

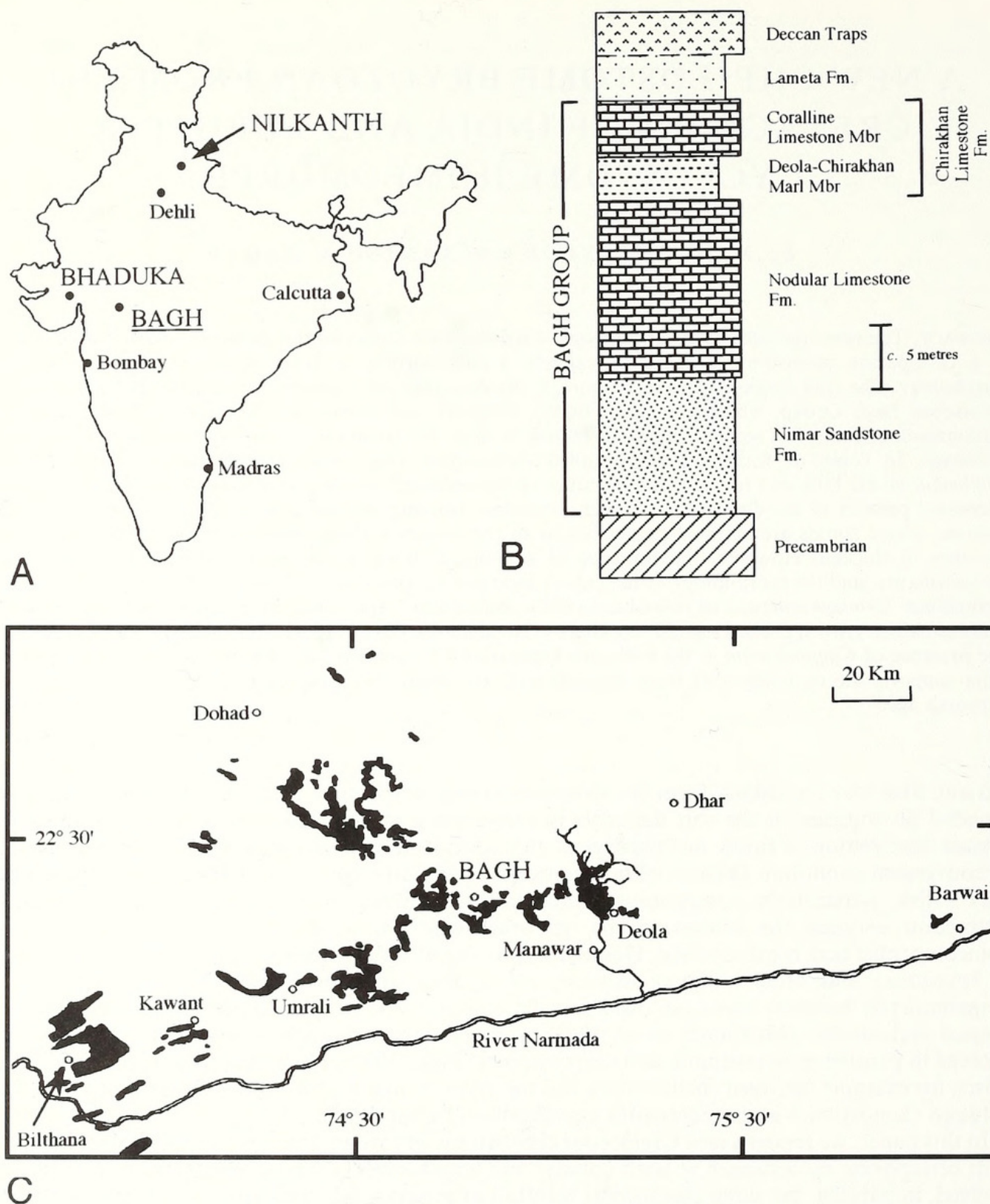
A NEW CHEILOSTOME BRYOZOAN FROM THE CRETACEOUS OF INDIA AND EUROPE: A CYCLOSTOME HOMEOMORPH

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ABSTRACT. The new 'malacostegan' cheilostome *Chiplonkarina* is an unusual genus previously misidentified as a cerioporine cyclostome because of extreme homeomorphy in both zooid-level and colony-level morphology. The type species, *C. dimorphopora*, is the dominant bryozoan in west-central India in the mid-Cretaceous Bagh Group, whose geology is briefly reviewed, and is recorded here for the first time in the Cenomanian of France. A second species, *C. bretoni* sp. nov., occurs in the Lower Cenomanian of France and Germany. In common with many free-walled cyclostomes (and other stenolaemates), the zooids of *Chiplonkarina* are long and tubular, and branches of the dendroid colonies have axial endozones with zooids orientated parallel to the direction of branch extension, bending through almost 90° into the surrounding exozone, where zooids are oriented perpendicular to the branch surface such that their lengthening caused branches to thicken. However, the presence of a cuticular layer in the interzooidal walls, fibrous wall microstructure, and the morphology of the colony base and overgrowths demonstrate that *Chiplonkarina* is a cheilostome. *Chiplonkarina* can be viewed as an early cheilostome 'experiment' in erect growth using a typically stenolaematous growth pattern seldom repeated by the numerous erect cheilostomes that evolved subsequently. The presence of *Chiplonkarina* in the Nilkanth Formation ('Upper Tal Shell Limestone') of Uttar Pradesh, India supports the correlation of these deposits with the Bagh Group and implies a likely Cenomanian-Turonian age.

HOMEOMORPHY in colony-form is pervasive among bryozoans. Even in the absence of well-founded phylogenies of the sort desirable in pinpointing specific instances of homeomorphy, the mosaic distribution of many morphological characters can only be explained by rampant parallel or convergent evolution. Degrees of homeomorphy vary. In some cases, homeomorphic taxa have only a few, particularly conspicuous characters in common, and close scrutiny easily permits distinction between the homeomorphs. In other cases, however, the difference between the homeomorphic taxa is more subtle. Homeomorphy can also be manifested at two hierarchical levels in bryozoans and other colonial animals: colony-level and zooid-level. Notable examples of homeomorphy between bryozoan orders at the colony-level are lyre-shaped fenestrates and lyre-shaped cyclostomes (McKinney *et al.* 1993), and the narrow-branched dendroid colonies which evolved in parallel in trepostomes and cryptostomes (Blake 1980). Homeomorphy at the zooid-level exists, for example, between cheilostomes and the cryptostome *Worthenopora* (Hageman 1991), and between cheilostomes and melicerititid cyclostomes (Taylor 1985).

In this paper, we report a new Cretaceous cheilostome bryozoan which is strongly homeomorphic with cerioporine cyclostomes at both colony- and zooid-levels. *Chiplonkarina* gen. nov. evidently evolved, in parallel, the same geometrical solution as cerioporines (and many other stenolaemates) for growing bushy colonies with cylindrical branches which could thicken proximally towards the colony base where breaking stresses were greatest. This was achieved by having long tubular zooids originating in an axial branch endozone and initially growing parallel to the branch axis at a high rate, but subsequently bending through about 90° outwards into the peripheral exozone where the zooids are perpendicular to the branch surface and growth rate would have been slower. Although a similar colony-form also occurs in the unusual cheilostome *Inversaria* (see Voigt and Williams



TEXT-FIG. 1. A, outline map of India showing locations of the type localities of the Bagh Group in Madhya Pradesh, and of the Bhaduka Limestone (Wadhwan Formation) in Gujarat, and the Nilkanth Formation in Uttar Pradesh. B, generalized vertical section of the Bagh Group and contiguous strata as developed in the Man River Valley near Deola, Madhya Pradesh; thicknesses of the constituent units of the Bagh Group vary considerably and are here scaled approximately according to median values; in some places, the Deola-Chirakhan Marl is absent and the Coralline Limestone rests directly on the Nodular Limestone. C, outcrop pattern of the Bagh Group plus Lameta Formation in the Narmada River Valley centred on the town of Bagh.

1973), most cheilostomes with thick dendroid branches employ frontal budding or other means of self overgrowth to grow thick-branched dendroid colonies, occasionally from an axial bundle of prismatic polymorphic zooids (e.g. *Dysnoetopora*, see Voigt 1970; *Heteroconopectum*, see Voigt 1983).

Chiplonkarina is locally common in the Cenomanian of north-west Europe but is much more abundant in the Bagh Group of Madhya Pradesh and Gujarat, west-central India (Text-fig. 1); indeed it is the commonest bryozoan in the Bagh Group, accounting for about 70 per cent. of the bryozoans by volume according to Guha (1987). Branching colonies of *C. dimorphopora* occur in great profusion (Pl. 1, fig. 1) in the uppermost unit of the Bagh Group, the Coralline Limestone, which was formerly used for building temples such as those at Mandu. Bose (1884, p. 71) remarked that the Coralline Limestone '...takes a fine polish, and the thick clusters of branching Bryozoa, of which it is largely made up, give it a most picturesque appearance.'

The principal aims of this paper are: (1) to describe the morphology of *Chiplonkarina*; (2) to establish its taxonomic affinities as a 'malacostegan' cheilostome and its striking homeomorphy with cerioporine cyclostomes (and other dendroid stenolaemates); and (3) to discuss aspects of its growth and functional morphology. Firstly, however, opportunity is taken to summarize aspects of the geology and palaeontology of the Bagh Group of west-central India because almost all of the literature on this important succession has been published in Indian journals which may not be easily accessible elsewhere.

GEOLOGICAL SETTING OF THE BAGH GROUP

The Bagh Group was deposited in the Narmada Basin (Trough), an intracratonic trough trending roughly west-east and following the line of the present-day Narmada River in Gujarat and Madhya Pradesh, west-central India (Acharyya and Lahiri 1991). The deposits are exposed in a series of small isolated outcrops (Text-fig. 1), mostly in river valleys to the north of the Narmada River, where erosion has cut through the overlying Lameta Formation and basalts of the Deccan Traps. These exposures extend over a total distance of about 275 km from Barwaha (Barwai) in the east to Naswadi in the west (Ahmad and Akhtar 1990). The outcrop in the Man River Valley near Manawar in Madhya Pradesh reveals the most complete and fossiliferous succession of the Bagh Group (Text-fig. 1B), although the thickest development occurs further west near Rajpipla in Gujarat. The Bagh Group is thought to be the product of a short-lived, eastwards marine transgression by an arm of the Tethys (Chiplonkar and Badve 1973; Jafar 1982). The deposits rest either with strong unconformity on the Precambrian or without obvious break on non-marine Upper Gondwana Group sediments.

Lithostratigraphy

The large amount of literature on the lithostratigraphy of the Bagh Group chronicles considerable discord between different research schools (summarized by Verma 1969; Guha 1976; Chiplonkar, Badve and Ghare 1977). For example, some authors have excluded the lowermost unit (Nimar Sandstone) from the Bagh Group (e.g. Dassarma and Sinha 1975; Singh and Srivastava 1981; Ahmad and Akhtar 1990), while others have used different names for stratigraphical units exposed in the western and eastern parts of the Narmada Valley (e.g. Poddar 1964; Dassarma and Sinha 1975). The main features of the Bagh Group succession were first established by Blanford (1869, p. 48) who described a section at Chirakhan in the Man River Valley as follows:

Coralline limestone	10 to 20 feet [c. 3–6 m]
Fossiliferous argillaceous limestone abounding in echinoderms (<i>Hemiaster</i>)	about 10 feet [c. 3 m]
Unfossiliferous nodular limestone	20 feet [c. 6 m]
Sandstone and conglomerate	20 feet [c. 6 m]

Bose (1884) provided a more formal nomenclature when naming the four successive units Nimar Sandstone, Nodular Limestone, Deola-Chirakhan Marl and Coralline Limestone, a scheme retained in essence by Chiplonkar and co-workers (e.g. Chiplonkar, Badve and Ghare 1977). However, alternative names for these four units have proliferated during the past few decades. For example, in the most recent revision of Bagh Group stratigraphy, Ramasamy and Madhavaraju (1993) distinguished three formations: Nimar Sandstone, Karondia Limestone, and Bryozoan Limestone. The Karondia Limestone Formation was originally proposed by Guha (1976) to replace the Nodular Limestone of earlier authors. The Bryozoan Limestone Formation is equivalent to the Barwaha Bryozoan Limestone of Pal (1971), the Chirakhan Limestone Formation of Guha (1976), and the Deola-Chirakhan Marl plus Coralline Limestone of older usage. Some authors (Roy Chowdhury and Sastri 1962; Sahni and Jain 1966) have interpreted the Deola-Chirakhan Marl as a weathering product of the harder limestone but this view is mistaken, as is clear from the differences in faunas between the marl and limestone. There is utility in distinguishing between the marly facies of the Deola-Chirakhan Marl and the typically cross-bedded limestones of the Coralline Limestone (see Chiplonkar, Badve and Ghare 1977) capped by an oyster bed (Chiplonkar and Badve 1980) in the classical sections along the Man River Valley. We therefore recognize these units as separate members of the Chirakhan Limestone Formation (Text-fig. 1B), as did Singh and Srivastava (1981) (the term Barwaha Bryozoan Limestone of Pal (1971) is inappropriate as this unit does not occur in the vicinity of Barwaha). The Nimar Sandstone and Nodular Limestone are retained as formations for the older units because these names are unambiguous and have been widely known since the work of Bose (1884).

The stratigraphical relationship between the Bagh Group and the overlying Lameta Formation, continental deposits with dinosaurian fossils (e.g. Brookfield and Sahni 1987; Mohabey *et al.* 1993), is generally regarded as unconformable, although Raiverman (1975) has suggested that the Bagh Group and Lameta Formation intercalate, and Jafar (1982) believed that they represented facies deposited synchronously.

