REVIEW OF THE AMMONOID SUBFAMILY VIRGATOSPHINCTINAE WITH SPECIAL REFERENCE TO ITS EVOLUTIONARY SUCCESSION IN THE INDIAN SUBCONTINENT ON THE GONDWANIAN TETHYAN MARGIN

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Abstract

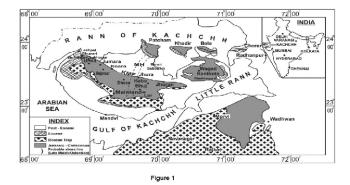
The Virgatosphinctinae is a geographically restricted Indo - East-African ammonoid subfamily, significantly present almost throughout the Kimmeridgian - Tithonian interval of Late Jurassic in India (Kachchh, Jaisalmer and High Himalayan belt), Pakistan and Medagascar. The investigation incorporates the review of Virgatosphinctinae generic evolutionary succession inclusive of limited heterochronic modalities of evolution and expressions. The subfamily includes a succession of six genera (Torquatisphinctes, Pachysphinctes, Katroliceras, Indodichotomoceras, Aulacosphinctoides and Virgatosphinctes). The generic differentiation within this subfamily is based mostly on the evolution and ontogenic positioning of their respective specialized rib sculpture from later part of the phragmocone to the body chamber. The evolution of the rib sculpture at genus/species level is analyzed and understood in terms of heterochronic evolutionary processes. The hypermorphic peramorphosis is observed as the dominant heterochronic evolutionary process in microconch and macroconch dimorph series. It includes a long phase of unidirectional hypermorphic peramorphocline interval with frequent presence of ammonoids in relatively fine textured sediments. The paedomorphic heterochronic expression is relatively much shorter lived, relatively poor in ammonoid density and diversity that too in relatively coarser sediments. The evolutionary succession of the Virgatosphinctinae has been used as the principal parameter for the refinement of geological time in the Kimmeridgian - Tithonian interval of West India.

Keywords

Ammonoid, Virgatosphinctinae, Heterochrony, Kimmeridgian, Tithonian.

Introduction

The Jurassic sedimentary succession of Kachchh (Fig. 1) in the western sector of India has



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been globally known for its rich invertebrate fauna, in particular the stratigraphically significant ammonoids through the early works of Sowerby (1840), Waagen (1873-75) and Spath (1927-33). These European scientists did never visit Kachchh yet they through the fossil collections sent to them in Europe succeeded well in highlighting the importance of the Kachchh Jurassic sedimentary succession in global context. In spite of the lack of desired stratigraphic information on the ammonoids studied by them, they could establish the general correspondence of the ammonoid succession in Europe to that of distant India along with their similarities and dissimilarities. However, these early studies failed to workout any independent refined stratigraphic framework based on indigenous successions of Kachchh ammonoids. Subsequent studies during the last 50 years on the Kachchh Jurassic in independent India included significant enlargement of data-bank which, however, unfortunately could not contribute much significant to the refinement of geological time in the Jurassic of Kachchh on the pattern of significant contributions in Europe in this direction. In this backdrop with a view to fill the above significant lacuna, the authors initiated a comprehensive study of Late Jurassic in Kachchh in the late 1980's. It was realized that the key to understanding of the integrated geological framework of the Kachchh Mesozoic crucially hinges on the refinement of geological time in this interval. The approach to refinement of geological time in the Kachchh Late Jurassic has been made through the study of evolutionary succession of the dominant ammonoid subfamily Virgatosphinctinae.

Already published results (Krishna and Pathak, 1991, 1993; Krishna et al., 1996a, 1996b) over the last many years include substantive progress in this direction. The present study includes significant new results besides updating the state of art in an integrated manner.

