

## Original article

Sexual dimorphism and polymorphism in a Callovian *Phlycticeras*  
(*Ammonoidea*) assemblage of Kutch, India<sup>☆</sup>*Dimorphisme sexuel et polymorphisme dans un assemblage callovien de Phlycticeras*  
(*Ammonoidea*) de Kutch, IndeSubhendu Bardhan<sup>\*</sup>, Sudipta K. Jana, Pinaki Roy

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**Abstract**

An assemblage of *Phlycticeras* Hyatt from a precisely dated zone of Middle Callovian in Kutch, India has been analyzed. Systematic study reveals that this sample can be divided into two size groups. The larger set shows different adult modifications leading to ornamental polymorphism. Polymorphs are very similar, if not identical, to different chronospecies of Europe, which range between Middle to Upper Callovian. They are grouped under well-known *Phlycticeras polygonium* (Zieten). The group of smaller specimens on the other hand, strongly resembles a species, which has been previously described as *Phlycticeras schauburgi* (Waagen) from the younger Upper Callovian horizons in Kutch. It has a peculiar ‘rooster’-like septacrinat keel in the venter near adult aperture. *Phlycticeras-Oecoptychius* have been considered as a possible dimorphic pair since long, but here shown to have many inconsistencies to support these views. Instead, sexual dimorphism is explored within *Phlycticeras* and *P. polygonium-P. schauburgi* is proposed as possible antidimorphs. A similar association is found in different stratigraphic assemblages of Europe. Interestingly these two morphs show parallel evolutionary changes within the *Phlycticeras* genus.

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**Keywords:** *Phlycticeras*; Callovian; Kutch; Polymorphism; Sexual dimorphism**Résumé**

Un assemblage de *Phlycticeras* Hyatt provenant d'une zone précisément datée du Callovien moyen de Kutch, Inde, a été analysé. L'étude systématique révèle que cet échantillon peut être divisé en deux groupes de taille. Les spécimens les plus grands montrent différentes modifications adultes menant à un polymorphisme ornemental. Les polymorphes sont très semblables, sinon identiques à différentes chrono-espèces d'Europe distribuées entre le Callovien moyen et supérieur. Elles sont regroupées ici au sein de l'espèce bien connue *Phlycticeras polygonium* (Zieten). D'un autre côté, le groupe de spécimens de plus petite taille ressemble fortement à une espèce décrite précédemment sous le nom de *Phlycticeras schauburgi* (Waagen) des horizons d'âge Callovien supérieur de Kutch. Elle possède un « rooster » particulier – une sorte de quille septacrinat ventrale, près de l'ouverture adulte. Depuis longtemps, *Phlycticeras-Oecoptychius* est considéré comme un possible couple dimorphe ; nous montrons ici que plusieurs incohérences discréditent cette hypothèse. En revanche, nous explorons le dimorphisme sexuel au sein du genre *Phlycticeras* et proposons la paire *P. polygonium-P. schauburgi* comme possibles antidimorphes. La même association est rencontrée dans différents assemblages stratigraphiques d'Europe. De façon remarquable, ces deux morphes montrent des changements évolutifs parallèles au sein du genre *Phlycticeras*.

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**Mots clés :** *Phlycticeras* ; Callovien ; Kutch ; Polymorphisme ; Dimorphisme sexuel**1. Introduction**

*Phlycticeras* Hyatt, 1900 is an important Middle Jurassic ammonite genus. It is neither diverse nor abundant but has a

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wide biogeographic distribution. Because of this, *Phlycticeras* helps in interprovincial correlation.

*Phlycticeras* was mostly described as ancillary taxa by the early workers while writing monographs due to paucity of specimens, but recently Schweigert and Dietze (1998) and Schweigert et al. (2003) comprehensively dealt with the phylogeny, dimorphism and palaeobiogeography of *Phlycticeras* based on numerous recent information. *Phlycticeras* is now believed to have ranged from the Upper Bajocian to Upper Callovian. The lineage, which consists of only few chronospecies, is characterized by phyletic anagenesis (Schweigert and Dietze, 1998). The early species (Bajocian–Bathonian) are mostly restricted to different areas of western Tethys. During the Callovian, *Phlycticeras* spread to Mexico (Sandoval et al., 1990), Kutch (Waagen, 1875; Spath, 1928; Jain, 1997), and other areas (Arkell et al., 1957).

The present Kutch collection, which includes a sizable sample of varying states of preservation as well as ontogenetic stages, have been made from three successive beds which belong to the Anceps Zone of the Middle Callovian. The population shows stunning variability in terms of shell shape and nature of ornamentation. The total range of intraspecific variation of Kutch population encompasses the forms, which closely resemble three different species of the Middle–Upper Callovian in Europe. These European species are *P. polygonium* (Zieten), *P. pustulatum* (Reinecke) and *P. waageni* Buckman. In a recent work Schweigert and Dietze (1998) have reevaluated these species and established their biostratigraphic distribution. *P. polygonium* has been found in the Jason Zone of the Middle Callovian, while *P. pustulatum* and *P. waageni* come from the Coronatum Zone, and Athleta Zone respectively (Schweigert and Dietze, 1998: fig. 2). They have considered these three species as chronospecies, which are highly variable and grade from one morph into another (Schweigert personal communication, 2008). Thus three successive chronospecies of Europe have been found in the same chronostratigraphic zone (Anceps Zone) in Kutch, which is precisely dated as the earlier Middle Callovian on the basis of other ammonite taxa, e.g., *Eucycloceras opis* (Sowerby), *Idiocycloceras perisphinctoides* Spath, and *Indosphinctes indicus* (Siemiradzki) (see also Jana et al., 2005). All the variants are distinct in ornaments,

connected by a few intermediate forms and they morphometrically overlap, thus the whole spectrum of variation in ornaments show discontinuous differences together with continuously expressed variation in size and shape. This phenomenon we have termed here as ornamental polymorphism (Reyment, 1988). The species which Waagen (1875) described as *Amaltheus pustulatus* and latter Spath (1928) described as *P. waageni* Buckman from Kutch also falls within the intraspecific range of variation of the present population. The population is described under *P. polygonium* as it is the oldest name and *P. pustulatum* and *P. waageni* have been considered as junior synonyms of *P. polygonium*. Other than *P. polygonium*, many other species have been described in Europe. For example, Mangold and Cariou (in Fischer, 1994) while revising d'Orbigny's (1847) material correctly designated 'Ammonites crastagallis' as *Phlycticeras*. This species however, strongly resembles European *P. polygonium* and Schweigert and Dietze (1998) synonymised the former with the later species. We have separately described *P. schauburgi* (Waagen), which co-occurs in the same beds with *P. polygonium* in Kutch. It is a smaller adult species with terminal modification of ventral keel. Both *P. polygonium* and *P. schauburgi* show little temporal changes and range up to the Upper Callovian in Kutch.

*Phlycticeras*–*Oecoptychius* Neumayr have been considered since long as the dimorphic pair. We have argued against this idea because of many morphological and stratigraphical inconsistencies. Instead, we here emphasize to seek dimorphism within *Phlycticeras* and propose dimorphism between *P. polygonium* [M] and *P. schauburgi* [m] in Kutch.

