

The taxonomic status of the genus *Hubertoceras* Spath: A new light on sexual dimorphism from the Callovian ammonites of Kutch, India

Rakhi Dutta, Subhendu Bardhan, Shubhabrata Paul, and Subhronil Mondal

ABSTRACT

The genus *Hubertoceras* was described under the subfamily Proplanulitinae from the middle to upper Callovian (Middle Jurassic) beds of Kutch. Recently we revisited the Kutch Proplanulitinae and proposed a new endemic subfamily Sivajiceratinae for them. The new subfamily consists of the genera *Sivajiceras*, *Kinkeliniceras*, *Obtusicosites* and *Hubertoceras*. Development of sexual dimorphism was widespread in Jurassic ammonite families and at the same time, there was a significant increase (especially from the Callovian) of isolated sexual variants, which could not easily be paired up. In the present endeavour, we have explored the status of *Hubertoceras* in the light of sexual dimorphism. The genus *Hubertoceras* is characterised by small adult size, evolute shell with biplicate ribs and well-preserved lappets, which speak for its microconchiate nature. We have also made an attempt to identify the probable antidimorph of *Hubertoceras* from the contemporary large genera with evolute shells described from Kutch.

Detailed morphological and morphometrical analyses indicated that *Obtusicosites* is likely the macroconchiate counterpart of *Hubertoceras*. The *Hubertoceras-Obtusicosites* pair satisfied all the paleobiological as well as geological prerequisites to form antidimorphs. Evolutionary trends between macroconchs and microconchs within the Sivajiceratinae lineage also showed parallelism.

Most of the Callovian ammonite genera of Kutch were strongly dimorphic. Intense competition for food, habitat and mates perhaps forced these genera to undergo character displacement. While the macroconchs remained less diverged being uniformly large, evolute and strongly ornate; the microconchs showed wide interspecific variation in the shape of lappets, some even lacked peristomal modifications. Different types of lappet or absence of it perhaps facilitated easy mate recognition system among other functions.

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Dutta, Rakhi, Bardhan, Subhendu, Paul, Shubhabrata, and Mondal, Subhronil. 2017. The taxonomic status of the genus *Hubertoceras* Spath: A new light on sexual dimorphism from the Callovian ammonites of Kutch, India. *Palaeontologia Electronica* 20.2.37A: 1-23
palaeo-electronica.org/content/2017/1954-antidimorph-of-hubertoceras

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Keywords: *Hubertoceras* (Ammonoidea); systematic position; sexual dimorphism; Middle Jurassic; Kutch, India

Submission: 27 October 2016 Acceptance: 21 July 2017

INTRODUCTION

One “has to be extremely careful when it comes to maintaining sexual relationships between hitherto blameless ammonites” (Lehmann, 1971)

Sexual dimorphism in ammonites was established since the origination of the Order Ammonoidea during the Devonian (see Makowski, 1962, 1963; Davis et al., 1996; Page, 2008; Klug et al., 2015). Only a few Paleozoic and Triassic families (five) showed dimorphism in terms of size and shape variation (Klug et al., 2015 and references therein). From the Jurassic onward sexual dimorphism became widespread. Out of 53 Jurassic families, sexual dimorphism occurred in at least 38 families (about 72%; see Callomon, 1963, 1969, 1981; Donovan et al., 1981; Davis et al., 1996; Klug et al., 2015), and the same trend persisted in the Cretaceous when out of 55 families sexual dimorphism was recorded in 37 families (about 67%; see Wright et al., 1996, Davis et al., 1996; Klug et al., 2015). Callomon (1963) provided detailed account of sexual dimorphism in many Jurassic ammonite families, for example, Graphoceratidae and Hildoceratidae of the Toarcian (Lower Jurassic) and Hammetoceratidae (Lower-Middle Jurassic). Howarth (1992) provided an account of dimorphism in the family Hildoceratidae from the Toarcian of Britain. Page (2008) mentioned the cryptic development of sexual dimorphism in the family Phylloceratidae of Lower Jurassic.

Many of the Callovian genera of Kutch ammonites are also found in Europe where many workers established sexual dimorphism in them. For example, Callomon (1963) established macro- and microconchs within the genus *Macrocephalites* Zittel, 1884 of England. Theirry (1978) also provided detailed account of sexual dimorphism in the genus *Macrocephalites* of the lower Callovian of Europe. Cariou (1980, 1984) elaborately dealt with the development of sexual dimorphism within the Middle Jurassic Reineckeidae from Europe. Cox

(1988) studied English Callovian perisphinctid ammonites and established sexual dimorphs in many genera. In a series of papers, Bardhan along with others also established sexual dimorphism in species from Kutch of different groups, e.g., Macrocephalitinae (Bhaumik et al., 1993; Datta et al., 1996), Eucycloceratinae (Jana, 2002; Jana et al., 2005), Reineckeidae (Kayal and Bardhan, 2005), Hecticoceratinae (Roy and Bardhan, 2007), Phylticeratinae (Bardhan et al., 2010), Pseudoperisphinctinae (Bardhan et al., 2012), Perisphinctinae (Roy et al., 2012) and Sivajiceratinae (Dutta and Bardhan, 2016; also see Callomon, 1993).

During the Jurassic, the nature of sexual dimorphism in ammonites took a turn in a new direction where microconchs had new kinds of mature modifications near aperture. The maximum number of dimorphic taxa with mature modifications in microconchs appeared during the Middle Jurassic. In the Jurassic antidimorphs, microconchs are relatively evolute and strongly ornamented with varying degrees of egression of the body whorl (Callomon, 1963, 1981).

Bardhan and Chattopadhyay (2003) attributed the great radiation of ammonites in the Jurassic to the nature of sexual dimorphism. Since two sexual variants within a species can be quite disparate, the ammonite taxa showed higher intraspecific variability. These facilitated rapid evolution. Stanley (1979) emphasized that sexual reproduction as well as sexual selection played a very important role in macroevolution. Bardhan and Chattopadhyay (2003) also related the rapid evolutionary diversification of ammonites with Mesozoic Marine Revolution (see Vermeij, 1977, 1987). The sudden increase of durophagous predation exerted much pressure on the prey communities of the shallow shelf areas, and ammonites responded against this selection pressure by strengthening their shell sculpture (Ward, 1981; Vermeij, 2002; Bardhan and Chattopadhyay, 2003; Zuschin et al., 2003; Kerr and Kelley, 2015). The great diversification

and increasing strength of ornaments in ammonites were perhaps possible because ammonite evolved a new kind of sexual selection i.e., strong and ornamental dimorphism.

Spath (1931) described the subfamily Proplanulitinae from the Middle Jurassic of Kutch. He included genera like *Cutchisphinctes* Spath, 1931, *Sivajiceras* Spath, 1930, *Obtusicoelites* Buckman, 1921, *Kinkeliniceras* Buckman, 1921 and *Hubertoceras* Spath, 1930 within this subfamily. No major revisionary work was completed on this subfamily after that of Spath (1931). We recently redesignated the Kutch Proplanulitinae into a separate, endemic subfamily Sivajiceratinae and considered the European Proplanulitinae as its sister group (Dutta and Bardhan, 2016). Sivajiceratinae has been characterised by evolute macroconchiate genera (*Sivajiceras*, *Obtusicoelites* and *Kinkeliniceras*). They have strong primary ribs furcating at the middle part of the flank and septal sutural patterns are complex. Microconchs (*Hubertoceras*) are lappeted, evolute and strongly ribbed. *Cutchisphinctes* was quite unrelated to the other four genera.

Earlier, Waagen (1875) and Spath (1931) while describing many species of *Hubertoceras*, occasionally mentioned the presence of lappets in some of them, but did not discuss the paleobiological significance of lappets. In the absence of any underlying hypothesis, many paleobiologically important features would escape notice of the concerned workers (cf. Gould and Vrba, 1982). Curiously, Arkell et al. (1957) in the Treatise described the genus *Hubertoceras* without lappets although the referred figure of the holotype (figure 403.2a, b) showed the presence of a prominent lappet in *H. omphalodes*, which spoke for its microconchiate status (cf. Callomon, 1963). Most of the species of *Hubertoceras* described by Spath (1931) were small with biplicate ribs and some of them also possessed lappets.

We here explored the actual taxonomic status of *Hubertoceras*. During the Callovian, Kutch was inhabited by many large (exceeding 150 mm diameter), evolute genera (for example, *Choffatia* Siemiradzki, 1898; *Indosphinctes* Spath, 1930; *Idiocycloceras* Spath, 1928; *Reineckia* Bayle, 1878; *Sivajiceras* Spath, 1930; *Obtusicoelites* Buckman, 1921 and *Kinkeliniceras* Buckman, 1921) whose inner whorls are more or less similar to adult *Hubertoceras*, which is small in diameter (maximum diameter=83 mm). One of the criteria of sexual dimorphism is based on the identity of the early ontogeny of putative sexual dimorphs, which

have different adult stages and adult size. Much new information recently emerged in working out dimorphic pairs in ammonites (see Davis et al., 1996; Klug et al., 2015). We here explored all possibilities of finding out the true sexual counter part of *Hubertoceras*.

GEOLOGICAL SETTING

During the Late Triassic to Early Jurassic, the origin of the Kutch Basin took place as a result of the Gondwana fragmentation (Biswas, 1977). The fossiliferous Bathonian-Callovian sediments are extensively exposed in the mainland of Kutch, particularly in Jumara, Keera, Jara and Jura in the NW of Bhuj, the district town of Kutch as well as in Ler-Fakirwadi and other areas situated south of Bhuj (Figure 1). The dome-shaped outcrops were formed due to successive tectonic activity and present outstanding fossil-bearing sections (Wynne, 1872).

The depositional setting of the Chari Formation, the main fossil-yielding unit was a shelf environment represented by the widespread development of siliciclastic ramp deposits, which includes different sub environments (Fürsich et al., 2004). The lower Callovian beds of the Chari Formation consist mainly of the shale-limestone association (packstone or wackestone), which suggests the outer ramp environment. The middle Callovian beds are dominantly siliciclastic and represent a shoaling upward phase (Datta, 1992; Fürsich and Oschmann, 1993). An alternation between greenish grey shale, occasionally gypseous and white fossiliferous limestone are characterised by the upper Callovian beds. Here, the sediments were deposited below the storm wave base in low energy environment within the outer ramp (Fürsich et al., 2004).

All the specimens (including types and the present collection) of the species of the subfamily Sivajiceratinae came from different localities within the mainland of Kutch (Waagen, 1875; Spath, 1931; Dutta and Bardhan, 2016) (Figure 1). The main geological sections are Jumara and Keera and other sections are Fakirwadi, Medisar, Badi, Gudjinsir, Walakhavas, Ler, etc. (for detailed stratigraphy/locality information and measurement list, see Appendix 1). In the present study, we tried to establish antidimorphic pairs between the species of *Obtusicoelites* and *Hubertoceras* genera. We, therefore, made a detailed analysis of the precise stratigraphy and locality information of the all specimens of *Obtusicoelites* and *Hubertoceras*.