Previous Work

But for early works of Waagen and Spath mentioned earlier very little of substance could be added about the Virgatosphinctinae ammonoids, the most dominating subfamily in the Kachchh Kimmeridgian - Tithonian sedimentary succession. It was Stoliczka who formulated the first lithostratigraphic scheme for Kachchh Mesozoic sediments in 1869. His scheme included a succession of four stratigraphic units as Patcham, Chari, Katrol and Umia Groups in ascending order. However, due to his untimely death, this scheme was later included in the work of Waagen (1871, 1873-75). Rajnath (1932), the first Indian worker on the Kachchh Mesozoic divided the Katrol Formation of mostly Kimmeridgian - Tithonian age into four informal members (K-I to K-IV) in ascending order. In Biswas's (1971, 1977) later Lithostratigraphic scheme for the Kachchh Mesozoic, the Katrol Formation is found included in the Jhuran Formaton with the same lower boundary yet different upper limit. Recently, Krishna and co-workers (Krishna, 1983, 1987, 1991; Cariou and Krishna, 1988; Krishna and Pathak, 1989, 1991, 1993; Krishna et al., 1996a, 1996b; Pandey, unpublished 1993) based on extensive field studies have favoured the retention of the old lithostratigraphic scheme of Stoliczka. The scheme has successfully withstood the test of time and is considered by us the best lithostratigraphic scheme for the Kachchh Mesozoic applicable to the entire basin with some minor clarifications and modifications. The entire Katrol Formation and basal part of Umia Formation of Stoliczka, as also followed by Spath (1927-33) and Rajnath (1932), correspond to the Kimmeridgian – Tithonian interval. While in terms of Biswas's scheme, the major part of Jhuran Formation corresponds to the Kimmeridgian – Tithonian interval.

Waagen (1871, 1873-75) made the first detailed systematic study of the Kachchh Mesozoic cephalopod fauna. He organized the Kachchh Kimmeridgian – Tithonian interval in a succession of two ammonoid assemblages. Spath (1924, 1927-33) worked out a succession of five distinct ammonoid assemblages in the Kimmeridgian – Tithonian interval based on the collections without precise stratigraphic information made by Blake, Smith, Rajnath and others. Recently Krishna and co-workers (Krishna, 2005; Krishna and Pathak, 1989, 1991, 1993; Krishna et al., 1996a, 1996b; Pathak, unpublished 1989; Pandey, unpublished 1993) developed a highly refined ammonoid stratigraphic framework in the Kimmeridgian – Tithonian interval of Kachchh with wide applicability in the entire Indo – East-African marine faunal province. The scheme includes 4 zones, 10 subzones and 19 horizons in part of Kimmeridgian and 4 zones, 10 subzones and 13 horizons in Tithonian.

Salient Features of the Present Study

The present study has been undertaken with the principal objective to review the earlier works and the development of the generic and species evolutionary succession in some detail in the subfamily Virgatosphinctinae. It is also endeavored to discuss the broad heterochronic framework in sequence stratigraphic context, in addition of the analysis of the ammonoid stratigraphic data in context of regional sequence stratigraphy.

The realization of the objective has been approached through the study of ammonoid faunal succession overwhelmingly dominated by the ammonoid subfamily Virgatosphinctinae to the extent of 80% in terms of individual specimens and 65-70 % by way of number of species. In fact the species evolutionary succession of Virgatosphinctinae in turn paved the way for high order chronologic resolution. Besides Virgatosphinctinae, five other Ammonitina subfamilies (Taramelliceratinae, Strebilitinae, Aspidoceratinae, Simoceratinae and Hybonoticeratinae), present in the Kachchh Kimmeridgian – Tithonian interval, although in much less proportion, have helped in precise long distance zonal / subzonal correlation across the Tethys based on either common or similar species to both the Tethyan margins (Schweigert et al. 1996). In special cases, informal heterochronic infraspecific evolutionary morphs have also been recognized within the range of species. The Virgatosphinctinae genera/species evolutionary succession (best developed and studied in Kachchh) is found to have evolved independently on the South Tethyan margin.

The principal handicap in earlier ammonoid stratigraphic refinement was absence of detailed stratigraphic differentiation, measurement and record of the studied sections along with precise positions of the collected ammonoids. Accordingly, this study is mainly based on the detailed measurement and record of lithocolumn which has been differentiated in to 31 sediment intervals and 163 beds / bands scoring several fold greater lithostratigraphic differentiation. The ammonoids have been precisely collected from 68 levels in the Kachchh Kimmeridgian – Tithonian interval in comparison to 5 broad imprecise stratigraphic intervals of Spath (1927-33). In addition to the Kachchh fauna, the precisely collected ammonoids from Tithonian of Jaisalmer (Fig. 2) have also been taken into account. At present the composite West Indian ammonoid zonation scheme (Pandey and Krishna, 2002; Krishna, 2005) includes 4 zones, 10 subzones and 19 horizons in part of Kimmeridgian and 5 zones, 14 subzones and 17 horizons in Tithonian. The recent study in the