Age

The age of the Bagh Group has been a matter of contention, with individual units having been assigned ages ranging from Valanginian to Palaeocene. Although present in reasonable numbers, ammonites in the Bagh Group are mostly poorly preserved steinkerns. The twenty-three named Bagh Group ammonite species point to a Cenomanian or Turonian age (Chiplonkar, Ghare and Badve 1977). The potentially informative inoceramids (of which forty-four nominal species have been distinguished; see Dassarma and Sinha 1975; Chiplonkar and Badve 1976*a*, 1976*b*) are in need of critical comparison with European species of known ages. The echinoid fauna, including *Mecaster meslei* (Peron and Gauthier) which first appears elsewhere in the mid Cenomanian, suggests a mid or late Cenomanian age (A. B. Smith, pers. comm. 1991). Jafar (1982) argued, on the basis of nannofossils, for a late Turonian age (*Eifellithus eximius* Zone) for the entire Bagh Group together with the overlying Lameta Formation. However, the diagnostic coccolith species is difficult to distinguish (J. R. Young, pers. comm. 1993), and some doubt exists over Jafar's age estimate.

Overall consideration of the biostratigraphical data points to a Cenomanian–Turonian age for the Bagh Group, possibly with parts of the Nimar Sandstone at the base of the sequence being Late Albian (Chiplonkar, Ghare and Badve 1977). However, the Nimar Sandstone, as commonly interpreted, is a heterogeneous unit: whereas the upper, more calcareous horizons are marine shallow shelf deposits (Bose and Das 1986) containing marine fossils similar or identical to those found in the overlying limestones, lower levels are fluvial/estuarine (Ahmad and Akhtar 1990), contain plant fossils of Upper Gondwanan affinities, and may be significantly older, perhaps Neocomian (Murty *et al.* 1963; Badve and Ghare 1977; Chiplonkar, Ghare and Badve 1977). Reflecting this upward change towards more marine facies with marine trace fossils, an oyster bed, and a *Jhabotrigonia-Turritella* Bed (Badve and Nayak 1984*a*), the upper part of the Nimar Sandstone, is sometimes recognizable as a separate unit (e.g. Sahni and Jain 1966) called the Amlipura Oyster Bed by Murty *et al.* (1963).

Depositional environment

Bose and Das (1986) interpreted the Nimar Sandstone as a transgressive wave-dominated sequence with upwards fining reflecting deepening of the basin. They regarded the succeeding Nodular Limestone as having been deposited below wave base. Unfortunately, the sedimentology of the carbonate-dominated, fossiliferous upper parts of the Bagh Group has never been studied in detail. The environment of deposition is best simply stated as shallow marine until the necessary research has been undertaken. Guha and Ghosh (1970) inferred a depositional depth of about 20 m on the basis of the bryozoan growth-forms present.

Hardgrounds within the sequence provide evidence of hiatuses in deposition and lithification of the sea-bed. They have been identified at three horizons: (1) at the top of the calcareous Nimar Sandstone at Mahakal, oysters and *Chiplonkarina* colonies are cemented to a hardground; (2) within the Nodular Limestone at Khod-Chikhali, a glauconitized hardground is bored by *Trypanites*; and (3) at the top of the Nodular Limestone at Zirabad, a hardground is bored by truncated *Gastrochaenolites* and encrusted by *Chiplonkarina* and oysters. Nodularity elsewhere in the sequence is suggestive of incipient cementation. From a biological perspective, this early lithification may have been important in creating hard substrates for colonization by epifaunal communities, including animals with hard skeletons whose remains would then have acted as further substrates ('taphonomic facilitation').

Palaeogeographically, the Narmada Valley was probably about 30–40 °S of the palaeoequator during the Cenomanian (e.g. Barron *et al.* 1981; Funnell 1990; Smith *et al.* 1994), although some reconstructions place it within the tropics (e.g. Howarth 1981; Badve and Nayak 1983).

Biota

The rich biotas of the Bagh Group have been described in numerous publications, including general accounts by Chiplonkar and Badve (1973), Dassarma and Sinha (1975), Badve and Ghare (1977) and Chiplonkar, Ghare and Badve (1977). Marine fossils occur abundantly in all units from the upper part of the Nimar Sandstone through to the Chirakhan Limestone. They are particularly numerous and show the best preservation in the Deola-Chirakhan Marl Member in the Man River Valley. Fossils from the higher energy deposits characterizing much of the upper parts of the Nimar Sandstone and the Coralline Limestone Member are typically broken and abraded to varying degrees. Bagh Group body fossils consist predominantly of bivalves (see Dassarma and Sinha 1975; Nayak and Badve 1985 and references therein), gastropods (Chiplonkar and Badve 1972*b*), echinoids (Chiplonkar and Badve 1972*a*), ammonites (see Chiplonkar and Ghare 1977; Ghare 1987 and references therein), bryozoans (see Taylor and Badve 1994 and references therein) and algae (Badve and Nayak 1983, 1984*b*), together with the brachiopod *Malwirhynchia* (Chiplonkar 1938), serpulid worms (Chiplonkar and Ghare 1976*b*), foraminifera (e.g. Rajsheker 1991) and occasional fish teeth (Chiplonkar and Ghare 1974). Burrows and trails are also recorded (Chiplonkar and Badve 1970; Chiplonkar and Ghare 1975; Badve and Ghare 1980), particularly from near the top of the Nimar Sandstone.

SYSTEMATIC PALAEONTOLOGY

Repository abbreviations. BMNH, The Natural History Museum, London; MACS, Agharkar Research Institute of the Maharashtra Association for the Cultivation of Science, Pune, India; VH, Voigt Collection, Universität Hamburg, Germany.

Order CHEILOSTOMATA Busk, 1852
 Suborder MALACOSTEGINA Levinsen, 1902
 Family ELECTRIDAE Stach, 1937
 Genus CHIPLONKARINA gen. nov.

Type species. *Chiplonkarina dimorphopora* (Chiplonkar, 1939), Cenomanian/Turonian, Bagh Group, Madhya Pradesh and Gujarat, India; Cenomanian of Sarthe and Charente Maritime, France; Turonian-?Coniacian of Turkmenistan, Uzbekistan and Tadzhikistan, FSU.

Other species. *Chiplonkarina bretoni* sp. nov., Lower Cenomanian of Calvados, France and Westphalia, Germany.

Derivation of name. After the late Professor G. W. Chiplotkar (1907–1991), an authority on the Indian Cretaceous (for an obituary, see Badve and Borkar 1991), and author of the type species of this new genus.

Diagnosis. Colony developing erect, subcylindrical, bifurcating branches from an extensive encrusting base; early astogeny unknown; erect branches with a narrow, thin-walled endozone surrounded by a thick-walled exozone; zooidal budding concentrated in the endozone; interzooidal walls compound, with the median zooidal boundary being crenulated and often brown in the exozone, interpreted as intercalary cuticle, flanked by a fibrous layer with fibres intersecting the wall surface at about 45°, and occasionally covered by a thinner indistinctly lamellar layer forming a zooecial lining; autozooids long and tubular, oriented parallel to branch growth direction in the endozone, bending through approximately 90° into the exozone to become perpendicular to the branch surface; gymnocyst lacking; cryptocyst narrow, pustulose, not shelf-like but forming a rim continuous with the more proximal parts of the vertical interzooidal walls; opesia ovoidal, sometimes slightly constricted medially or inverted pear-shaped, occupying a large proportion of the frontal area of the zooid; kenozooids common, irregularly distributed between autozooids, with which they are connected via tunnel-like pores; ovicells and avicularia not observed, presumed absent; pore chambers apparently absent.

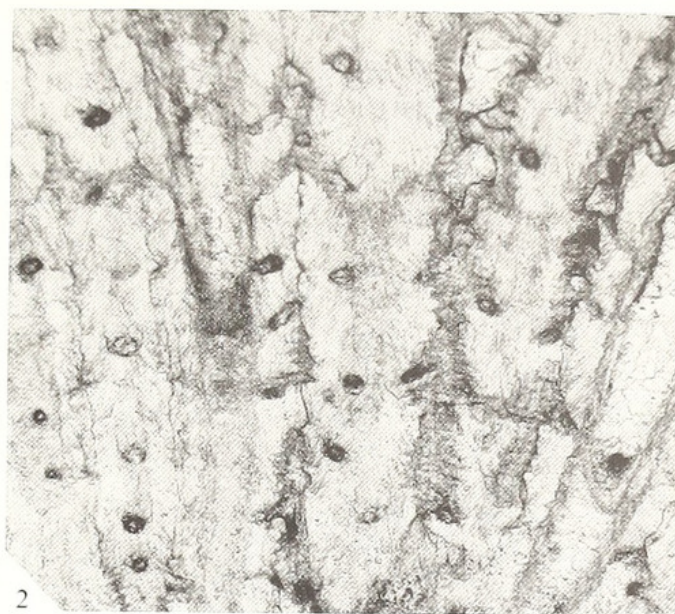
Remarks. Reasons for assigning *Chiplonkarina* to the malacostegan cheilostomes are given below (p. 649). Superficially, the new genus most closely resembles cerioporine cyclostomes such as *Ceriopora*, *Ceriocava* and *Heteropora* (see Nye 1976), and the Cretaceous cheilostome *Inversaria* (see Voigt and Williams 1973). In thin section, it can be distinguished from cerioporines by the fibrous microstructure of the walls, compared with the lamellar walls of cerioporines, and more particularly by the presence of a crenulated, typically brown layer (interpreted as the remnants of intercalary cuticle; see p. 646) running along the middle of the interzooidal walls. The large larval brood chambers characteristic of cerioporines, are lacking in *Chiplonkarina*. *Inversaria* has exozonal walls with ring diaphragms, calcified cap-like opercula and occasional avicularia, all of which are features not found in *Chiplonkarina*. Fractured interzooidal walls in *Inversaria* show

EXPLANATION OF PLATE 1

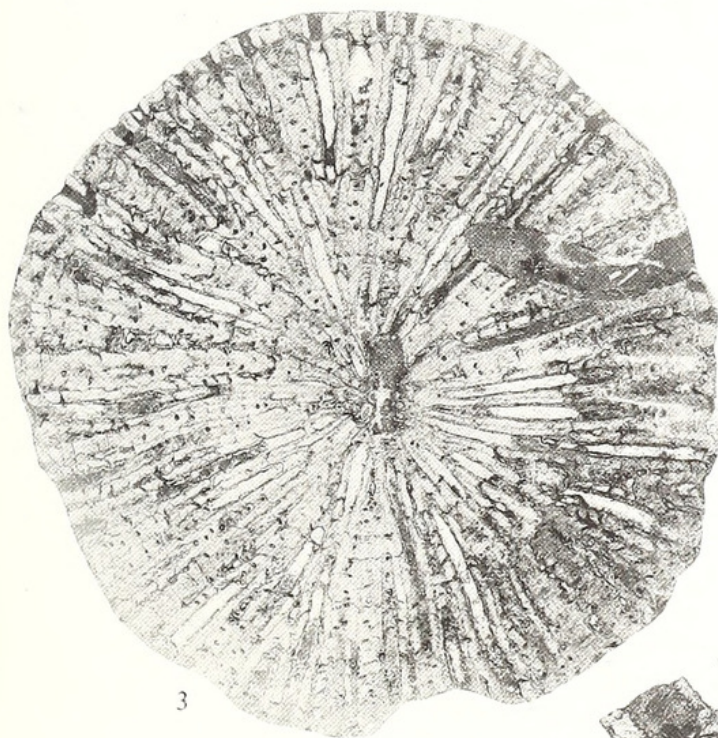
Figs 1–5. *Chiplonkarina dimorphopora* (Chiplonkar); thin sections photographed in plane polarized light. 1, BMNH D59430 \$1; Chirakhan Limestone Formation, Coralline Limestone Member, Badia-Chakrod section, Man River Valley, Madhya Pradesh, India; rock sample crowded with branches including one containing the bivalve boring *Gastrochaenolites* (arrowed); $\times 14$. 2–3, BMNH D59436 \$1; Chirakhan Limestone Formation, Deola-Chirakhan Marl Member, Sitapuri, Madhya Pradesh, India; 2, exozonal walls with interzooidal pores; $\times 75$; 3, transverse section of thick branch; $\times 15$. 4, BMNH BZ87 \$1; Upper Cenomanian; Port-des-Barques, Charente Maritime, France; tangential section through thick-walled exozonal zooids with zooecial lining layers; $\times 48$. 5, BMNH BZ 2477 \$2; Lower Cenomanian (*saxbii/orbigny* zones), Sables et Grès de Lamnay, Lamnay, Sarthe, France; beginnings of erect growth from an encrusting colony base; $\times 33$.



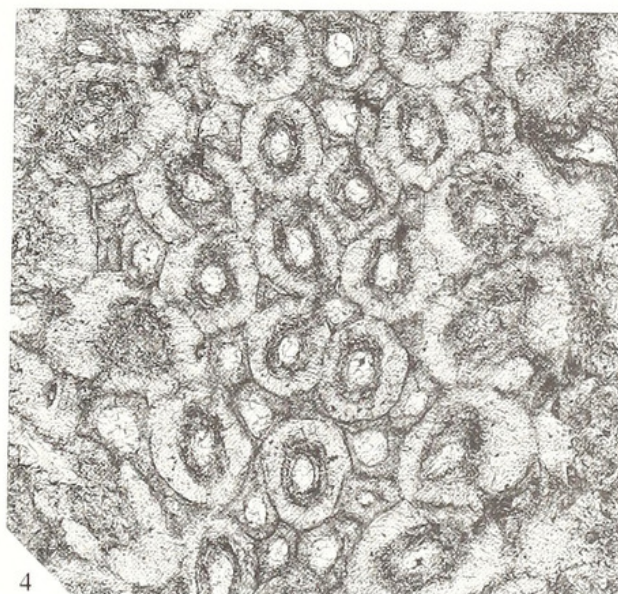
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median corrugations, suggestive of an intercalary cuticle, but the folds parallel wall growth direction (Voigt and Williams 1973, pl. 2, figs 2–3) whereas those in *Chiplonkarina* are perpendicular. An undescribed genus from the Albian–Cenomanian of southern England resembles *Chiplonkarina* in having stenolaemate-like branches with endozones and exozones, but the exozone comprises short, stacked, box-shaped zooids and not the long, tubular zooids found in *Chiplonkarina*. *Heteroconopeum* Voigt, 1983 from the Turonian has erect branching colonies and zooids somewhat similar in external appearance (Pl. 3, fig. 5) to those of *Chiplonkarina*. However, branch interiors consist of large polymorphic zooids which are overgrown by multilamellar files of autozooids visible on branch surfaces.