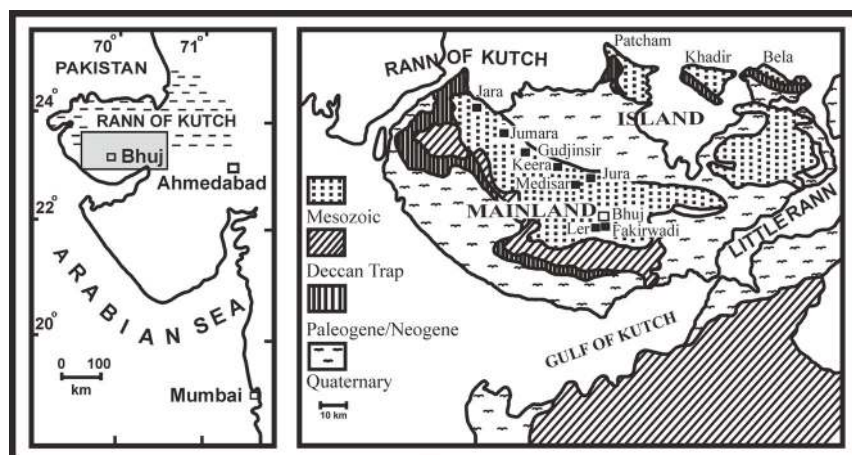


FIGURE 1. Geological map of Kutch showing the major localities (solid squares) from where fossils of the Sivajiceratinae have been collected (modified after Dutta and Bardhan, 2016).

The majority of the specimens of *Obtusicos-tites* and *Hubertoceras* came from the north of Bhuj sections like Jumara (24.5%), Keera (17.5%) and Jara (7%) (see Figure 1). The other main sections yielding specimens include Ler, Fakirwadi, Walakhavas and Samatra (collectively 28%), which are very closely spaced and are situated south of Bhuj. All the type specimens of *Obtusicos-tites obtusicos-ta* came from the ‘anceps’ and ‘athleta’ beds of Spath (1931). These beds spanned the middle to upper Callovian. In Jara, Jumara and Keera sections, we followed the high resolution lithostratigraphy recently made by Jana et al. (2000, 2005). Our precise collection from these sections also indicates the similar range of *O. obtusicos-ta* like the type specimens. Similarly a majority of specimens (including the types and the present collection) of different species of *Hubertoceras*, which were considered here as the antidimorphs of *O. Obtusicos-ta*, came from the same areas from where specimens of *O. obtusicos-ta* were also collected. The northern sections yielded most of the specimens (Jumara-33%, Keera-20.8% and Jara-4%) and the southern section collectively yielded 8% of the specimens (Fakirwadi-4% and Vanda-4%). Some specimens (25%), however, do not have any locality or stratigraphic information. Stratigraphic distribution of *Hubertoceras* specimens suggests that they were also essentially coeval with *Obtusicos-tites* specimen, i.e., ranging from the middle to upper Callovian (for detailed stratigraphic/locality information, see Appendix 2). Another species of *Obtusicos-tites* is *O. Devi*, and it is represented by 3 macroconch and 3 microconch specimens, all of which are type specimens. Most of the specimens came only from a single locality, Fakirwadi and

horizon, i.e., ‘athleta’ bed (Spath, 1931; also see Appendix 2). The above discussions suggest that the alleged antidimorphic pairs of *O. obtusicos-ta* and *O. devi* essentially co-occurred and had the same locality distribution in Kutch.

The stratigraphic and locality information and measurements of other genera of different families, which have been studied here for comparison, are listed in Appendix 3. The stratigraphic distributions of the studied species of the subfamily Sivajiceratinae of Kutch are shown in Figure 2.

MATERIAL AND METHODS

Our study material comprises the type specimens (n=40) and the present collection (n=174). We included specimens of Sivajiceratinae described from other region within the Indo-Madagascan Faunal Province (e.g., Collignon, 1958) in our analyses. The type specimens of Waagen (1875) and Spath (1931) are archived in the repository of the Geological Survey of India, Kolkata, India and Natural History Museum, U. K. The type specimens are mostly collected from Keera and Jumara sections (see Figure 1). The present collection is archived in the museum of Geological Sciences, Jadavpur University, Kolkata, India.

Search for the Taxonomic Status of *Hubertoceras* in the Light of Sexual Dimorphism.

Spath (1931) described the genus *Hubertoceras* from Kutch. He altogether included six species: *H. omphalodes* (Waagen, 1875), *H. dhosaense* (Waagen, 1875), *H. hubertus* Spath, 1931, *H. arcicosta* (Waagen, 1875), *H. mutans* (Waagen, 1875) and *H?* sp. nov. Spath, 1931 (Fig-

KUTCH					
	ZONE	SUBZONE	HORIZON	SPECIES RANGE	
CALLOVIAN	UPPER	<i>Peltoceras athleta</i>	<i>Peltoceras athleta</i>	<i>Peltoceras athleta</i>	
			MIDDLE	<i>Reineckeia reissi</i>	<i>Subgrossouvria aberrans</i>
	<i>Reineckeia reissi</i>	<i>Reineckeia reissi</i>			<i>Reineckeia reissi</i>
		<i>Reineckeia anceps</i>		<i>Indosphinctes indicus</i>	<i>Indosphinctes indicus</i>
	<i>Choffatia cobra</i>		<i>Choffatia cobra</i>		
	<i>Eucycloceras opis</i>		<i>Idiocycloceras persphinctoides</i>	<i>Idiocycloceras opis</i>	
			<i>Eucycloceras opis</i>	<i>Eucycloceras opis</i>	
	<i>Reineckeia anceps</i>		<i>R. tyranniformis</i>	<i>R. tyranniformis</i>	
			<i>Reineckeia anceps</i>	<i>Reineckeia anceps</i>	
	LOWER	<i>Macrocephalites formosus</i>	<i>Nothocephalites semilaevis</i>	<i>Nothocephalites semilaevis</i>	<i>Nothocephalites semilaevis</i>
				<i>M. formosus</i>	<i>M. formosus</i>
			<i>Macrocephalites formosus</i>	<i>Kamptokephalites lamellosum</i>	<i>Kamptokephalites lamellosum</i>
				<i>Kamptokephalites dimerum</i>	<i>Kamptokephalites dimerum</i>
		<i>Indocephalites diadematum</i>	<i>Kheraicerus bullatum</i>	<i>Kheraicerus bullatum</i>	<i>Kheraicerus bullatum</i>
				<i>Indocephalites diadematum</i>	<i>Indocephalites diadematum</i>
			<i>Indocephalites transitorium</i>	<i>Kheraicerus cosmopolitum</i>	<i>Kheraicerus cosmopolitum</i>
<i>Indocephalites transitorium</i>		<i>Indocephalites transitorium</i>			

FIGURE 2. The stratigraphic distribution of the studied antidimorphic pairs under the subfamily Sivajiceratinae of Kutch. Biozonation after Jana et al. (2000, 2005); Bardhan et al. (2012).

ure 3). He incorporated a few species of Waagen (1875) described under the genus *Perisphinctes*. Spath (1931) provided some diagnostic characters of *Hubertoceras* which are: biplicate ribs that occasionally disappeared on the venter and lacked thickened primary ribs; its species were evolute and compressed in adult stage with simplified suture (Spath, 1931; p. 284). We studied all the species described by Spath (1931) based on the type material obtained from several localities and horizons within the middle to upper Callovian of the mainland of Kutch. Our revision of the *Hubertoceras* spp. revealed that ribs never disappear on adult body whorl and in many cases, primary ribs are thickened to form bullae (see Figure 3.1, 3.3). Out of six species, the type specimens of three species have preserved lappets (i.e., *H. omphalodes*, *H. dhosaense*, *H. hubertus*) (see Figure 3.1-

3.7), and the rest are nearly complete with terminal constrictions preserved (Figure 3.8-3.10).

The holotype of *H. arcicosta* (Waagen, 1875, plate 58, figure 2) is a small adult shell (D=67 mm) and is reproduced here in Figure 3.9. Spath (1931, plate 79, figure 1a, b) provided another specimen of *H. arcicosta* with adult body chamber. In both specimens peristomal margins are not preserved. Although Spath (1931) included *H. arcicosta* within the genus *Hubertoceras*, it was found from the lower Callovian beds of Kutch. While mentioning the stratigraphic range of *Hubertoceras*, he categorically wrote 'the genus *Hubertoceras* was thus proposed for forms of the *anceps* and *athleta* beds (= middle to upper Callovian)' (Spath, 1931, p. 284). Because of this stratigraphic assignment as well as some morphological differences (for example, dense primary and secondary ribs), *H.*

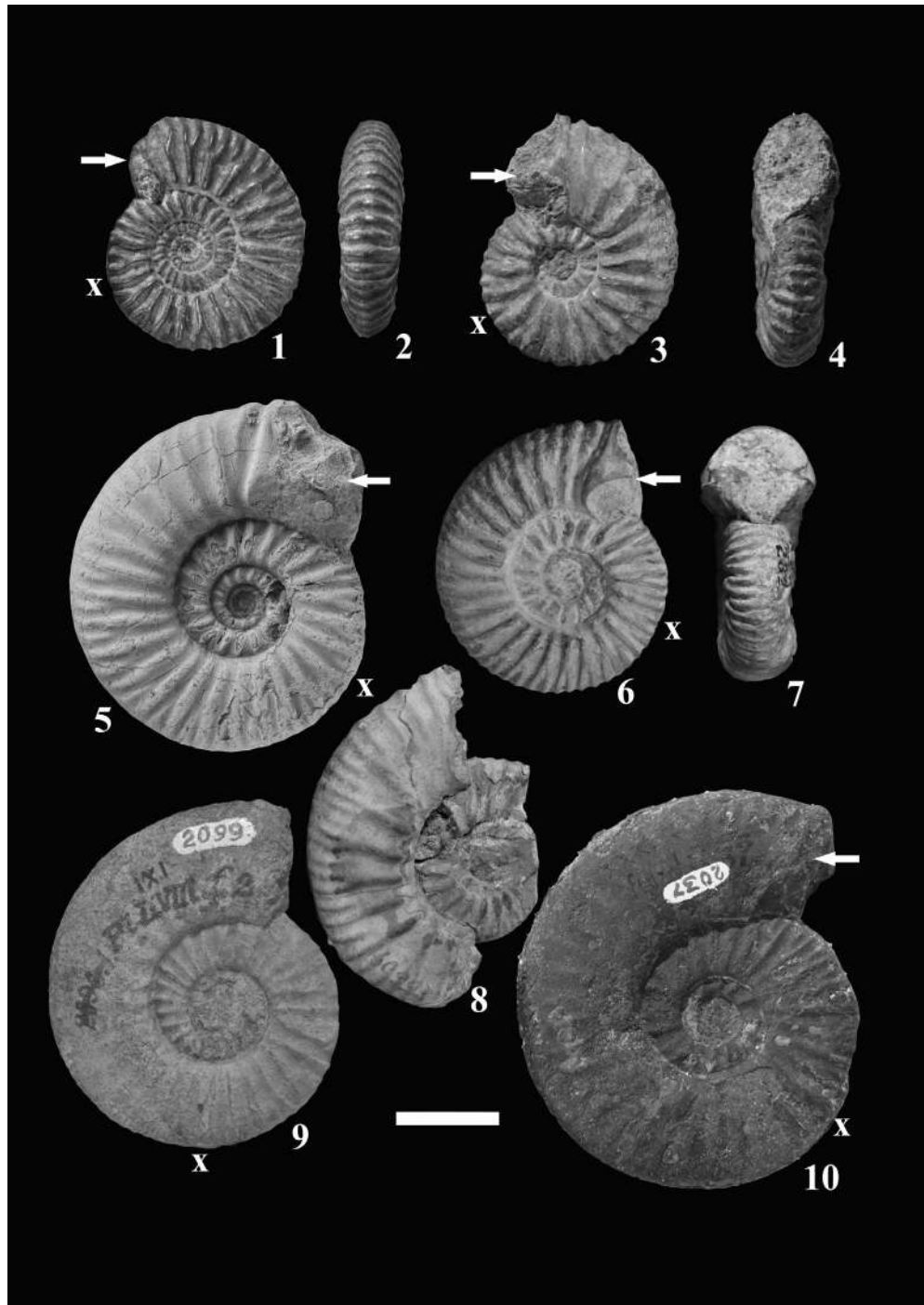


FIGURE 3. Representatives of Hubertoceras described by Spath (1931) from the Callovian of Kutch. **1-2.** Holotype of *Hubertoceras omphalodes* (Waagen), GSI no. 2030, lateral and ventral views; 'Perisphinctes anceps beds' of Vanda (=middle Callovian anceps beds). **3-4.** Holotype of *H. dhosaence* (Waagen), GSI no. 2035, lateral and apertural views; 'Perisphinctes anceps bed' of Keera (=beds nos. 5-7 of middle Callovian). **5.** Holotype of *H. hubertus* Spath; NHMUK no. C7686, lateral view. **6-7.** *H. hubertus* var. *densicostata*, GSI no. 16098, lateral and apertural views; ?anceps beds of unknown locality. **8.** *H?* sp. nov.; GSI no. 16099, lateral view; athleta beds of Fakirwadi (=athleta beds of upper Callovian). **9.** Holotype of *H. arcicosta*, GSI no. 2099, lateral view; 'Golden Oolite' of Keera (=bed no. 2 of lower Callovian). **10.** Holotype of *H. mutans*; GSI no. 2037, lateral view; 'Katrol group' of North Gudjinsir. Beds are following Jana et al. (2000, 2005). Commencement of body chamber and presence of lappets are indicated by 'x' and arrows respectively. GSI=Geological Survey of India, NHMUK=Natural History Museum, U.K. Scale bar equals 20 mm.