## 2. Geological setting

The Kutch basin was initiated during the Middle Jurassic fragmentation of Gondwana and soon began to receive a huge input of sediments due to repeated marine transgressions (Biswas, 1977). Jurassic rocks of Kutch are ranging in age from the Bajocian to Tithonian and cover nearly half of the area, including both the mainland and three 'islands' separated by an intervening expanse of salt flat locally known as the Rann (Fig. 1).

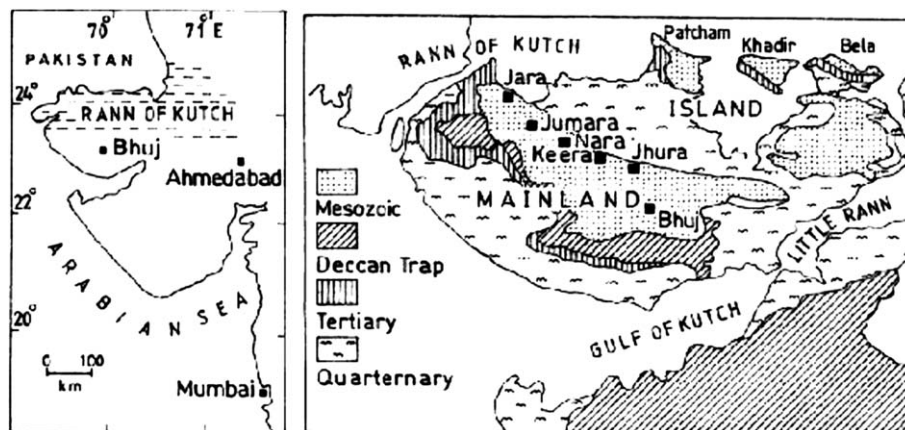


Fig. 1. Geological map of Kutch, showing the locality of Jara, Jumara, and Keera from where the present collection has been made.

The major lithostratigraphical units, in ascending order, are Patcham, Chari, Katrol and Bhuj formations. Among those the Patcham and Chari formations are present as inliers and are surrounded by the younger Katrol Formation. Despite the frequent spatiotemporal facies changes, ammonites are abundant in these two older formations (Jana et al., 2005). The Chari Formation is represented by a heterolithic facies association consisting of shale, limestone and sandstone, deposited in a mid-shelf environment. While the Lower Callovian part of the Chari Formation includes a dominantly shale-limestone (packstone/wackestone) association, the Middle Callovian starts with siliciclastics. Significant stratigraphical works and detailed facies analysis are now available (Datta, 1992; Fürsich et al., 1992; Fürsich and Oschmann, 1993; Jana et al., 2005). The arenaceous facies of the Middle Callovian represents a shoaling upward phase (Datta, 1992; Fürsich and Oschmann, 1993). This facies is monotonous in the field, consisting of yellowish grey sandstone that is commonly multistoreyed, massive with coarsening upward sequence and devoid of bioturbation. Close field study reveals the presence of three litho-units, i.e., a middle siltstone layer sandwiched between two sandstone beds. They are persistent, forming west-

east ridges on mainland Kutch, with increasing thickness and decreasing fossil-bearing horizons that reflect the direction of palaeoshoreline.

The specimens of the present study have been collected from Jara, Jumara and Keera sections of the Chari Formation. Phlycticeratin ammonites are mainly obtained from the three above-mentioned Middle Callovian beds of the Chari Formation. The distribution of two species of *Phlycticeras* and other co-occurring ammonite taxa in three sections are shown in Fig. 2.

### 3. Systematic palaeontology

Superfamily HAPLOCERATAE Zittel, 1884.

Family STRIGOCERATIDAE Buckman, 1924.

Subfamily PHLYCTICERATINAE Spath, 1925.

Genus *Phlycticeras* Hyatt, 1900.

**Type species:** *Ammonites pustulatus* Reinecke, 1818.

*Phlycticeras polygonium* (Zieten).

Figs. 3 and 4.

(Only important synonymy names are given; for detailed list see Schweigert and Dietze, 1998).

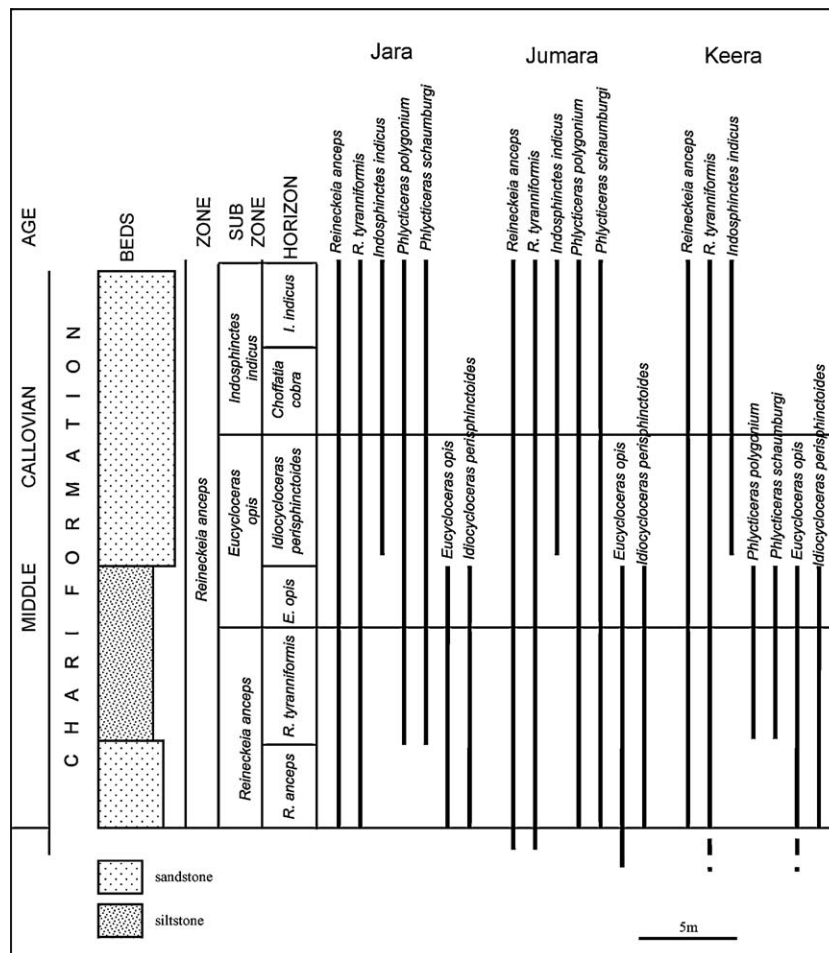


Fig. 2. Stratigraphic distribution of *Phlycticeras polygonium* and *P. schauburgi* along with other important ammonite species is shown against the regional lithostratigraphic units and biostratigraphic zonation of Kutch (sources for other ammonites distribution: Jain, 1997; Bardhan et al., 2002; Jana et al., 2005; Kayal personal communication, 2008).



