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TERTIARY BRYOZOA FROM WESTERN KACHCHH, GUJARAT – A REVIEW

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ABSTRACT

The Tertiary (Lutetian – Burdigalian) sequences of western Kachchh, Gujarat have preserved rich bryozoan assemblages, ninety-nine taxa of which are the main topic of this review article. The diversity and abundance of colonies are highly variable within and between formations, reaching their maximum during the deposition of the Khari Nadi Formation (Aquitanian). Fifteen fossil species of *Thalamoporella* Hincks, 1887, recognized in these sequences, have doubled the number of fossil taxa belonging to this genus to thirty, and have added much information on the Tertiary evolutionary history of this common extant genus. Three new genera, *Reniporella, Archoporella* and *Orbiculipora*, have considerably enriched our knowledge about their respective families. The presence of three out of five Tertiary steginoporellid genera makes Kachchh one of the main centres of diversity for this family. *Therenia indica* takes a conspicuous place in the phylogeny of the genus. Analysis of bryozoan growth forms indicates two episodes of deepening in the shallow pericratonic rift basin of Kachchh. The environment that supported a moderately diverse assemblage was restricted during the early Middle Eocene but gradually opened up and reached its zenith during the Early Miocene (Aquitanian) stage.

INTRODUCTION

The Kachchh region of Gujarat represents one of the classical areas of geology of peninsular India that has aroused the interest of palaeontologists from all over the world for the great Jurassic ammonoids, and then the Tertiary foraminifers. The pericratonic rift basin in the western margin of India has preserved a condensed section (about 900 metres thick) of Tertiary rock formations (Fig. 1) ranging from the Paleocene to Pliocene. Among the microbiota, large benthic Foraminifera form the major group, and have been successfully used for stratigraphical classification. These sequences (Table 1) have been classified on chrono-, litho- and biostratigraphical basis, the boundaries of which are somewhat parallel and seldom mutually transgressive. Based on larger benthic Foraminifera

Table 1 - Tertiary stratigraphy of Kachchh (after BISWAS, 1992).

AGE	FORMATION	LITHOLOGY
Middle Miocene-	Sandhan	Sandstones, minor
Photene	Unconformity	(No Bryozoa)
Early Miocene	Chhasra	Silty shales and impure
(Burdigalian)		Limestones.
Early Miocene	Khari Nadi	Variegated siltstones and
(Aquitanian)	Unconformity	sandstones.
Oligocene	Maniyara Fort	Foraminiferal
(Rupelian-Chattian)	Unconformity	limestones, shales, coral
		bioherms and lumpy claystones.
Middle to early L.	Fulra	Dense foraminiferal
Eocene		limestones.
(Lutetian-Bartonian)		
Early Middle Eocene	Harudi	Claystones/ limestones,
(Lutetian)	Unconformity	coquina, etc.
L. Paleocene to E.	Naredi	Claystones, limestones
Eocene	Unconformity	and gypseous shales.
(Thanetian-Ypresian)		(No Bryozoa)
Early Paleocene	Matanomadh	Volcanoclastics, shales
(Thanetian)	Unconformity	and sandstones. (No Bryozoa)
(Maastrichtian-Danian)	Deccan Trap	Basalt

(chiefly *Miogypsina*), an Aquitanian (25.2-20 MY) age had been assigned to the Khari Nadi Formation and Burdigalian (20.0-16.2 MY) to the Chhasra Formation (Biswas, 1992; Biswas and Raju, 1973; Raju, 1994, 1997).

d'Archiac and Haime (1853) first noted the occurrence of bryozoans in the Tertiary sequences of Kachchh. Tewari et al. (1960) reported two new free-living (lunulitiform) bryozoan taxa, Discoporella misrai and Anoteropora rajnathi from the 'Gaj Beds' (~ Chhasra Formation). Tewari and Srivastava (1967) reported nine new bryozoan species (Stigmatoechos striatus, Herpetopora? sehensis, Ellisina mianica, Bactrellaria? cheropadiensis. Ogivalia vinjhanensis. Nellia quadrangularis, N. kutchensis, Hippothoa narediensis and Tetraplaria turgida) from these sequences. The state of information on the Tertiary bryozoans from Kachchh remained at this level for a long time until the present author and his associates made an effort to study this fascinating group of fossils with a CSIR-supported project from 1995 to 1999.

Following the classification of Biswas (1992), different Tertiary lithologies of Kachchh (Table 1) were examined; some 6675 bryozoan colonies from 191 samples were studied; taxonomic classification and identification of bryozoans up to species level were undertaken, checked and vetted by eminent bryozoologists in different institutions in New Zealand, U.S.A., England and Australia. This resulted in a many-fold increase in bryozoan taxonomic diversity from the Tertiaries of Kachchh - from the 11 species of Prof. Tewari and his co-workers (listed above), the number of taxa increased to 99 species (including four from the earlier list) grouped under 62 genera and 38 families (APPENDIX I) [Guha (1999), Gopikrishna (2003), Guha and Gopikrishna (2004a-b, 2005a-f and 2007a-e)]. Three new genera - Reniporella Guha and Gopikrishna, 2004, Archoporella Guha and Gopikrishna, 2005 and Orbiculipora Guha and Gopikrishna, 2005 (Pl. I) - and 88 new species were recognised. Among the 38 families, 22 are represented by a single genus and 13 by only one species each. Of the 62 genera, 46 are represented by a single species representing a unique diversity. In peninsular India, such rich and diverse bryozoan assemblages match those retrieved from the Maastrichtian of



Fig. 1. Geological map of western Kachchh, Gujarat, showing sampling locations (after Biswas, 1992).

the Ariyalur, Vridhachalam and Pondicherry areas of the Cauvery Basin (Guha and Nathan, 1996).

The type specimens of 15 species of *Thalamoporella* are preserved in the Allan Hancock Foundation collection of species of this genus at Santa Barbara Museum of Natural History, California, USA. Other type specimens (including paratype specimens of 12 *Thalamoporella* species) are indexed and preserved at the Central Fossil Repository Unit (CHQ) of the Geological Survey of India, Kolkata – 700016. Post-

publication assignment of new type numbers for some 16 bryozoan species at the new repository is noted in APPENDIX II. Since type material of four species (*Discoporella misrai*, *Nellia quadrangularis*, *N. kutchensis* and *Anoteropora rajnathi*) of Prof. Tewari and his co-workers are misplaced, designated neotypes are preserved for future reference.