arcicosta had been provisionally excluded from the *Hubertoceras sensu stricto* (see also Dutta and Bardhan, 2016). It was rather closer to the microconch of *Kinkeliniceras*, which first appeared in the lower Callovian and was included here within *Kinkeliniceras*. *Hubertoceras mutans* (Waagen, 1875) is a problematic species both from morphological and stratigraphic reasons. The holotype of *H. mutans* is a small adult shell (D=83 mm) with entirely preserved outer whorl. Waagen (1875) mentioned that the ribbing of the holotype was “very faint on the body chamber, and it is almost impossible to count them” (p. 152). Perhaps he meant that it was biological and not due to the abrasion or lack of the shell remains. Stratigraphically, it came from the base of the ‘Katrol Group’ of the Oxfordian age (see also Spath, 1931), which is not within the range of *Hubertoceras* s. st. Even the Katrol Formation was not within the Oxfordian, it actually belongs to the Kimmeridgian (Shome and Bardhan, 2009). But Spath (1931) was confused with the stratigraphy of some of the specimens, which he illustrated as *H. mutans* (Spath, 1931, plate 54, figure 8a, b; plate 56, figure 7a, b; plate 60, figure 1a, b). The specimen (plate 54, figure 8a, b) which came from the younger Oxfordian may not belong to *Hubertoceras*. Another specimen (plate 56, figure 7a, b) is highly compressed and relatively involute. He was not sure about its stratigraphic occurrence and mentioned its occurrence questionably from his ‘anceps beds’. It is both morphologically and morphometrically similar to microconch of the older *Kinkeliniceras* (personal observation). One specimen (Spath, 1931, plate 57, figure 6 a, b) came from the ‘anceps’ horizon proper and is quite similar to *Hubertoceras* s. st. Spath (1931) also reiterated that it “is more like *H. omphalodes* than the type” (p. 318). We here synonymised it with the type species, *H. omphalodes*. *Hubertoceras?* sp. nov. is represented by a single specimen whose early part of outer whorl is broken, but the latter half consists of terminal whorl and Spath (1931, p. 323) mentioned “the mouth border almost intact except for the lateral processes” (see Figure 3.8). However, we found the mouth border broken and ribs are occasionally trifurcating in the outer whorl. We, in a previous attempt, considered it as the young phragmocone of *Obtusicoelites* (Dutta and Bardhan, 2016) and here placed it within *Obtusicoelites devi*.

All the species of *Hubertoceras*, therefore appeared to be small and lappeted or adult with nearly complete body chamber with lappets missing. They varied in size ranging from 45 mm to 83

mm with adult body whorl consisting of about three-fourths of the outer whorl. All species have biplicate ribs. This suggests that *Hubertoceras* is a microconchiate genus (cf. Callomon, 1963). Recently we combined some of the lappeted species (*H. omphalodes*, *H. dhosaense* and *H. hubertus*) of Spath (1931) within a single species, *H. omphalodes* (Dutta and Bardhan, 2016). They represent intraspecific variants and are essentially contemporaneous. Ontogenetically, *Hubertoceras* shows variation in shell involution (umbilical diameter/shell diameter i.e., U/D = 0.33-0.43), shell inflation (whorl width/whorl height i.e., W/H = 0.7-1.09) and ornamental density (primary ribs, P=7-15; secondary ribs, S=16-29) (Dutta and Bardhan, 2016).

Search for the Macroconchiate Counterpart of *Hubertoceras*

Klug et al. (2015) followed Davis et al. (1996) in formulating criteria to identify antidimorphic pairs. The important ones are: 1) a supposed dimorphic pair must be distinguished by at least one morphological trait (i.e., adult size, ornament, suture, etc.); 2) in a cladistic sense, the supposed pair must be monophyletic and forms a sister group; 3) they should be paleobiogeographically and paleoecologically congruent and; 4) secondary sexual features should be preserved in the shell for example, rostra, lappets, etc. Identical juvenile ontogeny is also very important prerequisite for proposing a hypothesis of sexual dimorphism. While looking for the possible macroconch of *Hubertoceras*, we kept all these criteria in mind.

Although the Callovian ammonites are among those which are best known in terms of sexual dimorphism, there remained a significant percentage of doubtful cases of sexual dimorphism from the Callovian to the Kimmeridgian (Davis et al., 1996). This situation was partly attributed to the rise in the numbers of microconch ammonoids that were very hard to pair up with any macroconchiate forms if the stratigraphic ranges and paleobiogeographic patterns were considered. Similarly, it was challenging to establish the macroconchiate counterpart of *Hubertoceras*. Our search for the macroconchiate counterpart of *Hubertoceras* included the genera within the Sivajiceratinae lineage as well as macroconchs of some other coeval genera of different lineages. We considered other genera because of the existence of great morphological disparity between dimorphs of a single biological species. They were often previously placed as distinct species within different taxonomic groups (e.g., see Callomon, 1963; Klinger and Kennedy,

1989; Jana et al., 2005). For this purpose, we have carried out extensive morphological and morphometrical comparisons. Two quantifiable characters like the whorl shape (W/H) and coiling (U/D) have been measured in *Hubertoceras* and all species of the potential macroconchiate genera.

The beginning of the middle Callovian in Kutch witnessed a rapid diversification of many large, evolute and ornamented ammonite macroconchite genera, including *Reineckeia* (Cariou and Krishna, 1988; Kayal and Bardhan, 2005); *Choffatia* (Bardhan et al., 2012); *Idiocycloceras* (Jana et al., 2005), *Indosphinctes* etc. These macroconchiate genera also show general similarity in shape (evolute) and nature of ornaments (strong ribs) with the macroconchiate genera of Sivajiceratinae lineage. We explored the possibility of finding the true macroconchiate counterpart of *Hubertoceras* within any of the above mentioned genera and Sivajiceratinae (Figures 4-5). For this we made bivariate plots (R-plots) involving degree of inflation (W/H) vs. degree of involution (U/D) of all these genera, including *Hubertoceras* (n=180).

Methods for Establishing Parallel Evolution

Another important prerequisite for establishing sexual dimorphism in a lineage is that both macroconch and microconch of the member species should show parallel evolution through time. Parallel evolution may be even found at higher taxonomic level between two distinct lineages (for example, see Monnet et al., 2011). Callomon (1963) considered this phenomenon within species as the strongest evidence in favour of sexual dimorphism. According to him, “the lineages must develop in pairs, in parallel like railway lines” (p. 33).

Evolutionary trends of different morphological characters of each dominant species within each genus of Sivajiceratinae are analysed. Median values of quantifiable characters like shell diameter (D), degree of involution (U/D), degree of inflation (W/H), number of primary (P) and secondary (S) ribs per half whorl are plotted for both macroconchs and microconchs based on sizable number of specimens (n = 110). Complete adult body whorl diameters of many macroconch specimens are not available. We, therefore, measured either the diameter of the incompletely preserved body chamber or reconstructed the diameter from the trace of the umbilical seam of body whorls. We counted primary and secondary ribs, from the adult phragmocones of specimens because in some species for example, *Sivajiceras paramorphum*,

the secondary ribs disappear on the adult body chamber. Parallel evolution between sexual dimorphs is expected to be persistent even within a lineage. We, therefore, tested this hypothesis at the genus-level incorporating all species of Sivajiceratinae of the Callovian. *Sivajiceras* is represented by *S. paramorphum* and two species of *Kinkeliniceras* (*K. angygaster* and *K. subwaageni*) and two species of *Obtusicosites* (*O. obtusicosta* and *O. devi*) are considered. We also tested this hypothesis at the species level for the genus *Sivajiceras* and *Obtusicosites*. *Sivajiceras* were represented by two species, i.e., *S. congener* of the upper Bathonian and *S. paramorphum* of the lower-middle Callovian and *Obtusicosites* also represented by two species, i.e., *O. obtusicosta* and *O. devi* of the middle and upper Callovian. We could not establish antidimorphic pairs in all species of *Kinkeliniceras* and it was therefore excluded from the analyses.

RESULTS

Search for Macroconch of *Hubertoceras* Outside Sivajiceratinae

Reineckeia anceps has evolute and inflated shell with strong tubercles, but the inner whorls lack tubercles and have bifurcating ribs (Cariou and Krishna, 1988; Kayal, 2009) like *Hubertoceras* (compare Figures 4.1 and 5.6). Numerous sharp primary ribs (P=12 at about the diameter of 13 mm) are the characteristic feature of inner whorls of *R. anceps* whereas in *Hubertoceras*, the primary ribs are strong and widely spaced (P=8 at about 21 mm diameter). However, this macroconch does not match with *Hubertoceras* since it is distinctly sulcate at the mid-venter, a typical symplesiomorphic character of the family Reineckeidae. Difference in subfamily level affinity is also evident in the sutural patterns. The first lateral lobe in *Reineckeia* is extremely long and slender ending with one branch (see Waagen, 1875, plate 58, figure 1b), whereas the first lateral lobe in Sivajiceratinae has five long terminating branches. Morphometrically, the macroconch of *R. anceps* is also quite distinct from *Hubertoceras* (Figure 6). Moreover, paleobiogeographically, *Hubertoceras* is restricted only to the Indo-Madagascan Faunal Province (Dutta and Bardhan, 2016), while *Reineckeia* comes from many regions including Kutch, Europe, South America, North Africa, etc. (Arkell et al., 1957; Cariou, 1984) and has a longer stratigraphic range (upper Bathonian to entire Callovian). Recently, Kayal (2009) established the dimorphism in