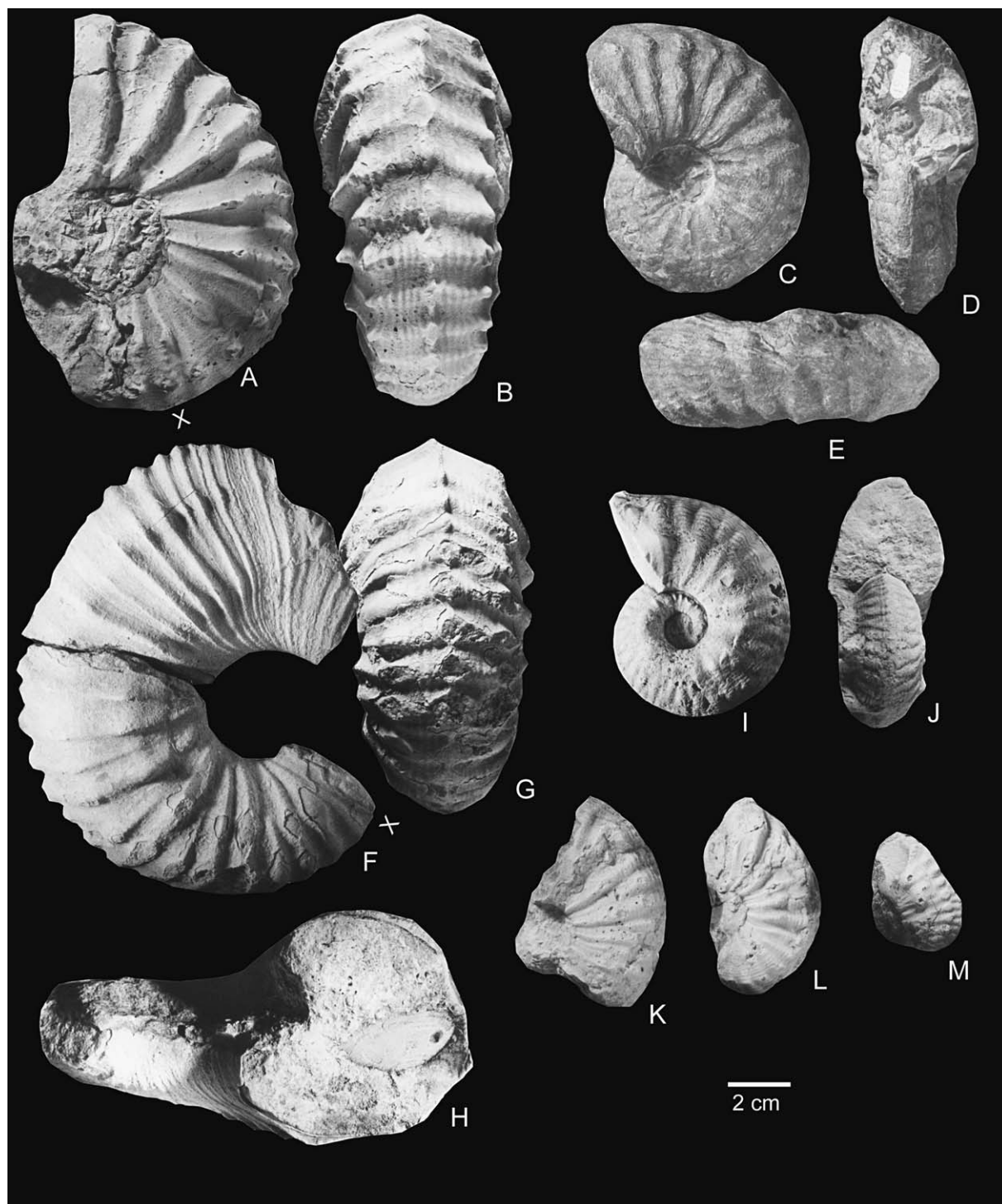


Fig. 3. *Phlycticeras polygonium* (Zieten). A–H. *Phlycticeras polygonium* var. *waageni*; A, B, lateral and ventral views respectively of specimen no. JUM/08/1, bed 6 of Keera; C–E, holotype, GSI (Geological Survey of India) Type no. 1915, from Athleta beds, far off north-east of Gudjinsir (Waagen, 1875); lateral (C), apertural (D) and ventral (E) views; fully septate, trace of the umbilical seam of body whorl indicates that body chamber occupied more than half of the outer whorl; F–H, near complete body chamber, phragmocone missing; note fine crowded ribs towards aperture (F) indicating mature modification; ventral (G) and apertural (H) views of the early part of the body chamber. Specimen no. JUM/08/N1, bed 4, Jara. I–M. *Phlycticeras polygonium*. Young individuals of different ontogeny; I, J, lateral and apertural views of specimen no. JUM/08/19, bed 3, Jara; K, lateral view of specimen no. 7, bed 4, Jara; L, lateral view of specimen no. JUM/08/12, bed 6, Keera; M, lateral view of specimen no. JUM/08/20, bed 4, Jara. Note polyschizotome ribbing.

