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Author(s): Dharendra K. Pandey, Christopher A. McRoberts, Manoj K. Pandit

Source: *Journal of Paleontology*, Vol. 73, No. 6 (Nov., 1999), pp. 1015-1028

Published by: Paleontological Society

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DIMORPHARAEA DE FROMENTEL, 1861 (SCLERACTINIA, ANTHOZOA) FROM THE MIDDLE JURASSIC OF KACHCHH, INDIA

DHIRENDRA K. PANDEY,¹ CHRISTOPHER A. McROBERTS,² AND MANOJ K. PANDIT¹

¹Department of Geology, University of Rajasthan, Jaipur 302004, India, <dhirendrap@hotmail.com>, and

²Department of Geology, State University of New York at Cortland, P.O. Box 2000, Cortland, New York 13045

ABSTRACT—The current classification of scleractinian corals based upon gross morphological features has been found unsatisfactory due to additional information from skeletal microarchitecture and microstructure. It is necessary to investigate microstructural details and limits in morphologic variation within and between different coral clades before a revised classification is constructed. Variations in morphologic characters and microstructural details from a population of *Dimorpharaea* de Fromentel, 1861 (Family Microsolenidae) from Upper Bathonian (Jumara Dome) strata in Kachchh are described. The data used include the diameter (D) and height (H) of the corallum, number of corallites in the colony (NC), number of septa in the mother corallite at the center of the colony (NS), minimum distance between centers of central corallite and corallite of the inner ring (C1), minimum distance between corallite centers of the outer ring (C2), septal density (DS) and trabecular density (DT). The principal components analysis reveals that most of the variation is explained by “size” related characters (D and H) while corallite density (NC and C1) and septal structures (DS and DT) contribute to the second and third principal component axes, respectively. The microarchitecture and distribution of characters observed in the Kachchh *Dimorpharaea* require a re-evaluation of familial-specific concepts and suggest that the population belongs to a single species, *Dimorpharaea stellans* Gregory, 1900, rather than four nominal species (*D. stellans*, *D. distincta*, *D. continua* and *D. orbica*) as has been assumed.

INTRODUCTION

THE CLASSIFICATION schemes for Mesozoic scleractinian corals have been unsatisfactory because of the poor understanding of morphologic character distribution and microstructural details within and between scleractinian clades. Although new information about skeletal microarchitecture and microstructures in Mesozoic corals has been recorded during the last two decades (e.g., Cuif, 1980; Cuif and Gautret, 1993; Gill and Lafuste, 1971; Gill, 1975, 1982; Gill and Russo, 1980; Roniewicz, 1982; Gill and Loreau, 1988; Lathuilière, 1990; Wendt, 1990; Roniewicz and Morycowa, 1993), the morphologic variability of most of the Mesozoic species and its relation to their paleoautecology are poorly known. The most appropriate characters (or character suites) for a particular taxonomic rank are not well defined. Answering these questions requires detailed examination of the distribution of morphological characters from numerous populations within and between members of different clades.

The Kachchh basin of western India (Fig. 1) has well-preserved, Middle Jurassic, nonreef-building corals whose microarchitecture or microstructure has not been studied in detail. The Middle Jurassic corals from Kachchh were first described by Gregory (1900), subsequently revised by Beauvais (1978), and more recently by Pandey and Fürsich (1993). Pandey and Fürsich (1993) also realized that because microarchitecture and microstructure are more significant in coral taxonomy than the apparent variability of some epigenetic or ecophenotypic morphological characters, such as size, shape, shallow to deep calicular pits etc., a more realistic systematic scheme for the Jurassic scleractinians using all available microstructural information should proceed after first identifying the limits of variability in morphology.

Examining the hitherto unknown microstructural features and limits of variation in the scleractinian fauna of Kachchh afford an excellent opportunity to utilize this taxonomic approach. This paper describes the microarchitectural and microstructural details and quantifies the limits of variation within a population of mid-Jurassic *Dimorpharaea* de Fromentel, 1861, from the Jumara Dome of Kachchh.

Dimorpharaea is a compound microsolenid. The corallum is

thamnasterioid, massive and low, with pedunculate to subpedunculate base. The colony is formed by circumoral budding around a central, occasionally eccentric corallite. The septa are thin, fenestrate, and pennular. The trabeculae are circular to elongate in cross-sections. The pennulae are subrectangular to subquadrangular in outlines, concave upward with fine teeth along the margins; pennulae of adjacent septa alternate. Menianae are discontinuous. The distal margin of the septa is finely beaded. The synapticalae between septa are common. The vesicular endothecal dissepiments are rare. The epitheca is thin and fragile with growth rugae.

The genus *Dimorpharaea* is readily distinguished from other members of the family Microsolenidae on the basis of its compound corallum and/or colony formation by circumoral budding, which is defined by the arrangement of corallites around a central, occasionally eccentric corallite. The closest ally of *Dimorpharaea* is *Microsolena*. The latter differs with respect to the circumoral arrangement of calices only in young colonies. Further, in *Dimorpharaea*, the septa are strongly bent, seldom run between adjacent corallites of the same ring, and are confluent

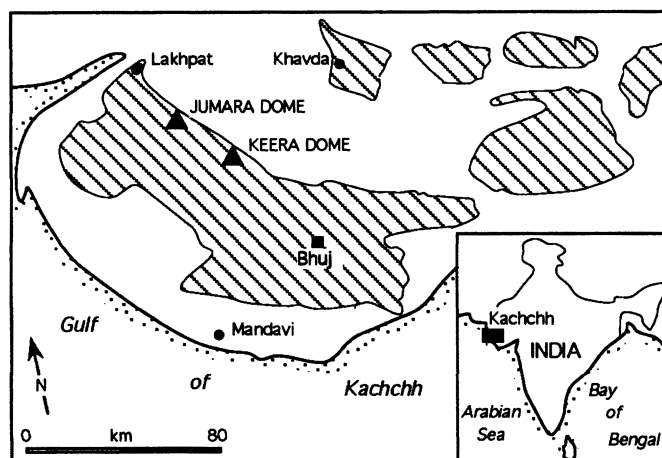


FIGURE 1—Location map showing Jumara Dome and Keera Dome localities along Indian coast. Hatched area represents extent of Jurassic-Tertiary outcrop in the Kachchh region.

TABLE 1.—Nominal species of *Dimorphopharaea* hitherto known from Jurassic. Their locations and the differences with the Kachchh species of *Dimorphopharaea stellans* GREGORY, 1900, are also given.

Nominal species <i>Dimorphopharaea</i> with author	Reference	Period	Locality	Differences with the Kachchh species <i>Dimorphopharaea stellans</i> GREGORY, 1900
<i>D. aequisepialis</i> BENDIKIDZE, 1949	p. 108, pl. 10, figure 4, pl. 11, figure 2	Upper Jurassic	South Ossetia (W. Asia)	Less dense corallites and greater number of septa in the central corallite
<i>D. contorta</i> (TOMES, 1978)	p. 441, pl. 18, figure 17; see Beauvais, 1972	Middle Jurassic	England (Paris basin)	Less density of septa (5 to 6 per 2 mm) and trabeculae (5 to 7 per 2 mm). Septa are never anastomosing
<i>D. convexa</i> DE FROMENTEL, 1861	Lathuilière, 1999, personal communication	Upper Jurassic	France (Paris basin)	Less dense corallites and greater number of septa in the central corallite
<i>D. desori</i> (KOBY, 1888)	p. 401, pl. 109, figure 7; see Beauvais, 1964	Upper Jurassic	Switzerland	Possesses less septal density (15 per 5 mm) and less trabecular density (7 per 2 mm)
<i>D. expansa</i> (ETALLON, 1859)	See Beauvais, 1964	Upper Jurassic	France (Jura)	Less dense corallites (minimum distances between centers of corallites of the adjacent rings vary from 7 to 8 mm and minimum distance between corallite centers of the same ring vary from 3 to 5 mm) and septa (10 to 13 per 5 mm)
<i>D. fromenteli</i> (TOMES, 1878)	Lathuilière, 1999, personal communication	Middle Jurassic	England (Paris basin)	The type from British Museum is misplaced. No detailed description available. The species should be dropped
<i>D. fungiformis</i> (MILNE-EDWARDS AND HAIME, 1851)	p. 141, pl. 30, figures 4, 4a; see Beauvais, 1970	Middle Jurassic	England (Paris basin)	A fungiform <i>Dimorphopharaea</i> measures minimum distance between centers of the corallites 2.8 to 5.7 mm, much less septal density near the periphery 5 per 2 mm and trabecular density 5 to 6 per 2 mm
<i>D. koechlini</i> (HAIME in Milne-Edwards, 1860)	p. 202; see Koby, 1887; Beauvais, 1964; Morycowa, 1974	Upper Jurassic	France (Paris basin)	Similar septal density (12 to 20 per 5 mm) and trabecular density (7 to 9 per 2 mm) to <i>D. stellans</i> , but latter lack in columella
<i>D. lentiformis</i> (KOBY, 1906)	See Koby, 1907; Beauvais, 1972	Middle Jurassic	France (Paris basin)	Large central corallite and much less septal density (4 to 5 per 2 mm) and trabecular density (3 to 5 per 2 mm)
<i>D. lineata</i> (EICHWALD, 1865)	p. 152, pl. 12, figure 3; see Flügel, 1966	Upper Jurassic	Crimea	Larger and less dense corallites
<i>D. lycetti</i> (DUNCAN, 1872)	p. 23, pl. 3, figures 7–9	Middle Jurassic	England (Paris basin)	This species is very poorly described and illustrated by Duncan. The septa and trabecular densities are not known
<i>D. muensteri</i> (RÖMER, 1836)	p. 21, pl. 1, figure 6	Upper Jurassic	N-Germany	Less dense septa
<i>D. tosaensis</i> EGUCHI, 1951	pl. 25, figure 3	Jurassic	Japan	Large central corallites (measuring about 7 mm in diameter). Trabecular columella
<i>D. verdanti</i> (KOBY, 1889)	See Beauvais, 1966, 1970b	Middle Jurassic	Switzerland	Less dense corallites (minimum distance between centers of corallites of the adjacent rings 6 to 10 mm and minimum distance between corallite centers of the same ring 3 to 7 mm), less dense septa (4 to 6 per 2 mm) and less dense trabeculae (density 4 per 2 mm)

