SYSTEMATICS OF THE OLIGOCENE TO MIOCENE REEF CORAL *TARBELLASTRAEA* IN THE NORTHERN MEDITERRANEAN

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ABSTRACT. Multivariate statistical analyses are used to distinguish species of the common reef-building coral *Tarbellastraea* at Oligocene and Miocene localities within the Aquitaine Basin, western Mediterranean, and central Paratethys regions; and to trace their distributions through geological time. Thirteen measurements or counts are made on thin sections of 126 colonies collected at 13 widely scattered localities, whose geological ages are newly updated. The data are analysed using average linkage cluster analysis and canonical discriminant analysis to distinguish clusters of colonies representing morphometric species. Names are assigned by qualitatively comparing measurements on the statistically recognized species with those of primary types of all previously described species of *Tarbellastraea.*

The results show that *Tarbellastraea* originated during the Oligocene (Rupelian) and became extinct during the Early Messinian. A total of 12 species (including two new species from the Italian Oligocene, and two species described previously as varieties) lived in the investigated areas during Oligocene and Miocene time. Except during the Oligocene, all but one species (*T. ellisiana*) were widespread. Although species richness within the genus remained constant at 5–7 species throughout much of its stratigraphical range, morphological disparity decreased significantly through time. The observed constancy in richness contrasts with the decrease reported overall in the Mediterranean reef coral fauna. Species originations were highest during the Burdigalian, when temperatures across the region increased. Species extinctions remained constant until the latest Miocene, when the extinction rate increased as cold Atlantic waters entered the Mediterranean.

New species described are *Tarbellastraea bragai*, *T. chevalieri*, *T. russoi* and *T. salentinensis*.

The extinct scleractinian genus *Tarbellastraea* Alloiteau, 1950 was one of the predominant reef-building corals on Mediterranean reefs during the Miocene (Chevalier 1962). During the Early and Mid Miocene, it was abundant in the diverse but small buildups that prevailed across the Mediterranean (Monleau *et al.* 1988) and European Atlantic regions (Cahuzac and Chaix 1993). During the Late Miocene, *Tarbellastraea* was one of two key framework builders of the large, well-developed reef systems that developed in the western Mediterranean (Esteban 1979; Martin *et al.* 1989; Pomar 1991). Despite the importance of *Tarbellastraea*, no stable taxonomy currently exists for distinguishing 'species' within the genus, and its stratigraphical duration and geographical range are debated. As a consequence, the evolutionary history of *Tarbellastraea* is poorly known.

Although several species of *Tarbellastraea* were described by authors in the nineteenth century (e.g. Reuss 1847, 1872; Milne Edwards and Haime 1850), the most comprehensive treatment of the systematics of the genus was that of Chevalier (1962). Chevalier (1962) described 12 species (five new) and seven varieties (six new) of Miocene western Mediterranean *Tarbellastraea*. He distinguished these species qualitatively using a large number of skeletal features, including colony shape, calice shape, calical relief, calice size, number of septa per corallite, columella structure, relative development of the primary and secondary septa, and calice spacing. His work was later questioned by taxonomists studying environmental variation in living Indo–Pacific species, because many of the features used by Chevalier (1962) had been found to vary widely in response to the environment (Best *et al.* 1984). Because of overlap among species in measurements made on corallite diameter, calice spacing, and number of septa per corallite, Oosterbaan (1988) synonymized five of the species recognized by Chevalier (1962) in the Burdigalian of the Aquitaine Basin. Best *et al.*

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(1984) further suggested that the overlap indicated that all of the species and varieties treated by Chevalier (1962) were probably only one species, *Tarbellastraea ellisiana* (Defrance, 1826).

Recent work on living Caribbean species of the closely related genus *Montastraea*, however, has shown that morphological differences among species may be much more subtle than previously appreciated, and that morphological overlap among species may be common in closely related species (Knowlton *et al.* 1992; Weil and Knowlton 1994). Three electrophoretically distinct sibling species within the *Montastraea annularis* complex differ primarily in morphological characters (involving colony form and calical relief) that have high environmental variation (Knowlton *et al.* 1992; Weil and Knowlton 1994). Nevertheless, sibling species within the complex can be distinguished morphometrically by applying multivariate statistical methods to measurements made on colonies from populations collected in different environments (Budd 1993). The statistical results show that no single character can be used to distinguish species within a complex, but ten or more characters must be considered in concert. Different types of morphological features are needed to distinguish species in different cases.

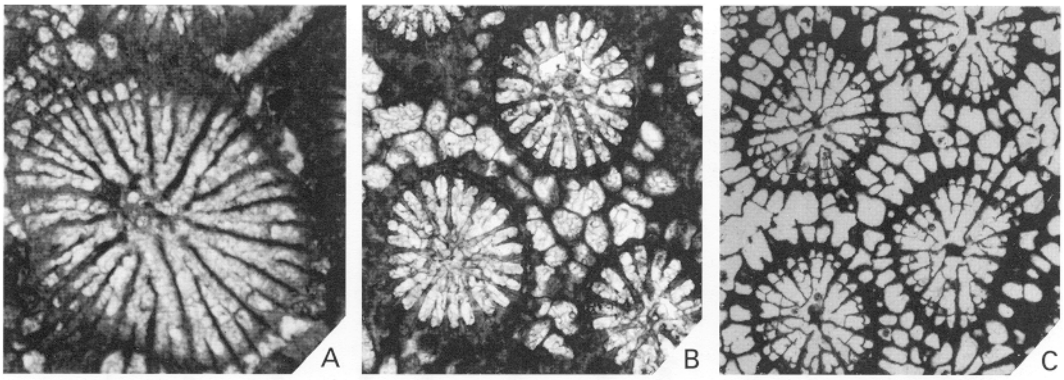
In this paper, we revise species of *Tarbellastraea* in some Mediterranean and European basins using a similar morphometric approach, derived from the methods of Budd and Coates (1992) and Budd (1993). Our approach is stratophenetic (*sensu* Gingerich 1979), and involves: (1) taking a number of linear measurements and counts on colonies in sample populations collected at a wide range of localities; (2) using multivariate statistical procedures, including cluster analysis and canonical discriminant analysis, to group colonies within pre-defined stratigraphical levels into clusters; and (3) statistically linking clusters into 'morphometric species' to trace their ranges through geological time. Comparisons are made with primary types, and names are assigned only after morphometric species have been recognized statistically. Because the approach is based on quantitative analyses of sample populations (i.e. > 5 colonies from any one locality), some of the difficulties associated with recognizing discrete morphological entities or 'morphometric species' in highly variable organisms, such as corals, are reduced.