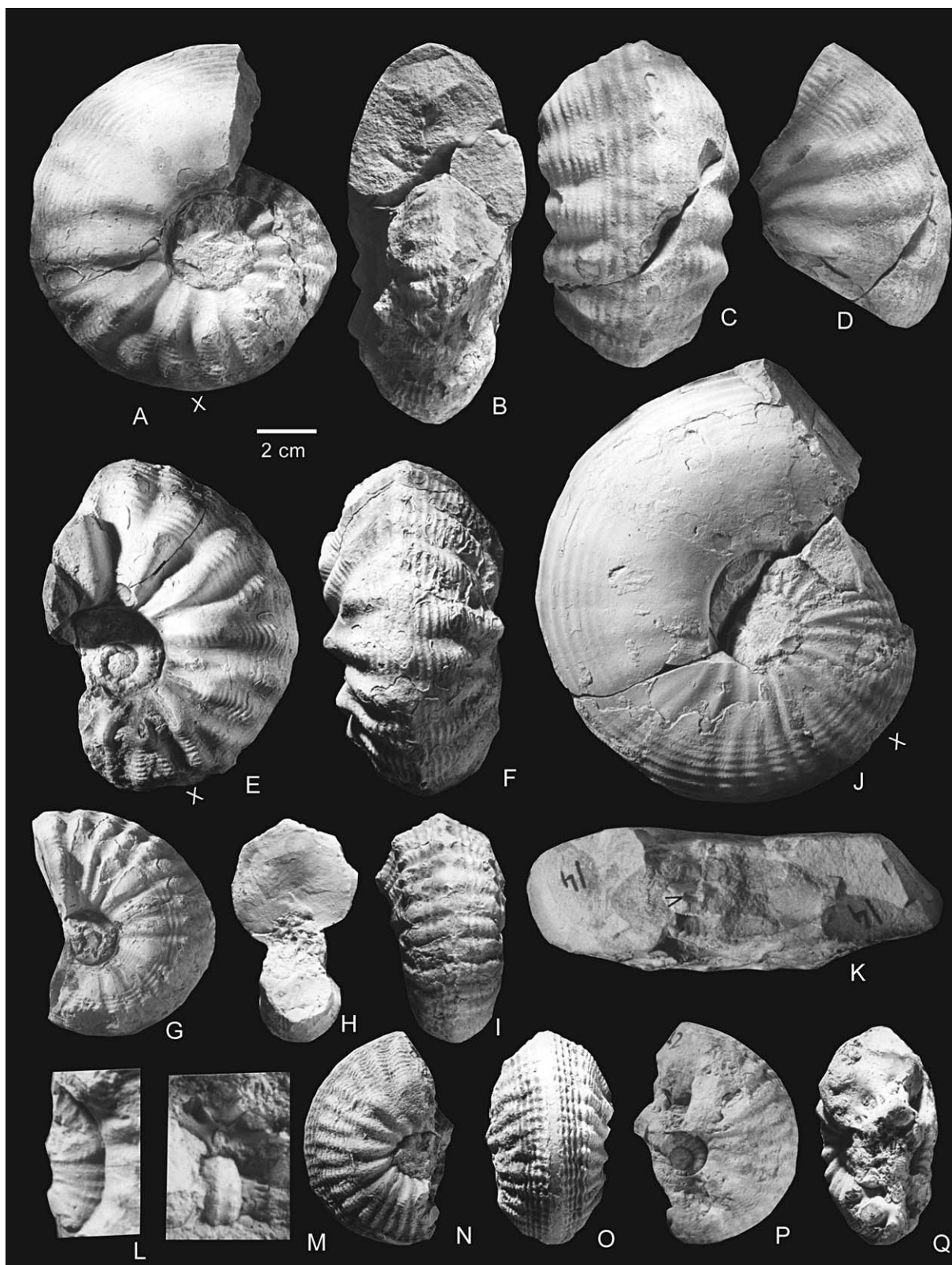


Fig. 4. *Phlycticeras polygonium* (Zieten). A–I. *Phlycticeras polygonium* var. *pustulatum*; A, B, lateral and apertural views. Specimen no. JUM/08/18, bed 10, Jumara; note weakening of radial ribs towards aperture (A); C, D, ventral and apertural views of body whorl fragment; specimen no. JUM/08/13, bed 4, Jara; E, F, lateral and ventral views of adult specimen; specimen no. JUM/08/15, bed 4, Jara; G–I shell with partially preserved body chamber; lateral (G), apertural (H) and ventral (I) views; specimen no. JUM/08/4, bed 6, Keera. J–M. *Phlycticeras polygonium* var. *polygonium*; J, K, lateral and apertural views of specimen no. JUM/08/14; near complete shell with three-fourths of the outer whorl occupied by body chamber; note disappearance of radial ribs, but strigation continues till to the preserved end; L, inner whorls of the same specimen showing ribbing on the flank,  $\times 2$ ; M, innermost whorl of the same specimen (see arrow in K); note presence of mid-ventral keel and ventrolateral tubercles,  $\times 2$ . N–Q. *Phlycticeras polygonium*; Young individuals of different ontogeny; N–Q, left lateral (N), ventral (O), right lateral (P) and apertural (Q) views of specimen no. JUM/08/N2, bed 9, Jara.

1846. *Ammonites pustulatus franconicus*–Quenstedt, p. 134, pl. 9, Fig. 22.
1847. *Ammonites pustulatus* Haan–d’Orbigny, pl. 154, Figs. 1–3.
1875. *Amaltheus pustulatus* (Reinecke)–Waagen, p. 40, pl. 9, Fig. 2.
1875. *Amaltheus polygonium* Zieten–von Ammon, S. 41.
1895. *Lophoceras polygonium* (Zieten)–Parona and Bonarelli, p. 91, pl. 2, Fig. 2.
1895. *Lophoceras lachati* n. f.–Parona and Bonarelli, p. 92, pl. 2, Fig. 3.
1915. *Strigoceras pustulatum* Rein–Loczy, p. 314, pl. 1, Fig. 3.
1919. *Strigoceras cristagalli* d’Orbigny sp.–Couffon, p. 22, pl. 13, Fig. 2.
1928. *Strigoceras polygonium* Zieten–Sayn and Roman, p. 150.
1928. *Phlycticeras waageni* S. Buckman–Spath, p. 90, pl. 13, Fig. 15.
1951. *Phlycticeras pustulatum* (Reinecke)–Jeannet, p. 105, pl. 32, Figs. 5–7.

1958. *Phlycticeras pustulatum* Reinecke var. *madagascariensis* nov.–Collignon, pl. 28, Figs. 113 and 114.
1967. *Phlycticeras polygonium* (Zieten)–Elmi p. 396.
1987. *Phlycticeras pustulatum* (Reinecke)–Callomon et al., p. 26 [Schicht 8a–d].
1988. *Phlycticeras polygonium* Zieten in Parona and Bonarelli–Cariou, Fig. 7.
1994. *Phlycticeras cristagalli* (d’Orbigny)–Mangold and Cariou, in Fischer, p. 141, pl. 60, Fig. 5.
1998. *Phlycticeras polygonium* (Zieten) var. *nodosum* Quenstedt–Schweigert and Dietze, p. 16, pl. 7, Fig. 5; pl. 8, Figs. 1–4 and 6–8.
1998. *Phlycticeras pustulatum* (Reinecke)–Schweigert and Dietze, pl. 9, Figs. 63 and 64.
1998. *Phlycticeras waageni* Buckman–Schweigert and Dietze, pl. 10, Fig. 1.

**Material:** The present study includes 17 specimens including the GSI (Geological Survey of India) type 1915. Measurements of the specimens are given in Table 1.

**Description:** Shell large, maximum diameter being 148 mm; inner whorls involute, becomes evolute in later whorls ( $U/D = 0.24$  to  $0.31$ ) and inflated ( $W/H = 0.73$  to  $1.0$ ). Umbilicus narrow, deep in inner whorls, margin gradual with steep wall. Innermost whorls (up to about 8 mm diameter traced) are also ribbed; primary ribs originate from either margin or slightly below the umbilical wall. Three rows of tubercles may appear at an early diameter of about 30 mm. Tubercles at the umbilical margin are prominent, which soon disappears at the later ontogeny, though still present in *P. polygonium* var. *pustulatum*. The other two rows of tubercles with variable strength, sometimes one is stronger than other, continue up to the adult stage. Primaries may bifurcate at the lateral tubercles and secondaries sometimes may furcate again at the ventrolateral tubercles, thus achieving a polyschizotome aspect. Secondaries, after crossing the ventrolateral margin, may go straight or slightly prorsiradiately towards the venter where they are interrupted by a smooth band at the mid-venter portion, which may be traced up to 80 mm diameter.

Adult end-phragmocone diameter may be attained at 95 mm. Adult body chamber assumes different morphologies leading to polymorphism and they show different kinds of mature modifications. *P. polygonium* var. *waageni* (number of adult specimens = 3) in early part of body chamber is strongly ribbed, mostly bifurcate with occasional short intercalatories. Two prominent rows of tubercles at the mid-flank and ventrolateral margin, the outer one being stronger. Tubercles are pyramidal in shape. Body whorl is highly inflated with polygonal whorl section; venter is broad, and obtusely fastigate with prominent discontinuous keel connected by lateral ribs that characterize the last two quarters of the body chamber. First quarter of the body chamber as well as entire phragmocone have a broad smooth tabulate venter. Last quarter of the body chamber includes ribs that become suddenly weak, but sharp and approximated. Longitudinal ribs are present at all stages of growth and are more prominent near the upper flank and ventral area.

