregular ridges and blunt spines.

Comparison: Among the fossil borage seeds the new genus has resemblance in overall shape, size, surface ornamentation with the Siwalik (Indian Pliocene Tatrot Formation) Boraginocarpus Mathur represented by the species Boraginocarpus lakhanpalii Mathur (Text-figure 3.2a, b) and to the Ogallala Formation (American Pliocene) genus Cryptantha Elias represented by Cryptantha coroniformis (Elias) (Textfigure 3.1a, b), C. auriculata (Elias) and C. chaneyi (Elias). The new taxon differs from Boraginocarpus Mathur in having a circular basal scar of attachment, a prominent knotty ventral keel running from the apical end to the basal end and irregularly shaped and haphazardly arranged ridges on the surface. From Cryptantha Elias the new genus is distinguished by the shape of the scar of attachment, presence of irregular ridges on the surface, more tapering apical end and well defined ventral keel. The living European as well as Indian Anchusa Linnaeus has shape of the seed and scar of attachment and size close to the new fossil genus but differs in its pitted surface, some irregular ridges around the collar and two ridges from apical end to basal part of collar. The above characters distinguish the Late Cretaceous Proboraginocarpus from other closely resembling living and fossil borage taxa.

Affinity: The present genus is close to Indian Pliocene genus *Boraginocarpus* Mathur in its small size, ovoid trigonal shape, surface structure comprising

irregular spines and a keel on the ventral side. *Proboraginocarpus* is treated as ancestor to *Boraginocarpus* during Late Cretaceous as the collar around the scar of attachment in the latter appears to have split along the ventral keel to give it an inverted 'v' shape instead of a circular one. The surface ornamentation also has modified into spines instead of ridges as in Late Cretaceous form yet retaining the overall shape.

Derivation of name: The genus is named to show it as a precursor to the Neogene genus *Boraginocarpus* Mathur known from Tatrot Formation (Pliocene), Siwalik Group, Indian Himalaya.

Proboraginocarpus balasinorensis A. K. Mathur & U. B. Mathur, sp. nov.

Plate 1, figures 1a-c, 2a-e, 3a-b, 4; Text-figure 3.3-4

Material: Eight specimens from Lameta Formation, Kheda District, Gujarat, India.

Holotype: Geological Survey of India, Kolkata Catalogue No. 20360.

Description: Seed small, bilaterally symmetrical, ovoid-trigonal in shape, 1-5-2.5 mm in length, 1.0-1.35 mm in maximum width, 0.9-1.4 mm in height. Apical end tapering to acutely rounded, basal end inflated, broad circular; lateral margins slightly convex and converging towards apical end from maximum width which lies in the basal 2/5 of the total length. Width is more than half the length. Scar of attachment is basal, circular with irregularly placed blunt spines on the collar. and a slight constriction behind (Plate 1, figure 1c); a well developed keel in ventral side running from collar of attachment scar at the basal end to the apical end (Plate 1, figures 1a, 2a; Text-figure 3.4) having short irregularly shaped ridges in the basal half giving it a knotty appearance (Plate 1, figures 1a, c, 2a, 3a); the basal end of the keel may have slight protrusion (Plate 1, figure 1b; Text-figure 3.3); irregularly shaped and haphazardly arranged ridges and blunt spines usually dense on dorsal surface.

Dimensions: Holotype: G.S.I. Catalogue No. 20360 (Length 1.85 mm, Height 1.04 mm, Max. Width 1.04 mm; Plate 1, figures 1 a-c; Text-figure 3.3);



Plate 1

Proboraginocarpus balasinorensis gen. et sp. nov. 1a-c. Holotype. GSI Catalogue No. 20360. L: 1.85mm; a-ventral view, b-lateral view c-enlarged view of ventral apical half. 2a-e. Paratype A GSI Catalogue No. 20361. L: 1.95mm; a-ventral view, b-lateral view, c-enlarged view of basal part, d-enlarged view of rounded tubercles, e-enlarged view of one tubercle showing depression in middle. 3a, b Paratype B. GSI Catalogue No. 20362. L: 1.74mm; a-ventral view, b-lateral view. 4. L: 1.70mm. showing poor surface ornamentation.

Paratype A: G.S.I. Catalogue No. 20361 (Length 1.95 mm, Height 0.90 mm, Max. Width 1.35 mm; Plate 1, figures 2a-e; Text-figure 3.4); Paratype B: G.S.I. Catalogue No 20362 (Length 1.74 mm, Height 0.96 mm, Max. Width 1.00; Plate 1, figures 3a, b)

