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On some new Late Bathonian paracenoceratids (Nautiloidea) from Kutch, India and their evolutionary and biostratigraphic implications

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With 10 figures and 1 table in the text

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Abstract: Three forms of *Paracenoceras* are reported, two of them new species, the third a new record in Kutch. These species, together with two other species of *Paracenoceras* come from a single horizon at a single locality in Kutch. Besides omnipresent and extensively studied ammonites, the present nautiloids help in placing a more authentic Bathonian-Callovian boundary in Kutch. A punctuational model of evolution is suggested here as nautiloid species show constancy of forms for long periods after their sudden origination.

Zusammenfassung: Von den drei aus der gleichen Lokalität beschriebenen Vertretern von *Paracenoceras* sind zwei neue Arten, während der andere zum ersten Mal aus dem Kutch beschrieben wird. Zusammen mit den häufigen Ammoniten erlauben sie eine verbesserte Grenzziehung zwischen dem Bathonien und dem Callovien. Da die Arten der Nautiloiden nach ihrer Entstehung sich über lange Zeit nicht merklich verändern, wird für sie ein punktuiertes Evolutionsmodell vorgeschlagen.

Introduction

The marine Mesozoic sequence of Kutch yields diverse faunas of which ammonites are particularly well-known. Nautiloids, though distributed throughout the sequence, have received much less attention in recent times. The first comprehensive account was by WAAGEN (1873-1875). It was revised and updated by SPATH (1927-1933), who also recorded many new forms. He made a major revision of post-Triassic nautiloid phylogeny and introduced five families of which four were new except Nautilidae. These families include twenty-eight genera of which sixteen are new. Accordingly SPATH regrouped all the Kutch nautiloids into three of his new families which are Paracenoceratidae, Cymatoceratidae and Hercoglossidae. The Cymatoceratidae are represented by a single genus *Procymatoceras*, which includes three species, namely *P. intumescense* (WAAGEN), *P.* sp. and *P.* cf. *perinflatum* (FOORD &

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CREEK) from different horizons. The Hercoglossidae are represented by only *Pseudaganides*, whose single species *P. kutchensis* (WAAGEN) is found from his Anceps Zone of the 'Middle Chari Group'. The genus *Paracenoceras* of the family Paracenoceratidae is the most dominant element and was represented by six species until recently. They are abundant and distributed throughout the Jurassic sequence. These species include, in order of decreasing abundance, *P. calloviense* (OPPEL), *P. kumagunense* (WAAGEN), *P. wandaense* (WAAGEN), *P.* cf. *lorioli* (LOESCH), and *P. hexagonoides* SPATH. Another species *P. jumarense* (WAAGEN) which SPATH (1927) doubtfully recognized, has curious transverse ribbing. WAAGEN based his *Nautilus jumarensis* on only three specimens, but many well-preserved new specimens show the ribbing unambiguously (BARDHAN et al. 1994b). All these are found in a restricted horizon in the lower Chari Formation at a single locality, Jumara, the type area of the Chari Formation (Fig. 1).

Recent systematic searches for nautiloids in the field have resulted in a rich haul of specimens, some of the species are either new or recorded for the first time from Kutch. *Cymatonautilus*, a biostratigraphically important marker, appeared briefly during the latest Early Callovian and was so far known only from western Europe (Enodatum Subzone), Madagascar and Saudi Arabia (TINTANT 1970, 1987). Recently, we have reported *Cymatonautilus* in Kutch from a horizon straddling between the Early and Middle Callovian (HALDER & BARDHAN 1996b).

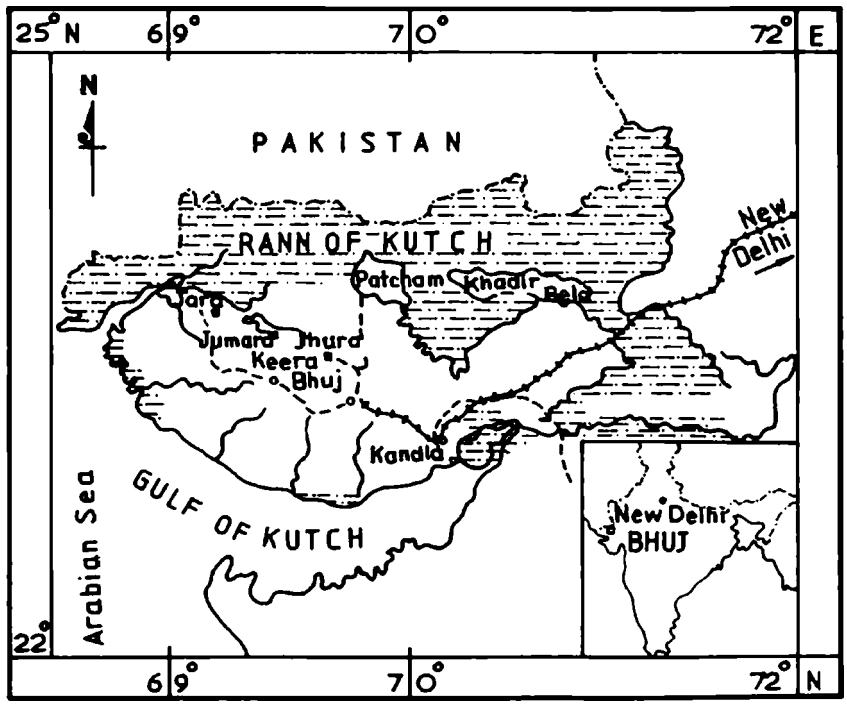

Fig. 1. Geographic location of Kutch with Jumara, the type area.

The present study reports three species of *Paracenoceras* from Jumara, two of them new, the other not so far described from Kutch. *P. noetlingi* n. sp. was previously reported from Baluchistan in the Indian sub-continent as *Nautilus giganteus* (NOETLING 1897). *P. prohexagonum* SPATH is a rare species, previously reported only from Somalia and Saudi Arabia (SPATH 1935, TINTANT 1987). These two species and *P.* n. sp. A are found together in the uppermost part of a cream-coloured limestone within the basal Chari Formation (Fig. 2) that also yields *P. jumarense* and *P. calloviense* (Fig. 3).