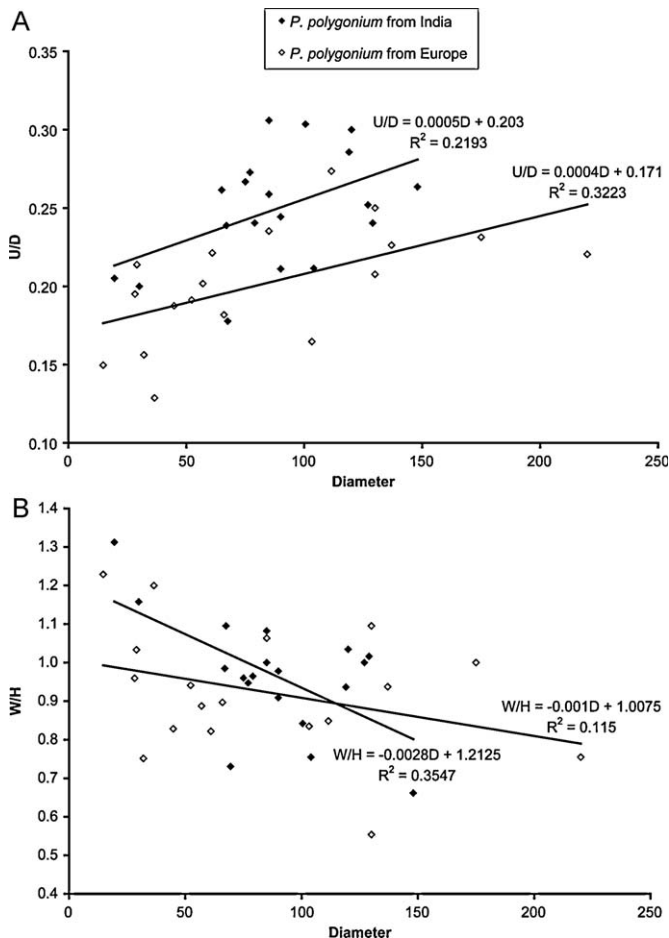


Fig. 5. Bivariate analysis involving degree of involution (umbilical diameter/shell diameter) vs. shell diameter (A) and degree of inflation (width/height) vs. shell diameter (B) of *Phlycticeras* spp. from Kutch as well as from Europe (other sources are: Waagen, 1875, Spath, 1928, Schweigert and Dietze, 1998, Schweigert et al., 2003).



Table 1

*Phlycticeras polygonium* (Zieten) dimensions. D = diameter of shell, U = umbilical diameter of shell, W = shell width, H = shell height.

Specimen no.	Description	Locality	D	U	W	H
JUM/08/01	Body chamber	Keera	127.00	32.00	63.00	63.00
JUM/08/10	Body chamber	Jara	100.50	30.50	48.00	57.00
JUM/08/15	Body chamber	Jara	120.00	36.00	60.00	58.00
JUM/08/16	Body chamber	Jumara	85.00	26.00	42.00	42.00
JUM/08/18	Phragmocone	Jumara	119.00	34.00	51.50	55.00
JUM/08/17	–	Jumara	–	–	53.00	64.00
JUM/08/04	Body chamber	Keera	85.00	22.00	46.00	42.50
JUM/08/N1	Body chamber	Jara	129.00	31.00	62.00	61.00
JUM/08/N2	Phragmocone	Jara	79.00	19.00	41.00	42.50
JUM/08/19	Phragmocone	Jara	77.00	21.00	36.00	38.00
JUM/08/11	Phragmocone	Jumara	62.00	16.00	32.50	31.00
JUM/08/14	Body chamber	Jara	148.00	39.00	45.00	68.00
JUM/08/08	Phragmocone	Jumara	75.00	20.00	24.00	25.00
JUM/08/07	Young specimen	Jara	–	–	31.00	38.00
GSI Type 1915	Phragmocone	Gudjinsir	90.00	22.00	44.00	45.00

*P. polygonium* var. *pustulatum* (number of adult specimens = 7) has early part of the body chamber equipped with two rows of tubercles, but umbilical tubercles are stronger and often forms bullae; the ribs are mostly bifurcating which fades after ventrolateral tubercles thus giving venter a look devoid of lateral ribs, but is characterized by strong and dense strigation. In the last quarter of the body chamber, ribs gradually become weak and may disappear. At the venter the strength of the serrated, discrete keel may attenuate, but continue till to the preserved end. Apertural whorl section varies from ovate to polygonal. Strigations present all throughout ontogeny; they appear incipiently near the lower flank, become more distinct towards the venter.

*P. polygonium* var. *polygonium* (number of adult specimens = 4) with almost no tuberculation at least in outer whorl of which the last three-fourth part is occupied by body chamber. Weak, mostly solitary ribs are present in the late phragmocone and early part of the body chamber. The ribs are mostly rectiradial, bifurcating and show sure sign of attenuation. In the last two-third of the body chamber ribs are weak to obsolete as evident both on shell remains and internal mould. The upper part of the flank and ventral area ornamented with prominent longitudinal ribs, which continue till to the end. Venter is abraded on the body chamber, which is relatively compressed with subtrapezoidal whorl section. Body chamber is also characterized by umbilical uncoiling.

**Remarks:** The variation in the degree of involution (umbilical diameter/shell diameter vs. shell diameter) and inflation (width/height vs. shell diameter) within the two populations of *P. polygonium* are shown in Fig. 5. It is clear that in both European and Indian populations, the shell becomes more evolute (Fig. 5(A)) and compressed (Fig. 5(B)) during ontogeny. The wide scattering of points especially in adult stage and relatively poor values of correlation coefficient are due to distinct adult variants, which show wide intraspecific variability with respect to these two morphometric characters. Intraspecific variability resulting in distinct adult forms has been termed as polymorphism and described in ammonites by many workers. For example, Tintant (1963, 1980) described

ornamental polymorphism in Kosmoceratidae and Dactyloceratidae, Meléndez and Fontana (1993) in Perisphinctidae and recently Gangopadhyay and Bardhan (2007) in the Cretaceous family Placenticeratidae. The phenomenon of polymorphism is commonly exhibited by discontinuous differences in ornament together with continuously expressed variation in size and shape (Reyment, 1988). Polymorphism as a modality of genetic intraspecific discontinuous variability (besides sexual dimorphism), has been the subject of much attention by many workers in palaeontological studies, e.g., in ostracods by Kamiya (1992) and Reyment (1988), and graptolites by Janusson (1973).

The variants although exhibit discontinuous variations in adult morphological characters, grade morphometrically. Moreover, all the variants have indistinguishable inner whorls and are stratigraphically coeval. For this, we have considered them as conspecific. *P. polygonium* var. *waageni* (Fig. 3(A–H)) corresponds well with the holotype of *P. waageni* (Fig. 3(C–E)) described from the younger Upper Callovian bed of Kutch (Waagen, 1875; Spath, 1928) as well as the European specimen (MBe 8324) of the same species from the similar stratigraphic horizon described by (Schweigert and Dietze (1998: pl. 10, Fig. 1). The holotype is a fully septate specimen while the European form is full-grown. Both the holotype of *P. waageni* and present variant have similar coarse solitary ribbing which are forwardly projected, and strong tuberculation. They also have similar mature modifications, e.g., ribs become relatively weak and approximated near the aperture.