Although generally uncommon in the European Cretaceous, *Chiplonkarina* occurs in sufficient abundance in some well-known French localities (notably around Le Mans) to make it somewhat surprising that the genus has not been previously recognized. Examination of the nineteenth century literature reveals only one possible example of *Chiplonkarina*: a species described from Le Mans (Cenomanian) and Grandpré (Albian) by Michelin (1841–48, p. 209, pl. 51, fig. 8a–b) as *Heteropora surculacea*. Reasons for believing that *H. surculacea* may belong to *Chiplonkarina* are the occurrence of widely varying branch diameters in one colony, and the ovoidal shapes of the zooidal apertures. The species was not considered by Walter (1975) when he redescribed the type material of Michelin's Albian and Cenomanian bryozoan species, nor was any material seen during a visit by one of us (PDT) to the MNHM in Paris during 1985. In the absence of Michelin's specimens (and of reliable topotypes), it is impossible to be certain about the affinities of *H. surculacea*.

Distribution. Cenomanian–Turonian (?Coniacian) of west-central India, Turkmenistan, Uzbekistan, Tadzhikistan and north-western Europe.

Chiplonkarina dimorphopora (Chiplonkar, 1939)

Plate 1; Plate 2, figures 1, 3, 5–6; Plate 3, figures 1–4; Plate 4, figure 4; Text-figures 2, 5

- ?1884 *Ceriopora dispar* Stoliczka; Bose, pp. 37, 40, 43.
- 1939 *Ceriopora dimorphopora* Chiplonkar, p. 100, pl. 3, fig. 5; pl. 4, figs 2–3.
- 1939 *Ceriopora conoformis* Chiplonkar, p. 100, pl. 3, fig. 3; pl. 4, figs 1, 5.
- 1939 *Ceriopora ellipsopora* Chiplonkar, p. 101, pl. 3, fig. 6; pl. 4, fig. 4.
- 1939 *Ceriocava micropora* Chiplonkar, p. 102, pl. 3, fig. 1.
- ?1967 *Laterocavea*; Tewari and Kumar, p. 37, pl. 3, figs 1, 4–6.
- ?1969 *Ceriopora dispar* Stoliczka; Verma, p. 46.
- ?1969 *Grammanotosoecia talensis* Kumar and Tewari, p. 221 [nomen nudum].
- 1974 *Ceriopora ellipsopora* Chiplonkar; Chiplonkar and Borkar, p. 36.
- 1974 *Ceriopora mamillaria* Chiplonkar and Borkar, p. 36, pl. 1, figs 1–3.
- 1974 *Ceriopora dimorphopora* Chiplonkar; Chiplonkar and Borkar, p. 37.
- ?1974 *Reptomulticava coquandi* d'Orbigny; Chiplonkar and Borkar, p. 37.
- 1974 *Tretocycloecia robusta* Chiplonkar and Borkar, p. 37, pl. 1, figs 4–6.
- 1974 *Ceriocava bhadukaensis* Chiplonkar and Borkar, p. 38, pl. 1, figs 7–9.
- 1974 *Ceriocava grandipora* Canu and Bassler; Chiplonkar and Borkar, p. 38.
- 1974 *Ceriocava micropora* Chiplonkar; Chiplonkar and Borkar, p. 39.
- 1974 *Ceriocava subramulosa* Chiplonkar and Borkar, p. 39, pl. 1, figs 10–12.
- 1974 *Semicea recta* (d'Orbigny); Chiplonkar and Borkar, p. 39.
- 1975 *Ceriopora dimorphopora* Chiplonkar; Guha and Ghose, fig. 2a.
- 1976a *Ceriopora dimorphopora* Chiplonkar; Chiplonkar and Ghare, p. 61, pl. 5, fig. 4.
- 1976a *Tretocycloecia robusta* Chiplonkar and Borkar; Chiplonkar and Ghare, p. 61, pl. 5, fig. 12.
- 1976a *Ceriocava grandipora* Canu and Bassler; Chiplonkar and Ghare, p. 61, pl. 5, fig. 10.
- 1976a *Ceriocava micropora* Chiplonkar; Chiplonkar and Ghare, p. 61, pl. 5, fig. 5.
- 1976a *Ceriocava subramulosa* Chiplonkar and Borkar; Chiplonkar and Ghare, p. 62, pl. 5, fig. 2.
- 1976a *Lateroeceia tapaswii* Chiplonkar and Ghare, p. 62, pl. 5, figs 7–9.
- ?1977 cerioporids; Mathur, p. 25, fig. 2A–E.
- 1980 *Ceriopora dimorphopora* Chiplonkar; Guha, p. 30, pl. 1, figs 2–8, text-fig. 1b.
- 1980 *Ceriocava nilkanthi* P. Singh, p. 260, figs 28–36.



TEXT-FIG. 2. *Chiplonkarina dimorphopora* (Chiplonkar). Cenomanian/Turonian, Bagh Group, Chirakhan Limestone Formation, Deola-Chirakhan Marl Member, Madhya Pradesh, India. Photographs showing variation in branch diameter. A, thickly branched colony giving rise to a single narrow branch (upper left); BMNH BZ2457; Badia-Chakrod section; $\times 3.2$. B–G, range of thick to thin branches from one locality; B, BMNH D59418; C, BMNH D59420; D, BMNH D59421; E, BMNH D59422; F, BMNH D59423; G, BMNH D59424; quarry west of Badia; $\times 1.6$.

- ?1985 *Ascopora* sp., Mathur, p. FM70, figs 1–4.
- ?1985 *Ceriocava nilkanthi* P. Singh, Raiverman and P. Singh, p. FM15, fig. 2e–f.
- 1988 *Ceriocava nilkanthi* P. Singh; P. Singh, p. 103, pl. 1, figs 6–8.
- 1988 *Ceriocava nilkanthi* P. Singh; P. Singh and K. I. Singh, p. 78, pl. 2, figs 6–8.
- 1990 *Ceriocava nilkanthi* P. Singh; V. Singh, p. 30, pl. 3, fig. 5 only, pl. 5, fig. 4.
- 1990 *Diplocava* sp., V. Singh, p. 30, pl. 3, fig. 3 only, pl. 5, fig. 3.
- 1994 '*Ceriopora*' *dimorphopora* Chiplonkar; Taylor and Badve, p. 181, fig. 2A, E–G.

Type. Chiplonkar (1939, pl. 3, fig. 5) figured as the holotype of this species specimen number B. H. U. No. B/2 in the collections of the Department of Geology of the Benares Hindu University. As this holotype and other material of *C. dimorphopora* was claimed to be lost, Chiplonkar and Ghare (1976a, p. 61) proposed as neotype specimen No. Gun. 27 in the collections of the Department of Geology at the Agharkar [formerly Maharashtra

Association for the Cultivation of Science (MACS)] Research Institute (ARI), Pune. Unfortunately, Chiplonkar and Ghare's neotype could not be located during February 1991, and has been missing from the ARI collections since 1976. Guha (1980, p. 33), apparently unaware of the paper by Chiplonkar and Ghare (1976a), which he does not cite, subsequently proposed another neotype, 'No. AKG/BRT/H93' in the collections of the Department of Geology and Geophysics, IIT, Kharagpur. Under Article 75 (e) of the Rules of Zoological Nomenclature, Guha's neotype designation is invalid and his specimen cannot replace the lost neotype (J. D. D. Smith, pers. comm. October 1991). Therefore, *C. dimorphopora* lacks a valid type specimen but, as the identity of the species seems uncontentious, it is considered unnecessary to designate yet another neotype.

Material. Cenomanian/Turonian Bagh Group, Madhya Pradesh and Gujarat, India. MACS Wal/1 (figured as *Ceriocava grandipora* Canu and Bassler, 1920 by Chiplonkar and Ghare 1976a, pl. 5, fig. 10), Nodular Limestone, Walpur. Gun/1 (figured as *Tretocycloecia robusta* Chiplonkar and Borkar, 1974 by Chiplonkar and Ghare 1976a, pl. 5, fig. 12), Nodular Limestone, Guneri. Kh 26/69 (figured as *Ceriocava subramulosa* Chiplonkar and Borkar, 1974 by Chiplonkar and Ghare 1976a, pl. 5, fig. 2), oyster bed near top of Nimar Sandstone, Khadlu. BW 49/2 (holotype of *Lateroecea tapaswii* Chiplonkar and Ghare, 1976a) and BW 49/3 (paratype of *Lateroecea tapaswii* Chiplonkar and Ghare, 1976a), Chirakhan Limestone, Deola-Chirakhan Marl Member, Barwaha.

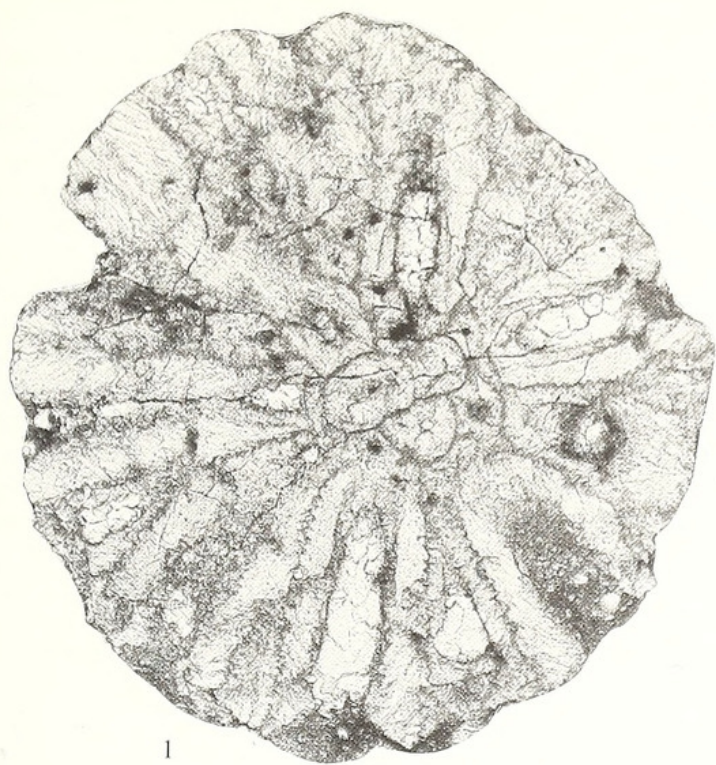
BMNH D59398, D59418–24, BZ 2438–41, BZ 2442 (sample), BZ 2443–4 (thin sections of colony-bases), BZ 2445, BZ 2628 (polished and etched specimen on SEM stub), Chirakhan Limestone, Deola-Chirakhan Marl Member, quarry west of Badia, Man River Valley, Madhya Pradesh. D59399, BZ 2446–51, BZ 2452 (sample), top of Nimar Sandstone, Bilthama, Bharuch District, Gujarat. D59397, D59430 (bryozoan-rich limestone with 2 thin sections), BZ 2453–5, BZ 2456 (sample), BZ 2457, Chirakhan Limestone, Coralline Limestone Member, Badia-Chakrod section, Man River Valley, Madhya Pradesh. D59431 (bryozoan-rich limestone with one thin section), Chirakhan Limestone, Coralline Limestone Member, Hatni River section, Jhabua District, Madhya Pradesh. BZ 2458–9 (samples), Chirakhan Limestone, Deola-Chirakhan Marl Member, Hatni River section, Jhabua District, Madhya Pradesh. BZ 2460, base of Nodular Limestone, Hatni River section, Jhabua District, Madhya Pradesh. D59433 (two thin sections), D59434 (two thin sections), D59435 (two thin sections), D59436 (two thin sections), D59437 (two thin sections), BZ 2461 (thin section of colony base), BZ 2462 (sample), Chirakhan Limestone, Deola-Chirakhan Marl Member, Sitapura, Man River Valley, Madhya Pradesh. BZ 2463, Nodular Limestone, Bhorgat, Man River Valley, Madhya Pradesh. BZ 2464, Chirakhan Limestone, Deola-Chirakhan Marl Member, Chirakhan, Man River Valley, Madhya Pradesh. BZ 2465–7, 2468 (three specimens), Nimar Sandstone, Kholar River section, Barwaha, Madhya Pradesh. BZ 2469 (sample), BZ 2470–2, top of Nimar Sandstone, Pipaldehla, Jhabua District, Madhya Pradesh. BZ 2473 (sample), base of Nodular Limestone, Mahakal, near Bagh Town, Madhya Pradesh. D59432 (rock with thin section), BZ 2474–6, top of Nimar Sandstone, Agarwara, Barwaha, Madhya Pradesh.