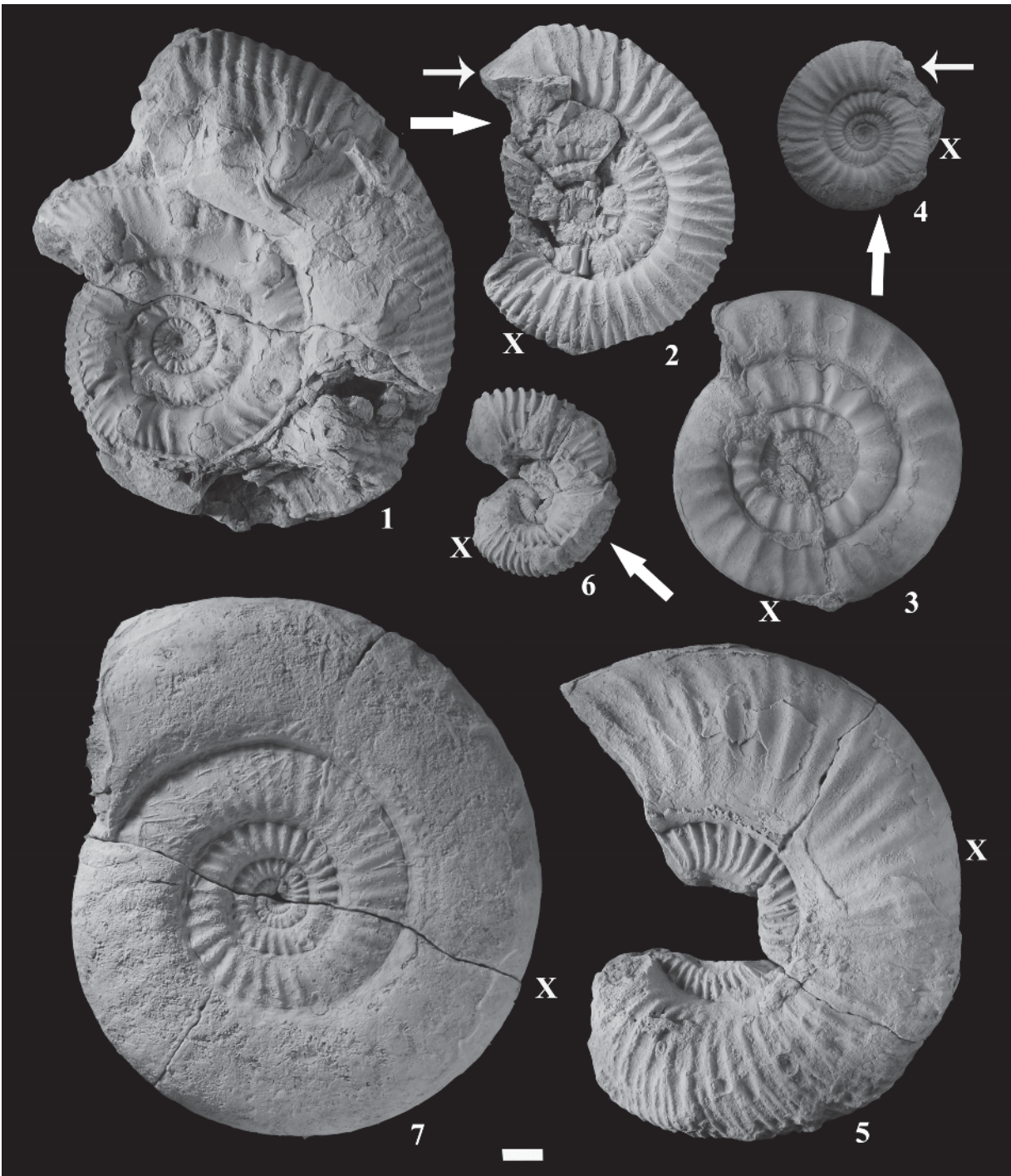


FIGURE 4. Different sexual dimorphic ammonites (non-Sivajiceratinae) contemporary to *Hubertoceras* during the middle Callovian in Kutch. Sexual Dimorphism among these species is well established and the pairs have been shown to be connected by large arrows. **1-2.** *Reineckia anceps* (M, JUM/R/90, bed 6, middle Callovian of Keera and m, JUM/R/44, bed 9, middle Callovian of Jumara, respectively). **3-4.** *Choffatia cobra* (M, JUM 33, bed 7, lower Callovian of Jumara and m, JUM 38, bed 7, lower Callovian of Jumara respectively). **5-6.** *Idiocyloceras perisphinctoides* (M, JUM 450, bed 8, middle Callovian of Jura and m, JUM 270, bed 6, middle Callovian of Keera respectively). **7.** *J Indosphinctes* sp. (M, JUM/IS/01, bed 11, middle Callovian of Jumara). Beds are following Jana et al. (2000, 2005). Note that microconch of *Indosphinctes* is still unknown. 'x' indicates the end of phragmocone. Small arrow indicates presence of lappets. Scale bar equals 20 mm. The sources are: Jana et al., 2005; Kayal, 2009; Bardhan et al., 2012, Dutta and Bardhan, 2016.

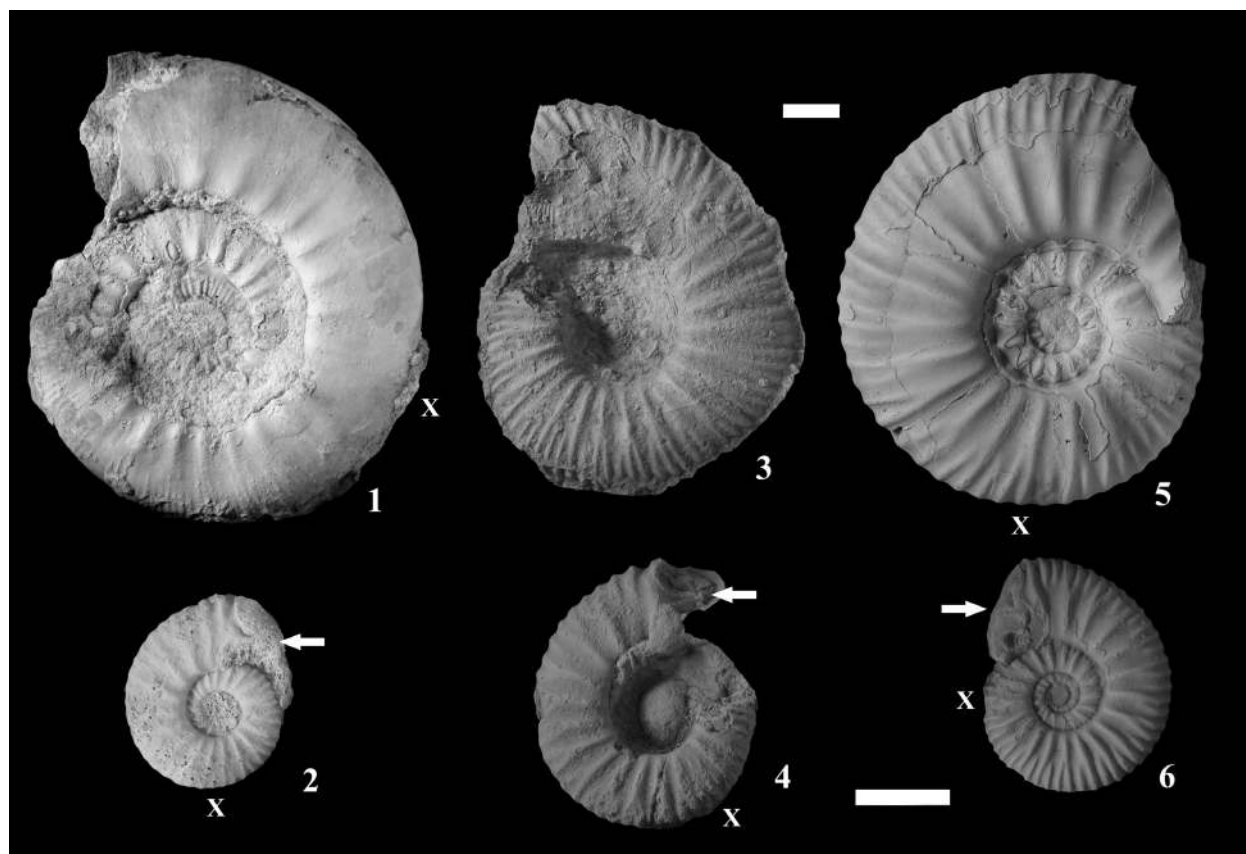


FIGURE 5. Supposed antidimorphic pairs within the subfamily Sivajiceratinae. **1-2.** *Sivajiceras paramorphum* (M, JUM/SP/2, bed 7, lower Callovian of Jumara and m, JUM/SP/22, bed 2, lower Callovian of Keera). **3-4.** *Kinkeliniceras angygaster* (M, JUM/KA/1, locality/stratigraphy unknown; m, JUM/KA/5, Medisar, Jura). **5-6.** *Obtusicoelites obtusicoelita* (M, JUM/OO/1, bed 11, middle Callovian of Jumara and m, JUM/OO/14, locality/stratigraphy unknown). 'x' indicates the end of phragmocone. Small arrow indicates the presence of lappets. Scale bars=20 mm. The sources are: Jana et al. (2000, 2005) for stratigraphic information and Dutta and Bardhan (2016) for taxonomy.

Reineckeia in Kutch where macroconch and microconch match well with each other (see Figures 4-5) and the microconch is quite distinct from *Hubertoceras*.

Another abundant and diverse genus of the middle Callovian is *Choffatia*. The type species *C. cobra* is characterized by evolute, depressed whorls with strong primary ribs (Figure 4.3) furcating at the outer flank. Their inner whorls are somewhat similar to inner whorls of *Hubertoceras* in having strong primary ribs and perisphinctoid umbilicus (shallow and wide). However, detailed examination revealed that there are many apomorphies of *Choffatia* not shared by *Hubertoceras*. For example, constrictions are present in the inner whorls of *C. cobra* which are lacking in *Hubertoceras*. The number of secondary ribs in *Choffatia* and their points of furcation also vary from that of *Hubertoceras* (for detailed description of *Choffatia cobra*, see Bardhan et al., 2012). The sutural pat-

tern of *Hubertoceras* broadly resembles that of *Choffatia cobra* (see Bardhan et al., 2012; figure 13b), but septal sutures are more ramified and complex in the later. Morphometrically, they are also disjunct (Figure 6). Bardhan et al. (2012) established antidimorphic pairs in *Choffatia* (see Figure 4.3-4.4) of Kutch in which microconchs are lappeted. But, *Choffatia* microconchs differ from *Hubertoceras* in many characters (e.g., ribbing patterns, number of ribs and shape of lappets) (Figure 4.4). Their paleobiogeographic distributions also suggest inhomogeneity; while *Hubertoceras* is endemic to Kutch and neighbouring areas, *Choffatia* in contrast, is widely distributed throughout the world. It is found in Africa (Tanzania, Ethiopia), Madagascar, Kutch, Europe (Italy, Spain, France, England), North and South America (Alaska, British Columbia, Mexico, Chile, Argentina) and central Asia (Turkmenistan) (Bardhan et al., 2012). Stratigraphically, *Choffatia* is long ranging (Batho-