The other present variant *P. polygonium* var. *pustulatum* of Kutch (Fig. 4(A–I)) is closely comparable with the European *P. polygonium* var. *nodosum* (Schweigert and Dietze, 1998: pl. 8, Figs. 1, 2, 4, 8) and some variants of *P. pustulatum* (Schweigert and Dietze, 1998: pl. 9, Figs. 1 and 2). Schweigert and Dietze (1998) also considered *P. polygonium* var. *nodosum* and *P. pustulatum* as closely related, but they separated the two species because of stratigraphic reason. The present variant resembles the European species in having relatively involute, tumid shell with coarse ornamentation. However, there are some forms which show relative weakening of ribs, widening of umbilicus and decrease in inflation – the typical features of

Table 2

*Phlycticeras schauburgi* (Zieten) dimensions. D = diameter of shell, U = umbilical diameter of shell, W = shell width, H = shell height.

Specimen no.	Description	Locality	D	U	W	H
JUM/08/05	Body chamber	Jumara	86.00	20.00	37.00	44.00
JUM/08/09	Body chamber	Jumara	–	–	32.00	45.00
JUM/08/E6	Body chamber	Jumara	–	–	23.00	35.00
JUM/08/12	–	Jumara	–	–	25.00	34.00
GSI type 1914	Body chamber	Gudjinsir	103.50	25.50	34.50	53.50

*P. polygonium* var. *polygonium* of Europe (Schweigert and Dietze, 1998: pl. 5, Fig. 1) as well as the third variant, *P. polygonium* var. *polygonium* described here (Fig. 4(J, K)).

In Europe these species (*P. polygonium*, *P. pustulatum* and *P. waageni*) range from Middle Callovian to Upper Callovian

and occur in succession (see Schweigert and Dietze, 1998: p. 31, Table 2). In Kutch they correspond to three variants of the same species, *P. polygonium*, which has a similar stratigraphic distribution. Unlike Europe, here, all the variants of *P. polygonium* are coeval and mostly co-occur in the same

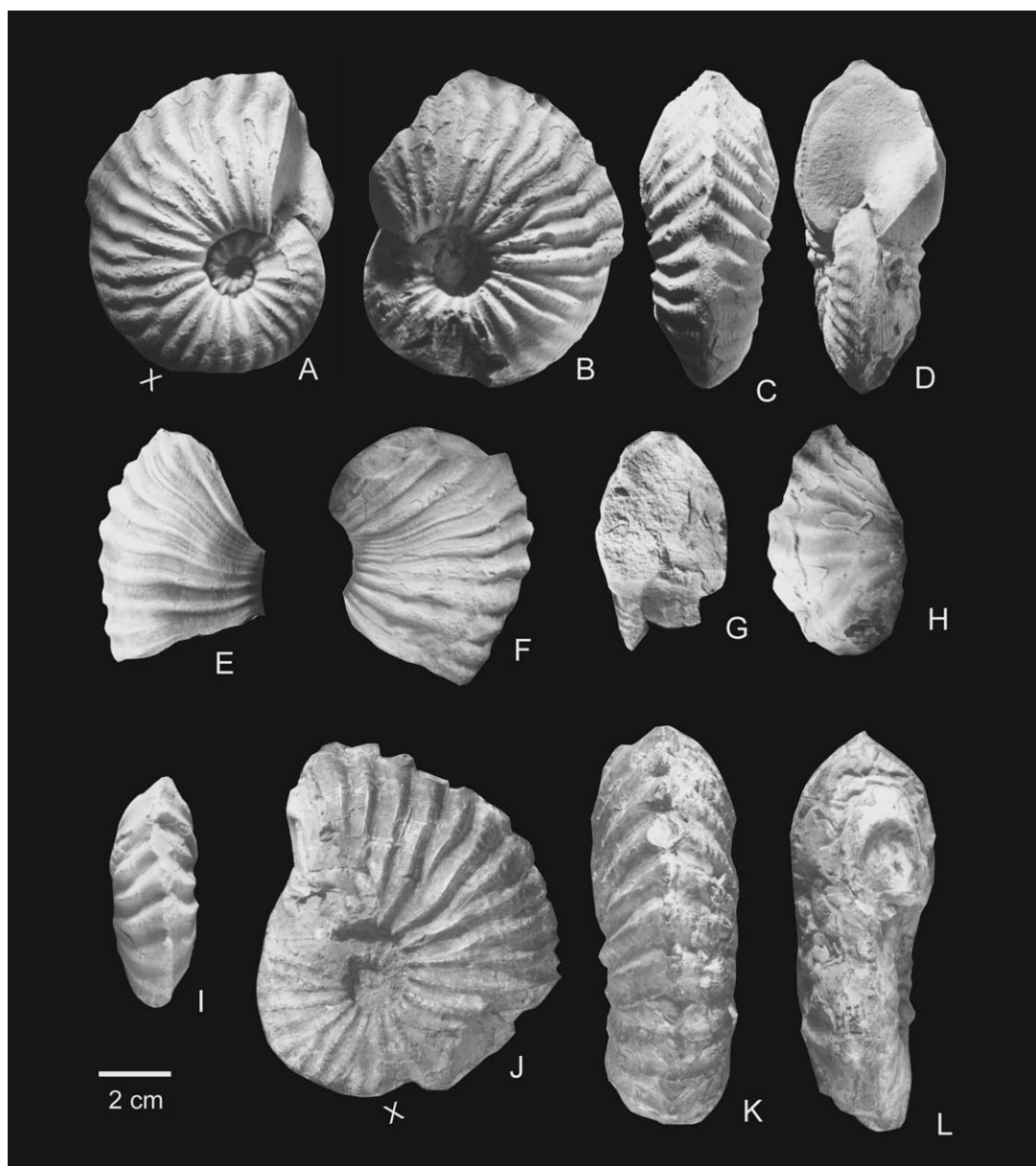


Fig. 6. A–L. *Phlycticeras schauburgi* (Waagen). A, B, left and right lateral views of specimen no. JUM/08/5, bed 9, Jumara. Note sudden appearance of ‘rooster’-like raised keel in last quarter of the body chamber; C, D, ventral and apertural views; E–G, left lateral (E), right lateral (F) and apertural (G) views of body whorl fragment; note approximation of fine ribs towards end; specimen no. JUM/08/9, bed 9, Jumara; H, I, lateral and ventral views of a body whorl fragment; specimen no. JUM/08/E6, bed 11, Jumara; J–L, holotype, GSI type no. 1914, Athleta beds, Gudjinsir (Waagen, 1875); lateral (J), ventral (K) and apertural (L) views.



beds (which show no evidence of condensation; Datta, 1992; Fürsich and Oschmann, 1993) of different localities (see Fig. 2). Because of the above mentioned reasons and observations we have considered all the three European chronospecies as conspecific and belonging to *P. polygonium*.

*Phlycticeras schauburgi* (Waagen).

Fig. 6.

- 1875. *Amaltheus schauburgi*–Waagen, p. 41, pl. 9, Fig. 1a–c.
- 1895. *Lophoceras schauburgi* (Waagen)–Parona and Bonarelli, p. 123.
- 1912. *Amaltheus schauburgi* (Waagen)–Smith, p. 1351.
- 1914. *Phlycticeras schauburgi* (Waagen)–S. Buckman, p. 98c.
- 1928. *Phlycticeras schauburgi* (Waagen)–Spath, p. 91, pl. 13, Fig. 15.
- 1998. *Phlycticeras polygonium* (Zieten)–Schweigert and Dietze, pars pl. 5, Fig. 2, pl. 7, Fig. 2.
- 1998. *Phlycticeras polygonium* (Zieten) var. *nodosum* Quenstedt–Schweigert and Dietze, pars pl. 8, Fig. 8.
- 1998. *Phlycticeras pustulatum* (Reinecke)–Schweigert and Dietze, pars pl. 9, Fig. 3.