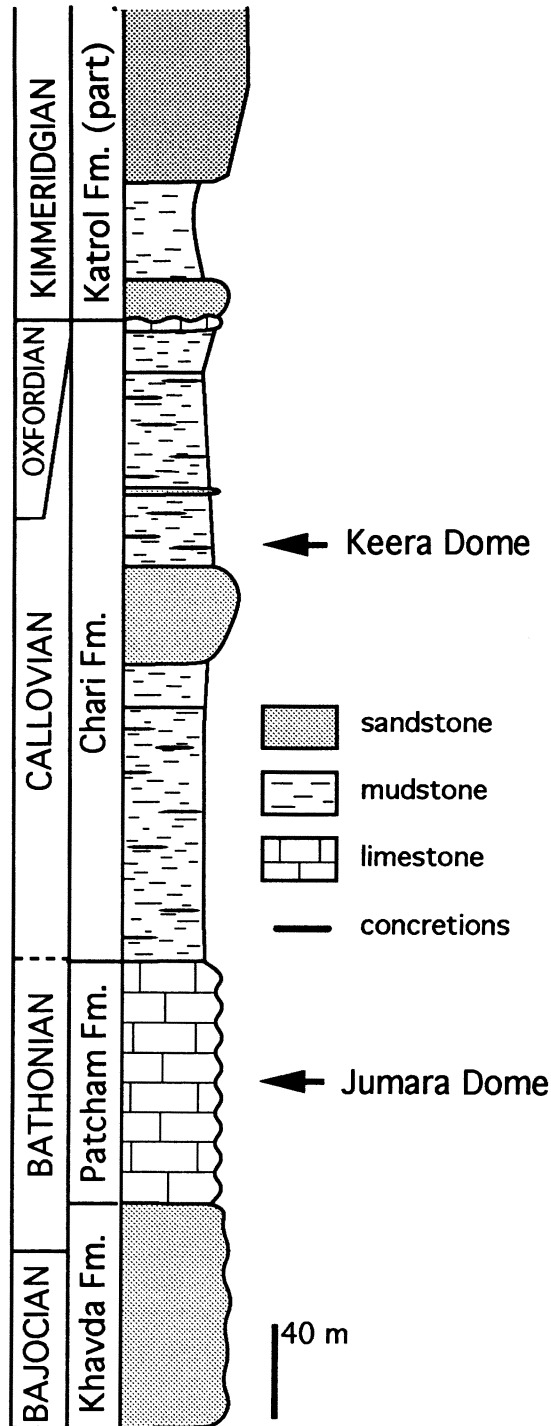


FIGURE 2—Generalized stratigraphic framework of Jurassic sediments of Kachchh showing the relative position of the two *Dimorphararea* localities: Jumara and Keera Domes, Kachchh, India.

between nearest corallites of the adjacent rings (also see Löser and Raeder, 1995). In contrast the septa in *Microsolena* are isotropic [term used for radial growth of the corallites by Dr. Lathuilière (personal commun.)]; straight and confluent equally with those of adjacent corallites of the same ring. Other characters typically regarded as important in generic or specific classification (e.g., septal density and trabecular density) are more or less uniform in most of the genera of the family Microsolenidae

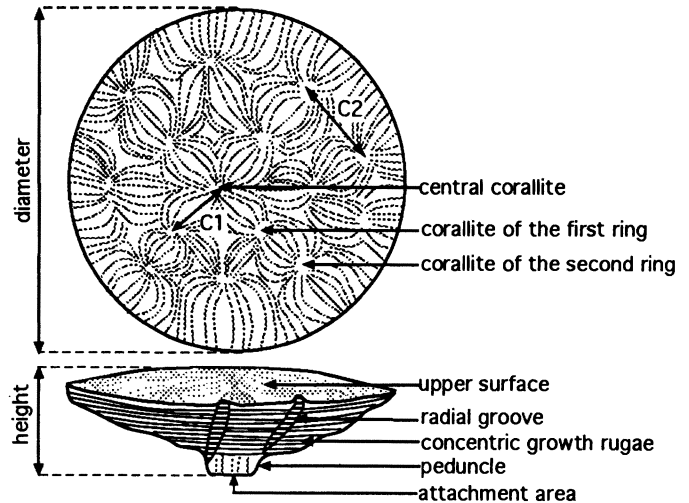


FIGURE 3—Schematic illustration of measured dimensions in *Dimorphararea*.

from Kachchh and are best regarded as familial characters. The distinguishing characteristic features of all other genera of the Family Microsolenidae occurring in Kachchh (e.g., *Kobyia*, *Tricycloseris*, *Trocharea*, *Microsolena*, *Trochoplegma*) are best summarized by Morycowa and Roniewicz (1995). Apart from 1) the kind of corallum, i.e., solitary (simple) or colonial (compound); 2) the mode of colony formation (budding), i.e., isotropic, partly circumoral or completely circumoral; 3) disposition of calices; 4) shape of the calicular fossa (in plan view), the above genera can also be distinguished on the basis of microarchitectures in trabeculae. Recently, one of the authors (DKP) in collaboration with Dr. Lathuilière, measured micro-dimensions such as septal density, trabecular density, trabecular width, pennular width, teeth density, interpennular height, height of pores and skeletal percentage in several representative specimens of abovegenera. They show a significant gradational relationship. However, individually they exhibit one or two diagnostic distinguishing characters. *Kobyia* possesses low septal and trabecular density (both five to six per 2 mm) and whereas *Dimorphararea* exhibits high value (seven to 12 and eight to 14 per 2 mm, respectively). *Tricycloseris* is characterized by very fine teeth and high density (10 per 100 μm) along the pennular rim. *Tricycloseris* and *Trocharea* show high skeleton percentage (56 and 62 percent). In addition pennulae are much more pronounced in *Kobyia*, *Dimorphararea*, *Microsolena*, and *Trochoplegma* than in *Tricycloseris* and *Trocharea*. *Kobyia* and *Dimorphararea* exhibit circumoral budding, and, in contrast, *Microsolena* possesses isometric growth. *Trochoplegma* and *Trocharea* are mostly solitary, and *Tricycloseris*, which is a small colonial coral, does

TABLE 2—Correlation matrix of standardized data values. Significant correlation coefficients are denoted by * and ** for chi-square probabilities of 0.01 and 0.001, respectively.

	D	H	NC	NS	C1	C2	DS	DT
D	1.00	0.85**	0.73**	-0.03	0.42**	0.44**	-0.20	-0.20
H	0.85	1.00	0.67**	-0.02	0.37**	0.51**	-0.19	-0.30*
NC	0.73	0.67	1.00	-0.14	0.08	0.13	-0.17	-0.25*
NS	-0.03	-0.02	-0.14	1.00	0.31*	-0.16	-0.03	-0.04
C1	0.42	0.37	0.08	0.31	1.00	0.55**	-0.21	-0.10
C2	0.44	0.51	0.13	-0.16	0.55	1.00	-0.19	-0.15
DS	-0.20	-0.19	-0.17	-0.03	-0.21	-0.19	1.00	0.49**
DT	-0.20	-0.30	-0.25	-0.04	-0.10	-0.15	0.49	1.00