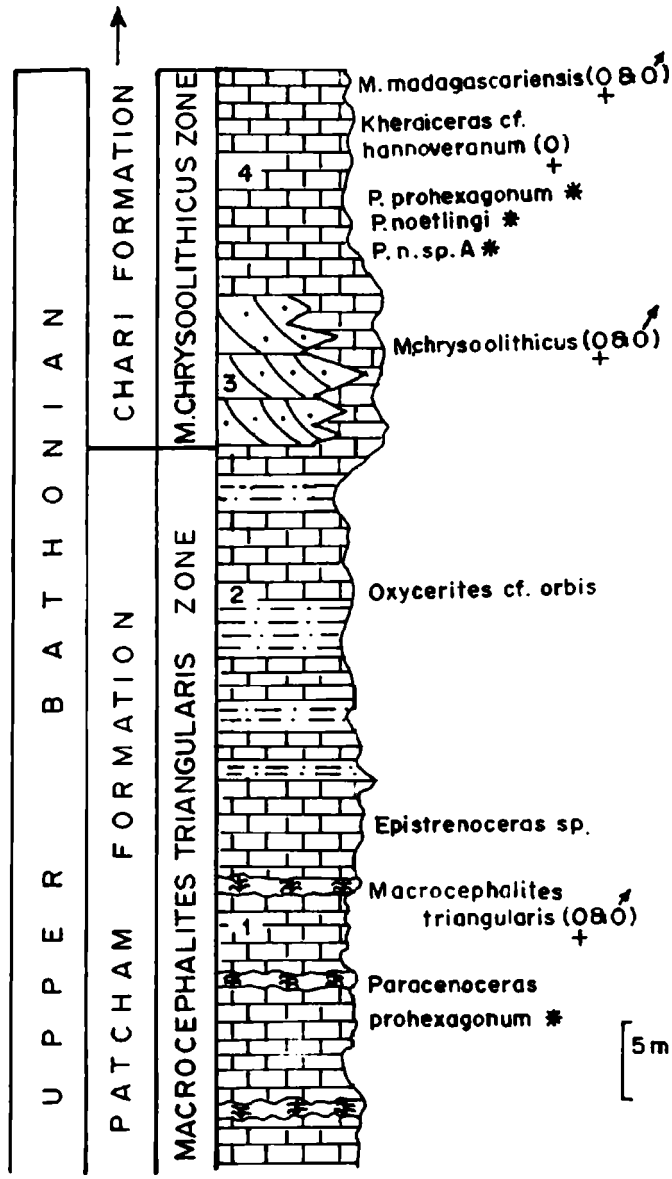

Fig. 2. Upper Bathonian stratigraphic section at Jumara with the distribution of the present species of *Paracenoceras* (see *) along with the key ammonites.

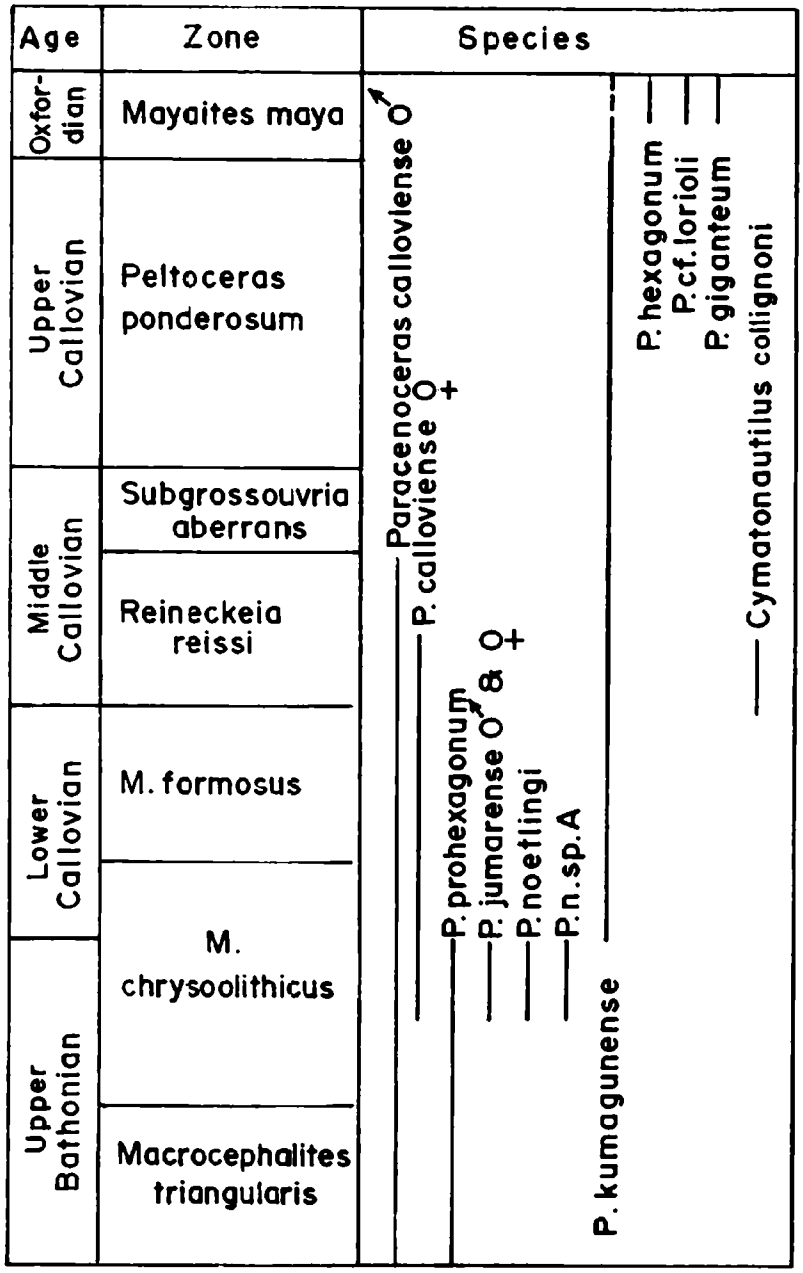

Fig. 3. Stratigraphic distribution of different paracenoceratid species in Kutch (modified from BARDHAN et al. 1994b, Fig. 2).

Stratigraphy

The Chari Formation, one of the major units of the Kutch Mesozoic is thick, persistent and exposed throughout the Kutch mainland (NATH 1932, BISWAS 1977, MITRA et al. 1979). It crops out in several structural domes including that of Jumara (Fig. 1) and attains a maximum thickness of 204 m (DATTA 1992). It ranges in age from the Callovian to Late Oxfordian and its lower boundary even straddles into the Late Bathonian (DATTA et al. 1996, HALDER & BARDHAN 1996a). The Chari Formation supports rich biota in

Jumara where the full sequence is exposed. It includes fifteen identifiable beds with lithologies mainly of limestone, shale and sandstone (BARDHAN et al. 1994a). Nautiloids particularly paracenoceratids are distributed throughout (Fig. 3). The present collection has been made mostly from the uppermost part of the basal cream-coloured limestone bed (Bed 4 of BARDHAN et al. 1994a and Bed 22 of NATH 1932) which is 15 m thick (Fig. 2). This limestone, massive with sparse comminuted shell fragments, is a wackestone and presumably deposited in an open shelf condition below the wave base (DATTA 1992). The lower part of the bed is less fossiliferous except some terebratulid brachiopods but the upper part is rich in fossils with great diversity. Ammonites are represented by *Macrocephalites madagascariensis* LEMOINE, *Indocephalites chrysoolithicus* (WAAGEN) and *Sivajiceras congener* (WAAGEN). Besides, scores of bivalves, brachiopods, corals and calcareous sponges also characterize this part.

It is interesting to note that both *P. noetlingi* n. sp. (= *Nautilus giganteus* D'ORBIGNY, NOETLING 1897, p. 8, pl. 4, fig. 5) and *P. prohexagonum* are also reported from limestone beds in Baluchistan and Somalia respectively (NOETLING 1897, SPATH 1935) perhaps indicating a strong facies control. *Paracenoceras* essentially represents a Callovian radiation and Bathonian forms are very rare (KUMMEL 1956). However, *P. prohexagonum* and its allied forms, and *P. speciosum* TINTANT are described only from the Bajocian and the Bathonian sediments (SPATH 1935, TINTANT 1987). In Kutch, the age of the limestone bed (Bed 4 of BARDHAN et al. 1994a) seems to be Late Bathonian with the occurrence of pre-Callovian *P. prohexagonum*, although nautiloids are generally not regarded as very time-diagnostic. BARDHAN et al. (1988) recorded *Bullatimorphites* sp. from this bed. It is an interesting specimen with a less depressed phragmocone and less contracted body chamber. It now appears to be a *Kheraiceras* and a distinct form from the other species of immediately overlying Callovian horizons. Significantly it bears coarse distant ribs till to the end of the observed body chamber and thus resembles strongly the well time-diagnosed *K. hannoveranum* (ROEMER) which comes undoubtedly from the Upper Bathonian of Europe (see also CALLOMON 1993). The immediately overlying bed at Jumara includes ammonites such as *Kamptokephalites lamellosus* (SOWERBY), *Dolikephalites subcompressus* (WAAGEN) and *Kheraiceras bullatus* (D'ORBIGNY) etc. which have their counterparts in European faunal horizons representing the Lower Callovian (CARIOU 1984, DATTA et al. 1996). Below the limestone the Patcham Formation includes two distinct lithofacies (Bed 1 and Bed 2 of BARDHAN et al. 1994a and Bed 24-26 of NATH 1932). The lower facies is an alternation of coralline rudstone and cream coloured wackestone containing ammonites which marks the first appearance of *Macrocephalites* in Kutch, i. e., *M. triangularis* SPATH, and other genera namely *Procerites hians* (WAAGEN) and *Epimorphoceras decorum* (WAAGEN). This suggests a definite pre-Callovian age of this level. The uppermost bed of the Patcham Formation is, on the other