**Material:** The present study is based on five specimens including the holotype (Geological Survey of India type No. 1914). Measurements are given in Table 2.

**Description:** Adult shell diameter ranges between 70 mm to 86 mm and the adult end-phragmocone diameter varies from 62 mm to 70 mm. Shell is compressed ( $W/H = 0.66$ ) with oval to lanceolate whorl section; flanks are gently to strongly curved, rapidly converging towards the venter. Inner whorls are less compressed ( $W/H = 0.9$ ). Umbilicus is small ( $U/D = 0.25$ ), umbilical margin distinct all through and umbilical wall is steep to over hanging during ontogeny. Ventrolateral margin is rounded. Shell is prominently ribbed, ribs originate from the umbilical margin, mainly rectiradiate and single up to the ventrolateral margin then may become slightly to strongly prorsiradiate while crossing over the venter. Bifurcating ribs occur occasionally and restricted mainly in the early and middle growth stages. The last quarter of the body chamber has mainly single ribs with occasional short intercalatories. Two rows of tubercles, which may be small, but distinct or feeble are present. One row is situated at one-third height from the umbilical margin and the other at the ventrolateral margin. The ventrolateral tubercles are relatively strong. The adult body whorl occupies two-third of the outer whorl. Venter floored with smooth band, which continues from early ontogeny up to the first quarter of the body chamber length. Precisely from this position appears a raised, high keel, which shows serration – another remarkable character which is unique to all these adult individuals. This makes venter truly extremely narrow in the last two quarters of the body chamber. Strigation present all through the shell, but becomes more prominent near the ventral region.

**Remarks:** Waagen (1875) described the present species as *Amaltheus schauburgi* from Kutch. Spath (1928) included

one additional specimen and renamed the species as *P. schauburgi*. Later Schweigert and Dietze (1998) split the species and included Waagen's type into *P. polygonium* and that of Spath's specimen in *P. waageni*. Their idea of splitting, perhaps, has been prompted by stratigraphic reasons. We have here retained the original name proposed by Spath and also added three more specimens. All of them have adult body chamber. Our specimens have the similar ribbing pattern and same body chamber length (two-third of the last whorl) as that of Waagen's and Spath's types. The common characteristic features of all these forms are the presence of raised, serrated keel at the last part of body chamber.

One of the specimens of *P. pustulatum* described by (Schweigert and Dietze (1998: pl. 9, Fig. 3) from Middle Callovian of Poitou, Western France has the same raised, serrated keel at the last part of the body chamber, but ribs do not conspicuously continue up to the venter and the shell is more inflated than our specimens. It has been included within the present species as a geographic variant.

The present species resembles strongly the contemporary *P. polygonium* and both have similar range of variability with respect to ornamentation and degree of inflation, especially in early stage. *P. schauburgi* however, has compressed body whorl with weak to very feeble tubercles and coarse, mainly solitary ribbing. Moreover, it has a peculiar “rooster-like”, raised mid-ventral keel found in the last quarter of the body chamber. Adult *P. schauburgi* is small ( $D = 103$  mm) in comparison to *P. polygonium* ( $D = 148$ ). Because of the similarities in inner whorls, stratigraphic contemporaneity (cf. Callomon, 1981; Davis et al., 1996) and parallel evolution of both morphs (for detail, see below), we suggest a dimorphic relation between *P. polygonium* [M] and *P. schauburgi* [m].

#### 4. Discussion

The *Phlycticeras-Oecoptychius* sexual dimorphic pair has been considered by many early workers (see Donovan et al., 1981 and references therein). Recently some German workers led by Schweigert (Schweigert and Dietze, 1998; Schweigert et al., 2003) have elaborately dealt with the nature of dimorphism in *Phlycticeras* and reiterated *Oecoptychius* as its microconchiate partner. The major reasons behind this matchmaking are similarities in some early ontogenetic characters and stratigraphic contemporaneity. Here, we argue that the claim does not appear to be very sound after close scrutiny.

Schweigert and Dietze (1998) mentioned that nuclei of *Phlycticeras* and *Oecoptychius* have identical sutures and some well-preserved *Oecoptychius* specimens have strigation. The significance of similarity of sutures between genera has been continuously debated since long. Schindewolf (1964) showed considerable differences in the earliest sutures of *Phlycticeras* and *Oecoptychius*. Callomon (in Donovan et al., 1981) believed that the sutures depicted by Schindewolf (1964) were not primary sutures and “the first incised sutures are almost identical”. Ammonite sutures are highly variable both ontogenetically and phylogenetically and therefore, cannot

be taken as a reliable guide to establish kinship. Klinger and Kennedy (1989: p. 243) clearly state “The role of sutural ontogeny in interpreting the phylogeny and its taxonomic value is disputable”. Wiedmann and Kullmann (1981: pp. 241–245) showed that haploceratid sutures in general closely resemble the oppelid sutures at the microconchiate level. Similarly, according to them, the suture of *Phlycticeratinae* is closely comparable with that of *Oppelidae*. The *Haploceratidae* and closely related family *Strigoceratidae* even show identical sutural patterns with some Cretaceous subfamilies. The sutural similarity between *Phlycticerat* and *Oecoptychius* may be due to convergence or may be symplesiomorphic character of the family *Strigoceratidae* in cladistic sense. Similarly, the appearance of strigation in some *Oecoptychius* specimens may be a primitive character of the different members of the higher clade.

Moreover, many other diagnostic characters of nucleus shell of *Phlycticerat*, are lacking in *Oecoptychius*. For example, *Oecoptychius* bears no tubercles at all, and most importantly, it lacks the ventral keel of *Phlycticerat* (see Schweigert and Dietze, 1998: pl. 9, Figs. 8, 10b, c, 11c, d). Instead, it has a ventral groove (Schweigert and Dietze, 1998: p. 26) at early stage or smooth band (Schweigert pers. comm., 2008). Recently Schweigert et al. (2003) correctly removed *Amblyoxites amblys* (Buckmann) from the phlycticeratid lineage because it lacks keel. We similarly question the supposed dimorphic relation between *Strigoceras* [M] Quenstedt (1886) and *Cadomoceras* [m] Munier-Chalmas, 1892 of Middle-Upper Bajocian. *Strigoceras* has hollow keel and it is thoroughly strigate with complex suture while *Cadomoceras* has smooth inner whorls and is devoid of keel and strigation with straight and simple suture (Arkell et al., 1957). Moreover, they have different palaeobiogeographic distribution.