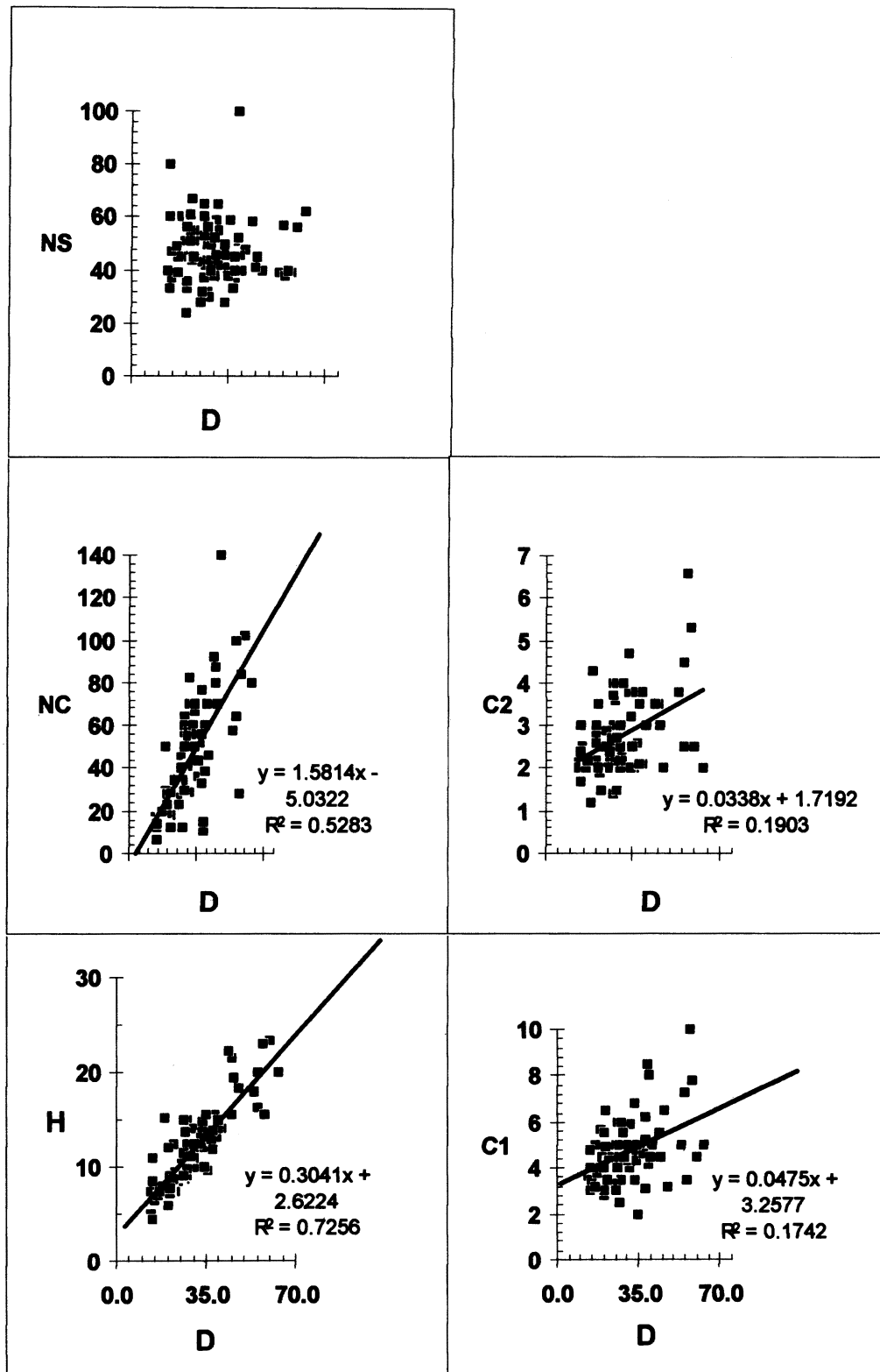


FIGURE 4—Scattergrams of size-related variables and the number of septa in *Dimorpharaea stellans* Gregory, 1900.

not show any distinct budding. Regarding porosity of the septa, two categories can be seen; one group with regularly perforated septa (*Kobyia*, *Tricycloseris* and *Trochraea*) and an other with fenestrate septa (*Dimorphararea*, *Microsolena*, and *Trochoplegma*).

Dimorphararea ranges from the Middle Jurassic to Cretaceous and is represented hitherto by the 14 Jurassic nominal species (Table 1; their locations and the differences with the Kachchh species of *Dimorphararea stellans*, are also given). In addition

TABLE 3—First three principal components extracted from correlation matrix.

	Principal component		
	I	II	III
Eigenvalue	2.866	0.860	0.624
Percent of total variance explained	65.97	19.77	14.25
Coefficient			
D	-0.895	0.152	-0.157
H	-0.893	0.114	-0.092
NC	-0.676	0.467	0.043
NS	0.020	-0.343	0.056
C1	-0.499	-0.577	-0.129
C2	-0.571	-0.359	-0.168
DS	0.329	0.159	-0.497
DT	0.355	0.042	-0.541

there are three more nominal species of *Dimorpharaea*; *D. defranciana* (Michelin, 1840), *D. pedunculata* Tomes, 1882, *D. concentrica* (Tomes, 1882), which could not be compared with the Kachchh species *Dimorpharaea stellans* because of their uncertain status (Lathuilière, 1989) and our poor knowledge of morphological characters.

Gregory (1900, p. 188–192), while describing *Dimorpharaea* from Kachchh, recognized four nominal species (*D. stellans*, *D.*

distincta, *D. continua* and *D. orbica*). The first three were differentiated on the basis of “tenuity of septa, less regular arrangement of corallites and the less pitted aspects,” which Beauvais (1978; Pandey and Fürsich, 1993) regarded as an intraspecific variation of *D. stellans*. The fourth species, *D. orbica*, is also considered a junior synonymy of *D. stellans* on the basis of present study (see below).

Most of the species have been reported from Paris Basin comprising southern England and Northern France. The information

TABLE 4—Specimen scores for the first three principal components. Gregory's type numbers (GSI No. . . .) have been followed by the letter corresponding with the species name; s—*stellans*, d—*distincta*, c—*continua*, o—*orbica*.

Specimen	Principal component scores		
	I	II	III
RUC1994I 620	-1.390	-0.283	0.476
RUC1994I 615	-1.217	0.325	0.533
RUC1994I 616	0.641	0.688	0.169
RUC1994I 945	-1.059	-1.272	0.672
RUC1994I 989	0.131	1.287	1.578
RUC1995I 321	-0.705	-0.897	1.729
RUC1995I 328	-1.220	-1.870	-2.688
RUC1992I 375	0.345	1.046	0.151
RUC1994I 613	0.301	0.628	1.613
RUC1994I 619	0.421	-0.255	0.558
RUC1994I 614	-0.124	-0.659	-0.097
RUC1994I 991	0.146	-0.524	0.976
RUC1994I 621	0.149	0.232	-0.698
JU/25/10	0.249	0.141	0.769
RUC1994I 987	0.516	0.340	0.518
RUC1994I 622	0.602	0.319	0.567
RUC1995I 323	-0.444	-0.419	-0.868
RUC1994I 618	0.926	0.001	0.202
JU/25/80	0.977	0.853	-0.116
RUC1994I 988	0.655	-0.580	1.905
JU/25/55	0.544	-0.171	0.688
RUC1994I 612	-0.235	0.410	-0.324
RUC1994I 983	0.356	-0.371	-0.699
RUC1994I 986	0.703	-0.725	-0.587
RUC1994I 999	0.732	1.106	1.032
RUC1994I 617	0.836	1.386	-1.560
RUC1994I 944	1.187	-0.987	0.588
RUC1994I 990	1.804	0.358	0.810
RUC1994I 985	1.512	-2.579	1.236
RUC1994I 984	1.560	-0.567	0.044
RUC1994I 982	1.992	1.053	0.773
RUC1994I 1088	2.181	0.046	-1.956
GSI No. 7008 s	1.644	-1.020	0.310
GSI No. 7007 s	0.361	0.947	0.209
GSI No. 7011 d	1.853	-1.402	-0.760
GSI No. 7009 s	0.169	1.016	0.431
GSI No. 7014 c	0.688	0.143	0.393
GSI No. 7015 c	1.704	-0.418	0.239
GSI No. 7013 c	-1.432	-0.398	-3.977
GSI No. 7012 d	0.239	0.573	0.662
GSI No. 7017 o	0.462	3.930	-0.607

TABLE 4—Continued.