The bryozoans, though restricted in spatial distribution, form an important group of microfossils among the Kachchh biota. The diversity and density of taxa in this group varies widely within and among lithological units. The updated taxonomic information on this colonial group from this area provided significant clues for deciphering the evolutionary history of many taxa. The overall changes in abundance, diversity and distribution of these bryozoans held key to important information regarding the changes in the microenvironment in which they were deposited.

Table 2 shows the summary of distribution of families, genera and species of Cyclostomata and Cheilostomata in different formations. Cyclostomes are restricted to the early Middle Eocene (Harudi Formation) and make up only around 4% of the Kachchh bryozoan colonies collected. The order is represented by seven species in seven genera in five families expressing unique taxonomic diversity and equitability. Cheilostomes are represented by 92 species in 55 genera in 33 families. Of the total 99 species of bryozoans (APPENDIX I), only 16 occur in more than one Formation. The family Calloporidae Norman, 1903 is represented by six genera; four others have three each, while 22 are represented by one genus each. 46 genera have one species each. Thalamoporella Hincks, 1887, an important constituent of the Kachchh bryofauna, is the most diverse genus with 15 species, which reveal some noteworthy features of its evolution. In all the formations, trends of taxonomic diversity (number of families, genera and species) of cheilostomes belonging to Anasca and Ascophora are somewhat parallel, but in general, the ascophorans are taxonomically more diverse than anascans (Table 2). While in other formations the number of specimens collected under these two cheilostome groups is similar, in the Harudi Formation the ascophorans are about five times more than the anascans. In general the Paleogene period was quite suitable for evolution of bryozoans, especially the cheilostomes (Zágoršek 1996), and according to Taylor and Larwood (1990), bryozoan radiation peaked during the Eocene. In the Kachchh Basin, the bryozoan radiation peaked during the Khari Nadi time (Aquitanian) with 55 species.

Table 2: Distribution of family/genus/species of Cyclostomata and Cheilostomata in different formations (F-family, G-genus and S-species with a number of colonies within parentheses).

	Cyclostomata			Cheilostomata						
					Anasca			Ascophora		
	F	G	S	F	G	S	F	G	S	
Chhasra (late Early Miocene)				7	7	10 (559)	9	9	11 (463)	
Khari Nadi (Early Miocene)				12	17	26 (1584)	15	22	29 (1490)	
Maniyara Fort (Oligocene)				3	3	5 (162)	6	6	6 (224)	
Fulra (Middle Eocene)				3	4	4 (104)	4	4	6 (107)	
Harudi (early Mid. Eocene)	5	7	7 (238)	6	6	9 (303)	5	6	9 (1441)	

In these formations, there exists some similarity in the diversity of taxa at different hierarchical levels. However, species belonging to a particular formation are generally unique and differ greatly from those of other formations. The Kojumdgieva similarity coefficients (Zágoršek, 1996) are low (Table 3) indicating a very dissimilar composition of bryozoan faunas among different formations. The value between the Khari Nadi and Chhasra formations, both being Early Miocene, is 45.83, indicating some degree of taxonomic coherence. Species belonging to the Harudi Formation are not found in any other younger horizons of the area. In the following sections, a review of important features and the significance of the Tertiary bryozoan assemblages from Kachchh is attempted.

Table 3: Kojumdgieva similarity coefficients among the species in different formations.

	FULRA	MANIYARA FORT	KHARI NADI
CHHASRA	7.38	36.9	45.83
KHARI NADI	11.78	29.46	-
MANIYARA FORT	30.0	-	-

SIGNIFICANCE OF THALAMOPORELLA SPECIES

The earliest occurrence of *Thalamoporella* Hincks, 1887, a commonly occurring cheilostome bryozoan of tropical and warm temperate waters, was reported from the Middle Eocene of Egypt, *i.e. T. bilfoliata* and *T. aegyptiaca*, by Ziko (1985). Subsequently these two species were interpreted as the rootstocks of two lines of evolution, one with distally directed and the other with proximally directed avicularia (Soule *et al.*, 1991). Pouyet and Braga (1993) described *T. sulawesiensis* from a suggested Eocene subduction zone on Sulawesi, Indonesia. Cheetham (1963) described *T. ocalana* from the Late Eocene Ocala Formation from peninsular Florida. *Thalamoporella* species are also widely distributed in the Mio-Pliocene and Pleistocene. The genus ranges from Middle Eocene to Recent, but extant taxa surpass the number of fossil species in both abundance and diversity.

Soule and Soule (1970) described tropical mid-Pacific *Thalamoporella*, and Soule *et al.* (1987) discussed in detail the evolution, systematics and biogeography of the family Thalamoporellidae Levinsen, 1902. Subsequent reports of *Thalamoporella* species without avicularia, with rounded avicularium mandibles, with acute or sub-acute avicularium mandibles and finally a review of known species worldwide (Soule *et al.*, 1992, 1999) increased understanding of this genus. Out of 58 species of *Thalamoporella* recorded in the literature (up to 1999), only fifteen species are reported from the Paleogene to Pleistocene. Fifteen new fossil species of *Thalamoporella* from the Tertiary (Lutetian-Burdigalian) sequences of Kachchh (Guha and Gopikrishna, 2004a) increased the number of fossil species of the genus considerably.

In general, the procedures adopted for species recognition by Soule *et al.* (1992, 1999), i.e. the presence or absence of avicularia, shape of avicularium mandibles and mean ratio (MR) of mean zooid length to mean avicularium length, were followed. Of the fifteen species of *Thalamoporella* occurring in the Harudi, Maniyara Fort, Khari Nadi and Chhasra formations (Table 4), the Khari Nadi Formation (Aquitanian) has the maximum number of eight species with 92% of the colonies, the Harudi Formation (Lutetian) has four species representing a meagre 4% of colonies, and the Chhasra (Burdigalian) and Maniyara Fort (Rupelian-Chattian) formations have three and one species, respectively. *T. kachchhensis* is the only species occurring in both the Khari Nadi and Chhasra formations. The Table 4: Checklist of different species of *Thalamoporella* described by Guha and Gopikrishna (2004) from the Tertiary sequences of western Kachchh, Gujarat, India (figures within parenthesis indicate number of colonies). Lithology and age of formations after Biswas (1992).