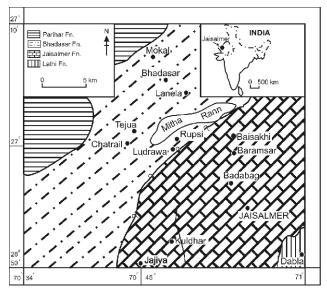


Figure 2

Tithonian of Jaisalmer (Pandey and Krishna 2002) has enabled inclusion of a new Natricoides Zone in between the Virgatosphinctoides Zone below and Communis Zone above and 4 subzones in the West Indian Tithonian ammonoid zonation scheme. The Communis Zone of Late Tithonian has been transferred from late Tithonian to late Early Tithonian.

Approach / Methodology to the Heterochronic Framework

According to Gould (1977) and McNamara (1986), heterochrony refers to changes in relative time of appearance and rate of development of characters already present in ancestors in either direction forward or backward. It includes two main processes Peramorphosis and Paedomorphosis (Fig. 3). Peramorphosis is characterized by introduction of new characters at

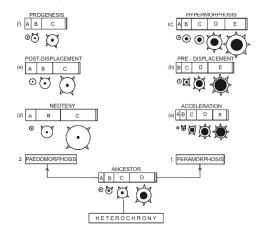


Figure 3

the terminus in the descendent taxon along with centripetal extension of existing features. It is in turn divided in to three types: (a) Acceleration (reduction in size), (b) Predisplacement (without change in size), and (c) Hypermorphosis (increase in size). Paedomorphosis is featured by removal of the existing characters from the terminal most part along with centrifugal extension of the remaining ontogenic stages from ancestral to the descendent taxon. It again includes three types; (a) Neoteny (increase in size),(b) Post-displacement (without change in size), and (c) Progenesis (reduction in size). The individual ammonoid spiral shells are uniquely favoured for heterochronic evolutionary studies since the spirals include all the successive ontogenic stages. The significance and application of heterochrony to evolution, particularly in ammonoids, has been dealt recently in several works (Alberch et al. 1979; Alberch 1980; Bonner 1982; House 1985; Dommergues et al. 1986; Dommergues 1987; Cariou and Sequerious 1987; Krishna and Cariou 1986, 1993; Krishna and Pathak 1991, 1993; Krishna et al. 1996a, 1996b; Pandey unpublished 1993).

Salient Features of the Ammonoid Subfamily Virgatosphinctinae

The ammonoid subfamily Virgatosphinctinae is known to range from late Early Kimmeridgian to late Late Tithonian in Kachchh. This subfamily was created by Spath in 1923 (Spath 1924, 1927-33) using the specialized virgatotome rib framework (Fig. 4). It has undergone

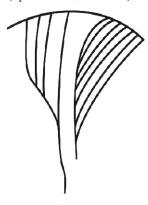


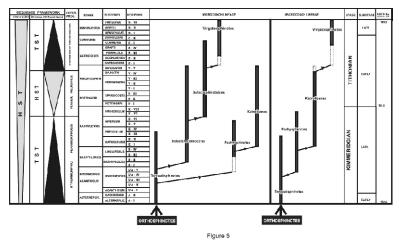
Figure 4

revision from time to time with regard to inclusion or exclusion of its constituent genera. It is largely restricted to the Indo – East-African marine faunal province comprising East- Africa, Madagascar, Western India, Pakistan and Himalayan belt on the South Tethyan margin. Currently based on the present comprehensive study this subfamily is restricted to include the genera Torquatisphinctes, Pachysphinctes, Katroliceras, Indodichotomoceras, Aulacosphinctoides and Virgatosphinctes (Krishna and Pathak 1991, 1993; Pandey unpublished 1993). The comprehension of phyletic transformation is also strengthened under heterochronic framework. The morphologically close genera Torquatisphinctes, Pachysphinctes and Katroliceras have been precisely differentiated from one another in terms of heterochronic framework as observed in their respective genotypes. The generic differentiation is mostly based on the ontogenic positioning

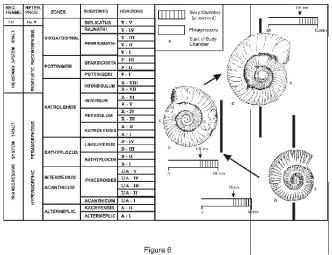
of their respective specialized rib sculpture from later part of phragmocone to the body chamber (Krishna and Pathak 1993).