Cenomanian/Turonian Wadhwan Formation, oyster bed at top of Bhaduka Limestone Member, Bhaduka, Gujarat, India. MACS Br 1 (identified as *Ceripora dimorphopora* Chiplonkar by Chiplonkar and Borkar 1974), Br 2 (holotype of *Ceripora mamillaria* Chiplonkar and Borkar, 1974), Br 3 (identified as *Ceripora ellipsopora* Chiplonkar by Chiplonkar and Borkar 1974), Br 4 (questionably assigned to *Chiplonkarina dimorphopora*; identified as *Reptomulticava coquandi* d'Orbigny by Chiplonkar and Borkar 1974), Br 5

EXPLANATION OF PLATE 2

Figs 1, 3, 5–6. *Chiplonkarina dimorphopora* (Chiplonkar). 1, 3, 5, Chirakhan Limestone Formation, Deola-Chirakhan Marl Member, Sitapuri, Madhya Pradesh, India; 1, BMNH D59433 \$1, transverse section through a thin branch (cf. Pl. 1, fig. 3); $\times 75$; 3, BMNH D59434 \$1, endozone (lower left) and inner exozone of a transversely sectioned branch showing corrugated inferred remnants of intercalary cuticle and fibrous wall microstructure; $\times 180$; 5, BMNH D59433 \$2, tangential section; $\times 22$. 6, BMNH D59397; Chirakhan Limestone Formation, Deola-Chirakhan Limestone Member; Badia-Chakrod section, Madhya Pradesh, India; photograph of well preserved branch bifurcating at its distal end; $\times 3.2$.

Figs 2, 4. *Chiplonkarina bretoni* sp. nov.; Lower Cenomanian; Carrière du Billot, Notre Dame le Fresnaye, Normandy, France. 2, VH 10565; transverse section; $\times 50$. 4, VH 10572; longitudinal section; $\times 15$. Thin sections photographed in plane polarized light.

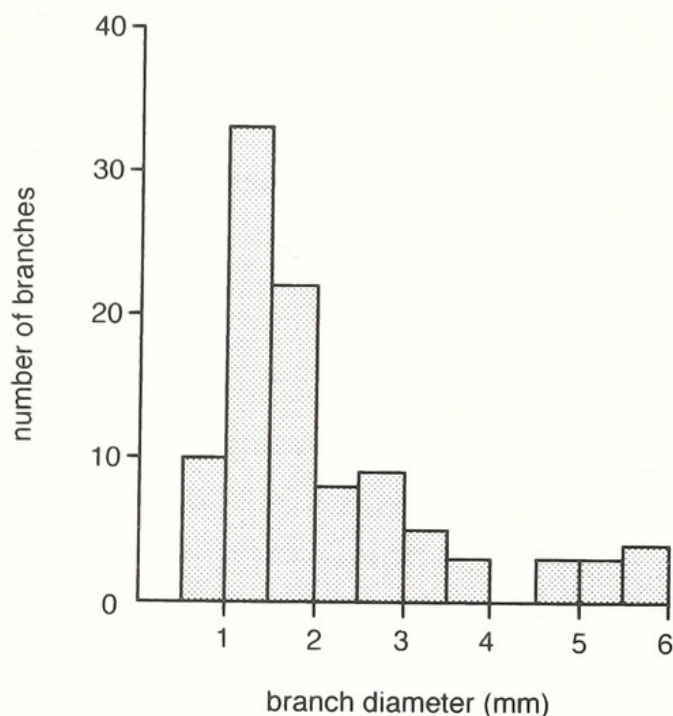


(holotype of *Tretocycloecia robusta* Chiplonkar and Borkar, 1974), Br 6 (holotype of *Ceriocava bhadukaensis* Chiplonkar and Borkar, 1974), Br 7 (identified as *Ceriocava grandipora* Canu and Bassler by Chiplonkar and Borkar 1974), Br 8 (identified as *Ceriocava micropora* Chiplonkar by Chiplonkar and Borkar 1974), Br 9 (holotype of *Ceriocava subramulosa* Chiplonkar and Borkar, 1974), Br 10 (identified as *Semicea recta* d'Orbigny by Chiplonkar and Borkar 1974).

French Cenomanian. BMNH D59401–4, Cenomanian (?Middle), ?Sables du Mans, Le Gasonfier, Le Mans, Sarthe. BZ 2696, Cenomanian, Le Mans. D58966, BZ 2697, Upper Cenomanian, Sables du Perche, Gr  ez sur Roc, Sarthe. BZ 2477 (two thin sections), Lower Cenomanian (*saxbii/orbigny* zones), Sables et Gr  s de Lamnay, Lamnay, Sarthe. BZ85–6, 87 (two thin sections), 88–9, Upper Cenomanian, Bed G (of Moreau 1976), Port des Barques, near Rochefort, Charente Maritime.

Diagnosis. *Chiplonkarina* with branches of widely varying diameters; autozooids with ovoidal opesia, narrow cryptocysts and apparent polarities that are often neither parallel to branch growth direction nor to the polarities of nearby autozooids; kenozooids numerous, especially in thick branches, intercalated between autozooids.

Description. Colony either entirely encrusting, sometimes with a hummocky surface, or more often becoming erect with cylindrical bifurcating branches of highly variable diameter (0.7–11 mm) (Text-figs 2B–G, 3).



TEXT-FIG. 3. Histogram of branch diameter in a sample of one hundred specimens of *Chiplonkarina dimorphopora* (Chiplonkar) collected from the Deola-Chirakhan Marl Member (Bagh Group) of Sitapuri, Madhya Pradesh, India. Note the wide but more or less continuous variation present in this sample.

Encrusting base often extensive, sometimes tubular (cavariiform) as a result of growth around an unpreserved substrate. More than one erect branch may arise from the encrusting base (Pl. 1, fig. 5). Secondary, lateral branches of small diameter often developed, diverging at approximately 90° from the exozone of the parent branch (Text-fig. 2A). Branches divided into an inner endozone with zooids orientated approximately parallel to branch growth direction, surrounded by an outer exozone with thicker-walled zooids orientated approximately perpendicular to branch growth direction and intersecting the branch surface at roughly 90° (Pl. 1, fig. 3; Pl. 2, fig. 1). Endozone narrow, varying from 0.24–0.53 mm in diameter. Exozone broad, accounting for most of the branch diameter, and highly variable in diameter. Wall thickness up to 0.05 mm in the endozone, 0.10–0.25 mm in the exozone. New zooids originate as interzooidal buds, initially triangular and located at triple junctions between existing zooids. Budding occurs in both the endozone and exozone. Distal branch growing tips not observed with certainty, but transversely fractured branches sometimes split along dome-shaped planes in the endozone which may represent former growing tips.

Interzooidal walls compound, interpreted as two exterior walls back-to-back. Median layer of interzooidal walls crenulated in exozone (Pl. 2, fig. 3; Pl. 4, fig. 4; Text-fig. 5), often with a brown deposit; crenulations perpendicular to wall growth direction, with a wavelength of 0.015–0.020 mm. Interzooidal wall microstructure

predominantly fibrous (Pl. 2, fig. 3), the fibres diverging from the crenulations and intersecting the wall surface at about 45°, giving the compound wall a chevron fabric when sectioned longitudinally. Lamellar zooecial lining up to 0.03 mm thick sometimes covering fibrous layer (Pl. 1, fig. 4). Secondary fibrous lining, found in a very few zooids, may represent intramural budding ('regeneration'). Pores (Pl. 1, fig. 2) present in interzooidal walls between autozooids and kenozooids (?lacking in walls between adjacent autozooids), parallel-sided, elongated transversely to wall growth direction, about 0.015–0.030 mm in diameter. Diaphragms very occasionally developed; distinctly U-shaped, concave distally, varying in thickness from 0.01–0.05 mm. Lamellar overgrowths sometimes present, with basal walls 0.015 mm thick giving rise to vertical walls 0.05 mm thick which rapidly attain a 'mature' thickness of 0.10 mm while bending slightly; appreciable endozone lacking in overgrowths.

Autozooids long, club-shaped tubes, moderately thin-walled in the endozone, bending into the exozone and becoming thicker-walled. Endozonal portions of autozooids may exceed 1 mm in length but their full extent and range is impossible to determine. Frontal outline of autozooids (Pl. 3, figs 1–4) on branch surface elliptical, variable in length and width, on average about $1.2 \times$ longer than wide, long axis (?indicating proximal-distal polarity) of variable orientation relative to branch axis in thick branches, but often parallel to axis in thin branches. Opesia occupying most of frontal surface, elliptical, on average about $1.3 \times$ longer than wide, sometimes slightly hourglass-shaped (Pl. 3, fig. 4). No frontal gymnocyst. Cryptocyst narrow, minutely pustulose (Pl. 3, fig. 4), not shelf-like (except in some zooids in lamellar overgrowths) but forming a typically funnel-shaped rim contiguous with the vertical interzooidal walls. Zooidal boundaries slightly grooved (Pl. 3, figs 2, 4). Closure plates and pore chambers not observed, presumed absent.

Kenozooids long, club-shaped tubes, intercalated between autozooids on colony surface. Frontal outline variable, some elliptical, others triangular, rectangular or of a more complex shape with concave sides, smaller than autozooids (Pl. 3, figs 1–4). Cryptocyst and opesia similar in morphology to those of autozooids.

Ovicells and avicularia lacking.

Dimensions (frontal dimensions in millimetres of ten autozooids).

	BMNH D59401 (Sarthe)	BMNH D59397 (Madhya Pradesh)
length	$\bar{x} = 0.24$; SD = 0.018; CV = 7.4; $r = 0.21$ –0.27	$\bar{x} = 0.28$; SD = 0.023; CV = 7.4; $r = 0.24$ –0.30
width	$\bar{x} = 0.20$; SD = 0.017; CV = 8.4; $r = 0.17$ –0.23	$\bar{x} = 0.23$; SD = 0.026; CV = 11; $r = 0.20$ –0.27
opesia length	$\bar{x} = 0.16$; SD = 0.017; CV = 10.8; $r = 0.14$ –0.18	$\bar{x} = 0.18$; SD = 0.016; CV = 8.6; $r = 0.17$ –0.21
opesia width	$\bar{x} = 0.12$; SD = 0.011; CV = 9.1; $r = 0.11$ –0.14	$\bar{x} = 0.14$; SD = 0.013; CV = 8.9; $r = 0.12$ –0.17

Remarks. The long synonymy of this species deserves comment. *Chiplonkarina dimorphopora* has been referred to no fewer than seven different cyclostome bryozoan genera and fourteen species. Confusion over its generic assignment undoubtedly stems from a difficulty in applying generic concepts to Mesozoic bryozoans. The erection of so many different species for *C. dimorphopora* is a result of several factors. First is the high variability in branch diameter. *Lateroecea tapaswii* Chiplonkar and Ghare, 1976a, for example, was established for thin-branched specimens. That this variability is not indicative of the existence of more than one species can be seen from the continuous variation in branch diameter found within sampled 'populations' (Text-fig. 3; see also Text-fig. 2B–G, and compare Pl. 1, fig. 3 with Pl. 2, fig. 1), and the occurrence of thick-branched colonies giving rise to lateral branches of narrow diameter (Text-fig. 2A). Specimens with uneven mamillated surfaces have also been given different species names (e.g. *Ceripora mamillaria* Chiplonkar and Borkar, 1974, *Ceriocava bhadukaensis* Chiplonkar and Borkar, 1974), although all of the mamillations observed fall more within the category of irregular bumps than potentially taxonomically significant, regularly-spaced monticules. The importance of this morphological variability has been accentuated by optimism about the possible stratigraphical value of different

morphotypes present in different units of the Bagh Group (M. A. Ghare, pers. comm. 1991). Erection of new names for occurrences of *C. dimorphopora* in the Wadhwan Formation of western Gujarat and Nilkanth Formation of Uttar Pradesh, and ignorance of previous publications have also led to taxonomic proliferation.

Guha (1980) understood the synonymy of the established species of '*Ceriopora*' from the Bagh Group which were known to him, but seems to have been unaware of the paper of Chiplonkar and Ghare (1976a) on bryozoans from the Bagh Group, and that of Chiplonkar and Borkar (1975) on a similar aged fauna from the Wadhwan Formation of Surendranagar District of western Gujarat. The original description by P. Singh (1980) of *Ceriocava nilkanthi*, a nominate species considered herein to be a junior synonym of *Chiplonkarina dimorphopora*, included material from both the Nilkanth Formation ('upper Tals') and from the Coralline Limestone of the Bagh Group. Singh quoted none of the palaeontological papers on the Bagh Group, and made no comparisons between his new species and established bryozoan species from the Bagh Group.

Specimens from the Upper Cenomanian of Port-des-Barques, Charente Maritime, France show some differences when compared with material from India and Sarthe, France. The Port-des-Barques specimens may develop very thick interzooidal walls (0.25 mm), twice the thickness typically found in *C. dimorphopora*, and the autozooids are somewhat larger: measurements made from a tangential section of BMNH BZ87 revealed zooidal lengths of 0.28–0.36 mm and widths of 0.24–0.28 mm (cf. dimensions given above). In view of the intrapopulational variability found in *C. dimorphopora*, however, these differences are deemed insufficient to justify species distinction without support from an intensive biometrical analysis.

Palaeoecology. Most specimens of *C. dimorphopora* from the Bagh Group consist of cylindrical branches from broken dendroid colonies (Pl. 2, fig. 6; Text-fig. 2). Despite the relatively robust construction of many colonies, it is rare to find specimens preserving more than one branch bifurcation, whereas the original colonies were probably bushy and would have contained a large number of bifurcations. Both mechanical and biological factors probably contributed to colony fragmentation. Many of the thicker branches contain *Gastrochaenolites* (Pl. 1, fig. 1), indicating boring by bivalves, which undoubtedly weakened the colony and promoted fragmentation. At least some of the branch breakage occurred while colonies were still alive: a thick-branched specimen (BMNH BZ 2445) has a fractured proximal end partly covered by a lamellar intracolony overgrowth. For most specimens, however, there is no such evidence for fragmentation during life and post-mortem breakage cannot be ruled out.