Our aim in this paper is to provide a consistent taxonomy that can be used to identify species of *Tarbellastraea*. Our work is unique in its focus on a single Mediterranean genus. It also considers several pre-Miocene occurrences of the genus, some of which are recorded for the first time. Like Chevalier (1962), as part of our revision, we interpret species origination and extinction events by considering the palaeogeography of the region. However, unlike Chevalier (1962), our interpretations are made within the context of updated higher resolution stratigraphies and current paleogeographical reconstructions. In the future, we plan to continue our study of *Tarbellastraea* by treating material from northern Africa and the Middle East, so that we can eventually examine evolutionary relationships among species. We believe that a thorough revision of the species of *Tarbellastraea*, as begun here, is an essential first step in reconstructing any meaningful phylogeny of the genus.

DIAGNOSTIC CHARACTERISTICS OF *TARBELLASTRAEA*

Because very little molecular or phylogenetic work has been done on scleractinian corals, most established Cenozoic genera have been defined on the basis of skeletal characters, that are easy to observe on upper calical surfaces (see Vaughan 1907; Lang 1984, for discussion). Using the morphological terminology of Wells (1956), in colonial scleractinians (except the suborder Astrocoeniina), species are generally distinguished by the architecture of the individual corallites (e.g. corallite diameter, number of septal 'cycles' *sensu* Wells 1956, fig. 240); whereas genera are distinguished by the degree of integration of corallites within colonies (e.g. plocoid *vs* cerioid colony forms, wall structure, development of costae), and by the development of the columella (Budd 1990).

Although *Tarbellastraea* was first designated as a new genus by Alloiteau (1950), its morphology was not described in detail until Alloiteau (1952) emphasized the small corallite diameter, often 'parathecal' wall structure, tabulo-vesicular coenosteum, and commonly lamellar columella of the new genus. Many of these characteristics are also possessed by seven other plocoid genera (Table 1), which, like *Tarbellastraea*, belong to the family Faviidae Gregory, 1990; differences between these eight genera are often difficult to detect without detailed microscopic examination. Nevertheless, with the exception of *Antiguastrea* Vaughan, 1919, *Tarbellastraea* is unique in its possession of a lamellar columella and a distinctive para- to septothecal wall structure. In both genera, the wall is primarily septothecal (i.e. formed by the thickening of the outer part of the septa), but it is sometimes reinforced by additional dissepiments, which are characteristic of true 'parathecal' walls (*sensu* Wells 1956, fig. 245). Two genera (*Plesiastrea* (*Palaeoplesiastraea*) and *Solenastrea*) contain species that resemble species of *Tarbellastraea* in almost every detail, except that they have spongy columellae and weak costae (Text-fig. 1).



TEXT-FIG. 1. Transverse thin sections of *Tarbellastraea* and two morphologically similar genera showing the differences in wall structure, columella form, and number of septal cycles among genera. A, *Antiguastrea cellulosa* (Duncan, 1863), type species of *Antiguastrea* Vaughan, 1919; SUI-84922-G; Upper Oligocene, Guayanilla, Juana Diaz Formation, Puerto Rico (Realini collection). B, *Solenastrea* sp.; SUI-84921-A; Langhian, Neffies, Languedoc, France (with the exception of its spongy columella, this species is almost identical morphologically to *T. reussiana* which occurs at the same locality). C, *Tarbellastraea ellisiana* (Defrance, 1826), type species of *Tarbellastraea* Alloiteau, 1950; SUI-84740-A; Lower Burdigalian, Cabanes, Saint-Paul-les-Dax, Bordeaux (France). All × 8.

The primary morphological differences between *Tarbellastraea* and *Antiguastrea* are similar in nature to differences that typically distinguish species. Species of *Tarbellastraea* usually have smaller corallite diameters and fewer septal cycles than species of *Antiguastrea*; however, clearly there is overlap (e.g. *Antiguastrea prava* Budd *in* Budd *et al.* 1992, from the Eocene of Panama, which has a corallite diameter of 3–4 mm and three cycles of septa). Nevertheless, the absence of *Antiguastrea* (as delineated in Table 1) from any of the Miocene units described herein (Chevalier 1962) suggests that vast majority of the species of *Tarbellastraea* in the present study may be descended from a common ancestor, and thus had an evolutionary history distinct from that of *Antiguastrea*. As mentioned above, studies similar to the present one are needed on (1) *Tarbellastraea* from the south-western and eastern Mediterranean and the Middle East and (2) *Antiguastrea* from the Mediterranean and the Caribbean regions, before a rigorous phylogenetic analysis can be performed to assess the taxonomic validity of distinguishing *Tarbellastraea* from *Antiguastrea*.

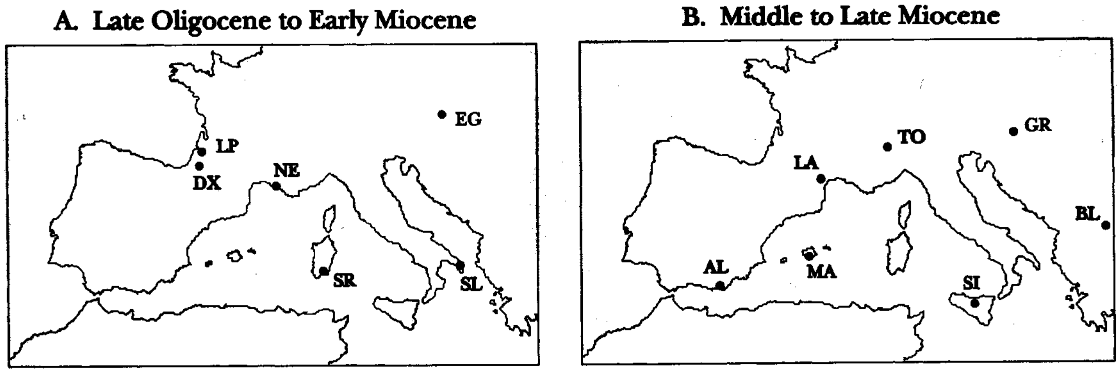
TABLE 1. Comparison of diagnostic morphological features in *Tarbellastraea* with those in morphologically similar genera (after Vaughan and Wells 1943; Wells 1956; Chevalier 1962). Following Vaughan and Wells (1943), synonyms for the genus *Montastraea* include: *Orbicella* Dana, 1846; *Phyllocoenia* Milne Edwards and Haime, 1848; and *Heliastrea* Milne Edwards and Haime, 1857.