SERIES/STAGES	FORMATIONS/ LITHOLOGY	Thalamoporella Species
MU. Miocene - Langhian-Messinian	Sandhan Sandstones, siltstones, lime Stones and conglomerate.	No Thalamoporella
L. Miocene - Burdigalian	Chhasra Claystones and limestones.	<i>T. kachchhensis</i> (40), <i>T. setosa</i> (3) <i>T. vinjhanensis</i> (10)
L. Miocene - Aquitanian	Khari Nadi Siltstones, sandstones, limestones and gypseous claystones.	T. arabiensis (17),T. rhombifera (2), T. kachchhensis (549), T. tewarii (6), T. kharinadiensis (2), T. voigti (6) T. transversa (1), and T. wynnei (4)
Oligocene - Rupelian-Chattian	Maniyara Fort Siltstones, sandstones, lime-stones and clay stones.	T. archiaci (1)
M.Eocene - Lutetian & Bartonian	Fulra Limestones	No Thalamoporella
M. Eocene - Lutetian	Harudi Sandstones, siltstones, limeston-es and shales	<i>T. domifera</i> (6), <i>T. minuta</i> (12) <i>T. reniformis</i> (6), <i>T. dorothea</i> (5)
U.Paleocene – L. Eocene Thanetian & Ypressian	Naredi Gypseous shales, limestones and claystones	No Thalamoporella

Kachchh species of *Thalamoporella* are distinctive in their occurrence, distribution and morphology when compared to species reported elsewhere. This assemblage has increased the number of fossil taxa of *Thalamoporella* i) from 15 to 30, ii) Eocene species number (*T. domifera*, *T. minuta*, *T. reniformis* and *T. dorothea*) from three to seven and iii) fossil species without avicularia (*T. reniformis*, *T. dorothea*, *T. archiaci*, *T. tewarii* and *T. wynnei*) from one to six. Further, some novel features observed in this assemblage are a) the smallest mean ratio (1:0.24) and or 8-shaped avicularium, as in *T. minuta*, b) four-sided erect colonies, as in *T. dorothea*, c) kidney-shaped opesiules, as in *T. reniformis*, d) transverse avicularia, as in *T. transversa*, and e) the smallest avicularia (= 0.140mm), as in *T. voigti*.

Cluster Analysis

The Tertiary species of *Thalamoporella* from Kachchh differ among themselves in terms of mean ratios and stratigraphical occurrence; and they show certain morphological similarities regarding the nature of avicularium mandibles and zooecia. An attempt was made to study the degree of similarity and their hierarchy on the basis of 25 different morphological characters (e.g. zoarial form, zooecial shape, shape and placement of avicularium, shape and size of opesiules, etc.) and to infer, if possible, the trends in evolution and morphogenesis of avicularia from Lutetian to Burdigalian (Guha and Gopikrishna, 2004a). Since species distinction was based mainly on avicularium characters, more importance was given to these than to characters with little or no significance.

Cluster analysis grouped the fifteen *Thalamoporella* species into three distinct assemblages (Table 5), each assemblage representing a particular set of similar morphological characters, especially features of the avicularium.

Table 5: Results of cluster analysis of *Thalamoporella* species giving the assemblage-wise grouping, occurrence, age, mean ratio (between zooid length and mean avicularium length) and shape of mandible. [Abbreviations: HA, Harudi; MF, Maniyara Fort; KN, Khari Nadi; CH, Chhasra.]

Species of Thalamo- orella	Asse mbla ge	Form- ation	Age	Mean Ratio	Shape of Mandible
T. vinjhanensis T. kharinadiensis T. kachchhensis T. domifera	Ι	CH KN KN/CH HA	late E. Miocene Early Miocene late E. / E. Miocene early Mid. Eocene	1:1.22 1:1.22 1:0.69 1:1.09	Acute Round Gothic- arch Round
T. wynnei T. tewarii T. archiaci T. reniformis T. dorothea	Π	KN KN MF HA HA	Early Miocene Early Miocene Oligocene early Mid. Eocene early Mid. Eocene	Avicula	aria absent
T. setosa T. voigti T. arabiensis T. rhombifera T. transversa T. minuta	III	CH KN KN KN KN HA	late Early Miocene Early Miocene Early Miocene Early Miocene Early Miocene early Mid. Eocene	1:0.92 1:0.28 1:0.76 1:0.98 1:0.52 1:0.24	Bristle- like Acute Acute Acute Acute Round

Assemblage I includes four species of *Thalamoporella* ranging in age from early Middle Eocene to late Early Miocene with avicularia of differing size and shape. Assemblage II has five species without avicularium that occur in successions that range in age from early Middle Eocene to Early Miocene. Assemblage III includes a complex group of six species with an age-range similar to that of Assemblage I. The four Early Miocene species of Assemblage III have acute mandibles of differing disposition, *i.e.* torqued and transverse, indicating a possible link in the evolution of these avicularium features. Further, Assemblage III includes the species *T. minuta*, having the smallest avicularia.

Soule *et al.* (1992, 1999) held that larger avicularia with a high mean ratio between mean zooid length and mean avicularium length, and rounded mandibles, are primitive features, while reduction in size of the avicularium and its absence were advanced features found in younger taxa. The features of the present assemblage of *Thalamoporella* species from Kachchh indicate that evolution of species without avicularia and a low mean ratio took place at an early date (early Middle Eocene). Alternatively, the reduction in size or loss of avicularia might represent some ecological change or alteration in the predator/prey relationship and not a linear progression (Dr. D. F. Soule, *pers. comm.*, 2003).

Astogeny and variability of Thalamoporella kachchhensis

Boardman and Cheetham (1969) noted the importance of zooecial size as the most consistently applicable index of astogenetic change. Even the range in zooecial size of a particular generation may be as great as the observed range of the parameter in the whole colony. In the zone of astogenetic change of a bryozoan colony, individuals in each generation in a distally directed series from the ancestrula express morphological characters unique to that generation (Boardman *et al.* 1969). There is a constant change in zooecial and apertural dimensions in zooecia belonging to different generations.