hand, an alternation of wackestone and marl containing sparse fragmentary ammonites. Recently, one of us (S. B.) along with others found *Epistrenoceras* sp. and *Oxycerites* cf. *orbis* (GIEBEL) from these two beds respectively. *Epistrenoceras* is a fleeting genus (sensu AGER 1984), appeared cryptogenically only during Late Bathonian and had worldwide distribution (see also WESTERMANN & CALLOMON 1988), while *Oxycerites orbis* is also a good index fossil, coming from the Upper Bathonian horizon of Europe. Thus, judging from this ammonite association which resolves the long-standing problem of the age of the Patcham Formation, the Bathonian-Callovian boundary may safely be placed between Beds 4 and 5.

Systematic palaeontology

Superfamily Nautilaceae DE BLAINVILLE 1825
FamilyParacenoceratidae SPATH, 1927
Genus *Paracenoceras* SPATH, 1927

Type-species: *Nautilus hexagonus* J. DE C. Sowerby, 1826

All the known species of *Paracenoceras* can be divided into two groups, one having adult diameter greater than 250 mm, the other consisting of smaller species not exceeding 100 mm in diameter (personal observation, see also TINTANT 1984, 1987). The former includes *P. verciacense* (LISSAJOUS), *P. hexagonum* (SOWERBY), *P. giganteum* (D'ORBIGNY), *P. macrum* TINTANT etc. The latter group consists of *P. speciosum* TINTANT, *P. sulcatum* TINTANT, *P. moreausum* (D'ORBIGNY), *P. parvulum* TINTANT, *P. dorsoexcavatum* (PARONA & BONARELLI) etc. and are considered as progenetic off-shoots of the former group (TINTANT 1987).

The knowledge about sexual dimorphism in nautiloid is still poor although examples are coming from Jurassic forms (TINTANT 1969, BARDHAN et al. 1994b, HALDER & BARDHAN 1996a). Unlike in ammonites the recognition of adulthood in nautiloids, which is a prerequisite for establishing sexual dimorphism (KENNEDY & COBBAN 1976, CALLOMON 1981, KLINGER & KENNEDY 1989), is very difficult. Sexual dimorphism in the paracenoceratid lineage is well-studied. Here dimorphism is limited to differences in relative adult size and ventral differentiation. In the clade of large forms, which also includes some of the present species, adult macroconchs are generally large, having diameters more than 300 mm (TINTANT 1969). The body chamber occupies half to one third of the last whorl. The flanks of the adult body chamber become flattened with the outer lateral sometimes depressed. The umbilical wall is steep to overhanging and the greatest width lies near the umbilical margin. The venter, which is rounded to flat in the inner whorls, becomes sulcate in the adult body chamber. Approximation of a few last septal sutures are noted. Microconchs, on the other hand, are smaller, not exceeding 100 mm, and resemble intermediate-sized macroconchs with nonsulcate venter.

Paracenoceras prohexagonum SPATH

Fig. 4; Fig. 5

1935 *Paracenoceras prohexagonum* nov. sp. – SPATH, p. 224; fig. 4a-c.
1987 *Paracenoceras* aff. *prohexagonum* SPATH – TINTANT, p. 92; text-fig. 15; pl. 7, fig. 1.

Material: Three specimens including two almost completely preserved adults (FI 10002 & FI 10003) from Bed no. 4 of Jumara and a juvenile (FI 10004) from Bed no. 1 have been collected. All the specimens are mostly covered with shell.

Fig. 4. Septal suture of *Paracenoceras prohexagonum* SPATH (FI 10003).

Description: Shell relatively evolute (U/D = 0.16), compressed (W/H = 0.9) to slightly inflated (W/H = 1.15), maximum diameter of adult shell 72 mm. The adult peristome has growth-conformable apertural outline with hyponomic sinus at the mid-venter. The body chamber occupies about 1/3 of the last whorl. Adult phragmocone diameter is about 50 mm. Maximum whorl width lies just above the umbilical margin. Flanks flattened in the early stage, become slightly bulged at the end-phragmocone and body chamber, with a slight concavity towards the outer flank near ventrolateral margin. Venter narrow to wide, slightly convex in early ontogeny, becoming sulcate at about 30 to 50 mm diameter and continuing increasingly to the end. Ventrolateral margin sharp, angular, forming keel-like ridge during later ontogeny. Umbilical margin rounded, umbilical wall steepening during growth. Septa relatively closely spaced with rounded, deep lateral lobe; umbilical and ventrolateral saddles short, angular; ventral lobe relatively shallow. Last two septa show approximation indicating maturity. Siphuncular position unknown. Shell smooth except for very fine growth lirae or with sharp ribbing on the venter of the adult body chamber in the inflated variant. Strength of the ribs increases ontogenetically and decreases from mid-venter to ventrolateral margins where they finally disappear. Flanks smooth to faintly ornamented with lirae. Both lirae and ribs form a deep hyponomic sinus on the venter.

Discussion: The present species shows wide intraspecific variation including ornamental polymorphism. One morph is more inflated (wider than high), slightly larger with prominent sharp, fine growth-parallel ribbing restricted to the venter of the adult body chamber. The other morph is compressed (higher than wide), smaller and smooth-shelled except very fine growth lirae. Both the morphs are hardly distinguishable in young stage since early whorls are smooth.

The present species was reported so far only from Somalia from an Upper Bathonian sequence (SPATH 1935). TINTANT (1987) recently reported Group of *Paracenoceras prohexagonum* from Saudi Arabia, ranging from the Late Bajocian to Early Bathonian. The Kutch form shows similarity with the Somali specimen in having sulcate periphery, concave sides and closely spaced septa. It differs in being relatively smaller and having shallow ventral lobe. But SPATH handled only a fragment of a specimen and the maximum diameter was reconstructed. The present form resembles *P.* aff. *prohexagonum* (TINTANT 1987) from Saudi Arabia, which has rounded ventrolateral margins, deeply

excavated venter and widely spaced septa with deep ventral lobe. Saudi specimens are highly inflated (W/H = 1.31-1.59), with fine growth striae forming acute angles on the mid-venter, whereas in the Kutch specimens they form obtuse angles. None of the Saudi or Somali specimens show any ribbing or ornamental polymorphism. *P.* sp., gr. *prohexagonum* SPATH (TINTANT 1987) differs from the present species mainly in being larger and more depressed, and having a larger umbilicus. Its venter is relatively large, with a rounded ventrolateral margin, while the present form has an angular ventrolateral margin and its venter is with distinct ornamentation on the body chamber at least in one variant.