	Genus	Colony form	Corallite diameter	Wall structure	Septal cycles	Palifom lobes	Columella	Exotheca
1.	*Tarbellastraea* Alloiteau, 1950	Plocoid	< 3·5 mm	Para- to septothecal	3–4 cycles	Weak or absent	Sublamellar to lamellar	Weak costae, tabulo-vesicular coenosteum
2.	*Antiguastrea* Vaughan, 1919	Subplocoid–plocoid	> 3·5 mm	Para- to septothecal	3–5 cycles	Weak or absent	Lamellar	Weak costae, tabulo-vesicular coenosteum
3.	*Cyphastrea* Milne Edwards and Haime, 1848	Plocoid	< 2·5 mm	Septothecal	2–3 cycles	Weak to strong	Papillose to spongy	Very weak costae, spinose coenosteum
4.	*Leptastrea* Milne Edwards and Haime, 1848	Subcerioid–plocoid	2–11 mm	Septothecal	2–5 cycles	Weak	Papillose	Weak costae, dense coenosteum
5.	*Montastraea* de Blainville, 1830	Plocoid	> 2·0 mm	Septothecal	3–4 cycles	Weak or absent	Spongy	Strong costae, tabular coenosteum
6.	*Solenastrea* Milne Edwards and Haime, 1848	Plocoid	< 3·5 mm	Septothecal	3 cycles	Weak	Papillose to spongy	Very weak costae, vesicular coenosteum
7.	*Plesiastrea* Milne Edwards and Haime, 1848	Plocoid	> 2·0 mm	Septothecal	3 cycles	Strong (rudimentary inner fan system)	Papillose to spongy	Strong costae, tabular coenosteum
8.	*Plesiastrea* (*Palaeoplesiastraea*) Chevalier, 1961	Plocoid	< 3·5 mm	Septothecal	3 cycles	Weak	Papillose	Very weak costae, vesicular coenosteum

RECOGNITION OF SPECIES USING MORPHOMETRIC METHODS

Material

A total of 127 colonies of *Tarbellastraea* was selected for analysis from collections made at 13 localities (Text-fig. 2; Table 2). All of the colonies were relatively well preserved and possessed the diagnostic criteria outlined above. The 13 localities are widely scattered across the Aquitaine Basin, western Mediterranean, and central Paratethys regions, and include the type localities for 14 of the 25 previously described species and varieties of *Tarbellastraea*. The localities consist of a range of different reef settings, including reef-complexes with lagoonal patch reefs (MA, SI), fringing reefs and patch reefs (SP, NE, DX, LP, GR, LD, AL), and smaller buildups (SR, BL). Two scattered coral horizons (EG, TO), in which true reef framework was not formed, have also been considered.



TEXT-FIG. 2. Maps showing 13 collecting localities. Abbreviations for localities are given in Table 2.

Most of the collections were made recently by either A. F. Budd (14 colonies at NE, 10 at EG, 10 at DX, 10 at LP, 5 at GR, 11 at BL, 11 at LD), F. R. Bosellini (8 colonies at SP, 5 at MA), J. C. Braga (9 colonies at AL), or A. Russo (4 colonies at SR). However, 30 additional specimens (2 colonies at NE, 18 at LP, 5 at TO, 2 at LD, 3 at SI) were selected from collections made by the late J. P. Chevalier and his predecessors at the Institut de Paléontologie, Muséum National d'Histoire Naturelle, in Paris, France (MNHN, I.P.). Wherever possible, at least ten colonies were selected from each locality; however, in the case of six localities, fewer specimens were available for analysis because of inadequate preservation (Table 2).

Six other localities where primary types of species and varieties of *Tarbellastraea* have been found include: the Vicentin area of northern Italy (Rupelian), the Landes region of southern France (Stampian), the Touraine region of north-west France (Langhian), the Vienna Basin of Austria (Badenian), the Granada region of Spain (Late Tortonian), and Malta (Late Tortonian to Early Messinian). The geographical proximity of (1) the Vienna localities to localities of similar age and environment in the Styrian Basin (GR; Table 2) and (2) the Granada localities to localities of similar age and environment in Almería (AL; Table 2), indicates that two of the six faunas may be partially represented in our present samples.

In order to determine geological age dates for the 13 localities, one of us (FRB) consulted with specialists on the local geology of each area, and conducted a thorough review of the most recent literature. The findings are summarized in Table 2. Age dates for the 13 localities vary in quality. In some cases (e.g. NE, DX, LP, EG, GR), microfossils have been rigorously investigated using up-to-date biostratigraphical methods. In others (e.g. SR, TO, LD), very little recent biostratigraphical work has been done. A second paper is currently in progress discussing these stratigraphical problems and the reef settings in fuller detail.

Because of the tendency for repeated evolution of similar morphologies over geological time within many scleractinian coral lineages (see Budd and Coates 1992), the 13 localities have been

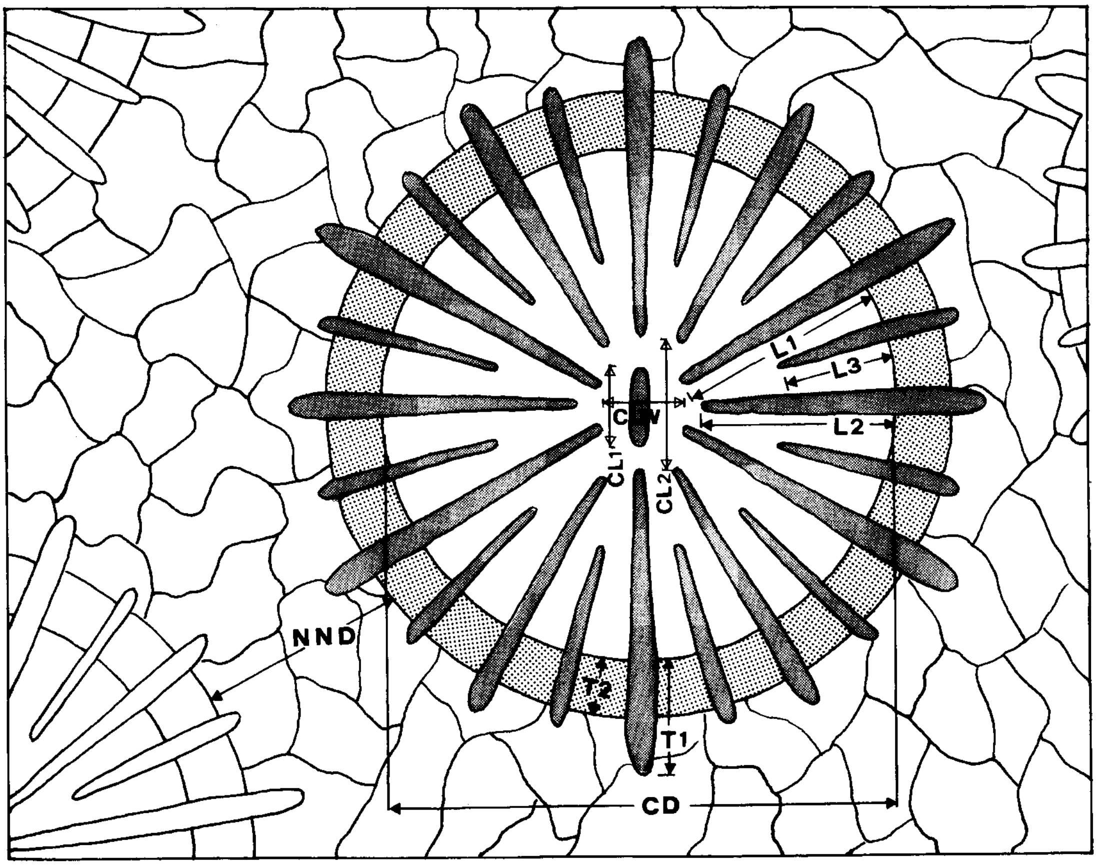
TABLE 2. Collecting localities for samples used in the morphometric analysis and their geological ages.