Specimen	Principal component scores		
	I	II	III
GSI No. 7016 o	-1.547	1.586	0.307
JU/25/75	-0.047	-1.359	-1.092
RUC1994I 691	-0.242	-2.181	-0.543
RUC1994I 692	0.416	-0.659	-0.399
RUC1994I 693	-0.036	-0.183	-1.624
RUC1994I 694	1.622	-2.051	0.795
RUC1994I 695	1.691	-0.555	-0.876
RUC1994I 696	0.882	-0.734	0.633
RUC1994I 697	-0.748	-0.967	-0.887
RUC1994I 699	-0.564	0.111	-1.124
RUC1994I 700	-0.757	0.679	-0.238
RUC1994I 701	-0.055	0.583	0.779
RUC1994I 702	-0.714	-0.153	1.252
RUC1994I 703	-0.158	0.048	-0.287
RUC1994I 704	-0.667	-1.032	-0.787
RUC1994I 705	-0.449	-0.099	1.145
RUC1994I 706	-0.779	0.045	1.323
RUC1994I 661	-0.248	-0.033	-0.249
RUC1994I 662	-0.342	0.723	0.875
RUC1994I 664	-0.029	1.084	0.555
RUC1994I 665	-1.168	-1.572	-0.375
RUC1994I 666	-1.311	-0.182	0.319
RUC1994I 634	-1.164	0.042	0.259
RUC1994I 635	-0.769	1.239	-0.350
RUC1994I 636	-1.336	0.092	1.534
RUC1994I 623	-1.018	0.433	0.066
RUC1994I 624	-1.094	0.459	0.079
RUC1994I 625	-1.025	0.303	1.372
RUC1994I 626	-0.460	-0.317	1.165
RUC1994I 627	-0.511	2.012	-0.939
RUC1994I 628	-1.321	0.284	-0.870
RUC1994I 629	-0.791	0.487	-0.091
RUC1994I 630	-1.460	-0.758	-0.444
RUC1994I 631	-1.224	-0.406	-0.647
RUC1994I 632	-1.039	0.446	0.101
RUC1994I 633	-1.018	0.932	-1.281
RUC1995I 319	-0.750	0.634	-0.139
RUC1995I 320	-0.017	-0.187	0.891
RUC1995I 322	-0.147	-1.124	0.162
RUC1995I 325	-0.325	-0.194	-0.235
RUC1995I 329	-1.055	0.675	-0.016
RUC1995I 330	0.368	0.152	-0.807
RUC1995I 336	-0.373	-1.706	-0.649
RUC1994I 1259	3.014	1.920	-2.094

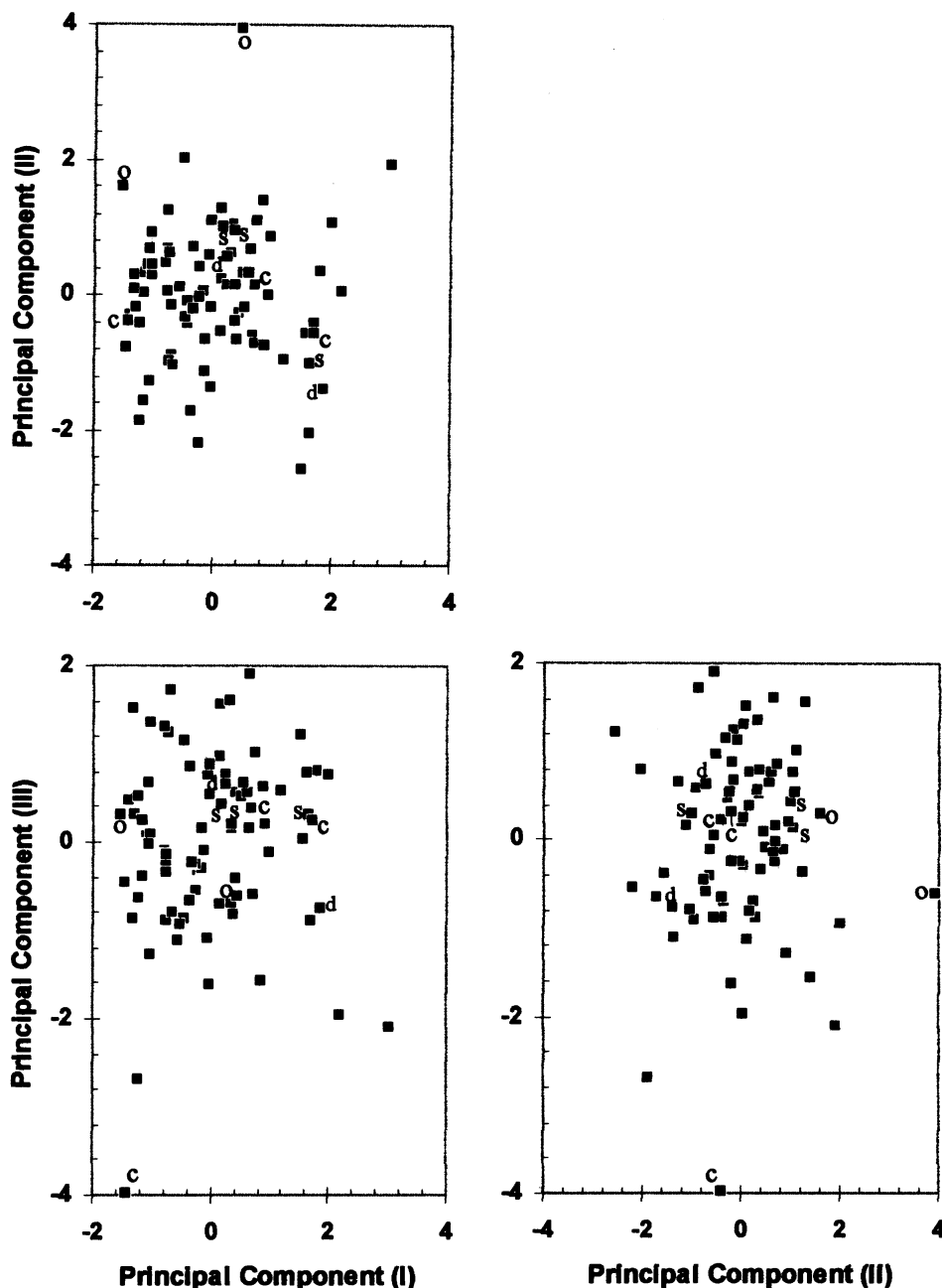


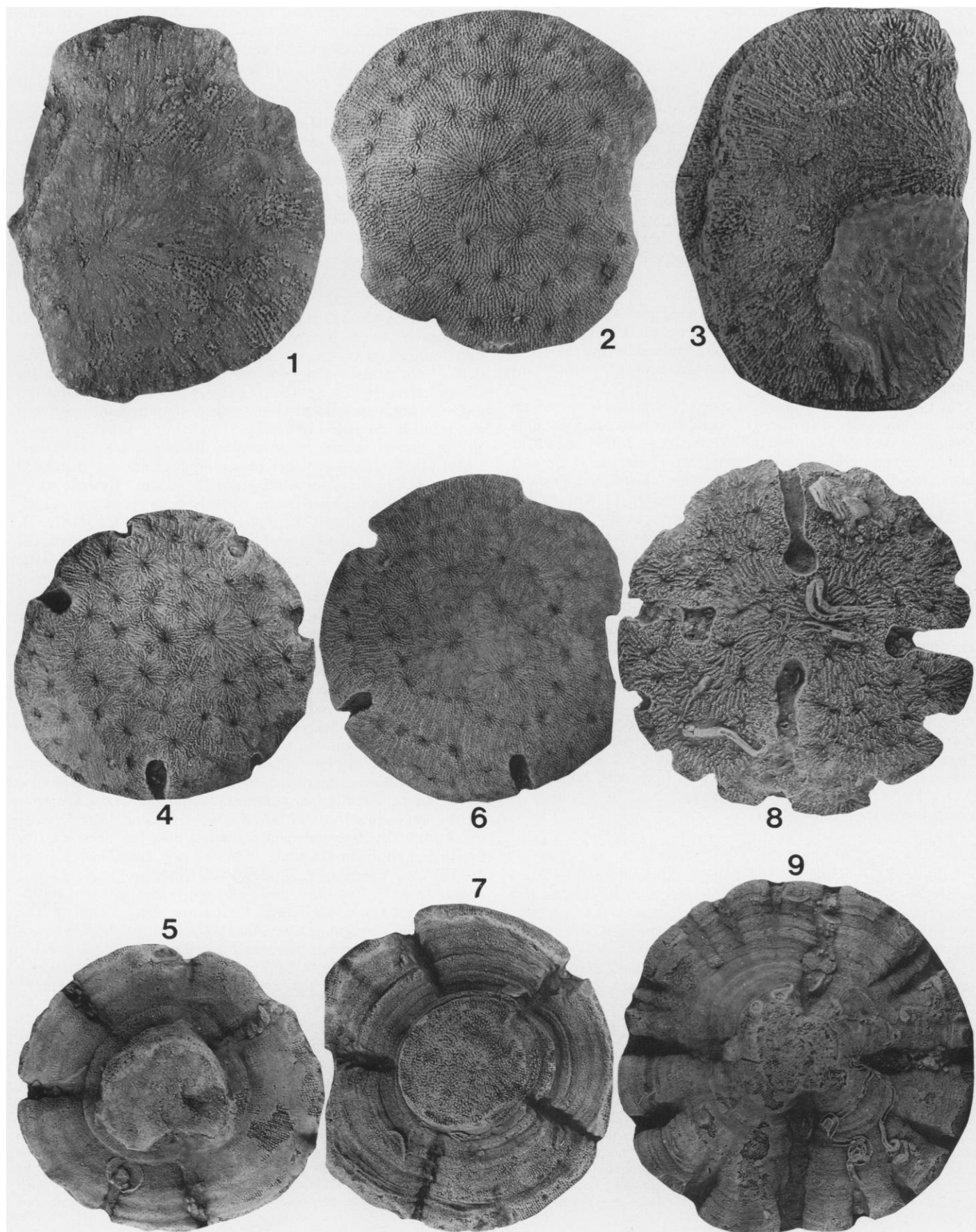
FIGURE 5—Specimen scores of first three principal components in *Dimorpharaea stellans* Gregory, 1900. Gregory's types have been followed by the letter corresponding with the species name; s—*stellans*, d—*distincta*, c—*continua*, o—*orbica*.

about *Dimorpharaea* in the Cretaceous is rather poor. The Kachchh species *Dimorpharaea stellans* differs from all European species of *Dimorpharaea* in exhibiting much higher values of septal and trabecular density (seven to 12 and eight to 14 per

2 mm respectively). A detailed microarchitectural and population study for European species is needed for any further comparison.