P. prohexagonum and allied forms are members of the group having maximum diameter less than 100 mm. Other members of this group in Kutch include *P. kumagunense* and *P.* n. sp. A. *P. kumagunense* is close to the present form in having a similar whorl section, a relatively open umbilicus with rounded margin, and a sulcate venter with increasing sulcation in later ontogeny. However, it differs from the latter in having slightly arched flanks and a relatively less pronounced angularity of ventrolateral margins. *P.* n. sp. A being involute, smooth-shelled with highly flared laterals presents a quite different look.

P. hexagonum ♂ is relatively evolute with arched flanks which become slightly depressed near the periphery of the body chamber and thus is closely comparable to *P. prohexagonum*. But it differs in having arched flanks all through. Besides, it is a much younger form of Early-Middle Oxfordian age (HALDER & BARDHAN 1996a). *P. prohexagonum* differs from *P. calloviense* ♂ in having a larger umbilicus, both ventral and lateral sulci, closely spaced septa, prominent angular ventrolateral margins and ornamental polymorphism.

Paracenoceras speciosum TINTANT, a small Early Bathonian form from Saudi Arabia has a similar narrow sulcation on the mid-venter but is involute with flat flanks, a shallow lateral lobe and is ornamented with both transverse and longitudinal fine striae. Longitudinal striae are reinforced on the ventrolateral margins giving rise to pronounced ribs (see TINTANT 1987). *Paracenoceras parvulum*, the smallest *Paracenoceras* species known (TINTANT 1984), has a wide umbilicus and sulcate venter and flanks on the body chamber. But it is

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Fig. 5. *Paracenoceras prohexagonum* SPATH. **A, B**: Left lateral and ventral views of the inflated variant, FI 10002, collected from Bed no. 4 of Jumara, with completely preserved adult body chamber. Note sharp, fine ribbing on the venter of the body chamber. **C-E**: Lateral, ventral and apurtural views of the adult completely preserved compressed variant, FI 10003, collected from Bed no. 4 of Jumara. Note smooth ventral surface. **F-H**: Juvenile specimen, FI 10004, collected from Bed no. 1 of Jumara. Lateral, ventral and apertural views. Note smooth venter with sulcus.

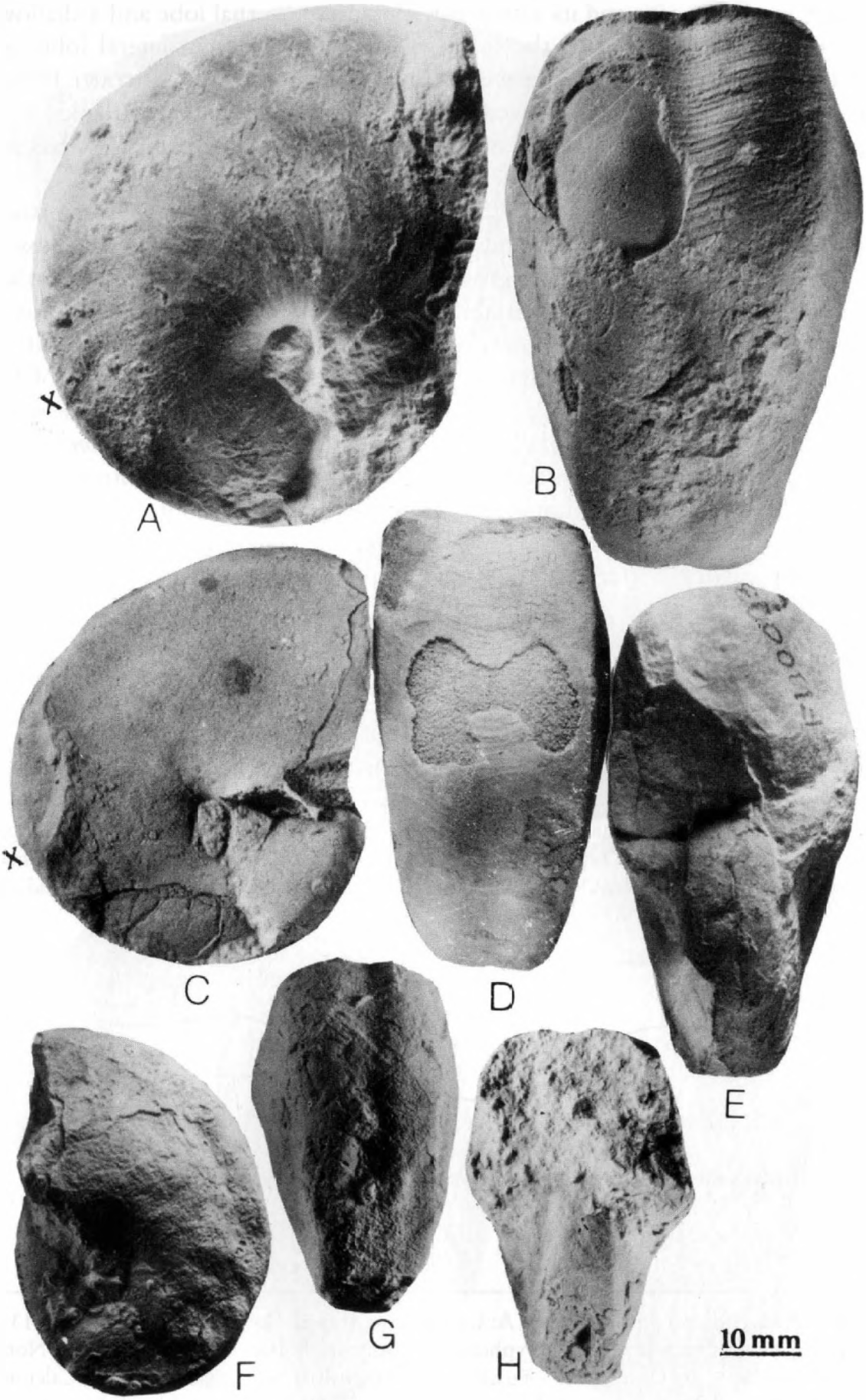

Fig. 5 (Legend see p. 550)

much smaller in size and its suture is with a deep external lobe and a shallow lateral lobe as opposed to the shallow external and deeper lateral lobes in *P. prohexagonum*. *P. dorso-excavatum*, another dwarf species (TINTANT 1984), is also close to the present species in having sulcate venter and flanks, and particularly two transverse ribs near the aperture, but it is smaller and has an occluded umbilicus and a shallow lateral lobe.

The similarities between the Early to Middle Callovian genus *Cymatonautilus* and the present species is wide and extensive. Both are characterized by a relatively wide umbilicus and grooved laterals and venter. *Cymatonautilus* shows a narrow intraspecific variability and has recently been interpreted as a fleeting genus which cryptogenically appeared during a very short interval of time with wide dispersal (HALDER & BARDHAN 1996b). A recent find of *C. collignoni* from the overlying horizon in Kutch is closely comparable with the ribbed inflated variant of *P. prohexagonum*. However, *C. collignoni* bears all-around ribbing from an early ontogeny and has a deeper ventral sulcus. This morphological and stratigraphical discontinuities prompted HALDER & BARDHAN (1996b) to consider *P. prohexagonum* to have been the precursor and the evolution perhaps took place in a punctuated manner through peramorphosis.

Paracenoceras noetlingi n. sp.

Fig. 6; Fig. 7; Fig. 8.

1897 *Nautilus giganteus* D'ORBIGNY – NOETLING, p. 8, pl. 4, fig. 5.