The Generic Evolutionay Succession in the Subfamily Virgatosphinctinae

The most observed heterochronic evolutionary process is peramorphosis in both microconch and macroconch lineages. It is characterized by addition of new characters at the terminus in the descendent taxon along with centripetal extension of existing features and distinct increase in size. This trend of evolution is found to range for a substantive interval of the total range from A-I Horizon of Alterneplicatus Zone to K-VI Horizon of Katrolensis Zone (c. 3.4 my), and later again from V-V Horizon of Virgatosphinctoides Zone to D-III Horizon of Densiplicatus Zone (c. 3.0 my) while paedomorphosis is observed relatively for much less distinctly shorter interval from K-VII of Katrolensis Zone to V-IV Virgatosphinctoides Zone (c. 2.5 my) (Fig. 5).



The earliest Virgatosphinctinae genus *Torquatisphinctes* appears at the base of A-I horizon of Alterneplicatus Zone through *Torquatisphinctes intermedius* Spath m and *Torquatisphinctes alterneplicatus* (Waagen) M. The genus *Torquatisphinctes* (in agreement with Krishna and Pathak 1993) is suggested to have evolved from *Orthosphinctes* by increase in size and number of single ribs, lower point of furcation of secondary ribs along with introduction of occasional triplicate ribs at the terminus (on the body chamber in microconch).



Microconch Lineages (Figs. 5 to 7): The heterochronic process involved is hypermorphic peramorphosis. *Torquatisphinctes* through cladogenesis branches into two *Torquatisphinctes* – *Pachysphinctes* – *Katroliceras* and *Torquatisphinctes* – *Indodichotomoceras* – *Aulacosphinctoides* – *Virgatosphinctes* and thus is interpreted to exhibit polymorphism with two microconch and single macroconch lineages.

Torquatisphinctes – Pachysphinctes – Katroliceras microconch lineage (Figs. 5 and 6): The first genus in this lineage, *Torquatisphinctes* appears at A-I Horizon of Alterneplicatus Zone through its species *T. intermedius* Spath m and ranges up to K-III Horizon of Katrolensis

Zone with T. bathyplocus (Waagen) m and T. torquatus (Sowerby) m. It is characterized by its depressed inner whorls, mostly biplicate ribs with frequent single intercalatries and few triplicate ribs in last quarter of body chamber between 69mm to 128mm diameter, particularly in relatively younger form e.g. T. torquatus (Sowerby) m. The significant stratigraphic hiatus underlying this fauna makes it difficult in Mainland Kachchh to precise the probable ancestor. However, the recent record of the morphologically close genus Orthosphinctes from earliest Early Kimmeridgian of Wagad in Kachchh is here suggested to be the ancestor of the genus Torquatisphinctes through introduction of triplicate ribs in terminal part of body chamber by way of hypermorphic peramorphosis. The genus *Pachysphinctes* appears at B-III Horizon of Bathyplocus Zone through the single microconch species Pachysphinctes linguiferus Spath m and ranges up to K-V Horizon of Katrolensis Zone. It is derived from *Torquatisphinctes (T. bathyplocus* (Waagen) m) through centripetal extension of triplicate ribs on the phragmocone with first appearance between 115mm to 135mm diameter and introduction of quadruplicate and multiplicate ribs along with somewhat abrupt modification (thickening and increase in spacing) in primary ribs at about 150mm diameter on the last quarter of body chamber along with size increase by way of hypermorphic peramorphosis. In this lineage Katroliceras appears next at the base of K-I Horizon of Katrolensis Zone through Katroliceras katrolensis (Waagen) m and continues up to V-V Horizon of Virgatosphictoides Zone with K. pottingeri (Sowerby) m, K. rajnathi Krishna and Pathak m and K. virgatosphictoides Krishna and Pathak m. It evolves from Pachysphinctes (P. linguiferous Spath m) through introduction of cuniform primaries that took place somewhere near the beginning of the body chamber between 73mm to 160mm diameter depending on the size and centripetal extension of the existing Pachysphinctes ontogenic stages again by way of hypermorphic peramorphosis from body chamber to phragmocone.