Locality	Abbreviation	Number of colonies measured	Age	Age reference
1. Vitigliano (Salento Peninsula, Apulia, Italy)	SP	8	Mid Chattian	Bosellini and Russo 1992
2. Carry-le-Rouet (La Nerthe, Bouches-du-Rhône, France)	NE	16	Late Chattian	Monleau *et al.* 1988; Nury 1994
3. Dolianova (Cagliari, Sardinia, Italy)	SR	4	Late Chattian-Aquitanian	Cherchi and Montadert 1984
4. Eggenburg (Vienna, Austria)	EG	10	Eggenburghian (i.e. Early–Mid Burdigalian)	Steininger and Senes 1971; Steininger *et al.* 1990
5. Cabanes (St.-Paul-lès-Dax, Landes, France)	DX	10	Early Burdigalian	Cahuzac and Poignant 1992; Cahuzac and Chaix 1993
6. Le Peloua and Mérignac (Bordeaux, Gironde, France)	LP	28	Early Burdigalian	Poignant and Pujol 1978; Cahuzac and Chaix 1993
7. Sciolze, Termô Fôrà, Albugnano, (Torino, Piedmont, Italy)	TO	5	Burdigalian–Langhian	Bonsignore *et al.* 1969; Clari *et al.* 1994
8. Leibnitz (Graz, Austria)	GR	5	Early Badenian (i.e. Langhian)	Friebe 1991*a*, 1991*b*
9. Pleven (Bulgaria)	BL	11	Early Badenian (i.e. Langhian)	Kojumdgieva *et al.* 1978
10. Autignac, Neffies and Seriège, (Beziers, Languedoc, France)	LD	13	Langhian	Magné 1978
11. Landro and Nicosia (Sicily, Italy)	SI	3	Late Tortonian	Catalano 1979; Grasso and Pedley 1988
12. Purchena and Los Marmoles (Almería, Spain)	AL	9	Late Tortonian	Martin *et al.* 1989
13. Cala Pi (Mallorca, Balearic Islands, Spain)	MA	5	Late Tortonian–?Early Messinian	Pomar 1991, 1993

subdivided into two major groups for the purposes of the statistical analyses: (1) Late Oligocene to Early Miocene (SP, NE, SR, EG, DX, LP, TO), and (2) Middle to Late Miocene (GR, BL, LD, SI, AL, MA). Because clusters of colonies are distinguished in our protocol only at the initial stages in analysis and subsequently linked together to form morphometric species, temporally subdividing the material in this way serves to reduce the overall number of taxa and evolutionary intermediates, and thereby enhances resolution at the critical initial stages of analysis when cluster nuclei are first detected. This procedure improves the capability for discriminating morphologically similar clusters that would otherwise intergrade and be less distinct in an all-encompassing statistical analysis of material from all localities and ages.

Characters

A total of 12 linear distances was measured on transverse thin sections of five to ten well-preserved corallites per colony (Text-fig. 3). The total number of septa ('NS') was also counted on each measured corallite. Measurements were only obtained from mature corallites on each colony.



TEXT-FIG. 3. Diagram showing nine of the 12 characters measured on transverse thin sections: CD (= CD–MIN), minimum corallite diameter; CL1, columella tubercle length; CL2, CLW, corallite centre width; L1, septum length (1st cycle); L2, septum length (2nd cycle); L3, septum length (highest cycle); NND, distance between corallites; T1, costa length; T2, theca thickness. Three additional characters that were measured were: CD–MAX, maximum corallite diameter; ST1, septum thickness (first cycle); ST2, septum thickness (second cycle). All measurements were made to the nearest 0·01 mm. On poorly preserved colonies, only CD–MIN, NND, and T2 were measured.

Corallites were judged to be mature if their highest septal cycle was relatively well-developed.

In general, these characters estimate the sizes of various corallite architectural features, and the size and spacing of corallites. They were selected because they represent a minimal set of diagnostic characters within a larger suite of characters used in previous morphometric work on fossil and living species of *Montastraea* (Budd 1991, 1993), a closely related genus which shares almost all of the same features (Table 1). In this previous work, morphometric species recognized using methods similar to those in the present study were found to correspond well with biological species recognized using molecular data. A few previously used morphometric characters of *Montastraea*, including several measurements related to skeletal density, spacing and trabecular thickness, could not be measured in the present study because of inadequate preservation. These measurements are sometimes taken more accurately in longitudinal section. Characters measured in the present study that are unique to *Tarbellastraea* include the dimensions of the columella tubercle (CL1, CL2), the thickness of the parathecal wall (T2) and costa length (T1).

The measurements and counts used in the present study are similar to those used by Chevalier (1962). However, again, as mentioned above, because of inconsistencies in preservation, not all of the characters treated by Chevalier (1962) could be measured, and analysed statistically. No measurements could be made of calical relief, or of the structure and development of the endo- or exotheca. Similarly, no measurements were made of overall colony size or shape. These characters are, however, treated qualitatively in the species descriptions.

Moreover, on some corallites, only some of the 12 characters (Text-fig. 3) could be measured, due to inadequate preservation. This is especially true of colonies from SP and SR, on which measurements of septal thickness (ST1, ST2) could not be reliably obtained. Because of missing data in these cases, morphological clusters were first distinguished by analysing only data from well-preserved material. Data from less well-preserved material were subsequently compared statistically with these initial morphological clusters.

In sum, the characters measured and statistically analysed in the present study are not the only characters that can be used to distinguish the species studied. They merely represent the characters with high species diagnostic potential based on previous work, and characters that could most easily and consistently be measured on the largest number of colonies in the assembled material.