Material: The holotype, described by NOETLING (1897) from the Polyphemus Limestone of Mazar Drik, Baluchistan is kept in the Repository section of the Geological Survey of India, Calcutta (Type no. 2913). It is refigured here in Fig. 7A and 8A. Two other specimens from the Lower Oolite Polyphemus beds of Mazar Drik are now in the Indian

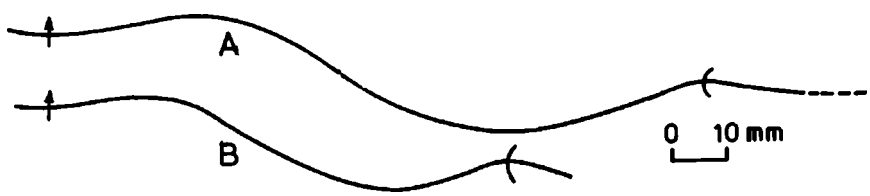

Fig. 6. Septal suture of *Paracenoceras noetlingi* n. sp. **A**: GSI Type No. 2913. **B**: FI 10110.

Fig. 7. *Paracenoceras noetlingi* n. sp. **A**: Lateral view of the holotype (GSI Type No. 2913). Septate, internal mould; from Polyphemus Limestone, Mazar Drik, Baluchistan. Note large umbilicus. **B, C**: Septate, internal mould; reposited in Indian Museum, Calcutta (H 48/658), collected from Polyphemus Limestone, Mazar Drik, Baluchistan. Lateral and apertural views. Note dorso-central siphuncle indicated by arrow (C).

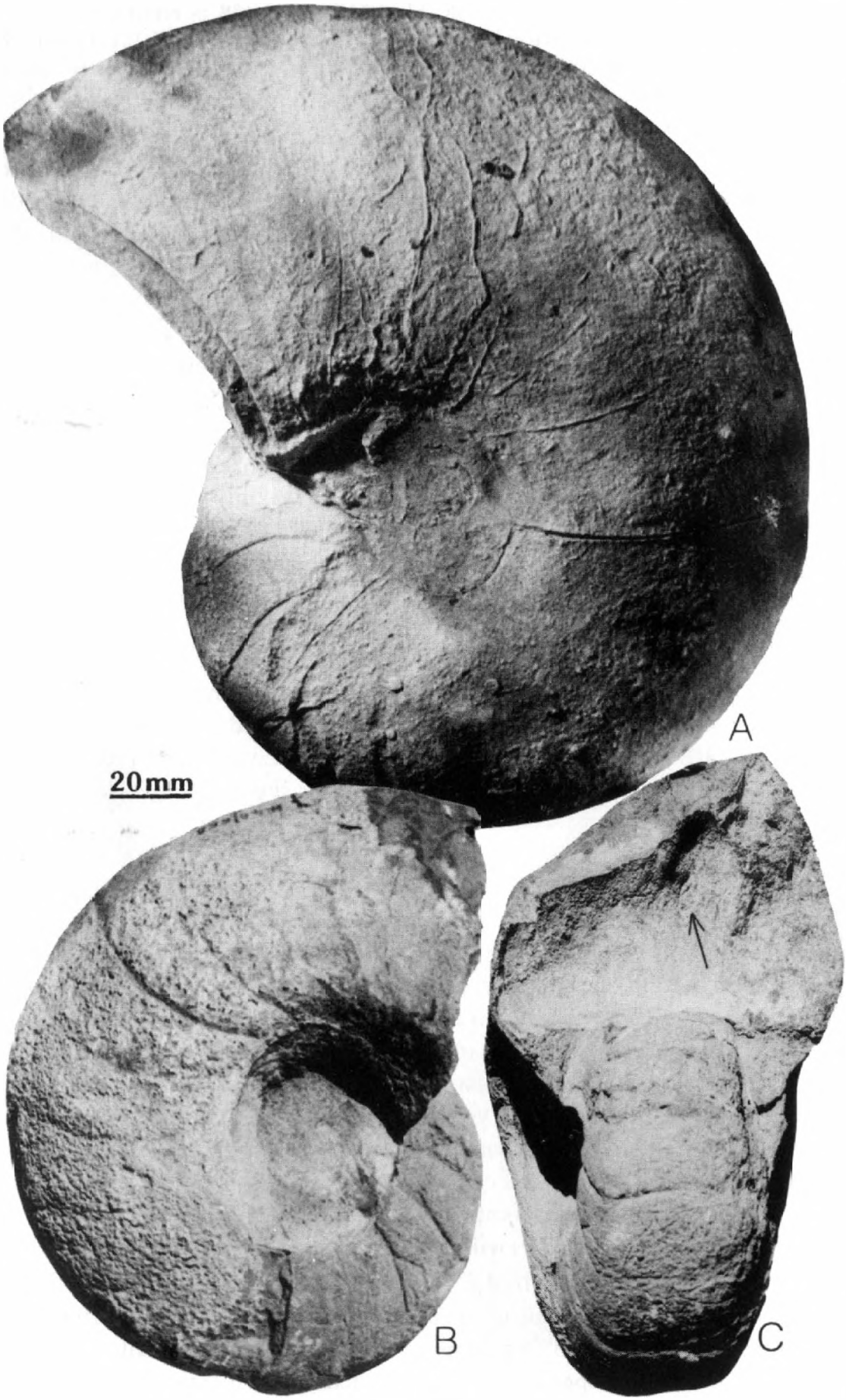

Fig. 7 (Legend see p. 552)

Museum, Calcutta (Type nos. H.48/658, H.48/817). H.48/658 is reproduced here in Fig. 7B, C and Fig. 8B. We have collected two specimens (FI 10110, FI 10111) from the cream-coloured limestone (Bed no. 4) in Jumara. All the specimens are mostly internal moulds and still septate except H.48/817, which retains a small part of the body chamber.

Description: Mostly internal mould, large size, maximum being 235 mm in diameter, still septate. Shell somewhat evolute (U/D = 0.2-0.3), umbilicus with steep wall, slightly overhanging near the dorsum. Flanks arched with broadly rounded ventrolateral and umbilical margins. Venter slightly arched to flat. Aperture sub-elliptical to sub-circular with width greater than height (W/H = 1.06-1.44). Siphuncle large (10 mm diameter), position wandering but always below the centre of the septum. Suture with very shallow ventral lobe and shallow, broad lateral lobe covering almost entire flank. Umbilical saddle very small, rounded near the umbilical margin. Sutural spacing wide (about 10 to 11 septa in a half-whorl from a diameter of 176 mm). Surface seems to be smooth with fine growth-conformable striae. Body chamber missing.

Discussion: The species is rare and reported so far only from Baluchistan as *Nautilus giganteus* D'ORBIGNY (NOETLING 1897). But true *Paracenoceras giganteum* (D'ORBIGNY) comes from the Upper Jurassic (Oxfordian) sequence in Europe (TINTANT 1987) and Kutch (HALDER & BARDHAN 1996a). NOETLING showed remarkable correspondence between his specimen and the European form which we do not. Besides morphologic differences there is stratigraphic heterochroneity between them. The holotype and other Baluchistan specimens, judging from their associated ammonoid taxa represent a Late Bathonian age (WESTERMANN & CALLOMON 1988). Kutch forms are morphologically indistinguishable from them and are also from the Upper Bathonian sequence.

P. noetlingi is comparable in size with other giant forms like *P. giganteum* (D'ORBIGNY), *P. hexagonum* ♀ (SOWERBY), *P. ennianum* (DACQUE), *P. calloviense blakei* (JEANNET) etc. Being large in size and openly umbilicate *P. giganteum* resembles *P. noetlingi* but differs in having a sulcate venter angular ventrolateral margins and deep ventral lobes.