Torquatisphinctes – Indodichotomoceras – Aulacosphinctoides - Virgatosphinctes microconch lineage (Figs. 5 and 7): In this lineage *Indodichotomoceras* is derived from *Torquatisphinctes* at the base of B-II Horizon of Bathyplocus Zone through *I. cf. zitteli* Spath m and continues up

to V-V Horizon of Virgatosphinctoides Zone with *I. inversum* (Spath) m, *I.* sp₁ m and *I. biplicatus* (Uhlig) m. Its evolution from *Torquatisphinctes* (*T. torquatus* (Sowerby) m) is realised through coarsening and sparsing of the primary ribs and their centripetal extension probably by way of hypermorphic peramorphosis.

The genus Aulacosphinctoides appears next at the base of K-VII Horizon of Katrolensis Zone through Aulacosphinctoides infundibulum (Uhlig) m and ranges up to C-I Horizon of Natricoides Zone with A. sparsicosta (Uhlig) m, A. willisi (Uhlig) m, A.

| SEQ. FRAMEW. | HETER. PROC. | ZONES | SUBZONES | HORIZONS | Body Chambi |
|----------------------|----------------------------|---------------|--------------------------|-----------|----------------------|
| IVE SYSTEM TRACT | PERAMORPHOSIS | DENSIPLICATUS | FREQUENS | D - III | 35 130mm (preserved) |
| | | | OPPELI | D - II | Phragmocone |
| | | | DENSIPLICAT. | D-I | X Start of Bo |
| | | COMMUNIS | SUBFREQUENS | С-П | Chamber |
| | | | COMMUNIS | C-I | |
| | | | KRAFTI | N - IV | |
| 88 | HYPERMORPHIC | NATRICOIDES | PUMPECKJI | N - III | |
| TRANSGRESSIVE | | | DOGHLAENSIS | N - II | |
| 28 | | | NATRICOIDES | N - I | d Zono |
| - | | | BIPLICATUS | v - v | → |
| ь | Sis | VIRGATOSPHIN. | RAJNATHI | V - IV | |
| TRACT | PAEDOMORPHOSIS | | PERRINSMITHI | V - III | |
| | | | | V - II | 0 85mm |
| SYSTEM | 8 | | | V - I | c Alle |
| SYS | 8 | POTTINGERI | SPARSICOSTA | P - III | |
| 9 | PROGENETIC | | | P · II | |
| STA | | | POTTINGERI | P - I | |
| HIGHSTAND | | | INFUNDIBULUM | K - VIII | |
| | | KATROLENSIS | INVERSUM | K - VI | |
| | HYPERMORPHIC PERAMORPHOSIS | | | K - V | |
| TRACT | | | PRESSULUM KATROLENSIS | K - IV | |
| ¥ | | | | K - III | |
| 2 | | | | к-п | |
| Е. | | | | K - I | . WALLANDER |
| TRANSGRESSIVE SYSTEM | | | LINGUIFERUS | B - IV | p magazin |
| | | BATHYPLOCUS | | B - III | |
| | | | BATHYPLOCUS | B - II | |
| | | | | B - I | 110mm |
| | | INTERMEDIUS/ | IPHICEROIDES | I/A - V | 1 |
| | | | | I/A - IV | |
| | | ACANTHICUM | | I/A - III | 0 143mm |
| | | AUAIT.IICOM | | I/A - II | 93mm a x |
| | | I | ACANTHICUM | I/A - I | 1 <u> </u> |
| | | ALTERNEPLIC. | KACHHENSIS | A - II | |
| | | | ALTERNEPLIC. | A - I | 0 124mm |