Thalamoporella kachchhensis Guha & Gopikrishna, 2004 (Pl. I, fig. 3) occurring in the Khari Nadi (Aquitanian) and Chhasra formations (Burdigalian) has large erect-rigid foliaceous bilaminar fronds and makes up about 9% of total bryozoan colonies from Kachchh and 26% of colonies in the Khari Nadi Formation. In this species at the bifurcation of a series of zooecia an adult zooid (mother zooid) gives rise to a pair of zooecia, one of which is decidedly shorter (S generation) in length than the other (L generation), or to one avicularium and one sibling zooid. These twin buds of unequal length grow independently by distal budding to form two linear series until they again give rise to mother zooids that are distally wider, generally shorter in length and have smaller apertural dimensions. Guha and Gopikrishna (2004a) studied (a) the stages of astogenetic repetition in zooidal series arising out of two dissimilar buds and (b) evolution of this species from the early to late phases of the Early Miocene.

Measurement of mean zooecial length of S and L generations and mother zooids in colonies of the Khari Nadi and the Chhasra formations indicate that maturity of zooids in colonies belonging to the older formation was attained by the 6th or 7th generation, whereas the same was attained by the 2nd or 3rd generation in zoaria of the younger formation. This was corroborated by the study of variation of zooecial, apertural and avicularium parameters like length, width, etc., and their ratios in successive generations on 20 colonies each from the Khari Nadi and Chhasra formations (Guha and Gopikrishna, 2004a, p. 48). Though the ratio of mean avicularial length to mean zooidal length was almost the same in the two formations, the dimensions of parameters of zooecia, avicularia and apertural height were significantly smaller in specimens from the Chhasra Formation than the Khari Nadi Formation. The zoarial growth form of T. kachchhensis being erect-rigid foliaceous, the chance of its influencing the time and stage of maturity of zooids in a colony and consequent increase in size was quite restricted. The environment of these formations might have a role to play. The Khari Nadi Formation, being chiefly arenaceous, might have helped zooecia to attain increased dimensions and maturity at 6th or 7th generation. In contrast, the Chhasra Formation, being chiefly argillaceous, might have motivated the zooids to attain early maturity with the appearance of mother zooecia in the 2nd or 3rd astogenetic stage where a bifurcating zooid would give rise to an avicularium, used as protective/cleaning apparatus. This might have been responsible for a luxuriant growth of T. kachchhensis to flourish more in the Khari Nadi Formation (549 colonies) than in the Chhasra Formation (40 colonies). Though these two formations show similarity in sustaining diverse bryozoan assemblages (Kojumdgieva similarity coefficients being 45.83, see Table 3), the change in microenvironment supported separate growth strategies for T. kachchhensis.

SIGNIFICANCE OF STEGINOPORELLID AND SCHIZOPORELLID SPECIES

The family Steginoporellidae Hincks, 1884 is well represented among the Tertiary cheilostome bryozoans from Kachchh, accounting for nearly 6% of total number of colonies (6675) collected. The presence of *Reniporella gordoni*, *Labioporella bassleri*, *L. hariparensis* and *Steginoporella bhujensis* (Guha and Gopikrishna, 2004b, 2007b) made the checklist of taxa under this family very impressive, with three out of the five Tertiary steginoporellid genera (*Steginoporella* Smitt, 1873, *Siphonoporella* Hincks, 1880, *Gaudryanella* Canu, 1907, *Labioporella* Harmer, 1926 and *Reniporella* Guha and Gopikrishna, 2004) being present. Such a generic diversity under one cheilostome family makes the present area potentially important for its evolution during the Tertiary.

The genus Steginoporella Smitt, 1873, known by more than 50 fossil and living species, has distinct phyletic lineages. Harmer (1900, 1926) proposed a classification based on the shape of the main sclerite of B-opercula of species under genus Steginoporella; the Kachchh taxon, Steginoporella bhujensis, can be placed under Group I-A in which several others like S. manzonii, S. cucullata, S. fragilis, S. turbarens, S. defixa, S. haidingeri, S. firma, S. simplex, S. lateralis, S. connexa and S. auriculata are also included (Pouyet and David 1979b). While reconstructing the spatial evolution of *Steginoporella*, Pouyet and David (1979a,b) recognised three radiation centres for the genus: a) an Eocene centre in the central part of the Americas, from Venezuela to USA, b) a Miocene centre corresponding to the present Mediterranean and c) a Pliocene centre of the Australian area. Pouyet and David (1979a, p.580) commented that "the headquarters of the genus Steginoporella is clearly the Indo-Pacific province: the Indian Ocean and the Western pacific. It is necessary to add the Caribbean province, but it is only of secondary importance." Most of the species associated with Group I-A of Harmer (1900, 1926), to which the present Kachchh taxon shows affinity, evolved during the second stage of radiation that took place in the European Tethyan province during the Upper Oligocene and Early Miocene. Thus, the presence of Steginoporella bhujensis in the Oligocene to Early Miocene horizons (Maniyara Fort, Khari Nadi and Chhasra formations) of Kachchh corresponds to the second radiation in the evolution of the genus. Recent species of this genus live in tropical marine environments. According to Pouvet and David (1979a,b), the geographical range of Steginoporella never extended beyond 40° North or South, and were within the regime of the most important warm ocean currents. Thus the presence of Steginoporella in this bryozoan assemblage, indicates that from the Oligocene to the Early Miocene (17-36 M.Y.) the Kachchh Basin experienced the influence of warm tropical oceanic currents suitable for optimum growth of these brvozoans.

Significance of Reniporella gordoni

While considering the probable phyletic relationship between the four Tertiary genera of the family Steginoporellidae, Pouyet and David (1979a, pp. 566-567; 1979b, p.796, fig. 6), considered the Eocene genus *Gaudryanella* Canu,1907, which lacks a visible calcified polypidian tube, as more primitive than *Steginoporella* and as the root stock of the family. However, the genus *Steginoporella* and the new monospecific genus *Reniporella* have calcified polypidian tube and show zooecial dimorphism (A-zooecia and B-zooecia), indicating a closer relationship between the two than any other belonging to the family Steginoporellidae. Thus, the Middle Eocene genus *Reniporella* from Kachchh may stand as a taxon more akin to the genus *Steginoporella* than to *Gaudryanella*. Fig. 2 shows the probable position of the genus *Reniporella* in the possible phyletic relations between the Tertiary genera (Pouyet and David, 1979b, p.796, fig. 6) of the family Steginoporellidae Hincks, 1884 (Guha and Gopikrishna, 2004b).