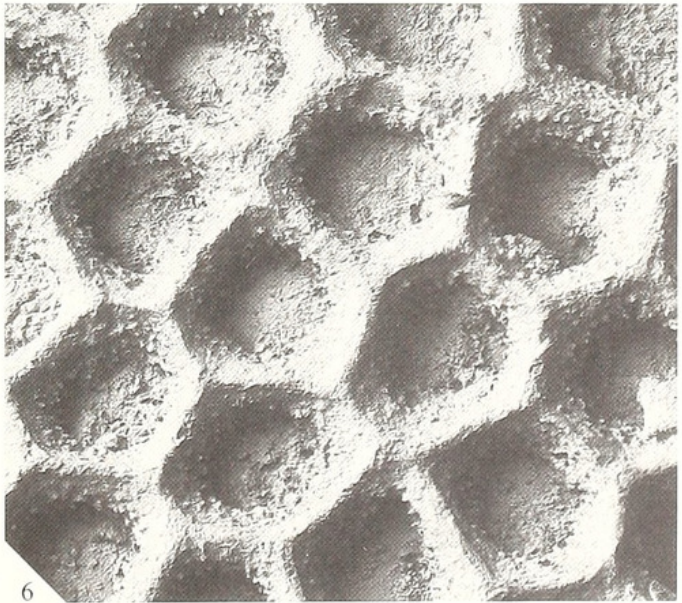
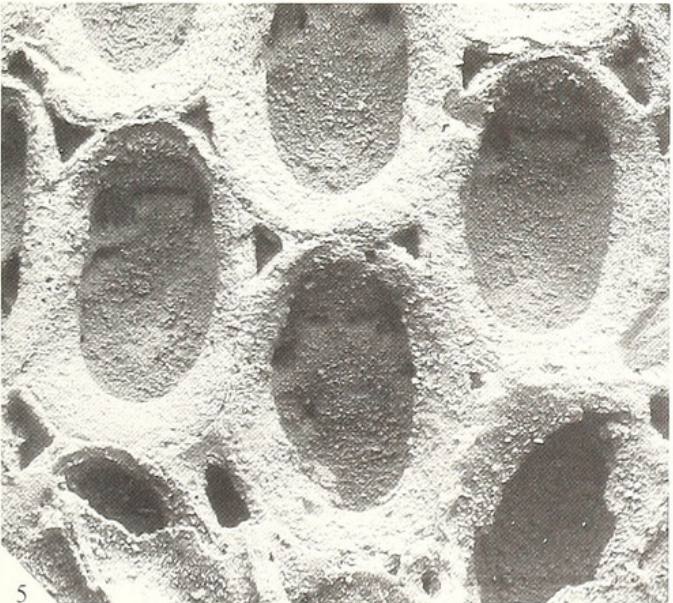
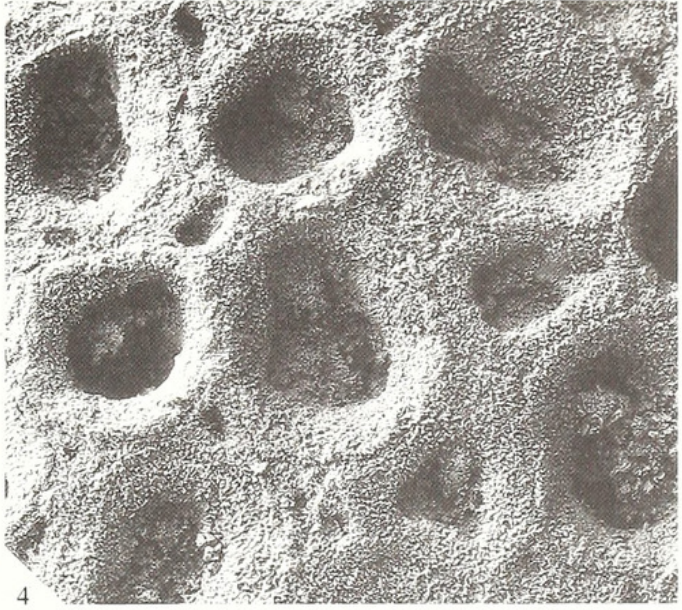
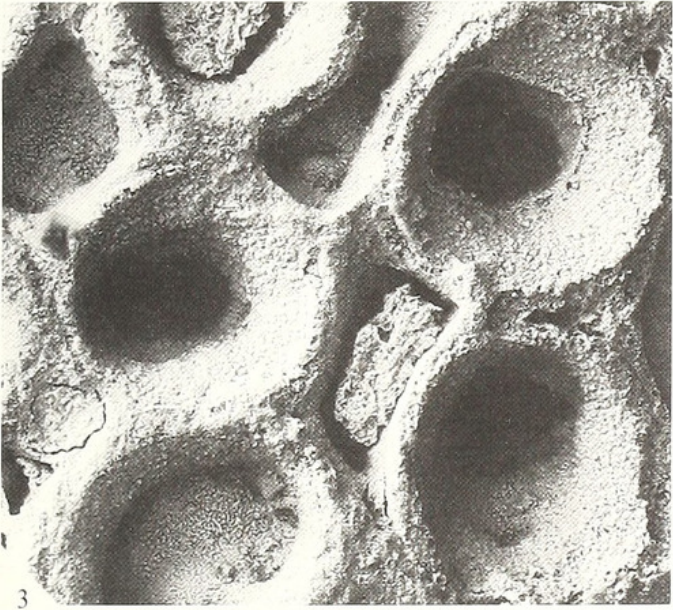
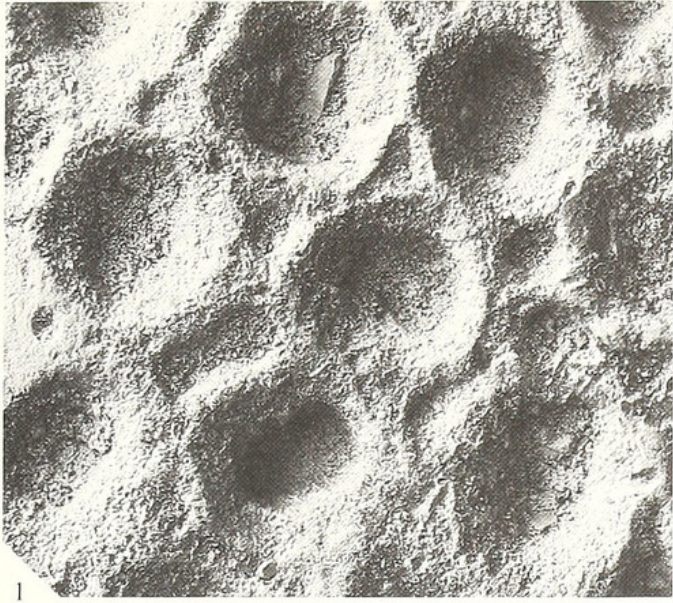
EXPLANATION OF PLATE 3

Figs 1–4. *Chiplonkarina dimorphopora* (Chiplonkar). 1, autozooids and space-filling kenozooids in a relatively well-preserved Indian specimens; BMNH D59397; Chirakhan Limestone Formation, Deola-Chirakhan Limestone Member; Badia-Chakrod section, Madhya Pradesh, India; $\times 80$. 2, typical coarsely-preserved autozooids and occasional kenozooids from a colony base; BMNH D59399; Nimar Sandstone Formation; Bilthama, Gujarat; $\times 80$. 3, autozooids with funnel-shaped 'cryptocysts' and a kenozooid with concave sides (centre) in a French specimen; BMNH D59401; Cenomanian; Le Gasonfier, Le Mans, Sarthe; $\times 135$. 4, French specimen with finely pustulose autozooidal and kenozooidal 'cryptocysts'; BMNH BZ 86; Upper Cenomanian; Port-des-Barques, Charente Maritime, France; $\times 80$.

Fig. 5. *Heteroconopeum janieresiense* (Canu), a 'malacostegan' cheilostome resembling *Chiplonkarina*, showing autozooids with small kenozooids at their corners; BMNH D55536; Turonian; Ruillé-Poncé, France; $\times 100$.

Fig. 6. *Ceriocava corymbosa* Lamouroux, the type species of *Ceriocava*, one of the cerioporine cyclostomes to which *Chiplonkarina dimorphopora* has previously been assigned; note the sharp edges of the interzooidal walls; BMNH D59139; Upper Bathonian; St Aubin-sur-Mer, Normandy, France; $\times 55$.

Scanning electron micrographs of uncoated specimens imaged using back scattered electrons.



Distribution. This species is volumetrically the dominant bryozoan in the Bagh Group (Cenomanian–Turonian, see above) of west-central India and is largely responsible for the term ‘Coralline Limestone’ as applied to the uppermost unit of the Bagh Group where the dendroid branches of *C. dimorphopora* are conspicuous on weathered and polished rock surfaces.

C. dimorphopora also occurs in the oyster bed at the top of the Bhaduka Limestone, the youngest unit of the Wadhwan Formation of the Surendranagar District, Gujarat (Chiplonkar and Borkar 1974). The Wadhwan Formation is regarded as a western lateral equivalent of the Bagh Group, and is thus most likely to be of Cenomanian–Turonian age (Chiplonkar and Borkar 1975).

Material of putative *C. dimorphopora* from the Lesser Himalayas (in the vicinity of Nilkanth on Text-figure 1A) is in need of restudy and the following preliminary remarks are based entirely on descriptions and illustrations from the literature. Mathur (1977) figured thin sections of ‘cerioporid’ bryozoans from the Tal Formation of the Garhwal region of Uttar Pradesh which strongly resemble sections of *C. dimorphopora* from the Bagh Group. His sections depict dendroid colonies with thick zooidal walls that have dark middle layers suggestive of the inferred intercalary cuticle found in *C. dimorphopora* from the Bagh Group. The bryozoans described by Mathur were said to be abundant in his Member 3 of the Tal Formation, including the so-called Singtali Formation (Mehrotra *et al.* 1976). There has been considerable debate about the age of the upper parts of the Tal Formation, with one school favouring a Permian and another a post-Palaeozoic (Jurassic–Early Palaeocene) age. The younger age assignment is based on records of various macrofossils (including belemnites) and microfossils, whereas apparent Permian algae, fusulines etc seemingly provide contradictory evidence. I. B. Singh (1981) reviewed the confusion over the age of the Tal Formation and made a clear distinction between older Tal Formation deposits, which are about 2000 metres thick and unfossiliferous, and the overlying Shell Limestone of the Mussoorie–Garhwal area, which is only thirty metres thick (see also Saxena 1985). The Shell Limestone was renamed the Nilkanth Formation by I. B. Singh (1979), although Bhatia (1985) argued that the Shell Limestone constitutes the Tal Formation *sensu stricto* and that, if anything, it is the thick underlying sequence which requires a substitute name. The Nilkanth Formation is interpreted as a high energy carbonate sand bar/shoal complex deposited in a shallow tidal sea (I. B. Singh 1979). It was formed during a marine transgression which flooded an arm of the Tethys along the Subathu–Dogadda Zone, probably contemporaneously with the transgression responsible for marine sediments of the Bagh Group along the Narmada Basin further south (I. B. Singh 1981). P. Singh (1980) described *Ceriocava nilkanthi* from the Nilkanth Formation and also recorded its presence in the Bagh Group. This species is here considered synonymous with *Chiplonkarina dimorphopora*, supporting correlation of the Nilkanth Formation with the Bagh Group, and implying a Cenomanian/Turonian age for the Nilkanth Formation.

European records of *Chiplonkarina dimorphopora* are from the Cenomanian of the Le Mans area, Sarthe, and the Upper Cenomanian of Port-des-Barques, near Rochefort, Charente Maritime, France.

Unregistered material of apparent *C. dimorphopora* from the former Soviet Union was seen recently by one of us (PDT) during visits to the All-Russian Scientific Research Geological Institute (VSEGEI) in St Petersburg, and the Palaeontological Institute of the Russian Academy of Sciences in Moscow. These specimens, which have not been studied in detail, are from the Turonian and ?Coniacian of Turkmenistan,

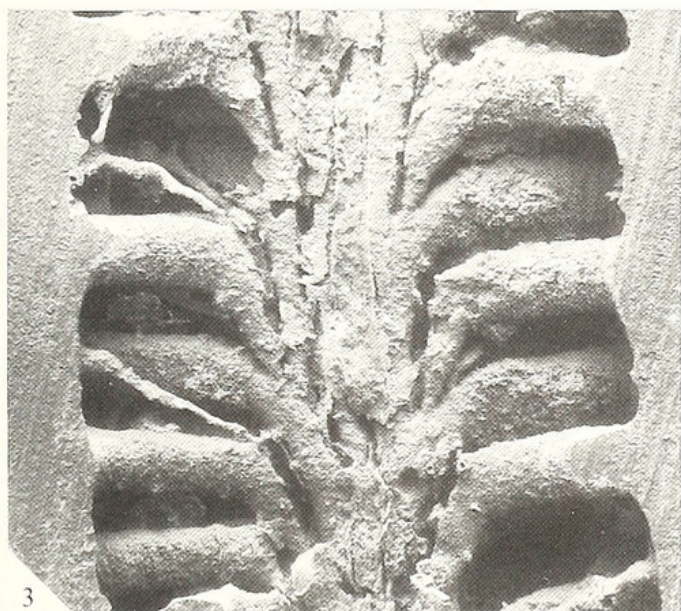
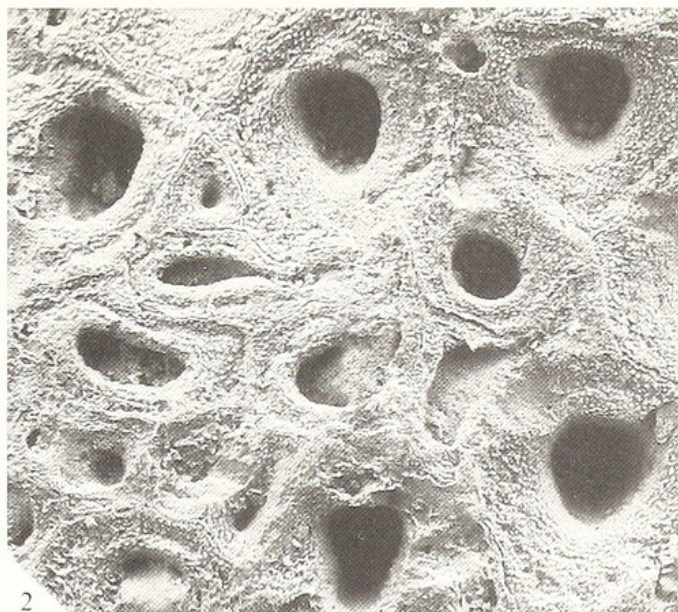
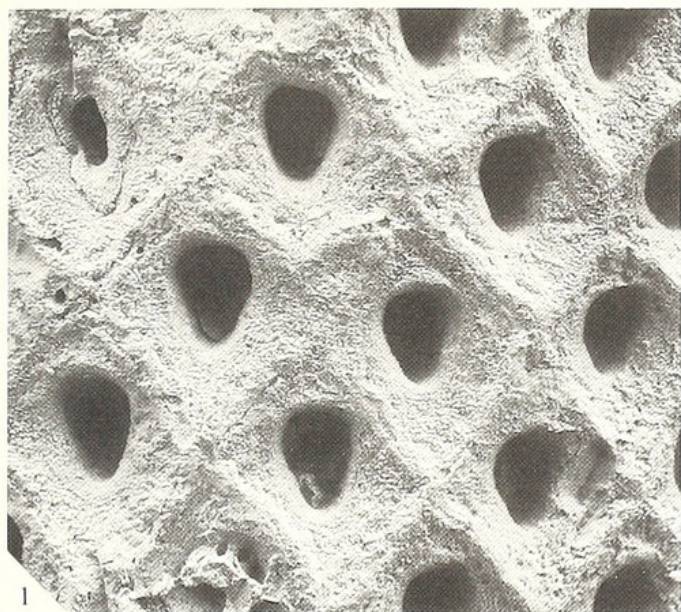
EXPLANATION OF PLATE 4