Figure 7

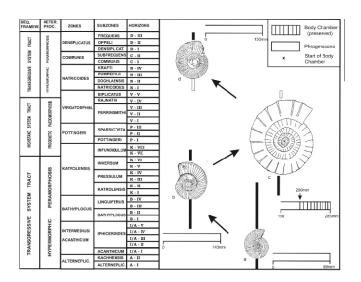


Figure 8

perrinsmithi (Uhlig) m, A. uhligi Spath m, A. tibetanus (Uhlig) m, A. natricoides (Uhlig) m, A. dhoglaensis Fatmi m, A. linoptychus (Uhlig) m and A. hyderi Fatmi m. It is suggested to evolve from Indodichotomoceras (I. inversum (Spath) m) through decrease in size and disappearance of coarser and sparser ribs and increased depression in whorl section through progenetic paedomorphosis. The youngest member of the generic lineage is Virgatosphinctes which appears at the base of N-III Horizon of Natricoides Zone through V. pompekji Uhlig m and continues up to D-III Horizon of Densiplicatus Zone with V. krafti Uhlig m, V. densiplicatus (Waagen) m and few other species. It is suggested to evolve from Aulacosphinctoides (A. sparsicosta Uhlig m) by way of increase in size and rib density (right from the early diameters) probably through hypermorphic peramorphosis.

Macroconch Lineage (Figs. 5 and 8): The single macroconch lineage identified within the subfamily Virgatosphinctinae is *Torquatisphinctes – Pachysphinctes – Katroliceras - Virgatosphinctes*. The heterochronic processes involved are almost the same as observed in the microconch lineages.

Torquatisphinctes – Pachysphinctes – Katroliceras – Virgatosphinctes macroconch lineage (Figs. 5 and 8): In this lineage, the genus Torquatisphinctes is found to range from A-I Horizon of Alterneplicatus Zone to K-II Horizon of Katrolensis Zone through T. alterneplicatus (Waagen) M and T. jurunensis Spath M. The genus Pachysphinctes appears first through Pachysphinctes granti Spath M at I/A-V Horizon of Intermedius / Acanthicum Zone and continues up to K-VII Horizon of Katrolensis Zone with P. major Spath M. It is derived from Torquatisphinctes (T. alterneplicatus (Waagen) M) through appearance of triplicate ribs at early diameters from 70mm onwards, introduction of quadriplicate and multiplicate ribs by way of hypermorphic peramorphosis. Later in this lineage Katroliceras appears next at the base of K–I Horizon of Katrolensis Zone through Katroliceras spathi Krishna and Pathak M from Pachysphinctes granti Spath M and ranges up to V-IV Horizon of Virgatosphinctoides Zone with K. giganteus Krishna and Pathak M and K. sp. M by way of introduction of cuniform primaries centripetally on later part of phragmocone from 150mm diameter onwards and centripetal extension of Pachysphinctes

ontogenic stages. The interval from K-VII Horizon of Katrolensis Zone to V-V Horizon of Virgatosphinctoides Zone is unfortunately almost devoid of macroconch forms, however, rare fragments indicate the continuation of *Katroliceras* till V-V Horizon of Virgatosphinctoides Zone. *Virgatosphinctes* is the next genus in this lineage, which appears through *Virgatosphinctes communis* Spath M at the base of C-I Horizon of Communis Zone and ranges up to D-III Horizon of Densiplicatus Zone with *V. frequens* (Oppel) M, *V. oppeli* Spath M and few other species of *Virgatosphinctes*. It appears to evolve from *Katroliceras* (K. sp. M) by way of marked increase in density of secondary ribs, most probably through mechanism of hypermorphic paramorphosis.

Based on the above heterochronic framework of generic evolution, it is found that from A-I horizon of Alterneplicatus Zone to K-VI Horizon of Katrolensis Zone (17 horizons) and again from V-V Horizon of Virgatosphinctoides Zone to D-III Horizon of Densiplicatus Zone (10 horizons), the Virgatosphinctinae generic evolution is unidirectional hypermorphic peramorphocline. The intervening interval of 9 horizons from K-VII Horizon of Katrolensis Zone to V-IV Horizon of Virgatoshinctoides Zone, the evolutionary process is undisputedly