Paracenoceras hexagonum ♀ is comparable in size with the present species but differs in having relatively smaller umbilicus, sulcate venter, sub-trapezoidal whorl section, subangular umbilical and ventrolateral margins and closely spaced septa with deeper ventral lobe.

SPATH (1927) noted that *P. ennianum* having flat venter even at a greater diameter than *P. hexagonum*, is closer to the present species but *P. ennianum* seems to have very angular ventrolateral margins and a much compressed section as obvious from the drawing in KUMMEL (1956, fig. 19).

We reported a macroconch of *P. calloviense* from Kutch although it differs in some aspects from its European counterpart (BARDHAN et al. 1994b). It differs from *P. noetlingi* by its involute shell of relatively smaller diameter (largest recorded adult specimen 190 mm in diameter while the present species is still septate) and stronger sinuosity in sutural pattern. European *P. callo-*

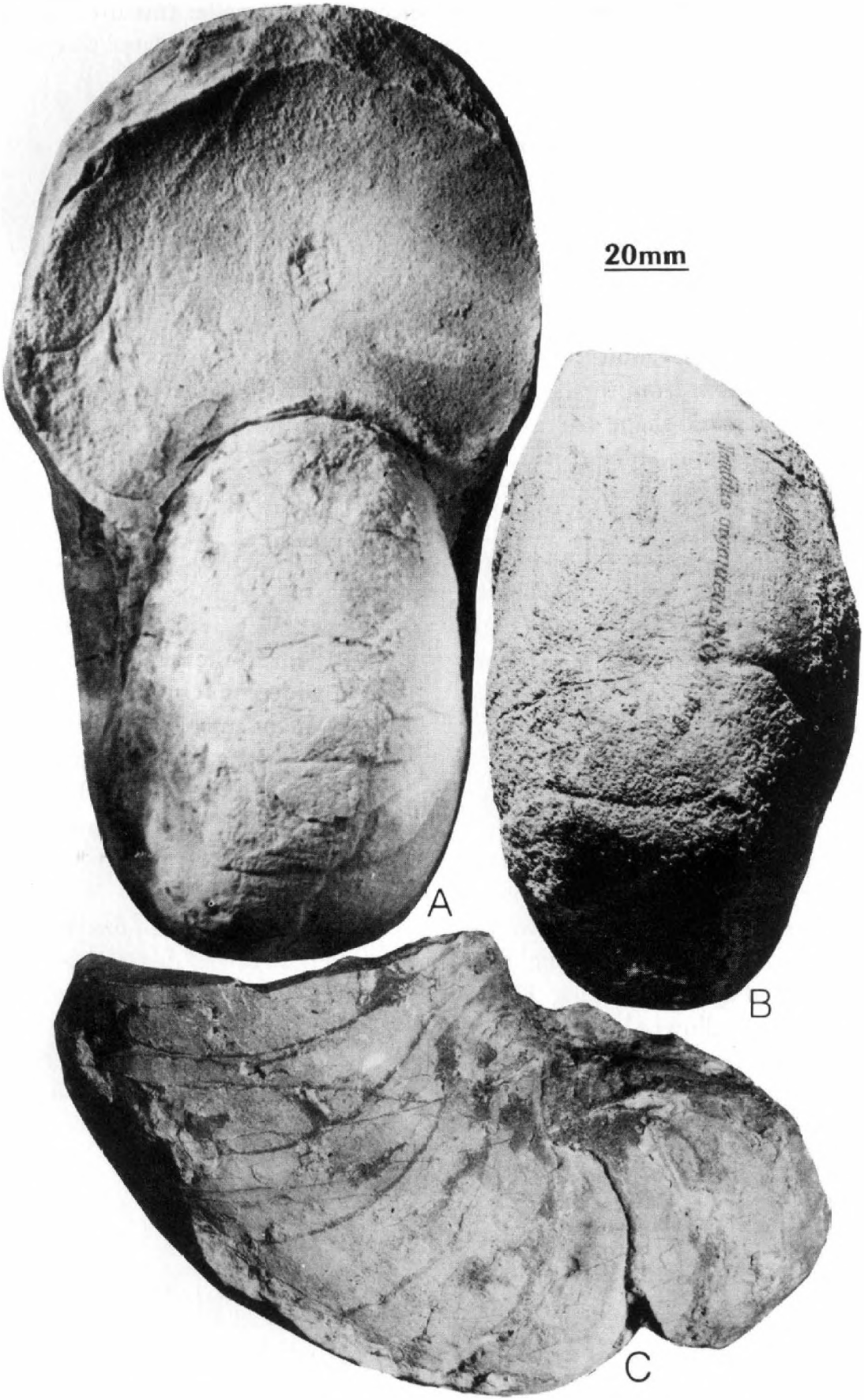

Fig. 8. *Paracenoceras noetlingi* n. sp. **A**: Apertural view of the holotype (GSI Type No. 2913) with dorso-central siphuncle. **B**: Ventral view of H48/658, reposited in Indian Museum, Calcutta. **C**: Septate specimen (FI 10110) from Bed no. 4 of Jumara. Lateral view.

viense blakei differs from the present species being smaller (matured phragmocone diameter 150 mm) and having sulcate venter in later ontogeny (TINTANT 1969).

Paracenoceras n. sp. A

Fig. 9; Fig. 10.

Material: Single specimen (FI 10120) collected from Bed no. 4 of Jumara, Kutch. Matured phragmocone, internal mould with shell remains.

Description: Highly inflated, strongly involute matured phragmocone with partially preserved body chamber. Maximum diameter observed being 90 mm which marks the adult end-phragmocone stage. Body chamber extremely short as evident from the trace of it, occupying only less than 1/3 of the last whorl. Apertural shape varies considerably during ontogeny, phragmocone at diameter 73 mm subrectangular, slightly depressed (W/H = 1.2). Whorl expands suddenly at diameter 85 mm near the end-phragmocone stage and becomes sub-trapezoidal, highly depressed (W/H = 1.6 at 88 mm diameter). Maximum flaring at umbilical margin giving rise to subangular umbilical shoulder. Whorl sides rounded to flattish in early stage, becoming slightly concave during maturity, converging always towards venter. Venter slightly arched, ventral width remains more or less constant in the major part of the last whorl but widens when shell starts sudden widening. Umbilicus remains occluded during much of the ontogeny, except slight uncoiling of the adult body chamber; umbilical wall increasingly steeper during growth. Suture not well-exposed, with deep lateral lobe and very shallow ventral lobe. Last few septa show approximation. The specimen is mostly an internal mould with shell remains; surface ornamentation as growth-conformable striae seen only on the venter with strong hyponomic sinus.

Discussion: The present form can be compared with *P. marocense* MILLER & COLLINSON in having slightly arched venter, strongly depressed whorl section and apertural flaring. However, the latter is openly umbilicate and its suture has shallower lateral lobe. The sulcate venter of *P. marocense* s.s. at its early ontogeny cannot be compared with the Kutch form as we are having a single specimen. Besides, MILLER & COLLINSON's species is reported from a much younger stratigraphic horizon in the Upper Jurassic.

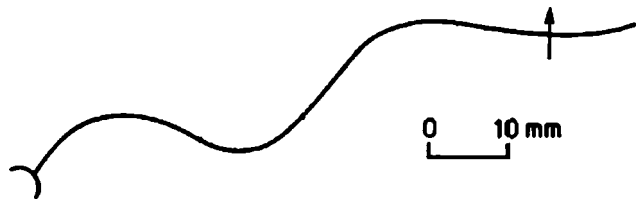

Fig. 9. Septal suture of *Paracenoceras* n. sp. A. (FI 10120).