Figs 1–3. *Chiplonkarina bretoni* sp. nov., Lower Cenomanian; Carrière du Billot, Notre Dame le Fresnaye, Normandy, France. 1–2, VH 10373, holotype; 1, group of autozooids showing typical shape of opesia; $\times 75$; 2, overgrowth of small kenozooids; note pustulose ‘cryptocysts’; $\times 85$. 3, VH 10383; epoxy mould showing shape of autozooidal chambers; narrow ‘pipes’ at the left may be knozooids; $\times 50$.

Fig. 4. *Chiplonkarina dimorphopora* (Chiplonkar); BMNH D59403; Cenomanian; Le Gasonfier, Le Mans, Sarthe, France; detail of transversely fractured branch (branch surface is towards the left) showing corrugations where double interzooidal walls have broken along the line of the intercalary cuticle; $\times 130$.

Figs 5–6. *Adeonellopsis yarraensis* (Waters); BMNH 1994.4.15.1; Recent, Otago Shelf (Munida Station Mu 88–29), New Zealand; a cheilostome with corrugations similar to those seen in the interzooidal walls of *Chiplonkarina*. 5, context view of fractured branch showing porous autozooids on either side of the median budding lamina and thick frontal walls; $\times 37$. 6, detail of frontal wall broken along the line of the corrugated intercalary cuticle; $\times 200$.

Scanning electron micrographs of uncoated specimens imaged using back scattered electrons.



Uzbekistan and Tadzhikistan. According to T. Favorskaya (pers. comm. August 1994), the species is particularly abundant in the Upper Turonian of Turkmenistan.

Chiplonkarina bretoni sp. nov.

Plate 2, figures 2, 4; Plate 4, figures 1–3; Text-figure 4

Derivation of name. After Gerard Breton who collected the holotype and other specimens.

Holotype. VH 10373, Lower Cenomanian (*carcitanensis* Zone); Carrière du Billot, Notre Dame le Fresnaye, Calvados, Normandy, France; G. Breton Collection. Other bryozoan species present at this locality were tabulated by Voigt (1986).

Paratypes. VH 10372, 10374–6, 10383 (epoxy mould), 10564 (twenty-six fragments), 10565–77 (thirteen thin-sections), locality details as for holotype. BMNH BZ 2629–33, Lower Cenomanian, Craie Glauconieuse, Villers-sur-Mer, Calvados, Normandy, France. BZ 2694–5, Lower Cenomanian, Mülheim, Westphalia, Germany.

Other material. VH 11650, Lower Cenomanian, Essen, Westphalia, Germany.

Diagnosis. *Chiplonkarina* with slender branches; autozooidal opesia inverted pear-shaped, apparent polarity parallel to branch polarity.

Description. Colony erect with cylindrical bifurcating branches (Text-fig. 4A) varying from about 1.1 to 2.4 mm in diameter. Branches divisible into a narrow endozone (0.30–0.57 mm in diameter) containing about ten to twenty zooids orientated approximately parallel to branch growth direction, surrounded by an exozone with thicker-walled zooids orientated approximately perpendicular to branch growth direction and intersecting the branch surface at about 90° (Pl. 2, fig. 4; Pl. 4, fig. 3). Wall thickness 0.02–0.03 mm in the endozone, 0.10–0.15 mm in the exozone. Interzooidal walls compound, interpreted as two exterior walls back-to-back. Median layer of interzooidal walls crenulated in exozone (Text-fig. 4B); crenulations perpendicular to wall growth direction, with a wavelength of about 0.020–0.025 mm. Interzooidal wall microstructure in thin section indistinctly fibrous (Pl. 2, fig. 2), the fibres diverging from the crenulations and intersecting the wall surface at about 45°, giving the compound wall a chevron fabric when sectioned longitudinally. Overgrowths occasionally present (Pl. 4, fig. 2), sometimes enveloping tubiculous and other fouling organisms. Lateral branches may be developed at high angles to parent branches. Autozooidal budding, except for that in overgrowths, mostly or exclusively endozonal.

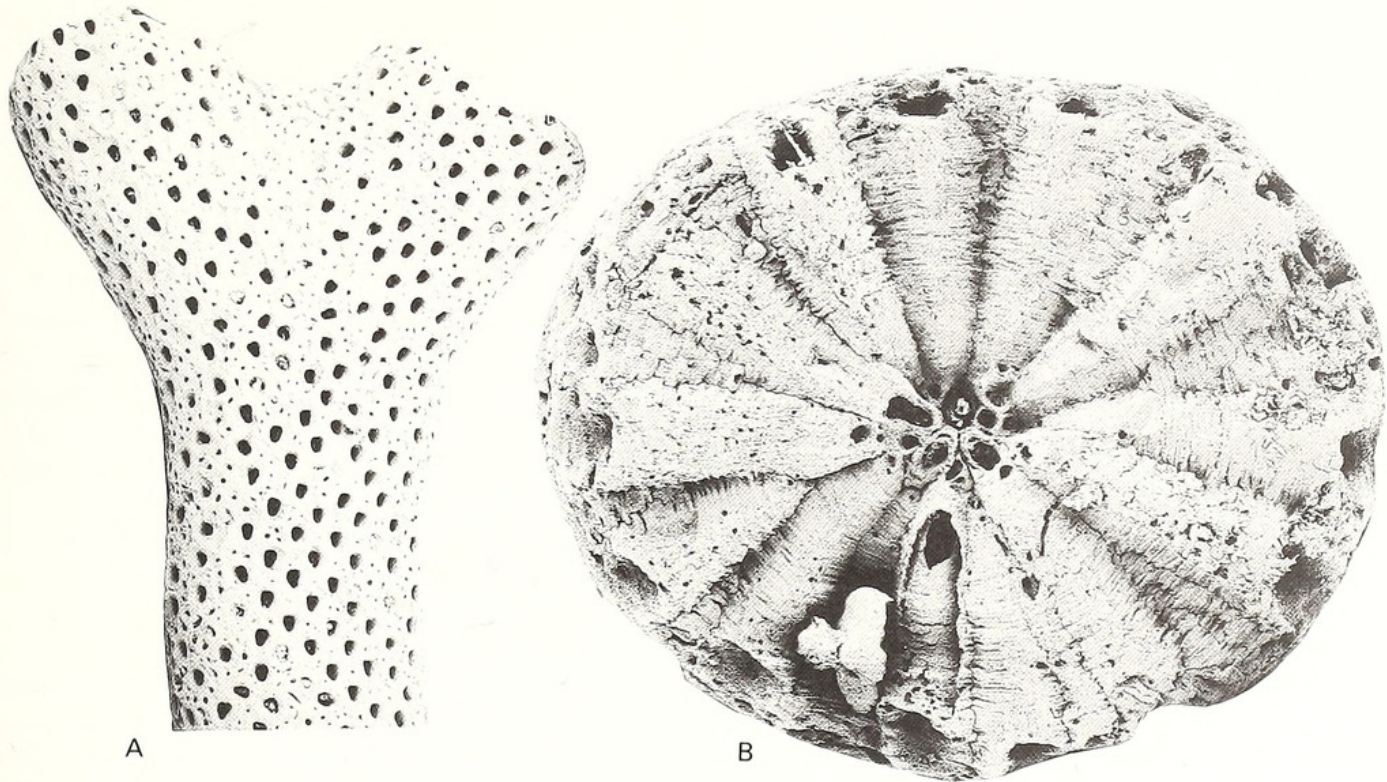
Autozooids tubular, elongate, club-shaped, bending through about 90° from the endozone into the exozone (Pl. 4, fig. 3). Frontal surface hexagonal or diamond-shaped (Pl. 4, fig. 1). Edges of zooids raised, bordered by a groove at the zooidal boundary. Opesia inverted pear-shaped, broadest close to the distal end. Cryptocyst minutely pustulose (Pl. 4, fig. 2), conspicuously funnel-shaped in erect zooids and smoothly continuous with the vertical walls, but more shelf-like in encrusting zooids comprising overgrowths. Closure plates and pore chambers not observed.

Kenozooids occasionally present singly between autozooids in erect branches but more commonly in aggregations at branch bifurcations (Text-fig. 4A), overgrowths, branch anastomoses and around the colony base. They are variable in frontal shape, and smaller than autozooids. Cryptocyst and opesia similar in morphology to those of autozooids.

Ovicells and avicularia lacking.

Dimensions (frontal dimensions in millimetres of ten autozooids from VH 10373).

	\bar{x}	SD	CV	range
length	0.39	0.020	5.1	0.35–0.42
width	0.33	0.022	6.5	0.29–0.36
opesia length	0.17	0.009	5.6	0.15–0.18
opesia width	0.14	0.009	6.2	0.12–0.15



TEXT-FIG. 4. *Chiplonkarina bretoni* sp. nov. Cenomanian, Essen, Germany; secondary electron micrographs of a coated specimen, VH 11650. A, bifurcating branch, $\times 11$. B, fractured distal end of branch showing narrow endozone surrounded by exozone with corrugated zooidal walls, $\times 35$.

Remarks. This species is characterized by inverted pear-shaped autozooidal opesia which are broadest near their distal ends. Lengths and widths of autozooids are larger than in *C. dimorphopora*, and these dimensions, as well as opesial length and width and branch diameter, are all less variable both within and between colonies than the equivalent dimensions in *C. dimorphopora*. Furthermore, there are generally fewer intercalated kenozooids in *C. bretoni* (although a specimen from the Cenomanian of Essen (Text-fig. 4) has a thicker branch and more abundant kenozooids than the French specimens), the autozooids frequently have a regular, close-packed quincuncial arrangement, and their apparent polarity is invariably parallel to branch length (Pl. 4, fig. 1).

Distal broadening of the opesia (Text-fig. 4A; Pl. 4, fig. 1) is unusual among cheilostomes where the opesia are generally broadest closer to their proximal margins. Correctly orientated branches of *C. bretoni* therefore give the appearance of being upside down, although the forks of branch bifurcations (Text-fig. 4A) and the direction of zooidal growth visible at fractured ends of branches dispel this impression. The unusual shape of the opesia raises the possibility that the zooids of *C. bretoni* may have reversed polarities relative to branch growth direction. For example, in the ascophoran cheilostome families Conescharellinidae and Batoporidae, the small rooted colonies have zooids whose orientation is reversed with respect to the direction of budding of the colony (Cook and Lagaaij 1976). The usual way of ascertaining zooid polarity in cheilostomes is from the positions of the orifice and ovicell, both of which are distal. Unfortunately, *C. bretoni* lacks ovicells, and there are no closure plates that might carry an impression of the operculum, indicating orifice position (cf. closure plates in other cheilostomes, e.g. Taylor 1988, pl. 43, fig. 3). Therefore, the vector of zooidal polarity cannot be confirmed.

Distribution. Lower Cenomanian: Notre Dame de Fresnaye and Villers-sur-Mer, Calvados, France; Essen and Mülheim, Westphalia, Germany.

PHYLOGENETIC POSITION

Identification of Chiplonkarina as a cheilostome

Indian specimens here described as *Chiplonkarina dimorphopora* have been repeatedly misidentified in the past as cyclostomes, most commonly *Ceriopora* or *Ceriocava* (Pl. 3, fig. 6). Both of the latter genera are traditionally classified (e.g. Bassler 1953; Nye 1976) within the cyclostome suborder Cerioporina, which ranges from Jurassic to Recent. Cerioporines have long, club-shaped autozooids with a free-walled skeletal organization (i.e. without calcified exterior frontal walls) and fixed-walled gonozooids (i.e. with calcified exterior frontal walls). Colony-form is very often dendroid, comprising subcylindrical, bifurcating branches which have an axial endozone surrounded by an exozone. Skeletal walls are thin in the endozone but become thicker as the zooids bend through about 90° into the exozone. Small polymorphs (kenozooids) are very often distributed between autozooids on the colony surface, although they are rare to absent in the genus *Ceriocava*.