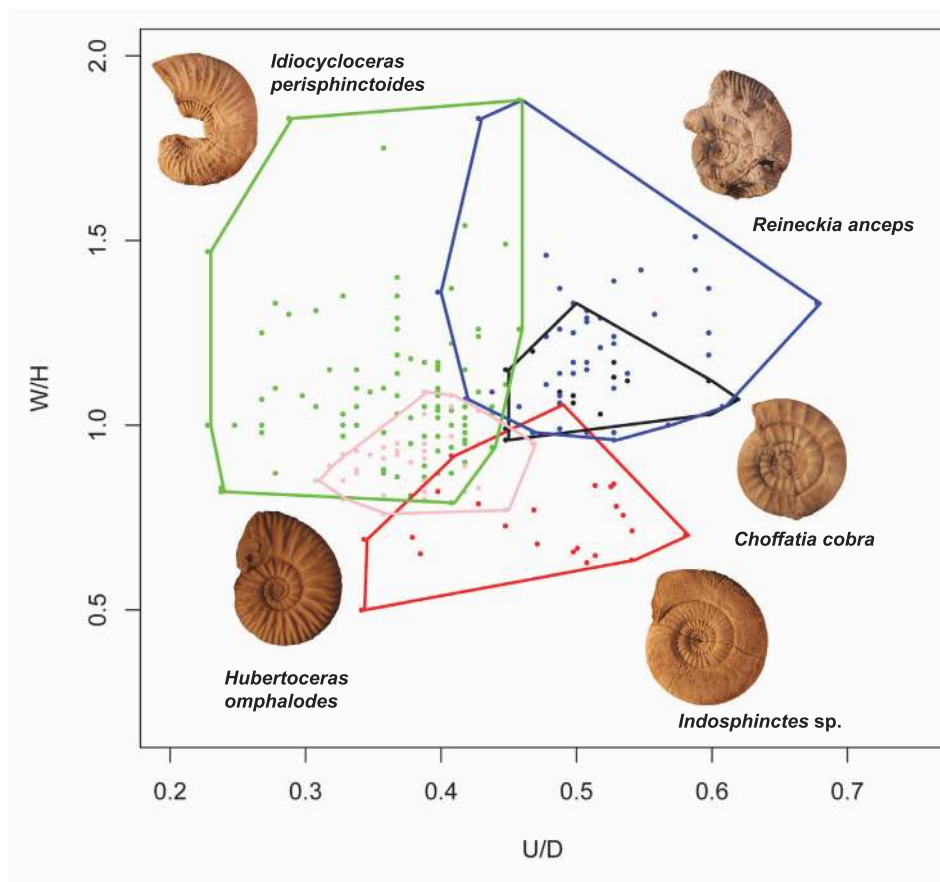


FIGURE 6. Bivariate growth graphs between *Hubertoceras omphalodes* and macroconchs of all contemporary (middle Callovian) species of different genera i.e., *Reineckia anceps*, *Choffatia cobra*, *Idiocyloceras perisphinctoides* and *Indosphinctes* sp. Cluster of morphological characters of *Hubertoceras* are separated from those of other genera. D=Diameter of the shell, U=Umbilical diameter, W=Width of the whorl and H=Height of the whorl. Measurements are taken at different ontogenetic stages of the specimens to accommodate intraspecific range of variability of each species. Photos are not to scale.

nian-Callovian) while *Hubertoceras* is restricted only to the middle and upper Callovian.

Similarly, for the case of *Idiocyloceras* the macroconchiate data do not fit with *Hubertoceras*. *Idiocyloceras* (M) is characterised by its more evolute, depressed to compressed whorl shape with distant primary ribs which are blunt, straight and finally disappear near the peristome (Figure 4.5). The whorl shape of *Idiocyloceras* in the inner part is compressed to depressed whereas *Hubertoceras* always have depressed inner whorls. *Idiocyloceras* have some overlapping areas with *Hubertoceras* (Figure 6). Both *Idiocyloceras* and *Hubertoceras*, also have similar bioprovincialism. They are mainly found in the Indo-Madagascan region as well as in Himalayan Tethys (Jana et al., 2005; Dutta and Bardhan, 2016). But, *Idiocyloceras* is biostratigraphically well constrained and restricted only to the *Idiocyloceras perisphinctoid*

horizon within the subzone *Eucycloceras opis* of the Anceps Zone in the middle Callovian of Kutch (Jana et al., 2005). *Hubertoceras* has a larger stratigraphic range spanning the middle to upper Callovian. Because of these stratigraphic heterochrony and the morphological disparity, *Idiocyloceras* is probably not the antidimorph of *Hubertoceras*. Another important clue of their different subfamily level affinity comes from their entirely different sutural patterns. Septal suture in *Idiocyloceras* is projected towards umbilical with a broad typical saddle envelop of lobes (Jana et al., 2005, text figure 15) while in *Hubertoceras*, auxiliary lobes are oblique and hang down to form a broad umbilical lobe. Besides, the antidimorph of *Idiocyloceras* is well established (Figure 4.5-4.6; also see Jana et al., 2005); although its microconchiate counterpart has an adult body size range and degree of involution similar to those of *Huber-*

toceras, the lack of lappet and nature of ribbing (strong and dense) readily distinguishes it (Figure 4.6) from *Hubertoceras*.

Indosphinctes is another abundant genus of the lower and middle Callovian of Kutch. Spath (1931) only described *Indosphinctes* from the lower Callovian beds, and we recently discovered a distinct middle Callovian species. *Indosphinctes* is a large genus with evolute and compressed shell and smooth body chamber (Spath, 1931; Dutta and Bardhan, 2017; Figure 4.7). Thus *Indosphinctes* may be a contender for the macroconchiate counterpart of *Hubertoceras*. Study of inner whorls, however, reveals that they are unrelated. In the inner whorls of *Indosphinctes*, primary ribs are dense (P=15 per half whorl at the 37 mm diameter), whereas in the same diameter the primaries are less dense and distant in the inner whorls of *Hubertoceras* (P=10). Moreover, furcation of ribs takes place at the higher flank in *Indosphinctes* whereas secondaries originate nearly at the mid-flank in *Hubertoceras*. Septal suture of *Hubertoceras* is very simple while it is highly complex and ramified in the genus *Indosphinctes* (see Dutta and Bardhan, 2017, figure 2.2). Stratigraphically, *Indosphinctes* spans from the lower to middle Callovian whereas *Hubertoceras* is from the middle to upper Callovian. Paleobiogeographically, *Indosphinctes* is a cosmopolitan genus distributed in Europe (England, France), Africa (Kenya), Asia (Turkey, Iran), Kutch, Japan, etc. (Arkell et al., 1957; Cox, 1988), whereas *Hubertoceras* is restricted only to the Indo-Madagascan Faunal Province with rare occurrence in the Himalayan Tethys (Dutta and Bardhan, 2016).

Search for Macroconch of *Hubertoceras* within Sivajiceratinae

Sivajiceras is a member of the subfamily Sivajiceratinae and thus phylogenetically related to *Hubertoceras* in having similar synapomorphic characters like depressed shell and strong primary ribs in the inner whorls (Dutta and Bardhan, 2016). General similarity of sutural patterns also speaks for their affinity at the subfamily level. *Sivajiceras* ranges from the upper Bathonian to the lower part of the middle Callovian (Roy et al., 2007; Dutta and Bardhan, 2016). Only in the early part of the middle Callovian, these two genera overlap stratigraphically. The Callovian species of *Sivajiceras* is represented by *S. paramorphum*. The macroconch is characterised by highly evolute and compressed shell with a smooth venter on the adult body whorl and shows some morphometric homogeneity with

Hubertoceras (Figure 7). Spath (1931) also reiterated 'that in ribbing [*Hubertoceras* species] resemble the young *Sivajiceras* throughout life' (p. 284). We argued that this similarity is due to the fact that they were phylogenetically close. *Sivajiceras* has constriction in early stage which is an apomorphic character, not present in the inner whorls of *Hubertoceras* (see Dutta and Bardhan, 2016). We recently discovered the microconch of *S. paramorphum* from the lower Callovian horizons, which was very similar to *Hubertoceras* (Dutta and Bardhan, 2016). But these two microconchs differ from each other in adult size and degree of involution (Figure 5.2). *Hubertoceras* was larger with more evolute shell. *Sivajiceras*, therefore, might not be the antidimorph of *Hubertoceras* since it has a longer stratigraphic range and has its own microconch.

Another important genus of Sivajiceratinae is *Kinkeliniceras*. It occurs mainly in the middle Callovian beds of Kutch. Adult *Kinkeliniceras* is rather relatively involute, compressed and has more number of ribs. The inner whorls of *Kinkeliniceras* are also involute, compressed and have denser primary ribs while the inner whorls of *Hubertoceras* are evolute, depressed and have distant primaries. Even the pre-adult shell of *Kinkeliniceras* differs from that of *Hubertoceras* in having a relatively involute shell with numerous fine ornamentation. In both *Kinkeliniceras* and *Hubertoceras*, sutural patterns are similar being less complex (Figure 8.4; Dutta and Bardhan, 2016, figure 6c). Morphometrically, *Kinkeliniceras* shows non-overlapping cluster with *Hubertoceras* (Figure 7). We recently described the microconch of *Kinkeliniceras angygaster*, which looks dissimilar to *Hubertoceras* in many respects (see Figure 5.4).

The genus *Obtusicoelites* is another macroconchiate form within the Sivajiceratinae. The dominant species, *O. obtusicoelites* is characterised by a large, evolute shell with strong ornamentation and complex sutural patterns. The type species, *Hubertoceras omphaloides*, differs from it by its size being small with a less complex suture and is characterized by lappeted peristome. *Obtusicoelites* and *Hubertoceras* are not only phylogenetically related, they share many apomorphic characters in their inner whorls. The depressed, evolute shell (Figure 8.1-8.2) with strong primary ribs characterises the inner whorls of both *O. obtusicoelites* and *H. omphalodes*. Moreover, they have bullae-like primary ribs on the adult shells (Figure 5.5-5.6). Another dimorphic pair, *O. devi* is established by the only types. Here, microconch differs from the

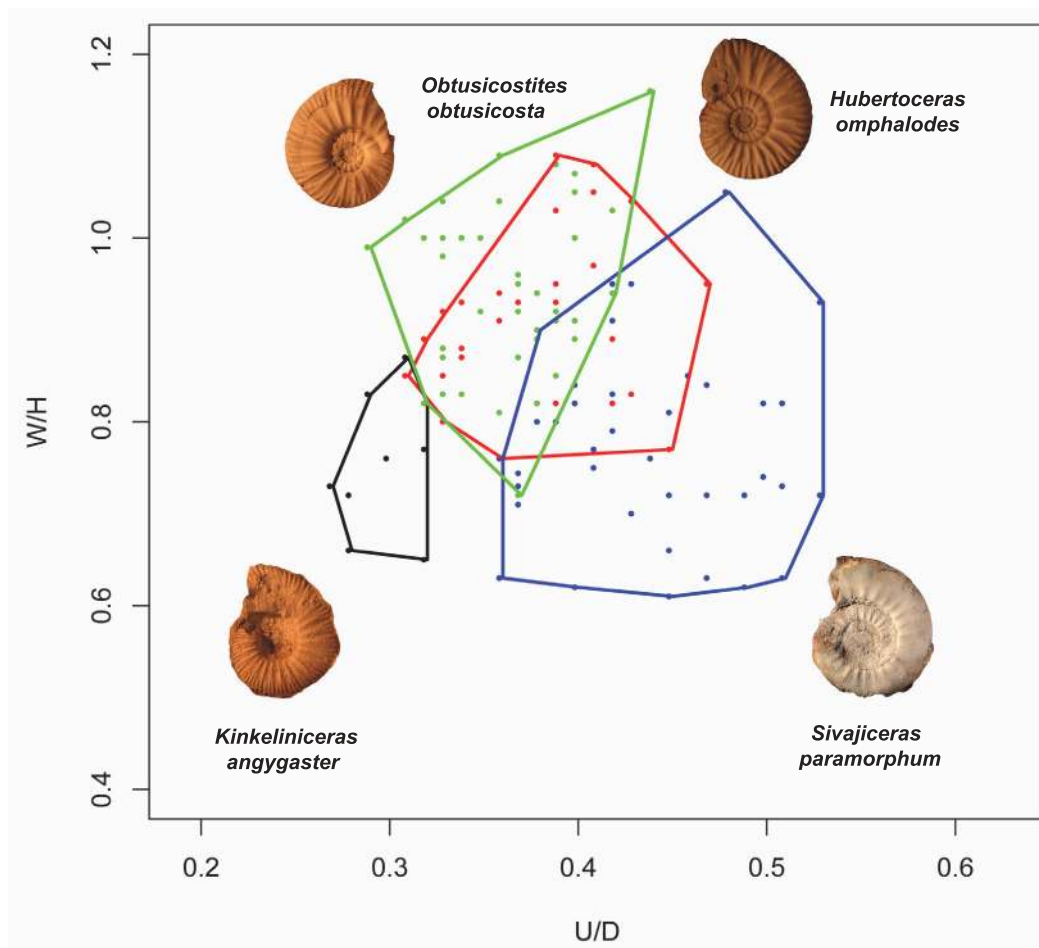


FIGURE 7. Bivariate growth graphs between *Hubertoceras omphalodes* and macroconchs of the subfamily Sivajiceratinae. Maximum homogeneity of points is shown between *Obtusicostites obtusicosta* and *Hubertoceras omphalodes*. D=Diameter of the shell, U=Umbilical diameter, W=Width of the whorl and H=Height of the whorl. Measurements are taken at different ontogenetic stages of the specimens to accommodate intraspecific range of variability of each species. Photos are not to scale.

macroconch by its small size and lappeted peristome.