Comparison: The new taxon has been compared with a number of present day seeds of Boraginaceae living in central and western India which include *Cordiya* myxa Linnaeus, C. rothii Roemer and Schimper, Ehretia aspera Roxburgh, E. laevis Roxburgh, Aenebia hispidissima de Candolle, Trichodesma indicaum Brown, Bothiospermum tenellum Fischer and Meyer, Heliotropium zeylanicum Lamarck, Cynoglossum lanceolatum Forskal and C. wallichi Don. The new taxon is distinct from the above mentioned present-day borage seeds in having an ovoid-trigonal shape, the narrow circular basal scar of attachment and the ventral keel. *Anchusa officinalis* Linnaeus (Text-figure 3.5a, b) resembles the new fossil taxon in ovoid triangular shape, tapering anterior and rugose surface ornamentation but is distinguished by the wide open invaginate scar of attachment, two lateral ridges running from basal to apical end, mostly smooth to pitted surface and short ventral keel restricted to apical half instead of knotty keel extending from apical end to basal end. Among the fossil borage seeds the new taxon compares well in shape, size and surface ornamentation with *Boraginocarpus lakhanpalii*



Text-figure 3. Line sketches of selected borage seeds from different horizons and locations of India, America and Europe. 1a, 2a, 3, 5a: lateral view; 1b, 2b, 4, 5b: ventral view; Bar = 1 mm. 1a, b. Cryptantha coroniformis (Elias) from Ogollala Formation (Pliocene), America. 2a, b. Boraginocarpus lakhanpalii Mathur from Tatrot Formation (Pliocene), India. 3-4. Proboraginocarpus balasinorensis gen. et sp. nov. from Lameta Formation (Late Cretaceous), India. 5a, b. Anchusa officinalis Linnaeus, native of Europe, also occurs in India.

Mathur known from the Tatrot Formation (Pliocene), Siwalik Group (Indian Himalaya) and *Cryptantha coroniformis* (Elias) known from the Ogallala Formation (America). The new taxon differs from *B. lakhanpalii* Mathur in having a circular basal attachment scar with collar, a prominent knotty ventral keel running from the apical end to the basal attachment scar and irregularly shaped and haphazardly arranged ridges on the surface. From *C. coroniformis* (Elias), *C. auriculata* (Elias) and *C. chaneyi* (Elias) the new form is distinguished by the shape of the attachment scar, presence of irregular ridges on the surface, more tapering apical end and well defined ventral keel.

Type Locality: 6 km NNW of Balasinor, Kheda District, Gujarat, India.

Horizon: Lameta Formation (Late Cretaceous).

Derivation of name: The species is named after the village Balasinor which is close to the locality from where material was collected by one of the authors (UBM).

EVOLUTIONARY TRENDS

In the Indian subcontinent, no significant work on fossil borage seeds has been published except by Mathur (1974) who described and illustrated Boraginocarpus lakhanpalii from the Tatrot Formation (Upper Siwalik) near Chandigarh. In contrast, the Boraginaceae seeds are well documented from the American Neogene (Berry 1926, 1928, Elias 1932, 1935, 1942, 1946, Brown 1935, Elias & Chaney 1941). Chandler (1961), while cataloguing Early Tertiary floras of southern England, described Boraginaceae (Ehretia spp.) seeds from Lower Bagshot Beds (London Clay) of Palaeocene age that is apparently the oldest horizon known for Boraginaceae seeds. The fossil seeds of herbaceous borages are identified by their shape, sculpture, and the characteristics of the scar of attachment (Elias 1946). The shape of seeds is influenced by their position in the fruit as four seeds are attached symmetrically around a common style and these are adpressed to each other on sides. According to Elias (1946), the fossil nutlets are either symmetrical GEOPHYTOLOGY



Text-figure 4. Evolutionarty trends in some Boraginaceae taxa

near the central plane (in fossil and living *Cryptantha* or *Krynitzkia*), or depart from this symmetry, perhaps because of differential pressure in the course of early growth, which results in the development of an equal number (two and two) of dextral and sinistral nutlets (in fossil *Biorbia* and living *Anchusa*, and others).

It has been shown that the living *Lithospermum* (with smooth nutlets) and *Anchusa* (with very corrugated nutlets) have developed from *Biorbia*, apparently ancestral to both of them, whose nutlets are slightly to moderately corrugated and species with intermediate surface texture are reported from Late Pliocene of High Plains (Elias 1946). The closeness in

shape and surface structure of Pliocene Boraginocarpus of Indian Tatrot Formation (Siwalik Group) and Cryptantha of American Pliocene Ogallala Formation is very significant in understanding the evolutionary trends of Boraginaceae. According to Elias (1946), there is great similarity in most Tertiary and even Cretaceous angiospermous arboreal leaves with living species, and the ensuing difficulty in differentiating fossil from living species, also indicate a slow differentiation of angiospermous trees. The American Biorbia is closer to the European Anchusa and its allies and according to Elias (1946) is apparently ancestral to European Anchuseae.