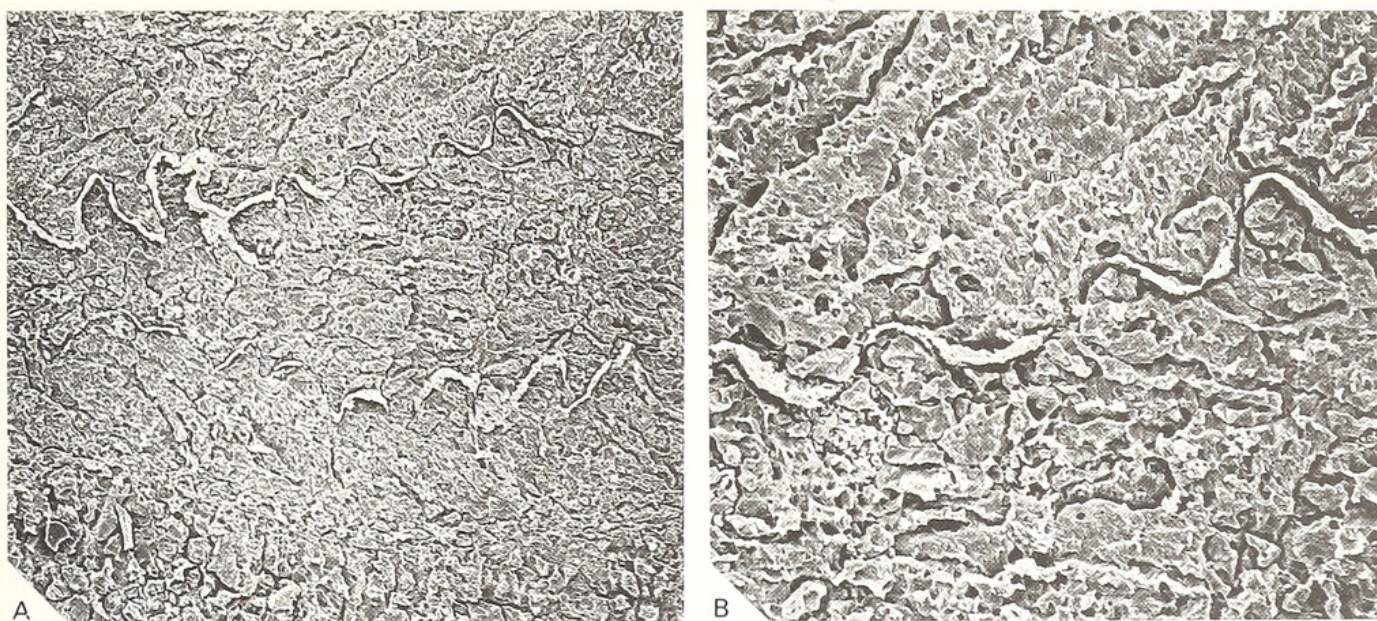
The meliceritid tubuliporine genus *Foricula* is another Cretaceous cyclostome with free-walled, club-shaped autozooids and a dendroid colony-form. *Foricula* has a superficial resemblance to *Chiplonkarina bretoni* but can be distinguished by its calcified opercula, an autapomorphy of the meliceritids (see Taylor 1994).

Except for the absence of gonozooids, which in any case have yet to be discovered in several cerioporines, *Chiplonkarina* has a basic morphology very like that of many cerioporine cyclostomes: autozooids are long, club-shaped and 'free-walled' (in the sense of lacking an exterior, gymnocystal frontal wall), kenozooids are interspersed between the autozooids, and colony branches are differentiated into a thin-walled endozone and thick-walled exozone. However, *Chiplonkarina* has several cheilostome features which show that its identification as a cerioporine, or indeed as a member of any suborder of cyclostomes, is incorrect.

1. *Double interzooidal wall structure.* The duplex structure of the interzooidal walls is the most striking and diagnostic feature demonstrating that *Chiplonkarina* belongs to the Cheilostomata. This is best seen in the exozone where the mid-line of the wall has a corrugated, sutured structure (Pl. 2, fig. 3). The folds are orientated transversely to wall growth direction, and are often associated with a brown coloration interpreted as a remnant of an organic cuticular layer (an intercalary cuticle, cf. Banta 1968). In polished and etched sections viewed using a high resolution SEM, this layer stands out in positive relief (Text-fig. 5), suggesting replacement of the organic material by a non-carbonate mineral. Specimens of *Chiplonkarina* sometimes fracture along the centre of the interzooidal walls where the cuticle was once situated. Such broken surfaces clearly show the corrugations (Pl. 4, fig. 4; Text-fig. 4B). The intercalary cuticle is also manifested on the colony surface by the slight grooves developed at zooidal boundaries (Pl. 3, figs 1–4). There is a clear contrast between the surface appearance of the double interzooidal walls of *Chiplonkarina* and the simple interzooidal walls of cerioporines where the zooidal boundary forms the sharp leading edge of the wall (Pl. 3, fig. 6).

In his detailed and thorough redescription of '*Ceriopora*' *dimorphopora*, Guha (1980, p. 31) noted that '...the outer boundary of the zooecial wall is transversely and irregularly corrugated.... This corrugation makes the suture lines between adjacent tubes serrated.' It is evident from this statement that Guha had observed the position of the intercalary cuticle but did not consider its morphological or systematic significance.

In all known cyclostomes vertical, interzooidal walls are interior walls secreted from both sides by an investing epithelium. Such interior walls lack a cuticular layer, and the walls have a unified structure. Many cheilostomes, however, have interzooidal walls which comprise two exterior walls arranged back-to-back. The calcified component of the wall of one of the zooids is separated from that of the other zooid by an intercalary cuticle which may be folded into corrugations, particularly along zooidal boundaries where frontal thickening is occurring (Pl. 4, figs 5–6; see Banta 1977; Carson 1978), and also basally (Tavener-Smith and Williams 1972, figs 76–77). Duplex interzooidal walls of this type have not been described in cyclostomes; the closest analogue among cyclostomes



TEXT-FIG. 5. Secondary electron micrographs of polished and etched sections of *Chiplonkarina dimorphopora* showing permineralized remnants of the crenulated intercalary cuticle; BMNH BZ 2628; Cenomanian/Turonian, Bagh Group, Chirakhan Limestone Formation, Deola-Chirakhan Marl Member; quarry west of Badia, Madhya Pradesh, India. A, cuticular remnants within opposite walls of a longitudinally sectioned zooid; bryozoan wall calcite and diagenetic calcite filling the zooidal chamber have similar textures in this preparation and cannot be differentiated; $\times 385$. B, detail of cuticular remnant; $\times 950$.

occurs in the Pliocene species *Blumenbachium globosum* where the colony consists of many subcolonies which at their junctions have back-to-back basal exterior walls with a folded cuticular remnant (Balson and Taylor 1982).

2. *Wall microstructure*. In thin section, the walls of *Chiplonkarina* have a fibrous appearance, the fibres intersecting wall surfaces at angles of 45° or more (Pl. 2, fig. 3). Similar fibrous fabrics are relatively common in cheilostomes (e.g. Ristedt 1977) but are absent or rare in cyclostomes where, when present, fibres are aligned in the plane of the wall and contribute to the laminar appearance of the wall in section (see Boardman *et al.* 1992, fig. 42a–b). Cerioporine cyclostomes have laminated wall microstructures, normally with the laminae parallel or subparallel to the wall surface, although higher intersection angles have been reported from some cerioporines (see Nye 1976, fig. 1E). Therefore, wall microstructure supports assignment of *Chiplonkarina* to the cheilostomes, and not to the cerioporine cyclostomes, but it should be stressed that this evidence must be seen in the light of our limited knowledge of skeletal microstructures and ultrastructures in bryozoans, especially cyclostomes.

3. *Pores in skeletal walls*. Interzooidal walls of *Chiplonkarina* are pierced by pores which are parallel-sided, canal-like structures often orientated obliquely to the wall surface (Pl. 1, fig. 2). In longitudinal sections of interzooidal walls between autozooids and kenozooids, pores may cross-cut the wall fibres approximately at right-angles, 'migrating' proximally with wall thickening. Lines of sectioned pores can then give a chevron appearance.

Both cerioporine cyclostomes and cheilostomes develop pores in interzooidal walls. In cerioporines and other cyclostomes, these pores are characteristically orientated at right-angles to wall surfaces, and generally decrease in diameter towards the centre of the wall where radial spines (seldom seen in fossils) often partly or completely occlude the pore (see Brood 1972; Boardman *et al.* 1992; Taylor and Jones 1993). A greater diversity of pore types occurs among cheilostomes, some

forming distinct pore chambers (or dietellae), and some partly occluded by rosette-plates (or septulae) perforated by many small holes (e.g. Ryland 1970, p. 87). Parallel-sided, canal-like pores are present in the thick interzooidal walls of the cheilostome *Herpetopora* (see Taylor 1988). The pores in *Chiplonkarina* are unlike those of known cerioporine cyclostomes but resemble the pores present in this Cretaceous cheilostome genus.

4. *Colony base and lamellar overgrowths*. The encrusting colony base in *Chiplonkarina* typically extends over a wide expanse of substrate. Zooids in the colony base differ from zooids in erect colony branches by being shorter and more box-shaped. Their endozone is poorly defined and short, comprising thin interzooidal walls which curve upwards for about 0.05 mm from the basal wall before giving way to the thick-walled exozone with interzooidal walls perpendicular to the basal wall. Lamellar overgrowths frequently show a similar structure; i.e. the zooids are short and have an abbreviated endozone. Growing edges of colony bases and overgrowths often have a ragged or stepped appearance. There is no fringing basal lamina.

Cerioporines, like most other multiserial stenolaemates, have colony bases and overgrowths with relatively smooth growing edges. A typically broad fringe of basal wall (or lamina) extends distally from the budding zone, and several ontogenetic generations of stacked new buds may be visible at this common bud.

Lamellar colony bases and overgrowths in cheilostomes are variable in appearance. A common condition, particularly among primitive and/or Cretaceous taxa, is for the growing edge to lack a fringing basal wall and to have an irregular outline as a result of 'intrazooidal budding' whereby new buds are formed discontinuously along the growing edge (see Lidgard 1985).

The irregular, lamina-free growing edges of the colony base and overgrowths in *Chiplonkarina* are more similar to cheilostomes with intrazooidal budding than to any known cerioporine cyclostomes. Furthermore, newly-formed autozooids in overgrowths may have a typically 'membraniporimorph' morphology of the type known in many malacostegan and pseudomalacostegan anascan cheilostomes.

Unfortunately, details of the early astogeny of *Chiplonkarina* are unknown. The morphology of the ancestrula in cerioporines and cheilostomes is very different and would provide important supportive evidence for the ordinal affinities of *Chiplonkarina*. In cerioporines and other cyclostomes, the ancestrula comprises a proximal, bulb-shaped protoecium leading to a distal tube terminated by the aperture. Cheilostomes lack a protoecium, and in most cases have ancestrulae essentially similar in shape to the later zooids in the colony.

5. '*Cryptocyst*'. No true cryptocyst, in the sense of a platform-like interior wall, is present in *Chiplonkarina*. However, the inner surfaces of the two back-to-back exterior walls forming the interzooidal walls constitute a 'cryptocystal rim' visible around the edges of the zooids when seen in frontal view. This cryptocystal rim is densely pustulose (Pl. 3, fig. 4), the gaps between the individual pustules being not much wider than the pustules themselves. Cryptocysts of a similar morphology are widespread among anascan cheilostomes, for example in *Conopeum seurati* (Canu) and *Akatopora circumsaepa* (Uttley) illustrated by Gordon (1986, pl. 1, fig. c and pl. 7, fig. c respectively), and in *Antropora tinctoria* (Hastings) depicted by Lidgard (1985, pl. 31, figs 2-5). Although the inner wall surfaces of many cyclostomes bear a variety of pustules and spinous processes (see Farmer 1979), these seldom reach the density found in *Chiplonkarina* and appear to be sparse in all cerioporine cyclostomes.

6. *Kenozooids*. Both cheilostomes and cerioporine cyclostomes may develop space-filling kenozooids between the autozooids. These can be of a similar surface morphology in the two groups with the exception that the kenozooids of cerioporines invariably have almost straight edges whereas those of cheilostomes can have concave edges (Pl. 3, fig. 5). Kenozooids with concave edges, resulting from indentation of their outline shapes by neighbouring autozooids, are a common feature in *Chiplonkarina* (Pl. 3, figs 1-4).

These features taken together permit confident assignment of *Chiplonkarina* to the Cheilostomata, and show that the cyclostome-like aspects of its morphology are homoplasies resulting from convergent evolution. Once accepted as a cheilostome, its systematic position within this order must be sought.

Affinities of Chiulonkarina within the Cheilostomata

Cheilostome bryozoans divide into two morphological grades: anascans and ascophorans. The latter are characterized by zooids with strongly calcified frontal shields, a feature clearly lacking in *Chiplonkarina* which is therefore of anascan grade. Among the anascans, the Malacostega are a primitive paraphyletic grouping of taxa with planktotrophic larvae and lacking the ovicells present in most of the remaining anascans for larval brooding purposes (Taylor 1987). In addition to the lack of ovicells, malacostegans typically have autozooids with simple skeletal morphologies and rarely possess the avicularian polymorphs found in so many other anascans. Ovicells are absent in *Chiplonkarina*, autozooids are relatively simple in form and avicularia wanting. Consequently, *Chiplonkarina* has a malacostegan morphological grade and can be provisionally assigned to the Family Electridae, one of the two recognized malacostegan families. Electrids first appear in the Upper Jurassic and are well-represented in the Cretaceous (e.g. Taylor 1986; Taylor and Cuffey 1992). It should be noted that the Electridae is itself likely to be paraphyletic but that redistribution of the constituent genera among monophyletic families awaits phylogenetic analysis.

Chiplonkarina seems likely to be closely related to *Heteroconopeum* (see Voigt 1983; Pl. 3, fig. 5) and to an undescribed cheilostome from the mid-Cretaceous of southern England (mentioned by Larwood 1976, p. 542 as a cheilostome encrusting a ramifying cyclostome colony). Both of these electrids have erect dendroid colonies and autozooids with similar frontal morphologies to those of *Chiplonkarina*.