Other prerequisites required to establish sexual dimorphism are geographical congruence and stratigraphical isochroneity of the two morphs (see Callomon, 1981; Davis et al., 1996). Although these two genera co-occur in many horizons and their uppermost stratigraphic ranges are the same, i.e., up to the Upper Callovian. The first *Oecoptychius* (*O. grossouvrei*) comes from the Upper Bajocian Parkinsoni Zone in Italy (Wendt, 1971) and the oldest records of *Phlycticerat* species (*P. aenigmaticum*) comes from the older Garantiana Zone of France. Schweigert et al. (2003) tried to show on the basis of other associated ammonite faunas that Wendt's material comes from the older Garantiana Zone, but they did not elaborate on this issue.

The palaeobiogeographic distributions of *Phlycticerat* and *Oecoptychius* are also not very compatible. *Oecoptychius* is mostly restricted to Europe and Spath (1928) reported only a single specimen from the Upper Callovian bed of Kutch. Westermann et al. (1984) reported *Oecoptychius* in the lowermost Callovian of Mexico. *Phlycticerat* on the other hand has been reported from Europe, India, Africa (see Arkell et al., 1957) and Mexico (Sandoval et al., 1990). Even in Kutch, the Middle Callovian horizon which yields the present numerous *Phlycticerat* specimens are totally devoid of *Oecoptychius*. Many other Kutch workers sampled extensively from these stratigraphic horizons for brachiopods (Mukherjee,

2002), gastropods (Das, 2003), bivalves (Rudra, 2007) and ammonites (Jana, 2002). Their vast collection is kept in the Repository of Jadavpur University Museum and the material lacks even a single *Oecoptychius*. Therefore, absence of *Oecoptychius* from these horizons may be real and not due to collection failure. However, in ammonites dimorphism, sex ratio varies greatly (Callomon, 1981), which may be constrained by many factors including biased collection, differential preservation and sexual segregation, which is also predominant in living cephalopod communities (see also Westermann, 1990; Shome and Bardhan, 2009). We argue (see below) that non-overlapping palaeobiogeography between *Phlycticerat* and *Oecoptychius* is not due to sexual segregation of two dimorphs but because of ecological incompatibilities of the two genera.

Ecologically, both *Phlycticerat* and *Oecoptychius* do not have comparable habitats. Highly lanceolate forms like *P. schauburgi* and depressed nodos forms with sharp ventrolateral margin like *P. polygonium* have been interpreted as shallow water nectobenthos (Batt, 1987; Westermann, 1990: Fig. 1). Trueman (1941) and Arkell et al. (1957) made important contribution in describing life orientation and possible floatation positions of diverse ammonite morphotypes based on calculation of centre of gravity, centre of buoyancy etc. According to them the life mode of *Oecoptychius* is believed to be as passive drifter like planktons (see also Kennedy and Cobban, 1976; Westermann, 1990).

In the superfamily Haplocerataceae, many groups are now known to have dimorphism; microconchs are small lappeted, but none is aberrantly coiled like *Oecoptychius* (see for detail Callomon in Donovan et al., 1981). Davis et al. (1996) recently extensively reviewed sexual dimorphism in the history of ammonites. They categorized many kinds of dimorphism in Jurassic ammonites. In oppelid lineage, *Taramelliceras*-*Creniceras* have been previously adjudged to be an established dimorphic pair (Palframan, 1966). In many instances these two taxa are contemporaneous and collected from the same localities. Davis et al. (1996) showed that *Creniceras*, which is lappeted, bears different juvenile characters (e.g., smooth shell) from that of *Taramelliceras*. The adult ornamentation of both genera is also quite different and there are no microconchiate mature modifications. These dissimilarities, they state, “do not improve phyletic understanding of the group”. Davis et al. (1996) therefore, have kept *Taramelliceras*-*Creniceras* as an example of “dubious sexual dimorphism”.

*P. polygonium*, like in Kutch, is also abundant in the Middle Callovian of Europe (Schweigert and Dietze, 1998). As the sample size is large, the forms like *P. schauburgi* described here, co-occurs with the macroconchiate *P. polygonium* group of forms (see Schweigert and Dietze, 1998: pl. 5, Fig. 2; pl. 7, Fig. 2; pl. 8, Fig. 8; pl. 9, Fig. 3). *P. schauburgi* is smaller in size, with body chamber preserved. Many mature modifications described here including the high, septicarinate keel also characterize all *P. schauburgi* like specimens of Europe. Even in the older species, the Lower Callovian *P. mexicanum* reported from Germany, two similar variants are readily apparent (see Schweigert and Dietze, 1998: pl. 4, Figs. 1 and 3).

Another important prerequisite for recognizing sexual dimorphic pair is the possession of similar evolving characters (Callomon, 1981; Davis et al., 1996). In the evolution of *Phlycticeras*, there is a progressive loss of umbilical tubercles in the lineage. In *P. mexicanum* it continues up to the adult stage in both variants (see Schweigert and Dietze, 1998: pl. 4, Figs. 1 and 3) while in younger *P. polygonium* umbilical tubercles are mostly restricted to the inner whorls (see Schweigert and Dietze, 1998: pl. 5, Fig. 3; pl. 6, Fig. 2). Remarkably, *P. schaumburgi* described here also bears umbilical tubercles only in inner whorls (see Spath, 1928: pl. 13, Fig. 15; Schweigert and Dietze, 1998: pl. 5, Fig. 3; pl. 6, Fig. 2).

Like the present study, a vast array of Jurassic ammonite species has been reported, which shows both dimorphism and non-sexual polymorphism in the same group (Ivanov, 1971, 1975, 1983; Matyja, 1986, 1994; Meléndez and Fontana, 1993; Parent et al., 2008). Many French workers also reported adult polymorphic variants within macroconchs and demonstrated sexual dimorphism within the same species (Marchand, 1976; Charpy and Thierry, 1976; Thierry, 1978; Contini et al., 1984). Some of their reports include only polymorphism independent of any sexual dimorphism. One of the famous examples where polymorphism affects both sexual antidimorphs is *Cosmoceras* Waagens (Tintant, 1963, 1976). This author showed that both morphs have variants, which exhibit variability in ornaments and they were previously grouped into different genera or subgenera. (Tintant, 1963, 1976) suggested that this ornamental variability may be attributed to nothing but intra-specific polymorphism.

Ornaments in ammonites might have various functions like protective, buoyancy regulation, sexually selected features etc. (for details see Kennedy and Cobban, 1976). Keels are believed to have a supporting function for siphuncular attachment or like other features of ventral ornament served to raise the shell free of the sea floor (Spath, 1923–1943). If our speculation regarding the necto-benthic life of *Phlycticeras* is correct then these above-mentioned functions of keel are highly relevant. But, why did *P. schaumburgi* suddenly develop extra-raised ('rooster' like) keel near the adult peristome? It effectively increases the diameter of the shell and in apertural section shell becomes truly lanceolate. We believe that this is another kind of mature modification near the peristome of microconch like lappets and ventral rostrum and it may be similarly a sexually selected feature related perhaps to sex recognition system. A similarly bizarre apertural modification has been found in the Lower Cretaceous microconch of *Mortoniceras* Meek, 1876, where aperture becomes lanceolate as the rostrum was raised and then recoiled on the ventral margin (Wright et al., 1996: Fig. 109h).

In conclusion, there are some inconsistencies to accept *Phlycticeras-Oecoptychius* as a dimorphic couple. We here propose another alternative within the *Phlycticeras* lineage itself. The nature of sexual dimorphism now satisfies many palaeobiological and stratigraphical prerequisites.

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