In many occasions, Spath (1931, p. 321-322) mentioned the identical nature of the inner whorls of *Obtusicostites* with adult *Hubertoceras*. For example, rounded whorl shape of adult *Hubertoceras* resembles the inner whorls of *Obtusicostites*, and there is great resemblance between the whorl thickness of *Hubertoceras* and the young *Obtusicostites*. Callomon (1963) emphasized that one of the criteria for the establishment of sexual antidimorphic pair is that the microconch is more or less the miniature version of the inner whorls of macroconch. Morphometrically, *Obtusicostites* shows maximum homogeneity with *Hubertoceras* (Figure 7) in comparison to other macroconchiate genera of middle-upper Callovian of Kutch. More importantly, they share similar paleobiogeographic (Indo-

Madagascar Faunal Province) and stratigraphic (middle to late Callovian) distributions. Ideally in any dimorphic species, sex ratio should be 1 but in ammonites it may vary 100:1 in favour of any variant (Callomon, 1981). Curiously, in the present *Obtusicostites obtusicosta* collection from Kutch, the sex ratio is close to 1 (M:m=1.15:1) and in case of *O. devi* the ratio is 1. Therefore, this antidimorphic pairs satisfy all the criteria in establishing the sexual dimorphism.

SYSTEMATIC PALEONTOLOGY

Abbreviations: * in front of the publication year in the synonymy list for the name-giving citation. v- in the synonymy list in front of the publication year indicates the specimens which were investigated in the present study. [M] and [m] designate macro-

conch and microconch respectively. The following letters are used to indicate shell parameters: D- diameter of the shell; U- diameter of the umbilicus; W- width of the whorl; H- height of the whorl from the umbilical margin; P- number of primary ribs per half whorl; S- number of ventral ribs (secondary plus intercalatory ribs) per half whorl.

Phylum MOLLUSCA Linnaeus, 1758
Class CEPHALOPODA Cuvier, 1795
Order AMMONOIDEA Zittel, 1884
Family PERISPHINCTIDAE Steinmann, 1890
Subfamily SIVAJICERATINAE Dutta and Bardhan, 2016
Type genus *SIVAJICERAS* Spath, 1930
Genus *OBTUSICOSTITES* Buckman, 1921

Type species. *Perisphinctes obtusicosta* (Waagen, 1875)

Diagnosis of the genus. Macroconch large (maximum D=165 mm) and evolute (U/D = 0.3–0.38). Bullae-like primary ribs characterise the shell. Microconch (maximum D=50 mm) lappeted and strongly ribbed.

Species included. *Obtusicostites obtusicosta* (M and m) and *Obtusicostites devi* (M and m).

Stratigraphical and geographical occurrences: middle to upper Callovian; Kutch, Madagascar Tanzania and Spiti, Himalaya.

Obtusicostites obtusicosta (Waagen, 1875)
Figures 3.1-3.4, 5.5- 5.6, 8

Holotype. GSI type no. 2032[M]

- v* 1875. *Perisphinctes obtusicosta*, Waagen, p. 146, pars, pl. 38, fig. 1a,b; p. 146, pl. 38, fig. 2; p. 146, pl. 38, fig. 3 a,b [M]
- v 1875. *Perisphinctes dhosaensis*, Waagen, p. 149, pl. 38, fig. 4 a-c [m]
- v 1875. *Perisphinctes omphalodes*, Waagen, p. 150, pl. 38, fig. 2 a,b [m]
- v 1931. *Obtusicostites obtusicosta* (Waagen); Spath, pl. 55, fig. 2; pl. 64, fig. 3 a,b [M]
- v 1931. *Obtusicostites waageni*, Spath, pl. 53, fig. 2a, b; pl. 80, fig. 1 a,b (m).
- v 1931. *Obtusicostites buckmani*, Spath, pl. 49, fig. 9; pl. 53, fig. 3 a,b; pl. 62, fig. 8 [M]
- v 1931. *Obtusicostites devi*, Spath, pars, pl. 45, fig. 5; pl. 52, fig. 2 a,b; pl. 65, fig. 3 [M]
- v 1931. *Obtusicostites devi*, Spath, pars, pl. 55, fig. 4 [M]
- v 1931. *Obtusicostites ushas*, Spath, pl. 52, fig. 6; pl. 53, fig. 1 a,b; pl. 56, fig. 1; pl. 57, fig. 3; pl. 63, fig. 6 [M]
- v 1931. *Kinkeliniceras crassiplanula*, Spath, pl. 58, fig. 4, 5; pl. 65, fig. 4 a,b [M]
- v 1931. *Obtusicostites* aff. *ushas*, Spath pl. 57, figs. 7a,b [m]

- v 1931. *Hubertoceras dhosaense*, (Waagen); Spath, pl. 74, figs. 50 a,b [m].
- v 1931. *Hubertoceras hubertus*, Spath, pars, pl. 57, fig. 4a-c; pl. 59, fig. 1 [m]
- v 1931. *Hubertoceras omphalodes*, (Waagen), Spath, pl. 49, figs. 7 a,b; pl. 61, fig. 4; pl. 65, fig. 2; pl. 67, fig. 9 [m]
1958. *Obtusicostites* aff. *obtusicosta*, (Waagen); Collignon, pl. 29, fig. 133 [M]
1958. *Obtusicostites ushas*, (Spath), Collignon, pl. 29, fig. 131 [M]
1958. *Obtusicostites buckmani*, (Spath), Collignon, pl. 31, fig. 143 [M]
1958. *Obtusicostites devi*, (Spath), Collignon, pl. 31, fig. 144 [M]
1958. *Kinkeliniceras kinkelini*, (Dacque), Collignon, pl. 29, fig. 135 [m]

Description

Macroconch. Species shows great ontogenetic changes in degree of involution and inflation. Inner whorls (D=50mm), are evolute (U/D = 0.3–0.38) and depressed (W/H = 1–1.09). Primary ribs are very strong, fewer and distant. Intermediate whorls (D = 57–115 mm) are still evolute (U/D = 0.3–0.39) but have more or less squarish whorl shape (W/H = 0.8–1). Primary ribs furcate below the mid flank into 2 to 3 secondary ribs which go straight across the venter. Primaries are low, broad and may form bullae. The end of the adult phragmocone (D = 124 to 159 mm) characterized by a shallow and broad constriction. Shell is compressed (W/H = 0.75–0.81) and relatively less evolute (U/D = 0.32–0.38). Flanks are flattish with strong primary and secondary ribs. Primary ribs on the inner flank forms characteristic bullae. Umbilicus has sloping wall and gradual margin. The numbers of primary and secondary ribs vary considerably during ontogeny. They increase from P (7–9) and S (30–33) in the inner whorls to P (9–11) and S (33–36) in the adult phragmocone. The adult body chamber occupies more than half of the outer whorl and is thoroughly and relatively densely ribbed. Umbilicus has inclined wall with gradual margin. Ribs continue and show no sign of attenuation at least up to the preserved end (D= 165 mm). Length of primaries increases in the body chamber, in the latter part of the body chamber, the primary ribs furcate higher on the flank.

The external saddle broad, with a deeply incised secondary lobe; the first lateral lobe is narrow and longer than the siphonal lobe, may have five terminating branches; the first lateral saddle is narrow with a deep asymmetrical lobe. The second lateral lobe is hanging, narrow and short. The sec-

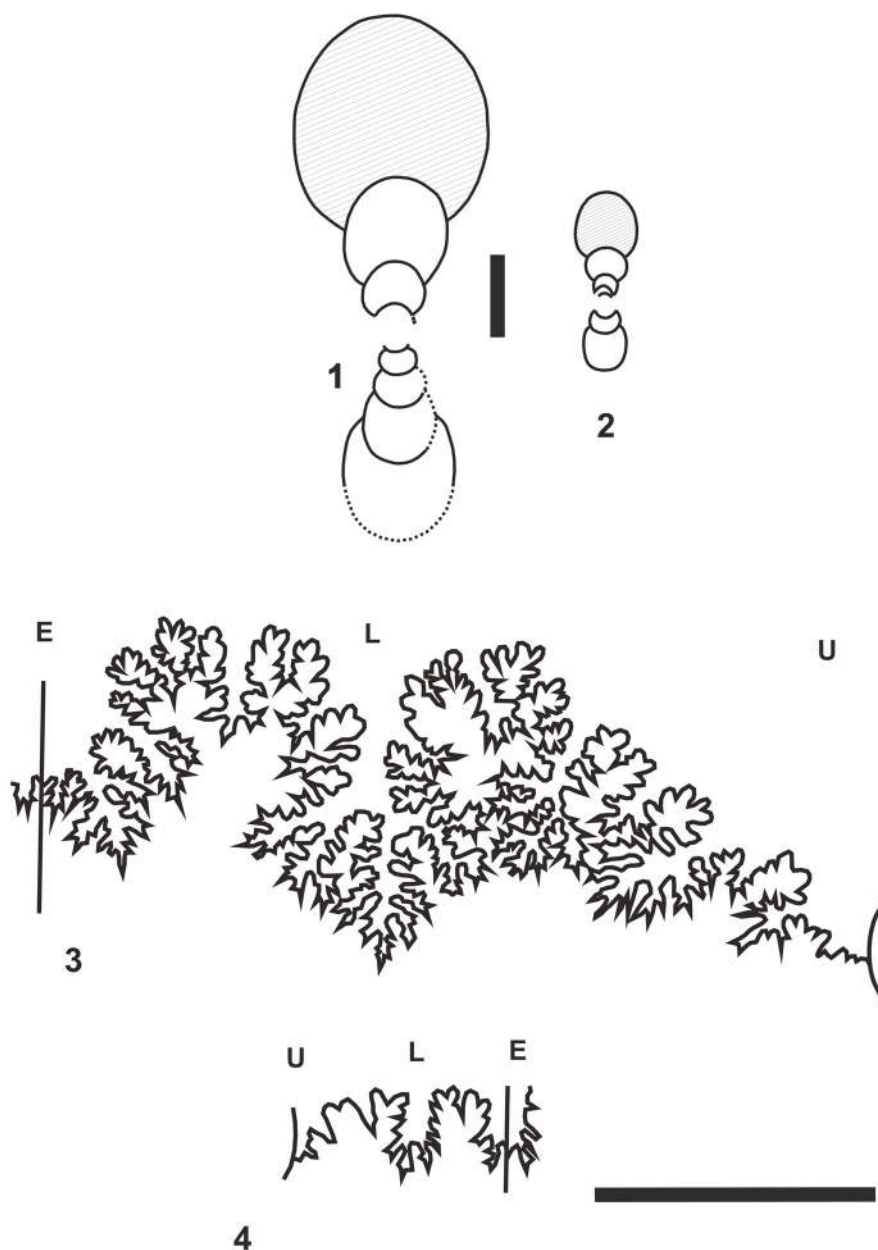


FIGURE 8. Transverse sections (body chamber hatched) of adult shells. **1.** *Obtusicostites obtusicosta* (M). **2.** *Hubertoceras omphalodes* (m). Note, for 1 and 2, overall similarity of whorl sections and depressed inner whorls with rounded umbilical edge. Septal sutural patterns. **3.** *Obtusicostites obtusicosta* (M) at diameter 150 mm, redrawn from Waagen (1875, plate 38, figure 2). **4.** *Hubertoceras omphalodes* (m) at diameter 48 mm, redrawn from Waagen (1875, plate 38, figure 4c). Scale bar equals 20 mm.

ond lateral saddle is also short and oblique with a very large secondary lobe. The second lateral lobe up to the umbilical suture hangs further down and forms a large umbilical lobe (see Figure 8.3).