The shape of the corallum within a species of a genus may

FIGURE 6—*Dimorpharaea stellans* Gregory, 1900. 1, View of the upper surface, RUC1994I 1259, Chari Formation of Keera Dome, $\times 2.5$; 2, view of the upper surface, note the central position of the central corallite and the oval to elongated outline of the calicular pit, RUC1994I 989, Patcham Formation of Jumara Dome, $\times 2.5$; 3, view of the upper surface, RUC1994I 1309, Chari Formation of Keera Dome; 4–5, JU/25/10, Patcham Formation of Jumara Dome, $\times 2.0$, 4, view of the upper surface, 5, view of the lower surface, note seven deep radial grooves; 6–7, RUC1994I 622, Patcham Formation of Jumara Dome, $\times 2.0$, 6, view of the upper surface, 7, view of the lower surface, note six deep radial grooves; 8–9, JU/25/55, Patcham Formation of Jumara Dome, $\times 2.0$, 8, view of the upper surface, 9, view of the lower surface, note fifteen deep radial grooves.



vary from thin expanded, discoidal, pedunculate, fungiform to elongate and tells nothing about the species.

GEOLOGIC AND DEPOSITIONAL SETTING

Jurassic sediments in the Kachchh basin overlay Precambrian rocks and are displayed in three east-west trending fault-bounded anticlinal ridges. Together they constitute five lithostratigraphic units from Bajocian to Tithonian in age: Khavda, Patcham, Chari, Katrol, and Umia (Fig. 2; Waagen, 1871; Fürsich et al., 1994a). The oldest Khavda Formation (Bajocian-Bathonian), exposed along the northern anticlinal range of the basin, unconformably overlies Precambrian strata (Biswas, 1977), whereas the youngest Umia Formation (Tithonian-Albian), best exposed along the southern anticlinal range is overlain by Deccan volcanics.

The Jurassic sediments were deposited in a pericratonic rift basin inundated by the extension of the southern margin of the Tethyan Seaway (Biswas, 1987; Fürsich et al., 1994b). The sediments range from nearshore, coarse-grained to deeper water, fine-grained siliciclastics. Carbonate sediments are mostly confined to older formations.

In the Middle Jurassic of Kachchh, scleractinian corals are rare and unevenly distributed in comparison to other benthos. *Dimorpharaea* de Fromentel, 1861 has been found at two localities representing different stratigraphic intervals. One hundred sixty-four specimens come from the Jumara Dome locality 1.25 km NNE of the village of Jumara (Fig. 1). The Jumara locality has been dated with ammonites as upper Bathonian (Calomon, 1993) and is part of the carbonate-dominated Patcham Formation, where the autochthonous corals colonized a soft substratum, generally in a low-energy environment (Fürsich et al., 1994b). An additional 14 specimens were collected from the Chari Formation at Keera Dome, 18 km SE of the Jumara locality (Figs. 1, 2). Chari Formation is argillaceous silts and intercalated sands representing low energy mid-shelf environments deposited during relative sea level low-stands (Fürsich et al., 1994b). Based on ammonoid identifications, the Keera Dome locality is considered Callovian in age (Spath, 1933). Although the corals from Keera Dome, found as nodules within a bioturbated calcareous unit, are interpreted as allochthonous, they were probably not transported far because the fragile epitheca are sometimes well preserved. Samples from both Jumara and Keera Domes were both bored and encrusted by a variety of encrusting serpulids, bivalves, and sponges.

MATERIAL AND METHODS

Transverse and longitudinal polished thin-sections were examined for details of skeletal microarchitecture and microstructure. For better differentiation between sediments and recrystallized skeletal elements, the thin-sections were soaked for a few hours in a methylene blue solution.

Dimensions of 85 specimens used in the quantitative analysis are shown in Figure 3. These measurements are a quantitative

representation of diagnostic morphological characters, which allow the comparison and correlation of different specimens within and between scleractinian corals. These include the diameter of the corallum (D), height of the corallum (H), number of corallites in the colony (NC), number of septa in the mother corallite at the center of the colony (NS), minimum distance between centers of central corallite and corallites of the inner ring (C1), minimum distance between corallite centers of the outer ring (C2), septal density per 1 mm (DS), and trabecular density per 1 mm (DT). The statistical computations were done in SYSTAT version 5.2 for the Macintosh computer (Wilkinson et al., 1992). All the specimens have been deposited in the collection of the Department of Geology, University of Rajasthan, Jaipur, India.

QUANTITATIVE ANALYSIS

Dimensions from *Dimorpharaea stellans* Gregory, 1900, from the Jumara Dome locality were examined statistically because they represent a coherent sample of 85 well-preserved individuals. Their measurements are provided in Appendix A. To facilitate interpretation between variables of different scales, the original data were converted to Z-scores (having a mean of zero and standard deviation of 1.0).

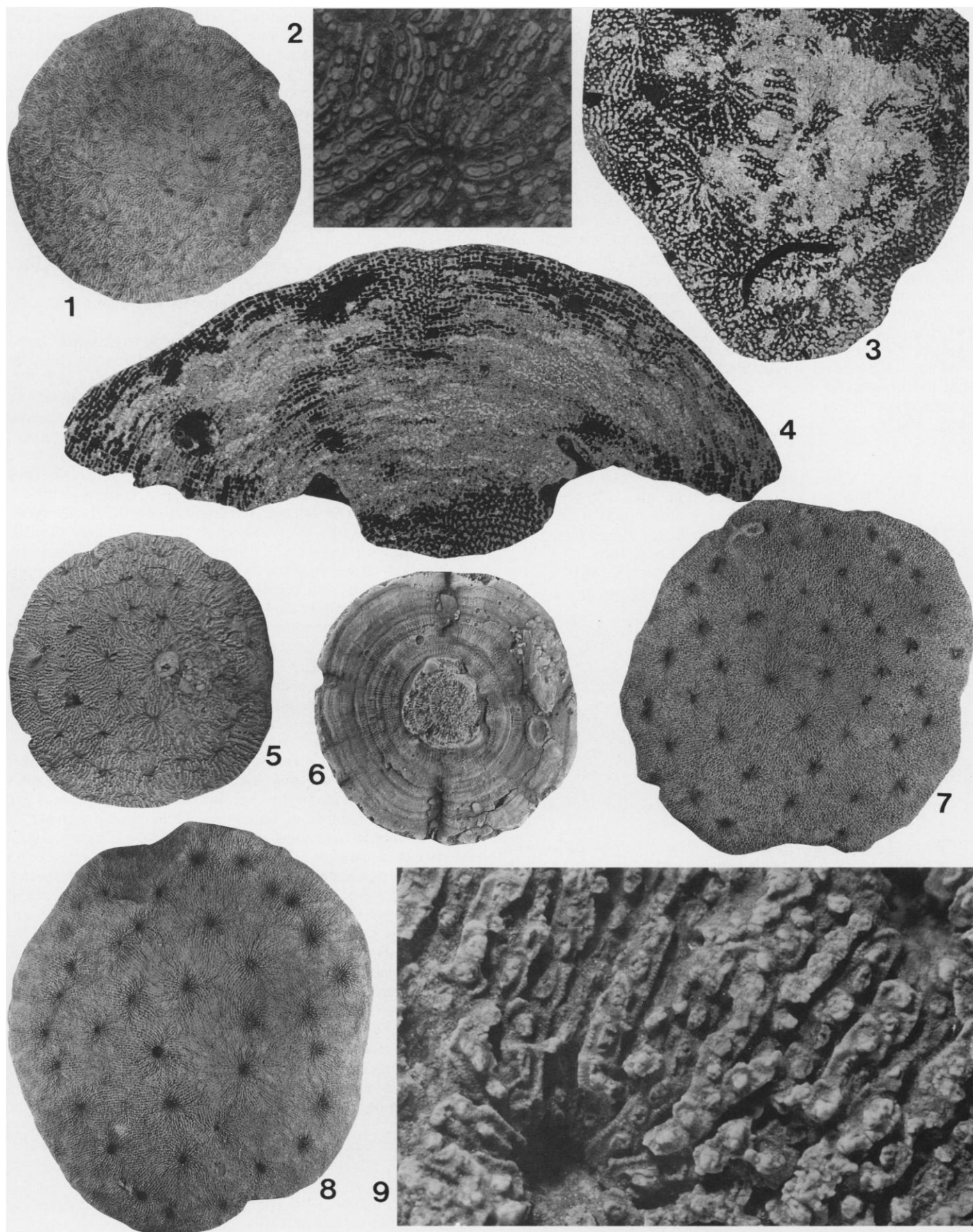
The correlation and covariance coefficients among eight variables (Table 2) suggest that most variables are not correlated and are highly variable. Among the 28 possible variable pairs, the *r* values between only nine variable pairs are highly significant, with $P < 0.001$. These are D-H, D-NC, D-C1, D-C2, H-NC, H-C1, H-C2, C1-C2, and DS-DT. In addition to these, NS-C1, H-DT, and NC-DT are also significant pairs, with $P < 0.01$. Most of the significant correlations occur among the "size"-related variables of diameter and height.