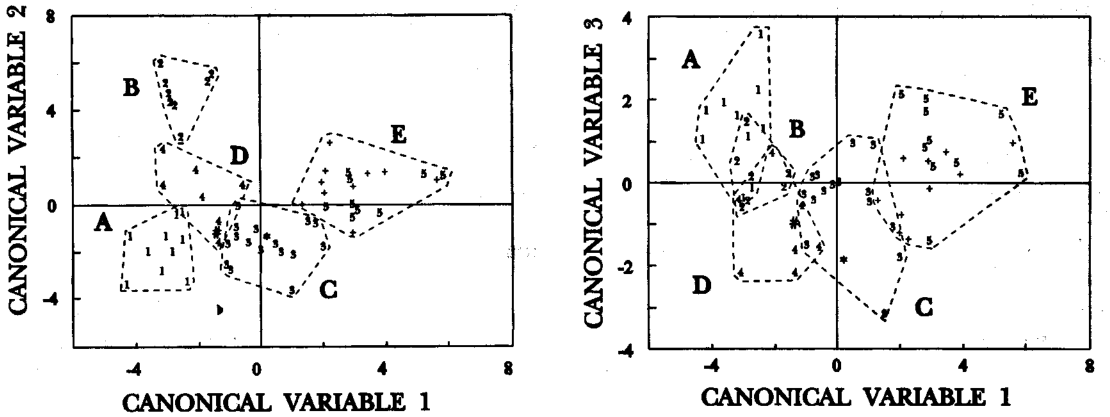
Statistical analyses

In order to recognize morphometric species, we used two major types of multivariate statistical procedures: (1) average linkage cluster analysis (UPGMA) and (2) canonical discriminant analysis. First, we analysed the measurement and count data for well-preserved colonies from each of the two stratigraphical levels and distinguished morphological clusters within each level. Then we compared less well-preserved colonies with the resulting morphological clusters. Finally we compared clusters between stratigraphical levels to recognize morphometric species. Our protocol is described in detail by Budd and Coates (1992) and Budd *et al.* (1994); the analyses were performed using the SAS version 6·09 for UNIX statistical procedures.

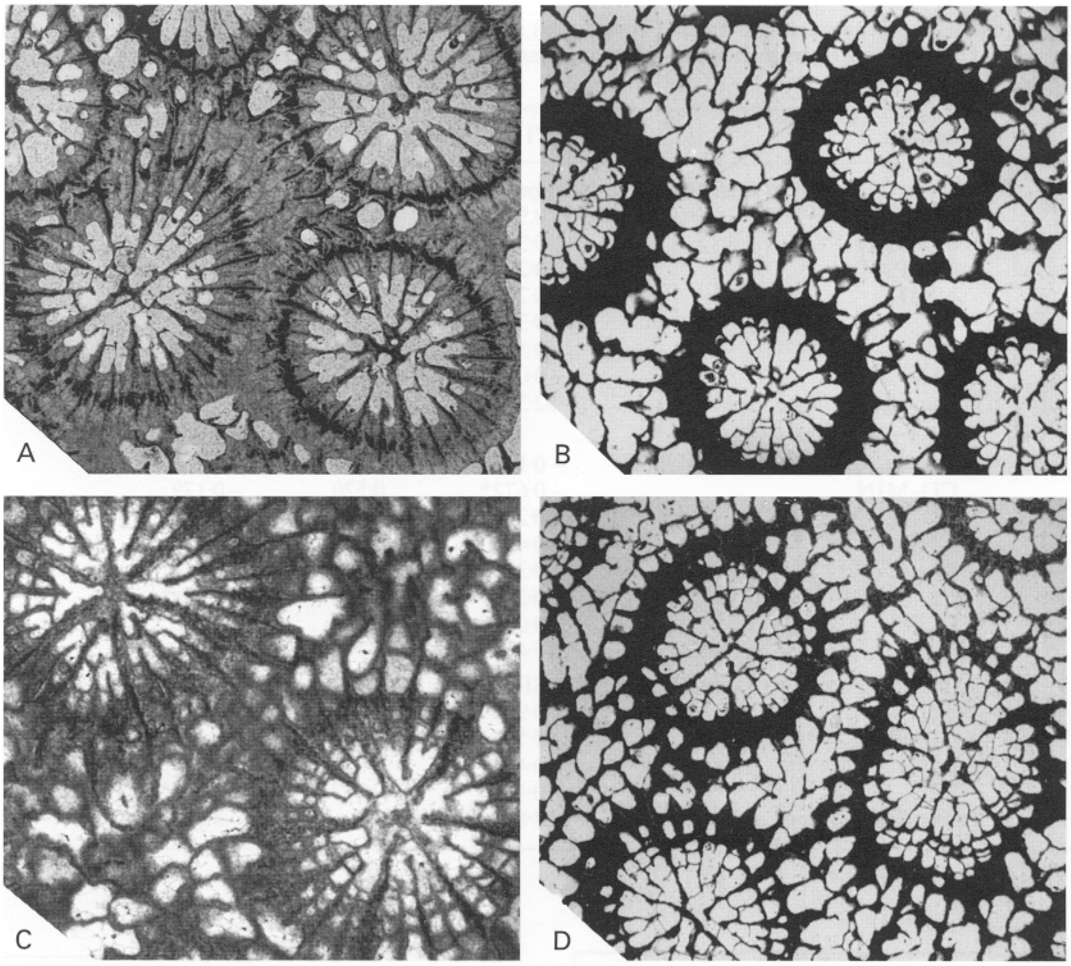
The first step involved performing average linkage cluster analysis on colonies from each of the two stratigraphical levels. In this initial cluster analysis, in order to prevent unknowingly assigning excessive weight to any one aspect of morphology, we selected a set of well-preserved, geometrically independent characters, with low Pearson's correlation coefficients (i.e. significantly less than 0·60). In the Upper Oligocene to Lower Miocene level, the characters consisted of NS, CD-MIN, NND, CL2, T1, T2. In the Middle to Upper Miocene level, the characters consisted of these six characters plus primary septum thickness (ST1). In the upper stratigraphical level, two ratios were also included: (1) the ratio between CD-MIN and CD-MAX ('CD-RAT') and (2) the ratio between ST2 and ST1 ('ST-RAT'). The first ratio served as an estimate of corallite ellipticity; the second served as an estimate of equality of the primary and secondary septa. Because the selected characters were found to have little or no correlation with corallite size (CD-MIN), no further transformations were made.

TABLE 3. Correlations between characters (Text.-fig. 3) and canonical variables (CV) in three final canonical discriminant analyses. Logarithms were taken in characters derived from linear measurements. *Heavily weighted characters.