Thomasson (1979), who carried out comprehensive palaeobotanical survey of the northern extent of the Ogallala Group, recorded Cryptantha, Biorbia, Lithospermum. According to Hilger et al. (2005) Borago L. and all the 16 genera of Tribe Boragineae, family Boraginaceae are native to the Old World and distributed in Asia, Africa and Europe. Milne and Abbot (2002), who worked on the origin and evolution of Tertiary relict floras, have shown that these are distributed throughout large part of the Tertiary in Northern Hemisphere and are now restricted to southeastern and western North America, East Asia and south-west Eurasia. On the basis of their molecular phylogenetic studies they suggested two refugial (warm humid) groups having geographical distribution centred on Japan/Korea/northeast China and southeast China/ Himalaya regions respectively. North Atlantic Land Bridge (NALB) which connected floras of Europe and North America was severed around 50 Ma, but from relict floras it appears that partial NALB allowed migration of floras between Europe and North America throughout the Tertiary (Milne & Abbot 2002). During Neogene it is indicated by the presence of closely related borage taxa Cryptantha in America, Biorbia in Europe and Boraginocarpus in India.

The distribution and proliferation of angiosperms during Late Cretaceous and their slow morphological modification (stasis) during Cenozoic could be due to allopatric speciation together with stabilizing selection (Milne & Abbot 2002). The slow change in morphological characters of leaves of fossil angiosperm

plants of Late Oligocene-Early Miocene Dagshai and Kasauli formations of north-western Himalaya is obvious from the fact that these can easily be compared with living plant taxa (Mathur et al. 1996). It can be surmised that the change in morphological characters like the replacement of well developed ventral knotty keel in Late Cretaceous Indian Proboraginocarpus to its splitting into an inverted narrow V-shape in Pliocene American Cryptantha, wide V-shape in Late Pliocene Indian Boraginocarpus and rudimentary and restricted to apical half in living European as well as Indian Anchusa are the slow evolutionary changes. Similarly there is change in the surface ornamentation from irregular ridges and blunt spines in Late Cretaceous Indian Proboraginocarpus to pointed closely spaced spines in Pliocene American Cryptantha and widely spaced relatively blunt spines and ridges in Late Pliocene Indian Boraginocarpus and pitted surface, some irregular ridges around the collar and two ridges from apical end to basal part of collar in living European as well as Indian Anchusa.

The origin of land mammals during Palaeogene in Old World and their spread to New World, diversification and extinction during Neogene is well established. It is therefore expected that the herbs that form their food also followed the same route of spread, diversification and extinction. Just as Cryptantha is an index fossil and restricted to middle early Pliocene of Ogallala Formation of America, Boraginocarpus is restricted to Late Pliocene Tatrot Formation of India. In order to understand evolutionary trends in this group of borage seeds the most important feature is the ovoidtrigonal shape of seeds that places them in common stock. The character that is most significant in identifying the taxa of same group is the development of a attachment scar. It is medium sized subcircular in Late Cretaceous Proboraginocarpus, trilobate in the Indian Boraginocarpus and the American Cryptantha and again wide circular in modern Anchusa. The other important character is the surface ornamentation. In Late Cretaceous Proboraginocarpus the ridges are more prominent than spines whereas in Pliocene genera Boraginocarpus and Cryptantha the spines dominate and in modern the ridges dominate over a more or less

smooth surface of *Anchusa*. The evolutionary links between the Late Cretaceous *Proboraginocarpus*, the Pliocene *Boraginocarpus* and *Cryptantha* and the modern *Anchusa* can be traced as shown in Textfigure 4.

DISCUSSION

The systematic study of the new borage taxon, first reported by authors (Mathur & Mathur 1985), is significant, as these seeds have been recovered from dinosaur egg bearing strata that are Maastrichtian in age (Srivastava et al. 1986). Sahni et al. (1996) described Seed Type I a, b and Type II from Lameta Formation of Jabalpur, India and compared Seed Type I a, b with Costatheca diskoensis and Type II with Spermatites elongates reported from Late Cretaceous of West Greenland. However, they (Sahni et al. op. cit.) were not definite about inter-relationship between the two. The morphological characters of Seed Type I a, b, i.e., prominent costae with deep furrows in between, small size (length 1.42 mm) is closer to Ehretia ehretioides (Reid & Chandler) described by Chandler (1961) from Palaeocene London Clay which is slightly larger in size being 1.5 to 1.75 mm in length, has longitudinal rows of costae and furrows and convex dorsal face. The genus Ehretia, belonging to family Boraginaceae, according to Chandler (op. cit.) is essentially tropical in the Old Wold. While dealing with paleogeographic and age implications on the basis of non-marine ostracodes of Lameta Formation, Bhatia et al. (1996) opined that Late Cretaceous assemblages from Asifabad and Takli have strong affinities with those of Central Asia which provided continuous terrestrial passage for the migration of Laurasian biotas to Peninsular India. The distribution and proliferation of angiosperms during Late Cretaceous and their slow morphological modification during Cenozoic has led earlier palaeobotanists to assign these fossil taxa to modern genera. But detailed SEM studies of such taxa may require their placement in genera having distinctive features from modern genera and an evolutionary lineage can then be developed in these genera as we find in Late Cretaceous Proboraginocarpus to modern Anchusa. The evolution and migration of mammals such

as horses is important in understanding the corresponding dispersion of vegetation in space and time around the globe.

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