| SEQ. FRAME. | HETER. PROC. | ZONES | SUBZONES | HORIZONS | |
|---------------------------|-----------------------|---------------|--------------|-----------|----------------------------|
| TST | Ну. Г. | | BIPLICATUS | v - v | Body Chamber |
| HIGHSTAND SYSTEM TRACT | PAEDOMORP | VIRGATOSPHIN. | RAJNATHI | v - Iv | (preserved) |
| | | | PERRINSMITHI | V - III | Phragmocone |
| | | | | υ - π | |
| | | | | V - I | x Start or body Chamber |
| | | POTTINGER | SPARSICOSTA | Ρ- Π1 | |
| | | | | P - II | 105 mm |
| | | | POTTINGERI | P-I | 1 → |
| | | | INFUNDIBULUM | K - VIII | |
| RANSGRESSIVE SYSTEM TRACT | MORPHIC PERAMORPHOSIS | | IN ONDIDOCOM | K - VII | 85 mm D 137 mm |
| | | KATROLENSIS | INVERSUM | K - VI | 75mm |
| | | | | K - V | |
| | | | PRESSULUM | K - IV | 113 mm |
| | | | | K-III | |
| | | | KATROLENSIS | K - 11 | ožmin ožmin |
| | | | | K - I | |
| | | BATHYPLOCUS | LINGUIFERUS | B - IV | |
| | | | | B - III | |
| | | | BATHYPLOCUS | В-П | |
| | | | | B-I | 3 20 MANAGE |
| | | INTERMEDIUS/ | | I/A · V | - Wallet |
| | | | IPHICEROIDES | I/A - IV | |
| | | ACANTHICUM | | I/A - III | |
| | | ~ | | 1/А - П | |
| - | | | ACANTHICUM | I/A - I | |
| | | ALTERNEPLIC. | KACHHENSIS | A - II | a |
| | | | ALTERNEPLIC. | A - I | |

Figure 9

progenetic paedomorphosis. Thus in the 36 horizon interval paedomorphosis is relatively short lived for only 9 horizons while the much larger interval of 27 horizons is found influenced by the peramorphic evolutionary process.

We also summarize one example each of intra-generic as also of intra-species heterochronic framework in the Indian Mesozoic ammonoid succession.

Intra-Generic Heterochrony

Torquqtisphinctes intermedius Spath – T. torquatus (Sowerby) – T. bathyplocus (Waagen) microconch lineage (Fig. 9): T. intermedius Spath m appear in A-I Horizon of Alterneplicatus Zone and is found to range until K-I Horizon of Katrolensis Zone. T. intermedius Spath m is known through incomplete specimens only in the present collections, however, the holotype of Spath (1927-33) includes body chamber. Next in the succession appears T. torquatus

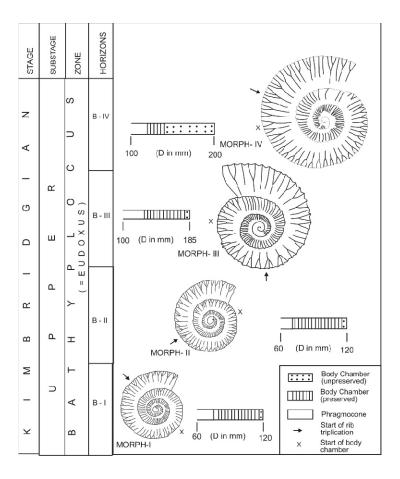


Figure 10

(Sowerby) m in I/A-IV Horizon of Intermedius / Acanthicum Zone and ranges up to K-III Horizon of Katrolensis Zone. It appears to evolve from *T. intermedius* Spath m through centripetal extension of existing rib sculpture by way of acceleration (peramorphosis). *T. bathyplocus* (Waagen) m appears in B-I Horizon of Bathyplocus Zone and ranges up to K-I Horzon of Katrolensis Zone. It is here interpreted as to evolve from *T. torquatus* (Sowerby) m through distinct increase in size and centripetal extension of existing rib sculpture by way of hypermorphic paramorphosis.

Microevolutionary Intra-Species Heterochrony (Fig. 10)

In specially favoured situations, there is observed unidirectional infraspecific microevolutionary heterochronic modifications within the species range. It is the first such effort of this kind in the South Tethyan margin Jurassic ammonoid succession. This allows the resolution of the Bathyplocus Zone into four (B-I to B-IV) and Katrolensis Zone in to eight (K-I to K-VIII) horizons (the older four horizons K-I to K-IV based on successive transient morphs within the range of *K. katrolensis* (Waagen) m while younger four horizons K-V to K-VIII based on first appearances of successive younger species *I. inversum* (Spath) m, *A. infundibulum* (Uhlig) m, *Hybonoticeras ornatum* Spath m and last appearance of *K. katrolensis* (Waagen) m). By way of examples