Microconch. Inner whorls ($D=7-15$ mm) are evolute ($U/D=0.41-0.44$) and depressed ($W/H=1.05-1.2$). Primary ribs are strong and widely spaced.

Adult phragmocone ($D=25-37$ mm) retains the same evolute ($U/D=0.4-0.42$) and depressed ($W/H=0.95-1.09$) shell. Primary ribs are rectiradiate and furcate into 2 to 3 secondaries, which are prorsiradiate and passing over the venter with a forward bend. In the adult body chamber, primary ribs ($P=12$ to 15) are strong bullae-like and split into 2

secondaries at the middle to slightly higher flank. Umbilicus has inclined wall with gradual margin. Shell may be compressed to slightly depressed ($W/H=0.68-1.09$) and shows wide variation in degree of involution ($U/D=0.33-0.43$). Peristome is marked by narrow, deep, long lappet with broad base which is preceded by deep terminal constriction.

The sutural pattern is simple, but broadly resembles the pattern of that of macroconch. The siphonal lobe is broad and short; the external saddle is not very broad, with a strong indentation in the middle; the first lateral lobe is narrow, longer than the siphonal lobe, with three asymmetrical branches; the first lateral saddle is relatively narrow with an incipient but distinct lobe at the middle; the second lateral lobe is short, oblique and not yet branched. Two auxiliary lobes are oblique and hang down to form a broad umbilical lobe (see Figure 8.4).

Remarks. The inner whorls of macroconch and microconch are essentially similar being depressed and evolute shell. Both have strong primary ribs. Microconch replicates the intermediate sized macroconch in having similar ribbing pattern and strength of ornamentation. Whorl shape and coiling are also more or less similar. While adult macroconch is always compressed and evolute, the adult microconch is more evolute and may be less compressed to depressed than that of macroconch. Septal sutural patterns are broadly similar between macroconch and microconch confirming subfamilies affinities but, sutural pattern of microconch is simple. The size ratio between macroconch and microconch (M:m) is 3:1 and sex ratio (M:m) is 1.15:1.

Obtusicoelites devi (Spath, 1931)

Figure 3.5-3.7

Holotype. GSI type no. 16076[M]

v* 1931. *Obtusicoelites devi*, Spath, pars, pl. 52, fig. 5 a,b; pl. 54, fig. 1a,b (M)

v 1931. *Hubertoceras?* sp. nov., Spath pl. 79, fig. 4 a,b [m]

v 1931. *H. hubertus*, Spath, pars, pl. 52, fig. 7; pl. 69, fig. 4 a,b; pl. 56, fig. 4; pl. 68, fig. 11 [m]

Remarks. This species is represented only by types. Spath (1931) described many *Obtusicoelites* and *Hubertoceras* species from higher stratigraphic horizons, i.e. his 'athleta' beds (upper Callovian). These forms have flattish flanks with a shallow umbilicus and more ribs compared to the older *O. obtusicoelites*, which has its highest abundance in the Middle Callovian. These 'athleta' species were synonymised and assigned to *O. devi* of

Spath in the present study. They included both macroconchs and microconchs. The holotype of *O. devi* is an adult septate specimen with half of the outer whorl (missing) occupied by the adult body chamber as evident from the trace of the umbilical seam. Reconstructed diameter is 198 mm and is considered here as macroconch. While describing the differences of these species with *O. obtusicoelites*, Spath (1931) correctly observed that *O. devi* had a weaker and denser costation of both primary and secondary ribs. In the adult phragmocone, *O. devi* has more ribs ($P = 14$, $S = 38$) than *O. obtusicoelites* ($P = 11$, $S = 36$). *Obtusicoelites devi* is more compressed ($W/H=0.67$) than *O. obtusicoelites* ($W/H=0.72$) in the adult phragmocone stage. Septal suture is simple.

Microconch of *O. devi* (maximum $D = 73$ mm) also has a finer and denser ribbing pattern ($P = 15$, $S = 38$). Primaries are relatively weak, and furcation takes place high on the outer flank. Both macroconch and microconch have planulate shape. The size ratio between macroconch and microconch (M:m) is 2.7:1 and sex ratio (M:m) is 1.

Parallel Evolution

Evolutionary trends of macroconchs and microconchs within the Sivajiceratinae lineage broadly show parallel changes (Figure 9, Appendix 4). Degree of involution (U/D) depicted the clearest evidence of parallel evolution. The degree of involution declines significantly (Mann-Whitney U Test with $\alpha = 0.05$) between *Sivajiceras* and *Kinkeliniceras*, followed by a significant increase (Mann-Whitney U Test with $\alpha = 0.05$) between *Kinkeliniceras* and *Obtusicoelites*. This trend is observed in both macroconchs and microconchs of the member species. In case of other parameters, although statistical significance of these changes is not always similar, directions of changes are similar in both macroconchs and microconchs.

We also tested the species level parallel evolution. For the genus *Sivajiceras*, the macroconchs and the microconchs of the two species i.e. *S. congener* and *S. paramorphum* show more or less parallelism of the diameter, degree of involution, degree of inflation, primary and secondary ribs (Figure 10). Same patterns are followed by the two species of *Obtusicoelites*, i.e., *O. obtusicoelites* and *O. devi* (Figure 11).

Moreover, new evolutionary characters for example, bullae-like primary ribs simultaneously appeared in the macroconch (*Obtusicoelites obtusicoelites*) and microconch (*Hubertoceras omphalodes*), and the number of ribs increased in the

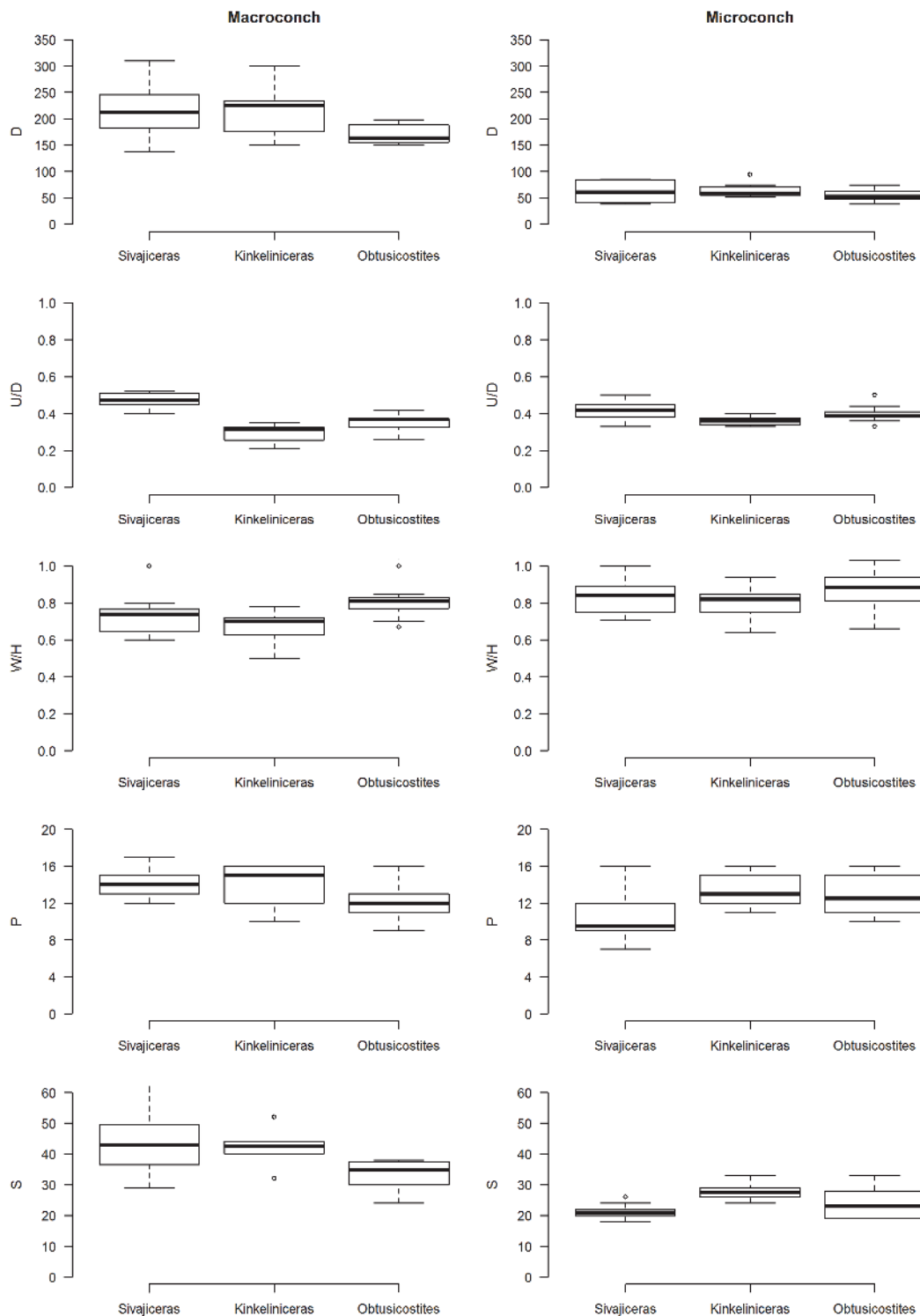


FIGURE 9. Parallel evolution of median values of different morphological characters for three successive genera (including M and m) within Sivajiceratinae is plotted. Note that both M and m within the lineage show parallel evolutionary trends. D, U, W, and H are the same as in Figure 4. P= Primary rib (per half whorl) and S= Secondary rib (per half whorl). The dark horizontal line in the middle of the each box represents the median values, top frame of the box represents 75th percentile, bottom frame of the box represents 25th percentile and the bars at the end of vertical lines represent the minimum and the maximum data values without outliers (open circles). Sources are: Waagen, 1875; Spath, 1931; Collignon, 1958; Dutta and Bardhan, 2016.