Significance of Thalamoporella reniformis

In respect to its kidney-shaped opesiules, general colonial growth habit, beaded nature of the lateral walls and smooth depressed frontal, *Reniporella gordoni* (Pl. I, fig. 1) has an overall similarity with *Thalamoporella reniformis* (Pl. I, fig. 2), occurring at the same horizon and locality (Guha and Gopikrishna, 2004b p.691, figs. 5a-b). Based on these similarities and the coexistence of the two species in the Middle Eocene Harudi Formation of Kachchh, one is inclined to infer that species with kidney-shaped opesiules under *Reniporella* and *Thalamoporella* might have evolved from a common ancestor or there might have been parallel evolution of these two taxa with a possible link between their respective ancestors.

Reniporella gordoni and Steginoporella rhodanica

While revising the systematics of the genus Steginoporella Smitt, 1873, Pouvet and David (1979a, pp. 575-577, fig. 6; 1979b, pp. 795-797, fig. 7) distinguished several groups of species and proposed probable phyletic lineages. They suggested a separate group, the S. rhodanica group (with the French Miocene species S. rhodanica Buge and David, 1967 at its base) to include S. alveolata Harmer, 1900 and S. truncata Harmer, 1900, two Indo-Pacific extant species. They left the antecedent of S. rhodanica as uncertain. Excepting the large kidney-shaped opesiules, the French Miocene species S. rhodanica is quite similar to Reniporella gordoni in zooecial and apertural aspects (Guha and Gopikrishna, 2004b p.691, figs. 5a-c). Both species have calcified polypidian tubes and the genera Steginoporella and Reniporella are considered close to each other among the Tertiary genera of the family (Fig. 2). If one assumes from the fossil record that loss of and/or reduction in size of opesiules on the zooecial frontal represent valid evolutionary changes with time, then species with large opesiules represent the oldest or most primitive taxa. Thus, Reniporella gordoni may stand as the possible precursor



Fig. 2. Probable position of the new genus *Reniporella* from Kachchh in the family phylogeny of the Tertiary steginoporellid genera (after Pouyet and David, 1979b, p. 796, fig. 6). Abbreviations: E, Eocene; O, Oligocene; M, Miocene; P, Pliocene and Q, Quaternary.

in the evolution of the French Miocene species *Steginoporella rhodanica* Buge and David, 1967, whose origin was so far unknown.

Evolution of *Therenia* David & Pouyet, 1978 (Fam. Schizoporellidae)

The phylogeny of the genus Herentia presented by David and Pouyet (1978) shows Herentia (Therenia) americana as the root stock of H. (T.) porosa group, with the French Miocene species H. (T.) falunica evolving as a side branch (Fig. 3). Gordon (2011) considered Herentia Gray, 1848 (a genus unrecognized by Bassler, 1953) and Therenia David & Pouyet, 1978 as separate genera. Since Therenia indica Guha and Gopikrishna, 2005 is from the Harudi Formation (Lutetian) of Kachchh, it may share the same position with $H_{\cdot}(T_{\cdot})$ americana and probably can be directly linked to H. (T.) falunica that has similar zooecial features as those of the Kachchh taxon (Guha and Gopikrishna, 2005a, 2007b). Further, in the Eocene palaeogeographical map of Briden et al. (1974; from Pouyet and David, 1979b, p.800), the present area of western Kachchh is shown within the Indo-Pacific realm. Recognition of T. indica from the Middle Eocene Harudi Formation of Kachchh extends the biogeographical distribution of the genus Therenia to the Indo-Pacific province from where no species belonging to this genus have so far been reported. David and Pouyet (1978, p.188) concluded, "The evolution of Herentia took place only in the Atlantic and its Caribbean and Mediterranean parts". However, presence of 49 colonies of T. indica (Pl. I, fig. 4) in a single locality of the Middle Eocene Harudi Formation of Kachchh would suggest that the evolution of Therenia took place in the Indo-Pacific province also.



Fig. 3. Attempt to show the probable position of *Therenia indica* of Kachchh (modified from the original phylogenic chart of *Herentia* Gray, 1848 with its two subgenera *Herentia* and *Therenia* given by David and Pouyet, 1978, p. 184, fig. 5).

SIGNIFICANCE OF KACHCHH SMITTINIDS

Among the ascophoran bryozoans from Kachchh, the family Smittinidae Levinsen, 1909 is distinguished by the presence of the greatest number of species. They are: *Hemismittoidea waiorensis*, *Houzeauina rakhadiae*, *Parasmittina auris*, *P. gujaratica*, *P. harudiensis* and *P. johni* (Guha and Gopikrishna, 2005d).

Hemismittoidea waiorensis from the Khari Nadi Formation (Aquitanian) is the first record of a fossil species of this genus, hitherto represented only by extant species. Until 2005, Houzeauina Pergens, 1889, was a monospecific genus with H. parallela Reuss, 1869, reported from the Eocene (Priabonian) Journal of the Palaeontological Society of India **Volume 58**(1), June 2013

Plate I

9



GUHA

EXPLANATION OF PLATE I

Representative figures of some selected bryozoan taxa from the Tertiary sequences of Kachchh.

1: General aspect of genotype colony *Reniporella gordoni* showing details of large reniform opesiules, beaded lateral walls, and squared opesial region.

2: Thalamoporella reniformis showing large unequal kidney-shaped opesiules.

3: General aspect of *Thalamoporella kachchhensis* colony, the most abundant *Thalamoporella* species of Kachchh. [Figs. 2-3. SEM courtesy: Irene McCulloch Foundation, USA]

4: General aspect of holotype specimen of *Therenia indica* showing details of avicularium and oral spines with small U-shaped proximal sinus.

5: Bilaminar genotype colony of Archoporella sepultica without ovicell.

6: Genotype specimen of *Orbiculipora gigantea* showing autozooecia, ooeciferous zooecia with large porous hyperstomial ovicell, small lenticular avicularia and apertural sinus with blunt condyles.

of Italy, being the type and only species. Recognition of *H. rakhadiae* from the Khari Nadi Formation (Aquitanian) increased the total number of species under this genus to two. Further, the stratigraphical ranges of *Hemismittoidea* and *Houzeauina* were extended up to the Lower Miocene (Aquitanian).

The four new species of *Parasmittina* Osburn, 1952 from the Middle Eocene (Lutetian) to Lower Miocene (Burdigalian) sequences of Kachchh are distinctive in their occurrence, distribution and morphology when compared to most of the extant species reported so far. Until 2005, *P. crosslandi* (Hastings, 1930) reported from the Neogene of Central America and *P. collum* (Canu & Bassler, 1920) as described from the Upper Eocene of Alabama by McKinney and Taylor (2003) are the two known fossil species of *Parasmittina*. The occurrence of three fossil species of *Parasmittina* (*P. auris, P. harudiensis* and *P. johni*) from the Harudi Formation (Middle Eocene, Lutetian) of Kachchh has increased our knowledge by adding more Paleogene species to this genus.