the case history of infraspecific heterochrony in Torquatisphinctes bathyplocus (Waagen) m is discussed here. Torquatisphinctes bathyplocus (Waagen) m is the youngest Torquatisphinctes in the well understood Torquatisphinctes – Pachysphinctes – Katroliceras lineage. It is characterized by the presence of triplicate ribs exclusively on the part or whole of the body chamber. Any centripetal extension farther on the phragmocone (peramorphosis) of the triplicate ribs results in the evolution of the descendent genus Pachysphinctes. However, within the Bathyplocus Zone, there is observed gradual centripetal extension of the first triplicate rib from near the close of the body chamber to near the start of the body chamber through intermediate positions in the successively younging morphs through the species range. This in turn allows unambiguous yet easy differentiation of the Bathyplocus Zone interval into four smaller intervals (horizons) characterized by the successive evolutionary transient morphs of T. bathyplocus (Waagen) m as morph I to morph IV in ascending order (Figure 10). These morphs (morph I to morph IV) of T. bathyplocus (Waagen) m are found to appear respectively at the base of B-I Horizon with first triplicate rib in the last quarter, at the base of B-II Horizon with first triplicate rib in the end of the second quarter, at the base of B-III Horizon with first triplicate rib in the beginning of the second quarter and at the base of B-IV Horizon of Bathyplocus Zone with first triplicate rib in the first quarter of the body chamber (Figure 10). The differentiation of Bathyplocus Zone in to four and Katrolensis Zone in to eight smaller intervals results in a chronological resolution respectively of the order of ca 200,000 years and 100,000 years per horizon. It compares well with the highest pre-quaternary resolution ever achieved in any part of the world.

Possible Genetic Link Between Heterochronic Evolutionary Changes and Sequence Stratigraphic Framework (Fig. 5)

The observed heterochronic evolutionary patterns are here analyzed against the sequence stratigraphic framework developed earlier (Krishna et al., 2000; Krishna, 2002, 2005). It is found that within the studied Kimmeridgian – Tithonian interval, there are interpreted, somewhat larger, two intervals of peramorphocline that are intervened by a relatively shorter interval of paedomorphocline. The two longer peramorphocline intervals are; 1. seventeen (17) Horizon long A-I Horizon to K-VI Horizon and 2. ten (10) Horizon long V-V Horizon to D-III Horizon, while the intervening paedomorphocline is nine (9) Horizon long, K-VII Horizon to V-IV Horizon. The two peramorphocline intervals are here found to broadly corresponds to two 2nd order TST's (Transgressive System Tract) while the intervening paedomorphocline corresponds to the intervening 2nd order HST (Highstand System Tract) in between the two 2nd order TST's. The heterochronic evolutionary change from peramorphocline to paedomorphocline takes place at the start of the MFI (Maximum Flooding Interval) in B-III Horizon. It is interpreted that the MFI maintains ne as stable maximum bathymetry from B-III Horizon to K-VI Horizon, while the precise MFS (Maximum Flooding Surface) is near the base of the K-II Horizon. The part of the MFI below the MFS registers extremely slow increase in bathymetry, so also extremely slow decrease of bathymetry in the part of MFI above the MFS.

The demonstration of the broad correspondence as above of the heterochronic evolutionary changes to 2nd order sequence stratigraphic framework suggests possible genetic links between

the two phenomena of ammonoid heterochronic evolutionary and sequence stratigraphic surfaces (Krishna et al., 2000, Krishna, 2005). In view of the possible governance of the 2nd order sequence stratigraphic framework by regional extensional tectonics, the major heterochronic evolutionary changes too appear to be heavily influenced by regional extensional tectonics. Within the paedomorphic interval here corresponded to HST, we also observe drastic reduction of ammonoid density, diversity and frequency; coarsening of texture, increase in sediment accumulation rate, decrease of bathymetry and increase of energy framework. However, similar genetic links require to be investigated in other intervals of the Jurassic on GTM (Gondwanian Tethyan Margin) and other parts of the world.

Conclusion

The ammonoid heterochronic evolutionary framework under the precise rigorest possible stratigraphic details as developed here suggests immense usefulness not simply in several fold improvement in geological refinement, but also in providing interesting clues to simultaneous governance of sedimentation pattern, sequence surfaces and biotic evolution by regional extensional tectonics.

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