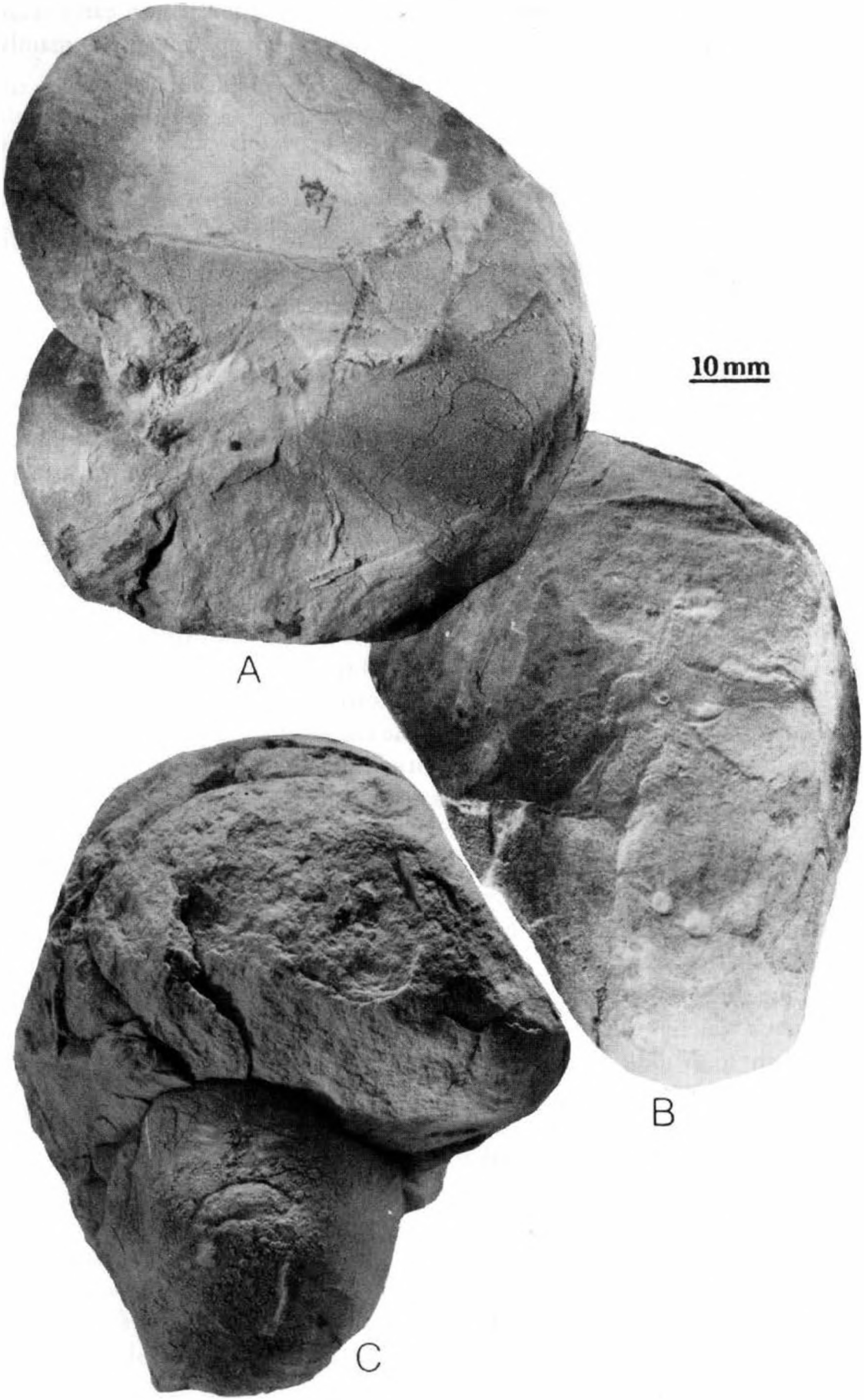

Fig. 10. *Paracenoceras* n. sp. A. Holotype, FI 10120, with shell remains, very small part of the body chamber preserved. Lateral (**A**), ventral (**B**) and apertural (**C**) views. Note extreme flaring at the end-phragmocone stage.

P. calloviense ♂ resembles the present species particularly in early stage and has stratigraphic contemporaneity. But the present species differs mainly in having depressed, flared adult body whorl and more sinuous suture.

Remarks

The present three species co-occur in a restricted horizon within a single locality, together with previously described *P. jumarense* and *P. calloviense*. These forms are the primitive paracenoceratids and the majority of them appeared simultaneously during the Late Bathonian time indicating a speciation event. *P. prohexagonum* appeared in the underlying coral biostrome, Bed 1 (Fig. 2) and continued upto this horizon. From it derived entirely a new genus *Cymatonautilus* during the late Early Callovian, which had a quick, wide geographic dispersion like a fleeting genus (HALDER & BARDHAN 1996b).

The larger clade, i. e., the post-Triassic nautiloids also had a rapid early expansion of diversity. *Cenoceras*, the only surviving genus that was able to cross the Triassic-Jurassic boundary, seemed to occupy what KUMMEL (1956, 1964) called "an ecologic vacuum" and showed a diversity explosion after the end-Triassic mass-extinction event. Out of 93 species 60 appeared in the Early Jurassic with world-wide distribution (TEICHERT & MATSUMOTO 1987) and the adaptive radiation was complete by the end of the Middle Jurassic. These species had the evolutionary potentiality to give rise to higher taxonomic categories. 4 out of 5 Mesozoic families arose from the *Cenoceras* stock during this short interval of time (KUMMEL 1964).

Paracenoceras, a genus of these newly evolved families, showed similar divergent speciation event. It arose during Middle Jurassic and by the end of Jurassic most of the species (35 out of 36) evolved (KUMMEL 1956).

In Kutch, *Paracenoceras* forms which lasted for a considerable geological time show remarkable morphological constancy (Fig. 3). For example, *P. calloviense* which is the most dominant species in Kutch and spanned the Late Bathonian to Middle Callovian showed remarkable morphological stasis (BARDHAN et al. 1994b). *P. prohexagonum* also remained relatively unchanged from the Late Bajocian to Late Bathonian (see also SPATH 1935 and TINTANT 1987). It is interesting to note that the longer geological distribution and remarkable constancy of form in paracenoceratid phylogeny was already noticed by WAAGEN (1873-1875). Other species, e. g., *P. kumagunense* spans the entire Callovian without any significant phyletic change (SPATH 1927-1933). *P. jumarense*, however, lasted briefly and restricted only within the Upper Bathonian. It appears, therefore, that the pattern of evolution in paracenoceratid lineage involves cladogenesis and is compatible with the punctuational model of evolution as proposed by ELDREDGE & GOULD (1972) and GOULD & ELDREDGE (1977).

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Table 1. Measurements (in mm) of *Paracenoceras prohexagonum* SPATH, *P. noetlingi* n. sp. and *P.* n. sp. A. **D** = Diameter, **U** = Umbilical diameter, **W** = Width, **H** = Height.