Disposition of avicularia on the zooecial frontal is varies between species of *Parasmittina* Osburn, 1952 (Gordon, 1984 and 1989; Gordon and D'Hondt, 1997; Hayward, 1980 and 1988; Hayward and Parker, 1994; Pouyet and Herrera-Anduaga, 1986; Ryland and Hayward, 1992 and Soule and Soule, 1973, 2002). The arrangement of avicularium on the frontal shield of adjacent distolateral zooecia, along with the distolateral torquing observed in *P. harudiensis* and *P. johni*, in the present Middle Eocene (Lutetian) assemblage were reported for the first time in species of this genus; and considered to be a primitive feature (Guha and Gopikrishna, 2005d).

NOTES ON HIPPOPODINID SPECIES

Among the three Paleogene formations (Harudi, Fulra and Maniyara Fort) of Kachchh, the Harudi Formation excels over the other two in terms of both species diversity and density (Table 2). Archoporella, the new hippopodinid genus with three new species (A. sepultica, A. capsulata and A. discidiata) described from the Fulra (Middle Eocene) and Maniyara Fort (Oligocene) formations (Guha and Gopikrishna, 2005b; see Appendix I), provides a unique importance to these Paleogene formations. A study of the variability of species of this new genus showed an unusually high variability of avicularial parameters. While apertural width (wa) is the least variable parameter in A. sepultica and A. capsulata, the zooecial width (wz) is generally the least variable in the former. Further, the zooecia of A. sepultica (Pl. I, fig. 5) are more equidimensional (mean wz/Lz = 1: 0.86) than A. capsulata (mean wz/Lz = 1: 0.69) and A. discidiata (mean wz/Lz = 1:0.71) (Guha and Gopikrishna, 2005b).

NOTES ON PETRALIID SPECIES

Two new petraliid cheilostome bryozoan taxa, *Orbiculipora gigantea* (Pl. I, fig. 6) and *Petralia mucropora*, were described from the Early Miocene (Aquitanian) Khari Nadi Formation of Kachchh (Guha and Gopikrishna, 2005c). Until 2005, the genus *Petralia* MacGillivray, 1869 within the monogeneric family Petraliidae Levinsen, 1909 was known to have only extant species (Gordon, 2011). The finding of the new genus *Orbiculipora* Guha and Gopikrishna, 2005 increased the generic diversity of the ascophoran family Petraliidae from one to two; and the presence of *Petralia mucropora* in the Aquitanian sediments of Kachchh added antiquity to the extant genus *Petralia*.

NOTES ON CALLOPORID SPECIES

Among the Tertiary bryozoans from Kachchh, the family Calloporidae Norman, 1903 has the highest diversity with six genera including eight species (Guha and Gopikrishna, 2007d). They are: *Aplousina* sp., *Copidozoum feddeni*, *Crassimarginatella blanfordi*, *C. ukirensis*, *Marginaria senguptai*, *Planicellaria kharaiensis*, *P. naliyaensis* and *Reptoporina chhasraensis* (see APPENDIX I). No other fossil species of *Marginaria* Röemer, 1841 have been reported beyond the Cretaceous Period. The presence of *Marginaria senguptai* in the Khari Nadi Formation of Kachchh has raised the upper age limit of the genus to the Aquitanian stage.

PALAEOECOLOGY OF BRYOZOANS FROM THE KACHCHH BASIN

The morphology of an organism reflects adaptive evolutionary or phenotypic responses to selected environmental pressures under which it lives. For fossil populations, the correlation between the morphology of an organism and the physico-chemical parameters of its environment for possible palaeoenvironmental interpretations is generally based on hard parts alone. Notwithstanding reservations expressed by Taylor (2005), the Bryozoa, with its variety of colony shapes, has been a useful palaeoecological indicator of sediments from the Ordovician to Holocene. In India information on palaeoenvironment have been recorded from the growth-form analysis of bryozoan colonies belonging to the Mid. Cretaceous Bagh Group (Beds) of Madhya Pradesh (Guha and Ghose, 1975), the Ariyalur Group (Maastrichtian) of Tamil Nadu (Guha, 1987 and Guha and Mukhopadhyay, 1996) and the tertiaries of Kachchh (Guha and Gopikrishna, 2005a).

Following the procedure of Nelson et al. (1988), eight major growth forms, viz, ENul (encrusting unilaminar), ENml (encrusting multilaminar), ERde (erect-rigid delicate), ERfo (erect-rigid foliaceous), ERfe (erect-rigid fenestrate), ERro (erect-rigid robust), EF (erect flexible) and FL (free-living) have been recognized among 6675 bryozoan colonies from the Harudi, Fulra, Maniyara Fort, Khari Nadi and Chhasra formations. The distribution of species number and density of colonies under each growth form along with the ER/EN (erect/ encrusting) ratio in different formations is shown in Table 6. The ENul growth habit is the most taxonomically diverse (56 species and 45% of total colonies) followed by ENml (three species and 16.5% of zoaria), ERfo (12 species and 13.6% of colonies), ERde (18 species and 12.6% of zoaria) and other four types (FL, ERfe, EF and ERro) together accounting for 12.1% of zoaria under 11species.

In general, the rocks of these formations are wackestones, packstones and mudstones with a fairly high content of terrigenous material. Five distinct taphonomic associations of bryozoan colonies with other organisms can be recognised: -(a) with algae; (b) with saddle-shaped shells of Foraminifera; (c) with bivalve shells, chiefly oysters; (d) with high-spired gastropod shells; and (e) with fossil barnacles (Guha and

Table 6: Formationwise distribution of species number (number of colonies within parenthesis) under different growth forms (for abbreviations see text) and ER/EN ratio of species under erect and encrusting growth form groups (same ratio of colonies within parentheses).