Five scatter plots (Fig. 4) indicate the relationship of diameter to the other five continuous variables. To show the relationship between size and other factors, a simple least-squares regression was conducted between diameter and the variables. The scatter evident in some of the bivariate plots (D-NS, D-C2, and D-C1) and the majority of other variables (not plotted) suggest that further multivariate analysis is necessary to determine the sources of variation within the sample set of *D. stellans*.

Principal components analysis.—The principal components analysis (PCA) was conducted to determine the sources and limits of variation within the sample set of Jumara corals. The principal components were extracted from a correlation matrix derived from the Z-scored data. Z-scored data has been used to buffer and eliminate the scale effects of raw data. The results of the PCA are presented in Tables 3 and 4 and in Figure 5.

Together, the first three principal components account for almost the total variance within the sample data (Table 3). The first principal component explains 66 percent of the total variance. The height and diameter and to a lesser extent the number of corallites and inter-corallite distances contribute predominantly to the first principal component. Given the contributions

FIGURE 7—*Dimorpharaea stellans* Gregory, 1900. 1, View of the upper surface, RUC1994I 613, Patcham Formation of Jumara Dome, $\times 2.0$; 2, part of the upper surface showing pennular septa and discontinuous menianae, note the outline of the pennulae in cross section, RUC1994I 985, Patcham Formation of Jumara Dome, $\times 15$; 3–4, RUC1994I 411, Patcham Formation of Jumara Dome, $\times 4.0$, 3, showing beaded nature of septa in transverse section, 4, longitudinal section, note the fenestrate nature of the septa; 5–6, RUC1995I 320, Patcham Formation of Jumara Dome, $\times 2.0$, 5, view of the upper surface, 6, view of the lower surface, note four deep and some shallow radial grooves; 7, view of the upper surface, note the depth of the central calicular pits and slight eccentric central corallite, RUC1994I 612, Patcham Formation of Jumara Dome, $\times 2.0$; 8, view of the upper surface, note the depth of the central calicular pit and pronounced eccentric central corallite, RUC1994I 617, Patcham Formation of Jumara Dome, $\times 2.0$; 9, part of the upper surface of the corallum showing fine teeth along the margins of the pennulae, RUC1994I 944, Patcham Formation of Jumara Dome, $\times 30$.



of the "size" related variables (especially diameter and height), it is reasonable to assume that the first principal component extracts most of the variation due to size effects. The second principal component explains 20 percent of the total variance and receives positive contributions from number of corallites and negative contribution from inter-calicular distances. The third principal component discriminates the variation among the septal parameters (septal density and trabecular density) and explains 14 percent of the total variance.

Scatter plots of the Principal Component Scores (Fig. 5; see also Table 4) indicate that the data points cannot be discriminated into different clusters, nor is there any clear trend among the sample specimens. The specimen scores of principal components hence preclude any discrimination of the data set into different groups. Further analyses that might extract groups of specimens (e.g., cluster and/or discriminant analysis) were not attempted due to the absence of any clearly identifiable clusters of points. It is for this reason together with the normal distribution of other variables that we interpret the collection of specimens to represent a single, highly variable species rather than the two or more, as has been previously reported for the extreme morphotypes (Gregory, 1900; Beauvais, 1978; Pandey and Fürsich, 1993).

SYSTEMATIC PALEONTOLOGY

Class ANTHOZOA Ehrenberg, 1834

Subclass ZOANTHARIA Blainville, 1830

Order SCLERACTINIA Bourne, 1900

Suborder MICROSOLENINA Morycowa and Roniewicz, 1995

Family MICROSOLENIDAE Koby, 1889

Genus DIMORPHARAEA de Fromentel, 1861

Type species.—*Microsolena koechlini* Milne-Edwards, H., 1860.

DIMORPHARAEA STELLANS Gregory, 1900

Figures 6.1–6.9, 7.1–7.9, 8.1–8.6

Dimorpharaea stellans GREGORY, 1900, p. 189, pl. 24, figs. 2–5;

BEAUVAIS, 1978, p. 63, pl. 5, fig. 6, pl. 7, figs. 2, 3; PANDEY AND FÜRSICH, 1993, p. 32, pl. 9, figs. 1, 2, 4–7, text figs. 19, 20.

Dimorpharaea distincta GREGORY, 1900, p. 190, pl. 24, figs. 6–8.

Dimorpharaea continua GREGORY, 1900, p. 191, pl. 24, fig. 9.

Dimorpharaea orbica GREGORY, 1900, p. 191, pl. 25, figs. 3, 4; BEAUVAIS, 1978, p. 63, pl. 5, fig. 7.

Dimorpharaea cf. *orbica* Gregory. PANDEY AND FÜRSICH, 1993, p. 33, pl. 9, fig. 8.

Revised diagnosis.—Pedunculate *Dimorpharaea*; calices shallow to superficial with distinct shallow to deep central calicular pits; fibrous trabeculae; pennulae with fine teeth along the margins (5 per 100 μm); menianae continuous and/or interrupted, occasionally pennular margins of the adjacent trabeculae of a septum show imbricating pattern; distal margin of the septa finely beaded or thick and continuous, depending upon the level of exposure of the septa on the calicular surface.

Description.—Corallum low, massive, thamnasterioid, bi-convex to discoidal, subcircular in plan view, with pedunculate to subpedunculate base (Fig. 3). Colony formed by circumoral budding around central occasionally eccentric (Fig. 7.7, 7.8), more or less large corallites. The notched edge and lower surface bear one to 15 long, narrow, radial grooves of varying depth (Fig. 6.5, 6.7, 6.9). Calices varying in number from 7 to 140 in adult

specimens, shallow to superficial with distinct shallow to deep central calicular pits. Septa thin, occasionally anastomosing (GSI Type no. 7008), fenestrate, composed of pennular and fibrous trabeculae (Fig. 8.3–8.6). Trabeculae circular, subcircular, suboval to subelongate in cross-section (Fig. 7.2). Fibers more or less diverge from the axis of the trabeculae (Fig. 8.4–8.6). Pennulae subrectangular to subquadrangular in outlines, concave upward with fine teeth (5 per 100 μm) along the margins (Fig. 7.9). Menianae discontinuous, occasionally pennular margins of the adjacent trabeculae of a septum show an imbricating pattern. The longitudinal section along the septal plane shows occasional continuous, wavy menianae. Pennulae of adjacent septa alternate. Distal margin of the septa finely beaded or thick and continuous, depending upon whether it terminates between the pennulae or along the pennulae. Synapticulae between septa common. Endothecal vesicular dissepiments rare (e.g., Fig. 8.2). Epitheca thin, fragile with growth rugae.