Character	CV1	CV2	CV3
1. Late Oligocene to Early Miocene (well preserved colonies only)			
NS	0.903*	−0·162	−0·015
CD–MIN	0·379	−0·345	−0·261
CD–RAT	−0·297	0·253	0·363
NND	−0·246	0·579*	−0·227
T1	0·324	0·562*	0·379
T2	−0·507	−0·017	0·491*
CLW	−0·036	−0·365	0·465*
Percentage variance explained	52·3	37·7	5·54
2. Mid to Late Miocene			
NS	−0·117	−0·141	0·316
CD–MIN	−0·672*	0·520	−0·179
CD–RAT	0·280	0·315	−0·178
NND	−0·426	0·650*	0·531
T1	0·326	0·725*	0·514
T2	0·267	−0·032	0·804*
CLW	−0·044	−0·084	−0·330
Percentage variance explained	45·4	38·7	15·9
3. Late Oligocene to Early Miocene (SP, SR unclassified)			
NS	0·900*	0·343	0·250
CD–MIN	0·513	−0·044	0·469*
NND	−0·464	0·527*	0·489*
T2	−0·438	−0·257	0·544*
Percentage variance explained	63·8	31·1	3·3

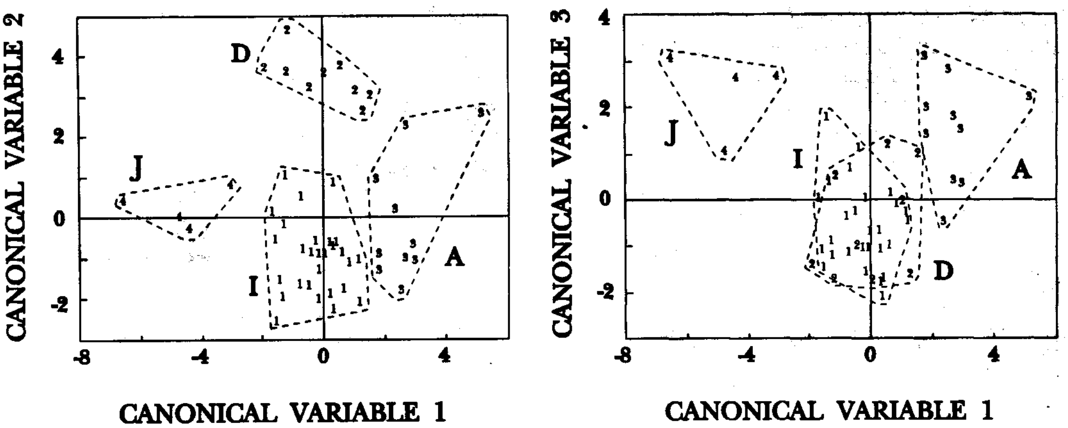


TEXT-FIG. 4. Plots of scores on the first three canonical variables in the canonical discriminant analysis of well-preserved Upper Oligocene to Lower Miocene colonies. Each point represents a colony mean. Symbols for each point refer to the cluster to which the colony was assigned. Dashed lines outline the range of variation within each cluster. Letters refer to morphometric species to which these clusters were later assigned. *, holotype of *T. carryensis* (MNHN, I.P.-R10521); #, holotype of *T. aquitaniensis* (MNHN, I.P.-R10518); +, topotypes of *T. ellisiana* (MNHN, I.P.).



TEXT-FIG. 5. Transverse thin sections of four of the five statistically recognized species in the Upper Oligocene to Lower Miocene. A, cluster 1 (morphometric species A), SUI-84718-A; B, cluster 2 (morphometric species B), SUI-51257-D; C, cluster 3 (morphometric species C), SUI-84765-C; D, cluster 5 (morphometric species E), MNHN, I.P., AFB # 135-C. All × 11.

Because ecophenotypic plasticity is high in colonial scleractinians and corallites within colonies are highly variable (see Budd *et al.* 1994 for discussion), we used Mahalanobis distances when performing cluster analyses, in order to reduce variational noise and to emphasize differences *among* colonies rather than *within* colonies, when recognizing species quantitatively. To establish a cut-off for cluster recognition on the cluster analysis dendrograms, we arbitrarily subdivided the corallites for each colony into two groups of 'colony halves' in colonies, and calculated Mahalanobis distances among all halves within each stratigraphical level. Only colonies with more than five measured corallites were subdivided. Cut-offs for cluster recognition were established where: (1) the highest number of clusters could be recognized, and (2) more than 85 per cent. of the two halves of each colony belonged to the same cluster. In the Upper Oligocene to Lower Miocene level, a total of 60 halved and four unhalved colonies (localities = NE, EG, DX, LP) were included in the initial analysis, and eight clusters were recognized using a cut-off, in which the halves of only three of the



TEXT-FIG. 6. Plots of scores on the first three canonical variables in the canonical discriminant analysis of well-preserved Middle to Upper Miocene colonies. Each point represents a colony mean. Symbols for each point refer to the cluster to which the colony was assigned. Dashed lines outline the range of variation within each cluster. Letters refer to morphometric species to which the clusters were later assigned.

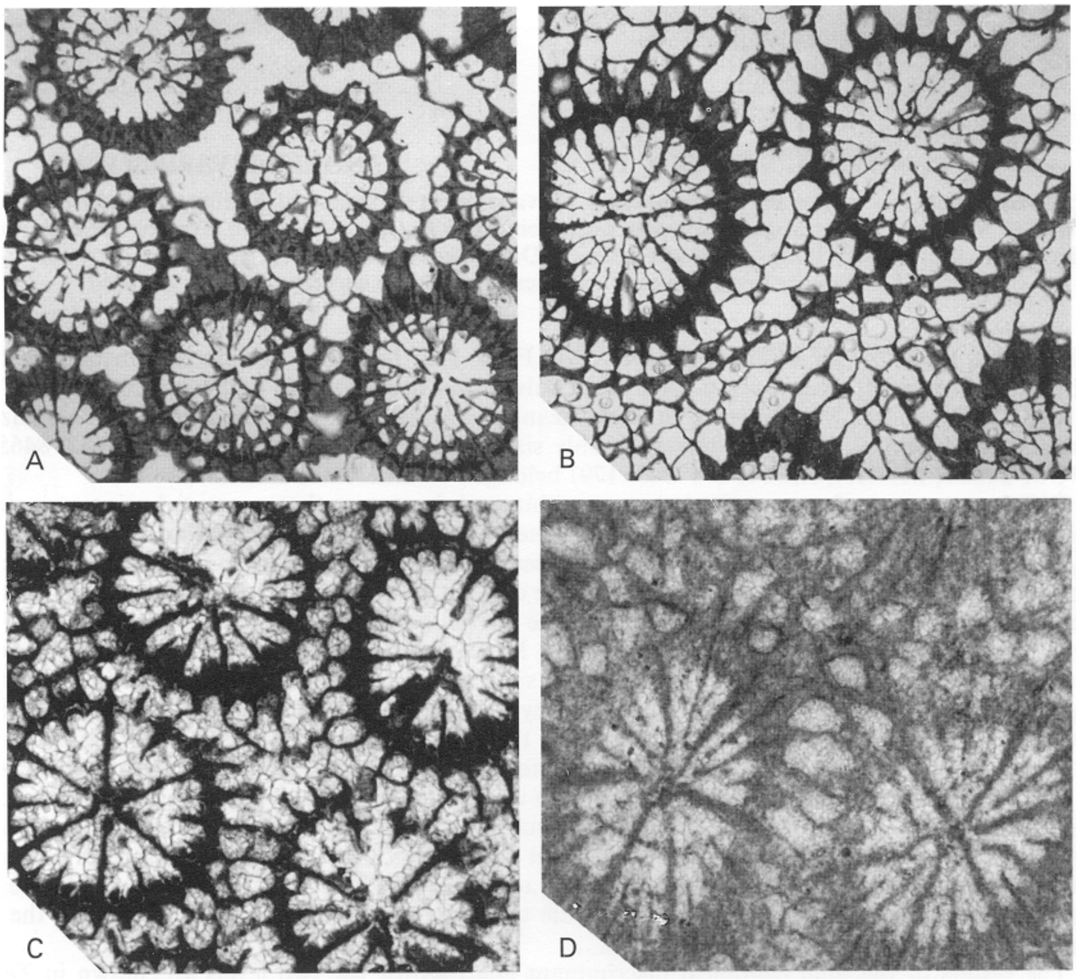
60 colonies (SUI 84735, 84764; MNHN, I.P.-AFB# 132) belonged to different clusters. In the Middle to Upper Miocene level, a total of 46 halved and five unhalved colonies (localities = TO, GR, BL, LD, SI, AL, MA) were included in the initial analysis, and seven clusters were recognized based on a cut-off in which the halves of only six of the 46 colonies (SUI 84704, 84652, 84658; IPUM 24884; MNHN, I.P.-AFB# 043, 179) belonged to different clusters.