Growth form	ENul	ENml	ERfo	ERde	ERro	ERfe	EF	FL	ER/EN
Formation (Age)									
Chhasra (Burdigalian)	04 (107)	01 (186)	06 (247)	04 (354)		01 (55)	01 (05)	04 (68)	2.4 (2.26)
Khari Nadi (Aquitanian)	31 (903)	03 (837)	04 (580)	07 (196)	01 (12)	04 (59)	02 (235)	04 (252)	0.53 (0.62)
M-Fort (Rup-elian-Chattian)	01 (01)	01 (80)	04 (76)	03 (136)	01 (39)	01 (54)			4.5 (3.77)
Fulra (Lutetian & Bartonian)	05 (109)		01 (03)	03 (68)	01 (31)				1 (0.94)
Harudi (Lutetian)	20 (1897)			06 (85)					0.3 (0.04)

Gopikrishna, 2005a). Association (b) is observed only in the Harudi Formation; (a), (c) and (d) are common in the Khari Nadi Formation, while (a) and (e) are common in the Chhasra Formation.

The fossiliferous bands within argillaceous parts of the Harudi Formation contain 66 % of total encrusting colonies retrieved; large shells of discocyclinid Foraminifera providing the chief encrusted surface. The ER/EN ratio is 0.3 for species and 0.04 for colonies, indicating that the bryozoan horizon within the Harudi Formation was developed in an inner shelf area (Schopf, 1969).

Large discocyclinids (often over 2.5 cm in diameter), having their broad equatorial faces buried in lime mud, form the bulk of the Fulra Formation. The general ambience of the basin during deposition was peculiar in supporting a restricted development of thickly-calcified bryozoan colonies. Though the scarcity of bryozoans continued during the deposition of the Maniyara Fort Formation, more diverse growth habits appeared. Multilaminar zoaria of *Turbicellepora* Ryland, 1963 encrusting algae, and erect-fenestrate species of *Reteporella* Busk, 1884 are notable additions. The high dominance of erect growth forms (ER/EN ratio for both species and colonies being around four) indicate a deepening of the basin and high turbulence.

The Aquitanian phase (Khari Nadi Formation) of the Kachchh Basin includes three out of five taphonomic associations mentioned earlier, maximum development of seven growth-forms (Table 6) and an appreciable number of FL colonies of the 'sand fauna'. The ER/EN ratio for this formation, both for number of species and colonies, is around 0.5. Two erect-flexible (EF) species of *Margaretta* Gray, 1843, and three encrusting multilaminar (ENml) species of *Turbicellepora* Ryland, 1963, reached their zenith. During this period, the Kachchh Basin became shallow, with flexible sandy substrates,

low rates of sedimentation and moderate wave energies; indicating an ecosystem that was most suitable to luxuriant growth of diverse bryozoan colonies. In an earlier section, similar inferences have been discussed on the effect of microenvironment on astogeny and variability of dimensions of zooecia, apertures and avicularia of *Thalamoporella kachchhensis*, showing that the Khari Nadi Formation provided better scope for bryozoan development than the younger Chhasra Formation.

The thick argillaceous sequences of the Chhasra Formation (Burdigalian) often contain hardgrounds with barnacles and other shelly material that supported encrustation by large mats of species of *Reptoporina* d'Orbigny, 1853, indicative of temporary emergence with cessation of deposition. A dominance of erect forms over encrusters (ER/ EN ratio more than two), high species diversity of ERfo group, and significant presence of erect-rigid fenestrate (ERfe) colonies indicate a possible deepening of the basin.

Though the area belonged to a stable pericratonic shelf, the variation in ER/EN ratio in formations showed two episodes of deepening (Rupelian-Chattian and Burdigalian) between periods of shallowing (Lutetian and Aquitanian).

Post Script

The author thanks Prof. A. K. Jauhri for requesting him to write this review paper on Kachchh bryozoans for the Prof. B. S. Tewari Commemorative Volume of the Journal of the Palaeontological Society of India. The study of bryozoans from Kachchh started in the 1960s under Prof. Tewari and his coworkers; and the present stage of its knowledge has created interest among a few new workers, such as Prof. Mohan A. Sonar and his students in Aurangabad, Maharashtra. The author hopes that in years to come more information will be available on fossils of this phylum from Kachchh.

ASIT K. GUHA

APPENDIX I

Distribution of the Tertiary Bryozoa belonging to different formations of western Kachchh, Gujarat with their family affiliation. Number of colonies within parenthesis. Abbreviations: HA-Harudi (Early Mid. Eocene), FU-Fulra (Mid. Eocene); MF-Maniyara Fort (Oligocene), KN-Khari Nadi (Early Miocene), CH-Chhasra (Late Early Miocene); (*) – new species and (**) - new genus and species.

FAMILY	Genera and species	НА	FU	MF	KN	СН
(Multisparsidae)	Idmidronea sp. (15)	+	-	-	-	-
(Incertae sedis)	Discosparsa lakhpatensis (10) *	+	-	-	-	-
(Oncousoeciidae)	Oncousoecia narediensis (129) *	+	-	-	-	-
(Plagioeciidae)	Plagioecia taylori (12) *	+	-	-	-	-
	<i>Tubigerina</i> sp. (6)	+	-	-	-	-
(Stomatoporidae)	Stomatopora illiesae (39) *	+	-	-	-	-
	Voigtopora reticulata (27) *	+	-	-	-	-
(Membraniporidae)	Biflustra mitiae (3) *	-	-	-	+	-
(Electridae)	Conopeum gohelaensis (7) *	-	-	-	+	-
	Herpetopora haimei (196) *	+	-	-	-	-
(Calloporidae)	Aplousina sp. (24)	+	-	-	-	-
	Copidozoum feddeni (4) *	-	-	-	+	-
	Crassimarginatella blanfordi (37) *	-	+	-	-	-
	C. ukirensis (10) *	-	-	-	+	-
	Marginaria senguptai (3) *	-	-	-	+	-
	Planicellaria kharaiensis (8) *	-	+	-	-	-
	P. nalivaensis (14) *	_	-	-	-	+
	Reptoporina chhasraensis (79) *	_	-	-	-	+
(Antroporidae)	Akatopora aidaensis (21) *	_	-	-	+	-
	Antropora gadhavii (14) *	-	-	-	+	-
(Quadricellaridae)	Nellia kutchensis (410)	-	+	+	+	+
	N. narayani (6) *	+	-	-	-	-
	N. quadrangularis (260)	_	-	+	+	+
	N. walasaraensis (4) *	_	-	+	-	-
(Vinculariidae)	Vincularia ramwaraensis (38) *	_	-	-	+	-
(Cupuladriidae)	Discoporella misrai (180)	-	-	-	+	+
(Chlidoniidae)	Crepis gurjarensis (226) *	-	-	-	+	+
(Microporidae)	Micropora vredenburgi (7) *	-	-	-	+	-
	Microporina biswasi (23) *	+	-	-	-	-
(Onychocellidae)	Onychocella torquata (20) *	-	+	-	+	-
	Floridina pentagonus (11) *	-	-	-	+	-
(Steginoporellidae)	Labioporella bassleri (5) *	-	-	-	+	-
	L. hariparenis (329) *	-	-	-	+	-
	Steginoporella bhujensis (51) *	-	-	+	+	+
	Reniporella gordoni (32) **	+	-	-	-	-
(Thalamoporellidae)	Thalamoporella arabiensis (33) *	_	-	-	+	-
	<i>T. archiaci</i> (1) *	-	-	+	-	-
	T. domifera (6) *	+	-	-	-	-
	T. dorothea (5) *	+	-	-	-	-
	T.kachchhensis (589) *	-	-	-	+	+
	T. kharinadiensis (2) *	-	-	-	+	-
	<i>T</i> minuta (12) *	+	-	-	-	-
	T reniformis (9) *	+	-	-	-	-
	T rhombifera (3) *	-	-	_	+	_
	1.momoljeru (5)	-	-	-	Ŧ	-