Name of the species	Specimen No.		D	U	W	H
P. prohexagonum	FI 10002	peristome	72	10	47	41
		body chamber	62	9	40	35
	FI 10003	peristome	65	9	36	37
		body chamber	53	7	27	30
	FI 10004	immature body chamber	45	6	26	25
		early stage	31	5	18	16
P. noetlingi n. sp.	GSI Type No. 2913	phragmocone	235	47	129	114
	Museum sp. No. H48/658	phragmocone	162	47	94	75
			106	33	58	50
	Museum sp. No. H48/817	end-phragmocone	151	31	92	87
		phragmocone	107	23	72	50
	FI 10110	phragmocone	195	47	107	98
	FI 10111	phragmocone	176	39	110	85
			166	37	–	76
P. n. sp. A	FI 10120	end-phragmocone	90	–	80	50
		phragmocone	73	–	48	40

References

AGER, D. V. (1984): The nature of the stratigraphical record. – 122 p.; Hong Kong (Macmillan Publishers Ltd.).

BARDHAN, S.; DATTA, K.; KHAN, D. & BHAUMIK, D. (1988): Tulitidae genus *Bullatimorphites* from Upper Bathonian Patcham Formation, Kutch, India. – Newsl. Stratigr., 20: 21-27; Berlin, Stuttgart.

BARDHAN, S.; DATTA, K.; JANA, S. K. & PRAMANIK, D. (1994a): Dimorphism in *Kheraiceras* SPATH from the Callovian Chari Formation, Kutch, India. – J. Paleont., **68** (2): 287-293; Ohio.

BARDHAN, S.; HALDER, K. & JANA, S. K. (1994b): Earliest sexual dimorphism in Nautiloidea from the Jurassic of Kutch, India. – N. Jb. Geol. Paläont. Abh., **193**: 287-309; Stuttgart.

BISWAS, S. K. (1977): Mesozoic rock stratigraphy of Kutch, Gujarat. – Quart. J. Geol. Min. Met. Soc. India, **49**, 3-4: 1-51; Calcutta.

CALLOMON, J. H. (1981): Dimorphism in ammonoids. – In: HOUSE, M. R. & SENIOR, J. R. (Eds.): The Ammonoidea: The evolution, classification, mode of life and geological usefulness of a major fossil group. – Syst. Assoc. sp. vol. **18**: 257-273; London (Academic Press).

– (1993): On *Perisphinctes congener* WAAGEN, 1875, and the age of the Patcham Limestone in the Middle Jurassic of Jumara, Kutch, India. – Geol. Bl. No - Bayern, **43**: 227-246.

CARIOU, E. (1984): Biostratigraphic subdivision of the Callovian Stage in the subtethyan province of ammonites, correlations with the subboreal zonal scheme. – In: MICHELSEN, O. & ZEISS, A. (Eds.): International Symposium on Jurassic Stratigraphy. – Geol. Surv. Denmark, **2**: 315-326; Copenhagen.

DATTA, K. (1992): Facies, fauna and sequence: an integrated approach in the Jurassic Patcham and Chari Formations, Kutch, India. – Unpubl. Ph. D. thesis, Jadavpur University, 167p.; Calcutta.

DATTA, K.; BHAUMIK, D.; JANA, S. K. & BARDHAN, S. (1996): Age, ontogeny and dimorphism of *Macrocephalites triangularis* SPATH - the oldest macrocephalitid ammonite from Kutch, India. – J. Geol. Soc. India, **47**: 447-458; Bangalore.

ELDREDGE, N. & GOULD, S. J. (1972): Punctuated equilibria: an alternative to phyletic gradualism. – In: SCHOPF, T. J. M. (ed.): Models in Paleobiology: 82-115; San Francisco (Freeman, Cooper and Co.).

GOULD, S. J. & ELDREDGE, N. (1977): Punctuated equilibria: the tempo and mode of evolution reconsidered. – Paleobiology, **3**: 115-151; Lawrence.

HALDER, K. & BARDHAN, S. (1996a): The Oxfordian (Upper Jurassic) nautiloid fauna of Kutch, western India. – N. Jb. Geol. Paläont. Abh., **201**: 17-32; Stuttgart.

– (1996b): The fleeting genus *Cymatonautilus* (Nautiloidea): new record from the Jurassic Chari Formation, Kutch, India. – Can. J. Earth Sci., **33**: 1007-1010; Ottawa.

KENNEDY, W. J. & COBBAN, W. A. (1976): Aspects of ammonite biology, biogeography, and biostratigraphy. – Sp. Papers Palaeont., **17**: 1-94.

KLINGER, H. C. & KENNEDY, W. J. (1989): Cretaceous faunas from Zululand and Natal, South Africa. The ammonite family Placenticeratidae HYATT, 1900; with comments on the systematic position of the Genus *Hypengonoceras* SPATH, 1924. – Ann. S. African Mus., **98**: 242-399.

KUMMEL, B. (1956): Post-Triassic nautiloid genera. – Bull. Mus. Comp. Zool. Harvard College, **114** (7): 494p.; Cambridge & Massachusetts.

– (1964): Nautiloidea - Nautilida. – In: MOORE, R. C. (Ed.): Treatise on Invertebrate Paleontology. – Geol. Soc. America, and Univ. Kansas Press, Pt. K, Mollusca **3**: K383-K466; Lawrence.

MITRA, K. C.; BARDHAN, S. & BHATTACHARYA, D. (1979): A study of Mesozoic stratigraphy of Kutch, Gujarat, with special reference to rock-stratigraphy and biostratigraphy of Keera dome. – Bull. Indian Geol. Assoc., **12** (1): 129-143; Chandigarh.

NATH, R. (1932): A contribution to the stratigraphy of Cutch. – Quart. J. Geol. Min. Met. Soc. India, **4**: 161-174; Calcutta.

NOETLING, F. (1897): Fauna of the Kellaways of Mazar Drik. – Palaeont. Ind., mem., ser. 16, 1 (1): 1-22; Calcutta (Geol. Surv. India).

SPATH, L F. (1927-1933): Revision of the Jurassic cephalopod fauna of Kachh (Cutch). – Palaeont Ind., new ser. 9 (2): 945p.; Calcutta (geol. Surv. India).

– (1935): Jurassic and Cretaceous Cephalopoda. The Mesozoic palaeontology of British Somaliland. – Geol. Palaeont. British Somaliland, 2: 205-228; London (Govt. of Somaliland Protectorate).

TEICHERT, C. & MATSUMOTO, T. (1987): The ancestry of the genus *Nautilus*. – In: SAUNDERS, W. B. & LANDMAN, N. H. (Eds.): *Nautilus*: the biology and paleobiology of a living fossil: 25-32; New York & London (Plenum Press).

TINTANT, H. (1969): Un cas de dimorphisme chez les *Paracenoceras* (Nautiloidea) du Callovien. – In: WESTERMANN, G. E. G. (ed.): Sexual dimorphism in fossil Metazoa and taxonomic implications. – IUGS, series A., 1: 167-184; Stuttgart.

– (1970): Les "Nautiles à côtes" du Jurassique. – Ann. Paleont. Invert., 55 (1): 53-96; Paris.

– (1984): Exemples de nanisme spécifique chez les Nautiloidés du genre *Paracenoceras* au Jurassique moyen. – Géobios, mém. sp., 8: 403-410; Lyon.

– (1987): Les Nautiles du Jurassique d'Arabie Saoudite. – Géobios, mém. sp., 9: 67-129; Lyon.

WAAGEN, W. (1873-1875): Jurassic fauna of Kutch. The Cephalopoda. – Palaeont. Ind., ser. 9 (1): 247p.; Calcutta (Geol. Surv. India).

WESTERMANN, G. E. G. & CALLOMON, J. H. (1988): The Macrocephalitinae and associated Bathonian and Early Callovian (Jurassic) ammonoids of the Sula Islands and New Guinea. – Palaeontographica, Abt. A, 203: 1-90; Stuttgart.

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