Differences among the recognized clusters within each level were then examined using canonical discriminant analysis on data for each corallite. Logarithmic transformations were used for measurement data when performing these analyses, because sample sizes in different clusters were not equal and because measurement data in some clusters were skewed toward larger values. In the analyses, unhalved colonies and colonies whose halves belonged to different clusters were left unclassified. In the Upper Oligocene to Lower Miocene level, study of Mahalanobis distances among clusters and canonical discriminant plots suggested that three of the eight clusters were not significantly different from the other clusters. They were therefore combined, yielding a total of five clusters. In the Middle to Upper Miocene level, three of the seven clusters were not significantly different from the other clusters, and were therefore combined, yielding a total of four clusters.

Posterior probabilities were then used to assign unassigned colonies to one of the clusters in both data sets, and a series of iterative discriminant analyses was run using colony means. In the series, misclassified colonies were reassigned to different clusters until the highest percentage of colonies was classified correctly. In the Upper Oligocene to Lower Miocene level, 96·9 per cent. of the 64 colonies were classified correctly. In the Middle to Upper Miocene level, 100 per cent. of the 51 colonies were classified correctly.

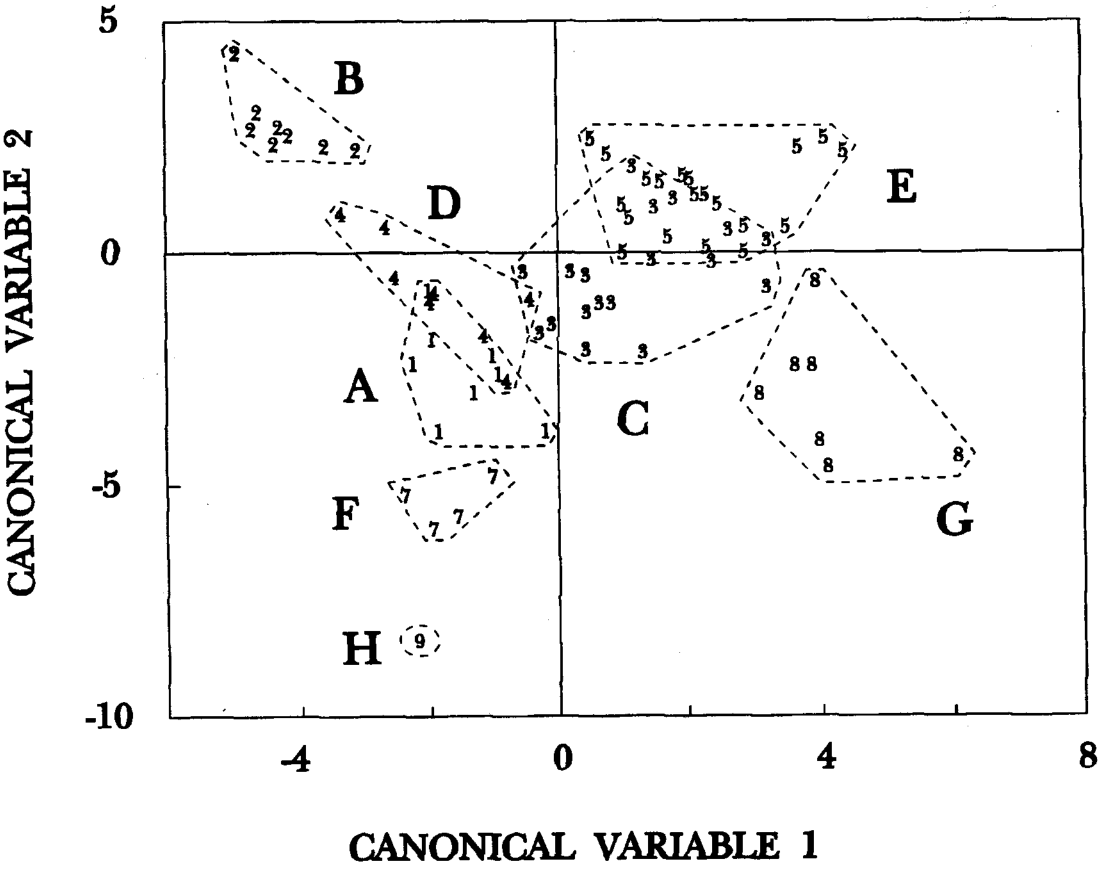
The results of the final canonical discriminant analyses for the two levels are shown in Text-figures 4–7, and correlations between the original characters (Text-fig. 3) and the canonical variables are given in Table 3. In the Upper Oligocene to Lower Miocene (Text-fig. 4), number of septa per corallite (NS) was most strongly correlated with the first canonical variable (Table 3) which distinguished clusters 1, 2 and 4 from cluster 3 and, to a lesser degree, cluster 3 from cluster 5. Characters related to distance between corallites (NND, T1) were most strongly correlated with canonical variable 2 (Table 3) which distinguished cluster 1 from cluster 2, and cluster 3 from cluster 5. These differences among clusters in number of septa and distance between corallites were clearly seen in thin sections (Text-fig. 5). Furthermore, theca thickness (T2) and size of corallite centre (CLW) were correlated most strongly with canonical variable 3 (Table 3) which distinguished cluster 1 from cluster 4.