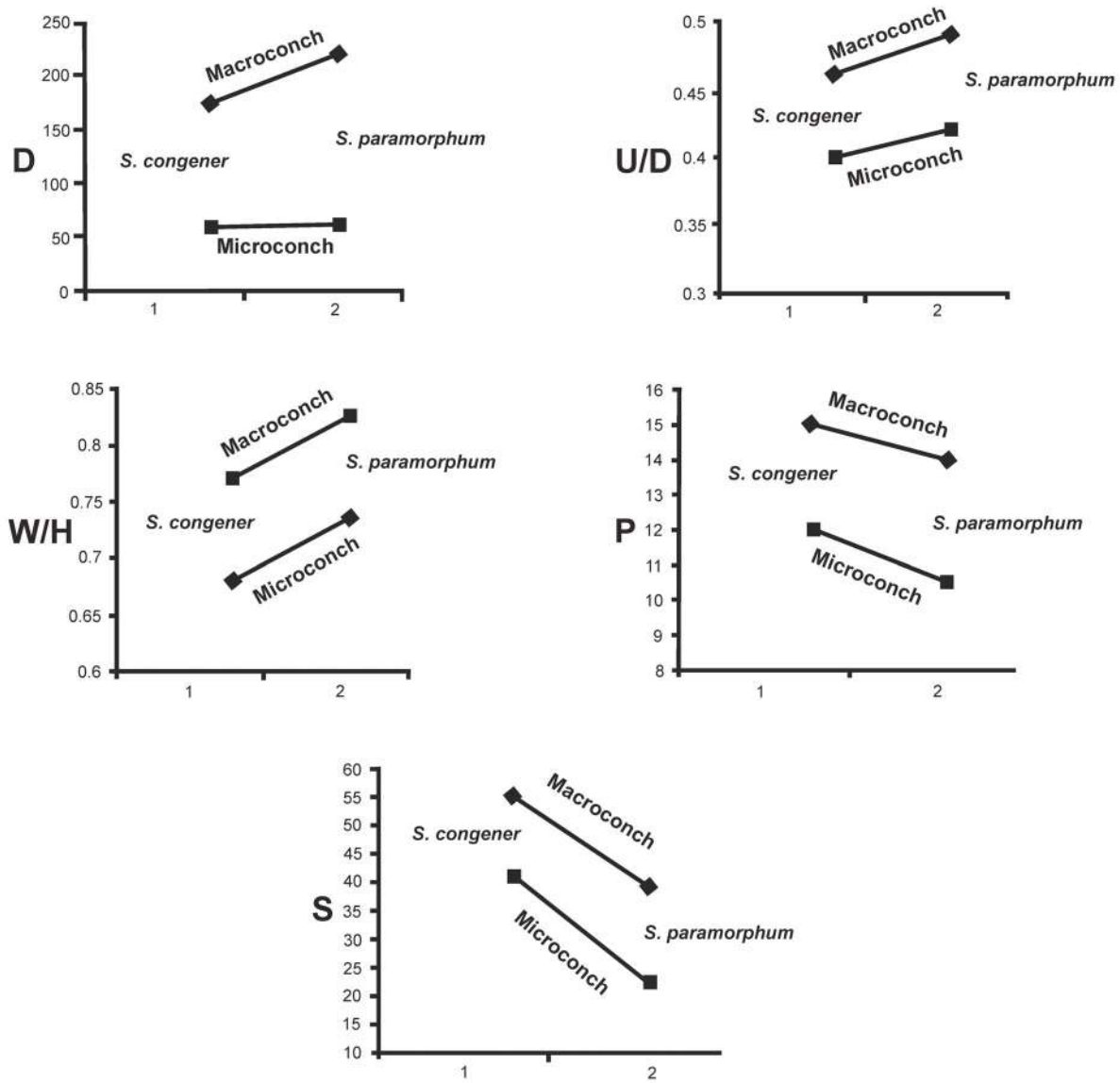


FIGURE 10. Parallel evolution of the species level for the genus *Sivajiceras* is plotted. Note that both M and m within the lineage show parallel evolutionary trends. Sources are: Waagen, 1875; Spath, 1931; Collignon, 1958; Callomon, 1993; Dutta and Bardhan, 2016.

dimorphic pair of *Kinkeliniceras angyaster*. The evolutionary loss of early constriction and rursiradate ribbing, which were the apomorphic traits of *Sivajiceras*, was reflected both in the antidimorphic pairs of *Obtusicosites* and *Kinkeliniceras* (see Dutta and Bardhan, 2016).

DISCUSSION

Middle Jurassic witnessed maximum development of sexual dimorphism in ammonites when antidimorphs evolved contrasting characters leading

to confusion for correct matching. Davis et al. (1996) also noted a significant increase of doubtful cases where it was very difficult to establish antidimorphic pairs especially during the Callovian. The same was true for the present *Hubertoceras* genus from Kutch.

Hubertoceras used to live sympatrically with macroconchiate genera, one of which ran a high chance of being the sexual partner. The contemporary macroconchiate genera were all large, evolved and strongly ornamented. Westermann (1990) collectively described them “*trachyostracans*” ammo-

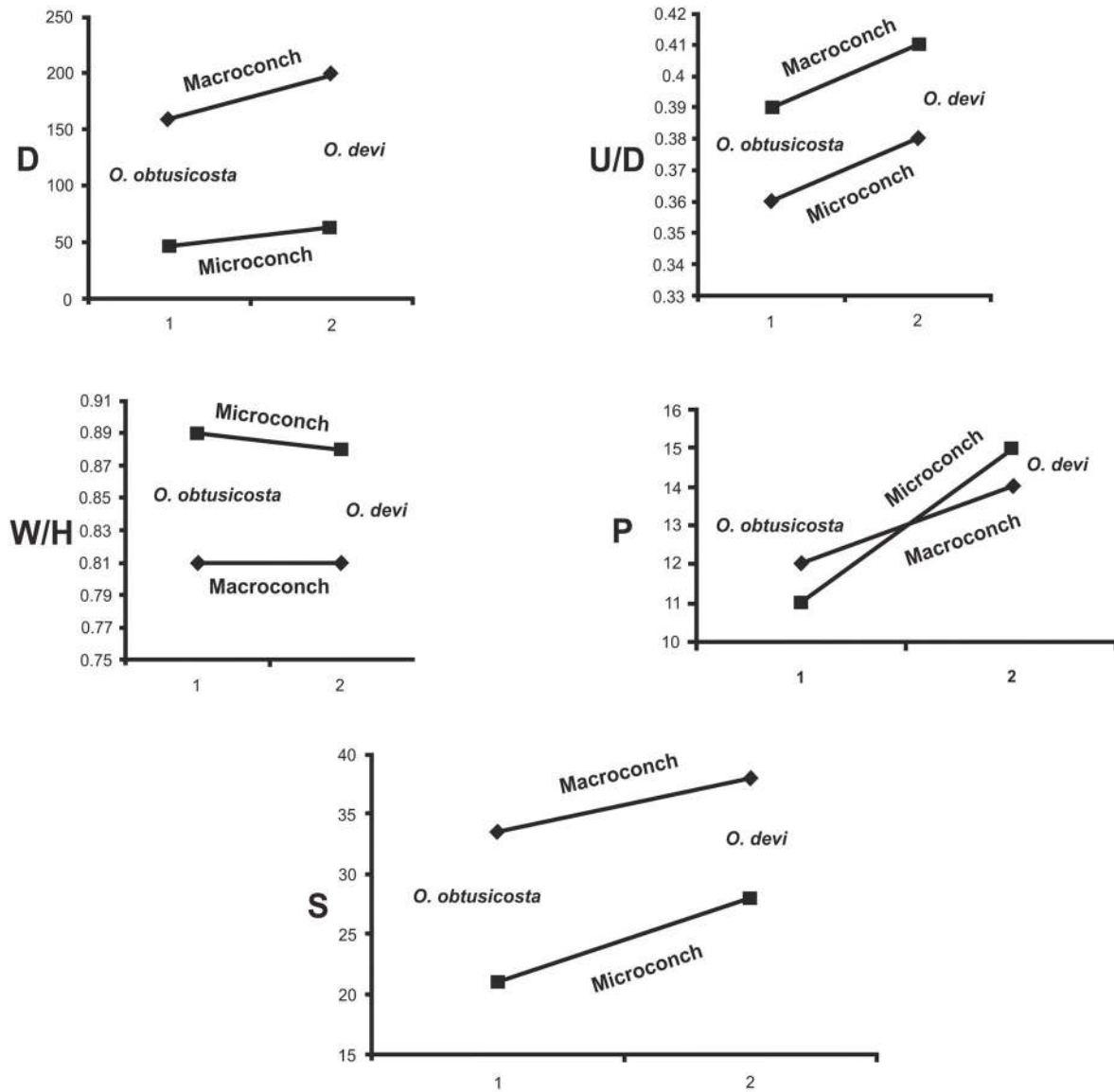


FIGURE 11. Parallel evolution of the species level for the genus *Obtusicostites* is plotted. Note that both M and m within the lineage show parallel evolutionary trends. Sources are: same as in Figure 10.

nites who lived in shallow waters (as was the Callovian Kutch basin; see Fürsich and Oschmann, 1993) and were nectobenthos (cf. Kennedy and Cobban, 1976; Batt, 1989; Tsujita and Westermann, 1998) and sluggish to moderately mobile (also see Ward, 1981; Seilacher and Gishlick, 2015). They were also strongly dimorphic whose microconchs were evolute, lappeted and having bifid ribs like *Hubertoceras*. This ammonite community faced competition for food, habitat and mates (Bardhan and Chattopadhyay, 2003; Jana et al., 2005). The functions of lappets have been variously interpreted (fabricational noise, Seilacher, 1974; Seilacher and Gishlick, 2015; change of hab-

itat or behaviour, Westermann, 1990; Davis et al., 1996; Klug, 2001; defence against predation or intersexual cannibalism, Keupp and Riedel, 2010; sexual characters, Landman et al., 2012). Many workers, however, believed its utility to facilitate mate recognition system among other functions (Kennedy and Cobban, 1976; Jana et al., 2005; Bardhan et al., 2010; Keupp and Riedel, 2010).

Eldridge (1974) mentioned that while competing for the same habitat, sympatric taxa displayed character displacement (also see Jana et al., 2005). While macroconchs of all Kutch genera remained more or less “neutral” in having similar size, shape and ornaments, their microconchs

diverge strongly away in their mature modifications. Similar size, perisphinctoid coiling (low whorl expansion rate with wide umbilicus), bifurcating ribs among the microconchs perhaps disrupted the “mate recognition” system (Bardhan et al., 2010). But, different types of lappets in different species (Figures 4-5) and absence of lappet in *Idiocycloceras* microconch perhaps, therefore, appeared as a sexual display, which facilitated easy recognition of the respective mates.

In conclusion, *Hubertoceras* Spath, 1931 of Kutch is a morph genus. Its microconchiate nature was established here based mainly on the presence of lappets. The antidimorph of *Hubertoceras* was elusive. Detailed search through morphological and morphometrical analyses including identical early ontogenetic characters as well as paleobiological and stratigraphic data suggests now that *Obtusicoelites* represents the best macroconchiate match. The *Obtusicoelites-Hubertoceras* dimorphic pair belongs to the Sivajiceratinae lineage where all genera are shown to be dimorphic. Evolutionary trends of many characters show parallelism between the macroconchs and the microconchs in the lineage.

ACKNOWLEDGEMENTS

We thank the Director of the Repository Section of the Geological Survey of India, Kolkata for granting access to the GSI material for study and photography. We acknowledge Z. Hughes for various supports and P. Hurst for the photography of type specimens housed in the Department of Earth Sciences, Natural History Museum, U.K. We thank C. Klug, University of Zurich, Switzerland for critically reviewing the manuscript and providing valuable suggestions. We thank the anonymous referee as well as the handling editor of the Journal for their critical reviews and suggestions. S.B. received partial aid from the DST (SERB-SR/S4/ES-638/2012), India. R.D. received aid from the UGC-BSR Scheme, Jadavpur University, Kolkata, India.

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APPENDIX 1.

Locality, stratigraphic information and measurements of all specimens (type as well as additional present collection) of Sivajiceratinae within the mainland of Kutch. For detail information of localities see Spath (1931); Waagen (1875); Figure 1. Available in PDF at palaeo-electronica.org/content/2017/1954-antidimorph-of-hubertoceras.

APPENDIX 2.

Precise stratigraphy and locality information of the all the specimens of *Obtusicosites* and *Hubertoceras*. Available in PDF at palaeo-electronica.org/content/2017/1954-antidimorph-of-hubertoceras.

APPENDIX 3.

Stratigraphic information and measurements of all contemporary macroconchiate (middle Callovian) species of different genera along with *Hubertoceras* (m). Available in PDF at palaeo-electronica.org/content/2017/1954-antidimorph-of-hubertoceras.

APPENDIX 4.

Results of Mann-Whitney U test for testing significance of change in morphological traits. Available in PDF at palaeo-electronica.org/content/2017/1954-antidimorph-of-hubertoceras.