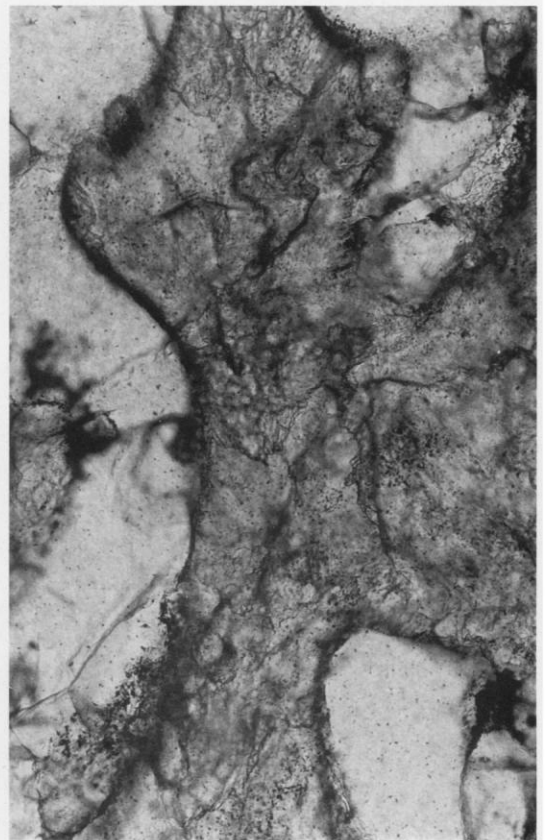
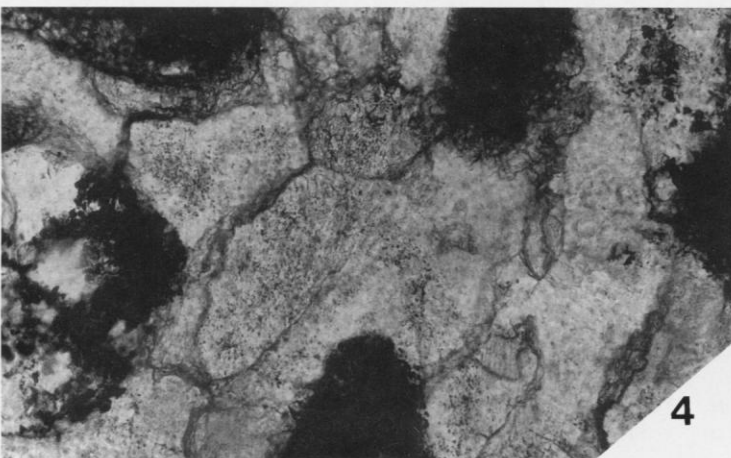
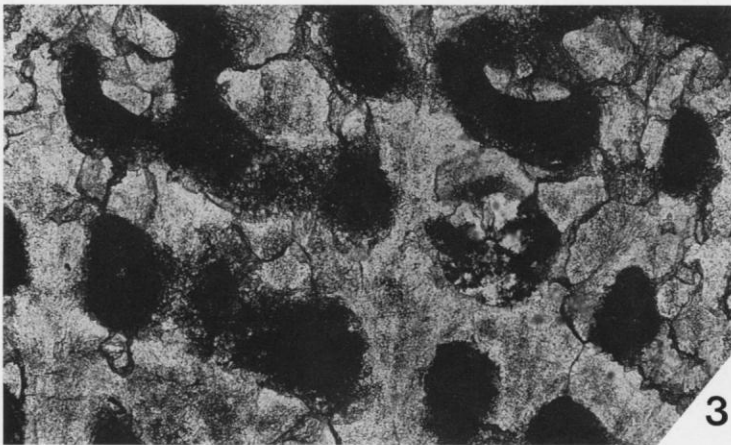
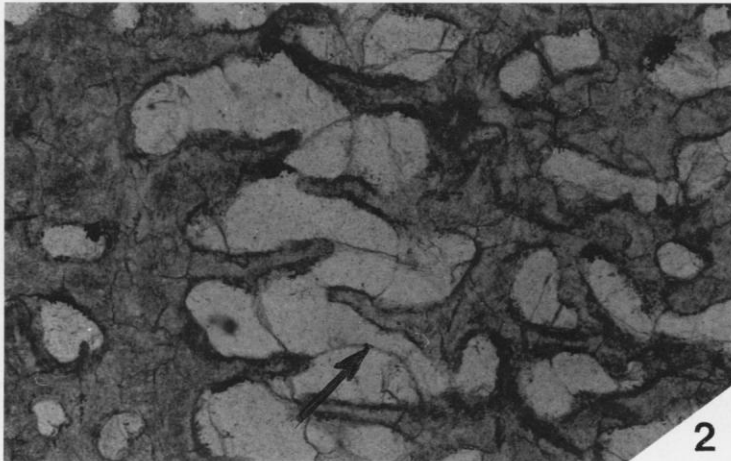
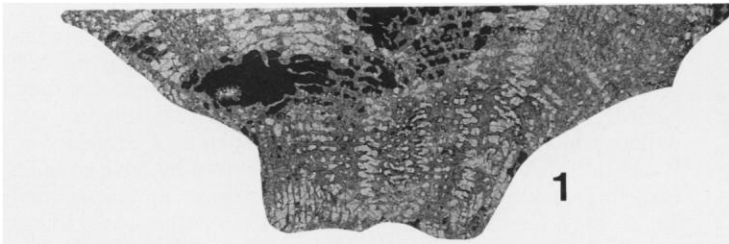
Material.—164 well-preserved specimens from upper Bathonian sediments of the Patcham Formation of Jumara Dome of Kachchh, India (RUC1992I 375; RUC1994I 37, 411, 612–706, 943–945, 982–991, 999, 1088; RUC1995I 319–370; JU/25/10, 55, 75, 80); an additional 14 specimens have been recovered from the Callovian sediments from the Chari Formation of Keera Dome, Kachchh, India (RUCI1994I 1309, 1259). Eleven type specimens (GSI, Calcutta Type No. 7007–7017) in the Gregory Collection.

Discussion.—The microarchitecture of the Kachchh specimens is similar to those of *Dimorpharaea* sp. from middle Callovian (Hathira) Israel (Gill, 1967). Although the original aragonitic skeletal material has been replaced by calcite, the microarchitecture is well preserved. In Figure 8.4–8.6, even the original traces of orientation of fibers can be seen.

The alternate arrangements of the pennulae of the adjacent septa has been misunderstood (Gregory, 1900; Milne Edwards and Heime, 1951). They identified the septa that are truncated along the pennulae as overgrowth of the stereoplasm along the lateral surface of these alternate septa. According to Gregory (1900), *Dimorpharaea orbica* differs from *D. stellans* on the basis of deep calicular fossae, large corallites, and more numerous (eight complete orders) septa. The study of a large number of specimens and a quantitative analysis of selected samples suggests that the diagnostic specific characters (intra-corallite distances, the number of corallites and maximum number of septa) are not in agreement with those used by Gregory (1900) for specific separation. The differences between *D. stellans* and *D. orbica* emphasized by Gregory (1900) are also not statistically distinct (see the section on PCA here in) and represent ecophenotypic variation; environmental stress resulted late maturity for budding. Thus, giving priority to *D. stellans*, *D. orbica* has been merged with it.

The European species from Inferior Oolite such as *D. oolitica* and *D. lycetti* (Duncan, 1872) do not differ in form, number and arrangement of corallites, fenestrate septa, moniliform distal margin of the septa, distinct and numerous synapticulae. However, because of the lack of information about the pennular structures and menianae, septal density and trabecular density of these species, any further comment must wait until more detailed information becomes available.

FIGURE 8—*Dimorpharaea stellans* Gregory, 1900. RUC1992I 375. 1, Longitudinal section, $\times 4.0$; 2, part of the longitudinal section showing vesicular dissepiment indicated by arrow, $\times 50$; 3, longitudinal section parallel to the septal plane exhibiting even distribution of pores, $\times 60$; 4–6, longitudinal section exhibiting microstructures, note the traces of fibers diverging from the axis of the trabeculae, $\times 150$.



PALEOECOLOGY

Gill (1982) suggested that the pennular structure in these corals is an indication of rhythmic alternating growth. Gill interpreted the rhythmic growth as a mechanical necessity. Recent study of an extant zooxanthellate coral, *Leptoseris fragilis* (Fungiina, Agariciidae) exhibiting pennular and perforated septa (Schlichter, 1991, 1992), probably indicates that the pennular architecture with perforated septa are characteristic of a comparative "deep-water suspension feeder" life habit (Lathuilière and Gill, 1995). This view is also supported by the record of the dominance of pennular corals, e.g., *Dimorpharaea*, *Microsolena*, *Trocharaea*, *Trochoplegma*, *Kobyia*, etc., in the coral bed of Patcham Formation of Jumara Dome, where coral colonized a muddy sea floor, well below the fair weather wave base, in a low energy environment (Fürsich et al., 1994b). Further, the high diversity of corals and associated fauna of coral bed (mentioned above) indicate that the coral grew in a warm, well-aerated, fully marine environment.

The notched edge and long, narrow, radial grooves of varying depth and number (Fig. 6.5, 6.7, 6.9) on the lower surface of the colony have been inferred to be connected with the commensalism with some worms, shrimps or crabs. The arguments in support the above inference are the continuity of the growth rugae and epitheca in to the groove, varying number of grooves in different colonies, varying depth and length in individual colony and gradual increase in depth of the grooves with the growth of the colony and perhaps also the size of the coral commensals.

CONCLUSIONS

The morphological and microarchitectural data on *Dimorpharaea* de Fromentel, 1861, from the Jumara Dome of Kachchh, India, provide a new means for comparison with other taxa of the Microsolonidae. Our study indicates that septal and trabecular density are more or less uniform in most genera of the microsolenids from Kachchh (see Pandey and Fürsich, 1993) and should not be utilized as specific or generic criteria. The diagnostic characters of mode of colony formation and pattern of septa readily distinguish *Dimorpharaea* from other genera of the family Microsolonidae.

Among the many possible morphological features observed in *Dimorpharaea stellans* Gregory, 1900, the distance between the centers of the central corallite and corallites of the inner ring, the distance between corallite centers of the outer ring, the number of corallites in a given density, and the maximum number of septa are here considered characters of specific significance. Most of the variation within *D. stellans* can be explained by factors related to size (diameter, height, and inter-corallite distances). Apart from size factors, septal parameters (number, density, and trabecular density) explain much of the rest of the variation within the studied sample. Without examining more material from different species, it is premature to conclude that the sources of variation within *D. stellans* would be the same in other species or useful in discriminating closely related species. Given that the several supposedly different but closely related species (e.g., *D. orbica*) appear to fall within the limits of variation in *D. stellans*, they are here considered as synonyms with *D. stellans*.