A close relationship between *Chiplonkarina* and the Upper Cretaceous genus *Inversaria*, although sharing a similar colony-form, can be discounted. *Inversaria* possesses conventional anascan avicularia (Voigt and Williams 1973, pl. 1, fig. 2, pl. 3, fig. 5), suggesting that it is not a malacostegan, although the absence of ovicells in the genus is problematical and may point to an alternative mode of larval brooding. The presence of horned calcified opercula (Voigt 1974) is an autapomorphy of *Inversaria*, and this genus also differs from *Chiplonkarina* in the orientation of the corrugations in the interzooidal walls marking the position of the intercalary cuticle: these corrugations are parallel to wall growth direction in *Inversaria* (Voigt and Williams 1973, pl. 2, figs 2–3) but are transverse to growth direction in *Chiplonkarina* (Pl. 4, fig. 4; Text-fig. 4B).

DISCUSSION

Colony growth

Bryozoan colonies grow by budding new zooids and/or by lengthening existing zooids. In most cheilostomes, but not in *Chiplonkarina*, zooids are box-shaped, rapidly attain their 'mature' size and do not increase in length during later ontogeny. Therefore, colony growth depends principally on the budding of new zooids, including new zooids budded on top of one another forming multi-layered colonies of increasing thickness. In addition to zooidal budding, the lengthening of existing zooids plays an important role in colony growth in many stenolaemates, as it did in *Chiplonkarina*. The tubular zooids of *Chiplonkarina* continued to grow during their ontogenies and allowed the dendroid colony branches to become considerably thickened. Similar thickening of dendroid colony branches in cheilostome bryozoans is normally accomplished by the frontal budding of new zooids (notably in various 'celleporids', e.g. Voigt 1970), not by the distal growth of existing zooids.

Growth of dendroid (or ramose) branching colonies in bryozoans and other animals necessitates that distal growth rate decreases away from the branch axis (e.g. Key 1990); uniform distal growth rates across the colony surface would produce a hemispherical form. As in dendroid stenolaemates,

Chiplonkarina had maximal budding rates and linear growth rates in the axial endozone which forms the distal growing tips of the branches. However, budding was not restricted to the endozone. The substantial enlargement of branch surface area with increasing diameter demanded that zooidal budding continued into the exozone because this increase could not be entirely accounted for by wall thickening, intercalation of kenozooids or enlargement of autozooidal surface area.

Details of the mode of zooidal budding in erect branches of *Chiplonkarina* are unclear. Sections generally reveal new buds first becoming visible at the foci of triple junctions between walls of existing zooids. No mother-daughter relationship is apparent and the pattern of budding corresponds to the interzoecial category defined for dendroid stenolaemates by McKinney (1975). New buds are presumably linked via interzooidal pores, at an early stage in development, to the mature zooids in the colony, but this is difficult to ascertain from sections. At least some of the putative kenozooids intercalated between autozooids in the exozone may be immature autozooids. Careful serial sectioning would be needed to determine whether such 'kenozooids' do indeed develop into autozooids with growth.

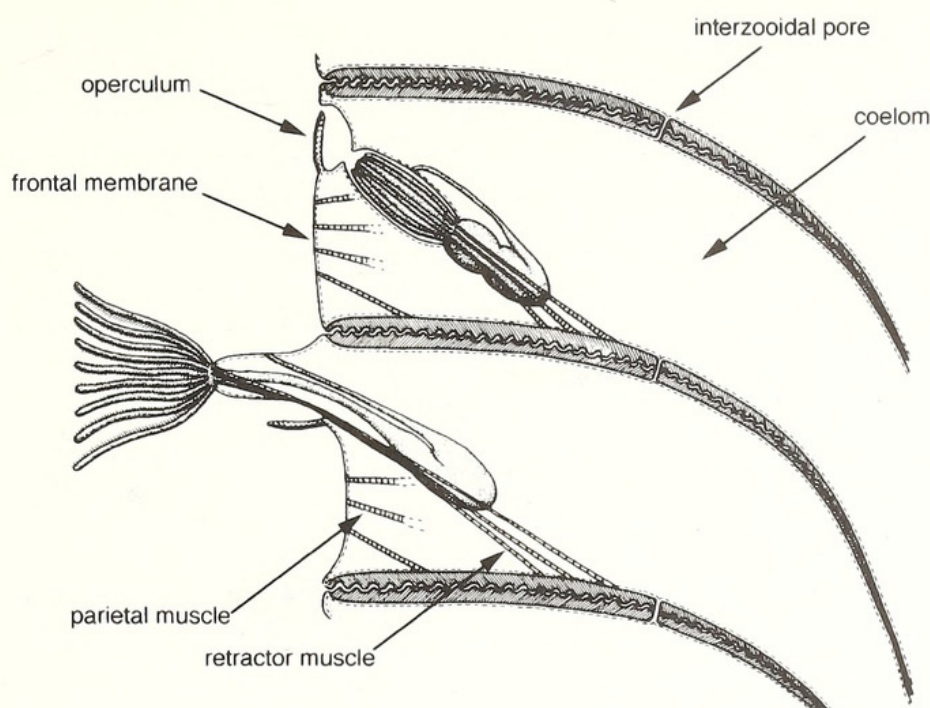
Continued distal (vertical) growth of individual zooids is possible in *Chiplonkarina* because the zooids are open-ended and not constricted by a frontal wall. The absence of a frontal wall permits similar vertical growth in the Recent anascan *Antropora tinctoria* (Hastings), although to a much lesser degree (Lidgard 1985, p. 278). The gymnocystal or cryptocystal frontal wall developed in most cheilostomes imposes a limit on the upward growth of the zooidal chamber. The frontal wall itself can be thickened, as in many erect ascophorans in which thickened proximal zooids reinforce the colony base (e.g. Cheetham 1971), but the zooidal chamber does not lengthen (excepting peristomial prolongation around the orifice). It seems possible, therefore, that the presence of frontal walls in cheilostomes may have acted as a constraint prohibiting the evolution of more clades with the stenolaemate-like growth patterns found in *Chiplonkarina* and *Inversaria*. Only taxa with negligible frontal walls had the 'preadaptation' necessary to evolve stenolaemate-like dendroid colonies.

With distal growth of the zooidal skeleton, the polypide and associated musculature must also have migrated distally. It is not known whether this migration occurred episodically, perhaps linked to the cycles of polypide degeneration-regeneration which characterizes bryozoans, or more gradually. The skeletal walls show no evidence of periodic changes in thickness suggestive of episodic growth.

Functional morphology

(a) *Feeding currents.* Branch diameter in *Chiplonkarina dimorphopora* is extremely variable. McKinney (1986) looked at between-species variability in bryozoans with dendroid erect branches (his radial category) and found that branch diameters in species with maculae were significantly greater than in species lacking maculae. Maculae are surface disruptions representing chimneys of excurrent water flow which appear to be necessary in bryozoans with broad surfaces where colony margins alone are insufficient to vent all of the filtered water. McKinney identified a polarization between species with branches less than 2 mm in diameter which are non-maculate, and those with branches more than 2 mm in diameter which are maculate in all stenolaemates and in many cheilostomes. In *Chiplonkarina dimorphopora*, the large, presumably age-related variation in branch diameter means that the species is unusual in spanning the division between these two size categories. Branches of *C. dimorphopora* have a modal diameter of between 1 and 1.5 mm, but range from 0.7 to 11 mm. Maculae cannot be identified in either thin- or thick-branched specimens. It seems likely that thick branches of *C. dimorphopora* would have developed excurrent chimneys with no skeletal expression and perhaps transitory existence. Such chimneys occur in many living cheilostomes (see McKinney 1990 for a review of feeding in bryozoans).

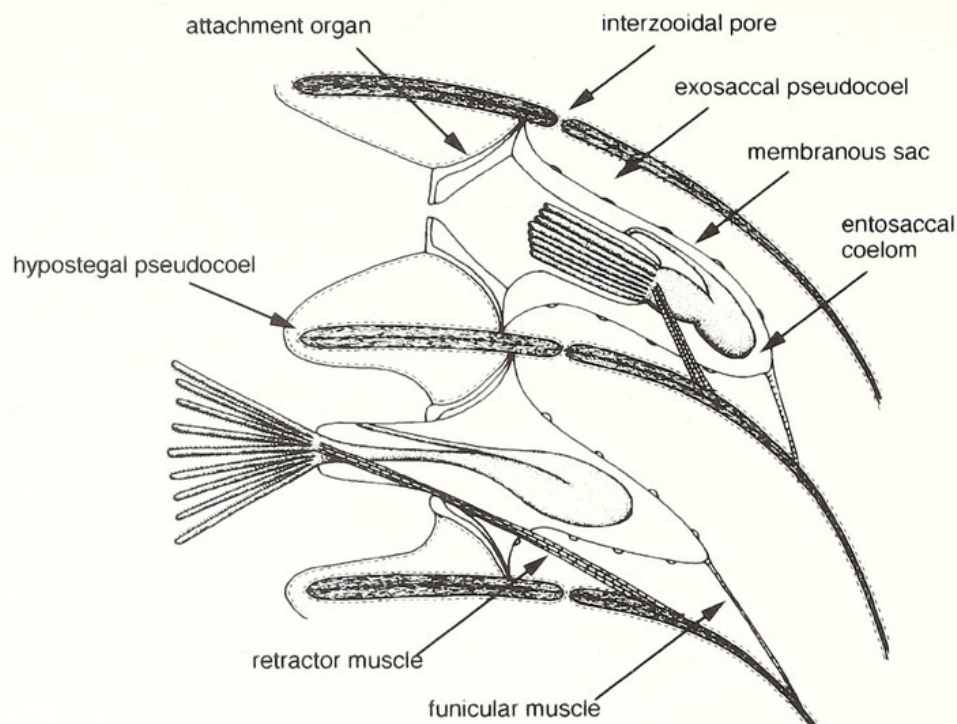
(b) *Soft tissue distribution.* Text-figure 6 shows a reconstruction of soft tissue distribution in *Chiplonkarina* and can be compared with a dendroid ceriopore (or similar free-walled stenolaemate) shown in Text-figure 7. There are two main areas of contrast: the interzooidal walls, and the mechanism of tentacle protrusion.



TEXT-FIG. 6. Reconstruction of soft part morphology in *Chiplonkarina*. Two zooids are shown, one with the tentacle crown expanded and the other retracted.

As noted above, the interzooidal walls of *Chiplonkarina* are duplex structures comprising back-to-back exterior walls including a cuticular layer at the centre of the wall. The two halves of the wall were secreted by discrete epithelia belonging to adjacent zooids. No soft tissue continuity would have existed over the growing ends of the walls (cf. soft tissue connections through pores in the walls which can be inferred). Yet it is clear that growth rates were similar for both sides of the wall. Indeed, the suture-like intergrowth of the medial cuticle implies a close coordination between the neighbouring zooids responsible for wall growth. Interzooidal walls of cerioporines are interior walls lacking a cuticle and secreted by an epithelium which wraps over the ends of the walls and is continuous from one zooid to the next. A hypostegal pseudocoel also links adjacent zooids over wall ends, enclosed by an outer epithelium and cuticle. This more 'integrated' condition presumably does not pose the same potential problems of coordination of growth rates, or of a median plane of weakness formed by the organic cuticle, both of which would have pertained in *Chiplonkarina*.

Anascan cheilostomes, like *Chiplonkarina*, and cyclostomes employ fundamentally different methods for eversion of the tentacles (see Taylor 1981). In both groups, this is accomplished hydrostatically by the contraction of muscles pulling on membranes and forcing coelomic/pseudocoelomic fluids into the tentacle sheath, which then everts and pushes the tentacles out through the orifice. In anascans, the muscles involved are parietal muscles attached to the flexible frontal membrane, which would have occupied most of the frontal surface in zooids of *Chiplonkarina*, and anchored to the lateral or basal walls of the zooid. Two sets of muscles are apparently responsible for tentacle protrusion in cyclostomes: atrial dilator muscles which widen the atrium and force exosaccal pseudocoelomic fluid proximally, and annular muscles of the membranous sac which squeeze the entosaccal coelom. Whereas the typically box-shaped anascan zooid provides a suitably large surface area of depressible frontal membrane, the typically tubular cyclostome zooid furnishes a large surface area of compressible membranous sac. Analogy with living anascans leads to the conclusion that the polypide of *Chiplonkarina* would have been positioned at a shallower depth (i.e. more distally) within the tubular zooidal skeleton than are the polypides of cerioporine cyclostomes. A greater proportion of the older, proximal parts of the zooidal chambers would have been devoid of actively functional soft parts but were presumably still



TEXT-FIG. 7. Reconstruction of soft part morphology in a cerioporine cyclostome with tubular zooids similar in shape to those of *Chiplonkarina*. Two zooids are shown, one with the tentacle crown expanded and the other retracted. Compared with *Chiplonkarina* (Text-fig. 6) note deeper, more proximal location of the polypide within the tubular zooidal skeleton and lesser elevation of the expanded tentacle crown.

filled with coelom and lined by epithelium. Although a few *Chiplonkarina* zooids have calcified basal diaphragms, serving to reduce the length of the living chamber, these are lacking in most zooids, although the existence of non-calcified, membranous diaphragms cannot be ruled out. It is well-known that cheilostome tentacle crowns are characteristically protruded to a greater degree than those of cyclostomes: in cheilostomes, the tentacle sheath may be everted outside the orifice, held on top of the introvert, whereas in cyclostomes the level of the mouth seldom extends beyond the skeletal aperture (cf. McKinney 1988). Therefore, *Chiplonkarina* zooids can be inferred to have had the ability to protrude their tentacles further above the colony surface than cerioporine zooids occupying skeletons of a similar tubular shape.

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