12

	$T_{setosa}(3) *$	-	_	-	_	+
	T towarii (6) *	_	_	_	+	-
	T transversa(1) *	_	_		· -	
	T. vinibaronsis (10) *	-	-	-	'	-
	T. vinjnanensis (10)	-	-	-	-	Ŧ
	1.Volgii (6) *	-	-	-	+	-
	1.wynnel (4) *	-	-	-	+	-
(Cribrilinidae)	Puellina (C.) larwoodi (726) *	+	-	-	-	-
	Gen and sp. indet. (3)	-	-	-	+	-
(Trypostegidae)	Trypostega rossae (3) *	-	-	-	+	-
(Arachnopusiidae)	Arachnopusia kankawatiae (40) *	-	-	-	-	+
(Romancheimdae)	Each anolla, ach annuag (5) *	+	-	-	-	-
	Eschareita asnapurae (5) *	-	-	-	–	-
	Escharolaes cuneijormis (5) *	+	-	-	-	-
	E. multispinosa (2) *	+	-	-	-	-
(Smittinidae)	Hemismittoidea waiorensis (4) *	-	-	-	+	-
	Houzeauina rakhaalae (3) *	-	-	-	+	-
	Parasmittina auris (25) *	+	-	-	-	-
	P. gujaratica (67) *	-	-	-	+	+
	P. harudiensis (596) *	+	-	-	-	-
	<i>P. johni</i> (3) *	+	-	-	-	-
(Bitectiporidae)	Schizomavella decorata (70) *	-	-	-	+	+
(Schizoporellidae)	Schizoporella sowerbyi (3) *	-	-	-	+	-
	Therenia indica (49) *	+	-	-	-	-
(Stomachetosellidae)	Cigclisula ramparensis (3) *	-	-	-	-	+
(Porinidae)	<i>Porina</i> sp. (3)	-	-	-	+	-
	Tremotoichus fulraensis (88) *	-	+	+	+	-
(Margarettidae)	Margaretta fusiformis (180) *	-	-	-	+	+
	<i>M. rajui</i> (62) *	-	-	-	+	-
(Hippopodinidae)	Archoporella sepultica (37) **	-	-	+	-	-
	A. capsulata (31) *	-	+	-	-	-
	A. discidiata (37) *	-	+	-	-	-
(Gigantoporidae)	Cosciniopsis parilis (3) *	+	-	-	-	-
	<i>C. tuberosa</i> (6) *	-	-	+	-	-
(Lanceoporidae)	Calyptotheca aviculifera (156) *	-	-	-	+	+
	C. subhexagonalis (23) *	-	-	-	+	-
	C. subrectangulata (5) *	-	-	+	-	-
(Microporellidae)	Microporella waghotensis (7) *	-	-	-	+	-
	<i>M</i> . sp. (2)	-	-	-	+	-
(Petraliidae)	Petralia mucropora (7) *	-	-	-	+	-
	Orbiculipora gigantea (18) **	-	-	-	+	-
(Petraliellidae)	Hippopetraliella megafera (3) *	-	-	-	+	-
(Didymosellidae)	Tubiporella bispinosa (3) *	-	+	-	-	-
(Siphonicytaridae)	Siphonicytara confusiata (4) *	-	+	-	-	-
	S. hexaserialis (3) *	-	+	-	-	-
(Mamilloporidae)	Anoteropora cookae (45) *	-	-	-	+	+
	A. rajnathi (81)	-	-	-	+	+
	A. aff. latirostris (39)	-	-	-	+	+
(Celleporidae)	Buffonellaria cornuata (5) *	-	-	-	+	-
	Lagenipora chedopadiensis (5) *	-	-	-	+	-
	Turbicellepora canui (357) *	-	-	-	+	-
	T. naniberensis (15) *	-	-	-	+	-
	<i>T. rostrata</i> (694) *	-	-	+	+	+
(Phidoloporidae)	Iodictyum megapora (3) *	-	-	-	+	-
(Reteporella granti (3) *	-	-	-	+	-
	R. quadripora (161) *	-	-	+	+	+
1		1	1	-		

APPENDIX II

Post-publication assignment of new type numbers for some bryozoan species at the new repository – Central Fossil Repository of the Geological Survey of India, Kolkata.

Name of Species	Nature of Type	Published number	New Type Number
Reniporella gordoni	Holotype	K085/020/001	21175
Thalamoporella arabiensis	Paratype	-	21180
T. domifera	Paratype	-	21176
T. dorothea	Paratype	-	21177
T.kachchhensis	Paratype	-	21181
T.minuta	Paratype	-	21178
T. reniformis	Paratype	-	21179
T.rhombifera	Paratype	-	21182
T.setosa	Paratype	-	21186
T. tewarii	Paratype	-	21183
T. vinjhanensis	Paratype	-	21187
T.voigti	Paratype	-	21184
T.wynnei	Paratype	-	21185
Archoporella sepultica	Holotype	K038/017/001	21188
A. capsulata	Holotype	K015/019/001	21189
A. discidiata	Holotype	K015/018/001	21190

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