Dimorpharaea, one of the common genera of the family Microsolonidae, is characteristic of a comparatively deep-water suspension-feeder life habit, and colonized a soft bottom in a warm, well aerated, low energy, fully marine environment, well below the fair-weather wave base.

ACKNOWLEDGMENTS

The specimens studied here were collected in a joint fieldwork program between the years 1992 and 1997, with F. T. Fürsich

(Würzburg); J. Callomon (London) and A. K. Jaitly (Varanasi) in connection with a project funded by National Geographic Society (grant 3597-87), the Deutsche Forschungsgemeinschaft (grant Fu 131/18-1) and Department of Science and Technology, New Delhi (award no. ESS/23/016/95). This contribution was written while DKP and CAM were supported as Alexander von Humboldt-Stiftung Fellows and further revised by DKP in India with the support of fund given by Department of Science and Technology, New Delhi. We thank also to H. Schirm, Würzburg, who carried out the photographic work, and A. Budd, B. Lathuilière, and an anonymous reviewer for critical remarks leading to an improved manuscript.

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APPENDIX A

Original measurements of *Dimorpharaea stellans* from Jumara Dome. Gregory's types numbers (GSI No. . . .) have been followed by the letter corresponding with the species name; s—*stellans*, d—*distincta*, c—*continua*, o—*orbica*.

Specimen	D (mm)	H (mm)	NC	NS	C1 (mm)	C2 (mm)	DS	DT
RUC1994I 620	13.3	7.4	17	40	3.0	2.2	4	5
GSI No. 7016 o	13.5	5.0	11	80	3.6	2.0	5	4
RUC1994I 633	14.0	11.0	7	60	4.8	3.0	5	5
RUC1994I 636	14.0	4.5	12	33	4.0	1.7	4	4
RUC1994I 625	14.2	8.5	14	47	3.0	2.4	4	4
RUC1994I 666	14.5	6.4	15	36	3.5	2.5	4	5
RUC1994I 628	16.3	7.0	19	49	5.0	2.0	5	5
RUC1994I 630	16.7	7.5	20	39	3.2	2.2	5	5
RUC1994I 634	17.0	8.0	21	45	3.8	2.0	4	5
RUC1994I 615	18.4	7.3	30	60	4.0	1.2	5	4
RUC1994I 616	18.6	15.1	50	45	5.7	4.3	4	4
RUC1994I 623	19.5	7.0	28	51	4.5	2.0	4	5
RUC1994I 626	20.0	12.0	19	36	3.0	3.0	4	4
RUC1994I 702	20.0	8.8	20	33	4.0	2.2	4	4
RUC1994I 945	20.0	6.3	27	24	2.8	2.8	5	4

APPENDIX A

Continued.

Specimen	D (mm)	H (mm)	NC	NS	C1 (mm)	C2 (mm)	DS	DT
RUC1995I 329	20.0	6.0	23	56	4.0	2.6	4	5
RUC1994I 635	20.4	8.3	24	61	5.5	2.2	4	5
RUC1994I 627	21.0	7.2	12	61	6.5	3.5	4	5
RUC1994I 629	21.0	9.0	28	51	4.9	2.0	4	5
RUC1994I 632	21.0	7.7	24	55	4.0	2.0	4	5
RUC1994I 624	21.5	7.2	18	51	4.3	1.9	4	5
RUC1994I 706	21.9	8.5	23	44	3.5	2.0	4	4
GSI No. 7013 c	22.0	12.5	21	67	4.5	2.5	7	6
RUC1994I 631	22.4	8.7	23	45	4.3	1.5	5	5
RUC1994I 700	22.6	7.5	25	51	5.0	2.5	4	5
RUC1994I 662	22.8	9.5	35	55	4.5	2.5	4	4
RUC1994I 705	24.0	8.6	34	43	3.3	2.9	4	4
RUC1994I 665	25.3	8.9	26	28	3.0	2.0	5	5
RUC1994I 697	25.9	11.0	23	32	4.0	2.7	5	5
GSI No. 7009 s	26.0	15.0	26	53	6.0	2.2	4	4
RUC1995I 319	26.0	9.0	23	60	4.0	2.4	4	5
RUC1994I 989	26.5	10.5	42	65	4.0	3.0	3	4
RUC1995I 320	26.5	11.5	40	37	4.5	2.7	4	4
GSI No. 7007 s	26.8	13.7	33	55	5.0	3.7	4	4
RUC1995I 321	27.0	8.7	46	42	2.5	1.4	4	4
RUC1992I 375	27.3	15.0	12	50	5.0	4.0	4	4
RUC1994I 701	27.3	12.5	35	57	4.3	2.5	4	4
RUC1995I 328	27.3	9.0	34	32	3.5	3.0	6	6
RUC1994I 664	27.5	9.8	40	56	6.0	2.2	4	4
RUC1994I 613	27.8	11.0	50	44	5.5	2.2	3	4
RUC1994I 619	28.0	11.7	50	30	5.2	3.6	4	4
RUC1994I 614	28.2	10.0	64	38	4.8	2.5	4	5
RUC1994I 699	28.4	12.0	38	57	5.5	1.5	5	5
RUC1994I 621	28.7	9.8	50	44	5.3	4.0	4	5
RUC1994I 991	28.7	11.5	57	38	4.2	2.7	4	4
RUC1995I 325	28.8	11.2	30	40	4.5	2.7	4	5
JU/25/10	29.0	12.0	60	50	5.0	2.4	4	4
RUC1994I 703	30.0	12.4	42	52	4.5	2.5	4	5
RUC1994I 704	30.0	10.0	42	38	4.3	2.0	5	5
RUC1994I 987	30.0	14.0	57	53	5.0	3.0	4	4
RUC1994I 661	30.5	11.0	41	46	5.0	2.2	4	5
GSI No. 7012 d	30.6	12.0	55	59	5.0	2.4	4	4
RUC1994I 622	31.2	11.8	82	55	5.9	2.4	4	4
RUC1995I 323	31.2	10.0	70	65	4.0	2.0	5	5
RUC1994I 693	31.5	12.5	29	42	5.0	4.0	5	5
RUC1994I 618	33.0	13.3	60	41	4.8	4.7	4	4
JU/25/80	33.5	14.2	50	46	6.8	3.8	4	4
RUC1994I 988	33.7	14.8	67	41	3.5	2.5	3	4
JU/25/55	34.0	12.0	70	50	4.3	3.2	4	4
RUC1995I 322	34.0	10.0	50	28	5.0	2.0	5	4
RUC1994I 691	35.0	15.5	56	38	2.0	2.5	5	5
RUC1994I 612	35.7	9.7	44	59	5.0	2.0	4	5
RUC1994I 983	36.0	13.2	36	33	5.0	3.8	4	5
JU/25/75	37.0	12.7	52	33	4.6	2.6	5	5
RUC1994I 986	37.5	14.0	77	35	6.2	2.6	4	5
RUC1995I 336	37.7	11.8	56	40	3.1	2.1	5	5
RUC1995I 330	37.8	13.8	33	45	5.2	3.5	4	5
GSI No. 7017 o	38.6	12.0	15	100	8.5	2.1	4	4
RUC1994I 999	38.6	15.5	11	51	4.4	3.8	3	4
RUC1994I 617	39.0	13.0	39	52	8.0	3.8	4	5
RUC1994I 692	39.5	14.0	60	46	4.2	3.0	4	5
RUC1994I 696	40.0	15.0	70	40	4.5	3.0	4	4
GSI No. 7014 c	41.0	14.0	46	48	5.0	3.0	4	4
RUC1994I 695	44.0	22.2	92	58	5.5	3.5	5	4
GSI No. 7008 s	44.8	21.5	80	41	4.5	3.5	4	4
RUC1994I 944	45.0	15.5	87	43	4.5	3.0	4	4
RUC1994I 990	45.8	19.4	70	45	6.5	3.0	3	4
RUC1994I 985	47.5	18.3	140	40	3.2	2.0	4	4
RUC1994I 984	53.7	18.0	58	39	5.0	3.8	4	4
RUC1994I 982	55.3	16.3	64	57	7.3	4.5	4	4
RUC1994I 694	55.5	20.0	100	38	3.5	2.5	4	4
RUC1994I 1259	57.0	23.0	28	40	10.0	6.6	4	4
RUC1994I 1088	58.0	15.5	84	39	7.8	5.3	4	5
GSI No. 7011 d	60.0	23.4	102	56	4.5	2.5	4	5
GSI No. 7015 c	63.0	20.0	80	62	5.0	2.0	4	4
Minimum	13.3	4.5	7	24	2.0	1.2	3	4
Maximum	63.0	23.4	140	100	10.0	6.6	7	6
Mean	30.5	11.9	43.2	47.3	4.7	2.6	4.2	4.5
SD	11.56	4.13	25.14	11.90	1.32	0.89	0.62	0.55