In the Middle to Upper Miocene (Text-fig. 6), corallite diameter (CD-MIN) was correlated most strongly with the first canonical variable (Table 3), which distinguished cluster 4 from clusters 1 and 2, and clusters 1 and 2 from cluster 3. Characters related to distance between corallites (NND, T1) were correlated most strongly with canonical variable 2 (Table 3) which distinguished cluster 2 from cluster 1. The differences among clusters in corallite diameter and distance between corallites are clearly seen in thin sections (Text-fig. 7). Furthermore, theca thickness (T2) was correlated most strongly with canonical variable 3 (Table 3) which distinguished clusters 1 and 2 from clusters 3 and 4.

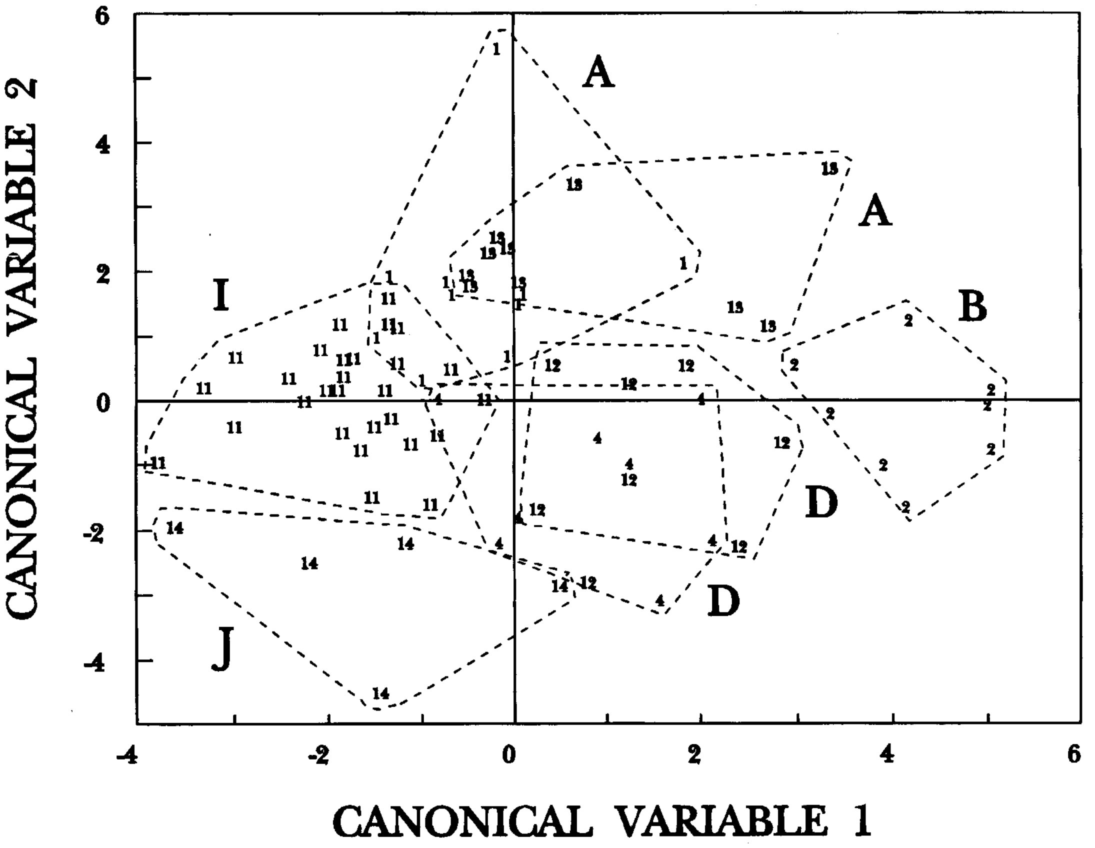


TEXT-FIG. 7. Transverse thin sections of the four statistically recognized species in the Middle to Upper Miocene. A, cluster 3 (morphometric species A), SUI-84673-H; B, cluster 2 (morphometric species D), SUI-84671-G; C, cluster 1 (morphometric species I), SUI-84703-E; D, cluster 4 (morphometric species J), SUI-84659-A. All ×11.

The next step in our protocol for recognizing morphometric species involved comparing statistically the canonical discriminant results above, with data from less well preserved colonies collected at SP and SR. Measurements and counts on these colonies, similar to those in the analyses above, could only be made for four characters (Text-fig. 3): CD-MIN, NND, T2, NS. It is important to note, however, that these four characters were found to be the most important in distinguishing clusters in the analyses above. To make the statistical comparisons, a series of canonical discriminant analyses was run with data for the 64 Upper Oligocene to Lower Miocene colonies above, eight colonies from SP, and four colonies from SR. This analysis was run using four characters (CD-MIN, NND, T2, NS) and five groups (the five Upper Oligocene to Lower Miocene clusters in Text-fig. 4). The 12 newly added colonies were left unclassified. The results (Text-fig. 8) showed that the 12 newly added colonies did not lie within the margins of any of the five Upper Oligocene to Lower Miocene clusters recognized earlier. Instead, seven of the colonies from SP formed a separate group with high values on CV1, which was correlated most strongly with number of septa per corallite (NS) (Table 3). Similarly, the four colonies from SR formed a group with low values on CV2, which was correlated most strongly with distance between corallites (NND) (Table 3). A single colony from SP had exceedingly low values on CV2 and CV3, which were correlated most strongly with distance between corallites (NND) and size (CD-MIN) respectively (Table 3).



TEXT-FIG. 8. Plot of scores on the first two canonical variables in the canonical discriminant analysis of Upper Oligocene to Lower Miocene colonies including SP and SR. Each point represents a colony mean. Symbols for each point refer to the cluster to which the colony was assigned. Dashed lines outline the range of variation within each cluster. Letters refer to morphometric species to which these clusters were later assigned.



TEXT-FIG. 9. Plot of scores on the first two canonical variables in the canonical discriminant analysis of three Upper Oligocene to Lower Miocene clusters and four Middle to Upper Miocene clusters. Each point represents a colony mean. Symbols for each point refer to the cluster to which the colony was assigned. Dashed lines outline the range of variation within each cluster. Letters refer to morphometric species to which these clusters were later assigned.

We therefore interpret the two groups and the one odd colony to represent three distinct clusters, yielding a total of eight clusters in the Upper Oligocene to Lower Miocene.

In the final step of our protocol for recognizing species, we compared the eight clusters in the Upper Oligocene to Lower Miocene with the four clusters in the Middle to Upper Miocene level using another series of canonical discriminant analyses. An initial analysis showed that no overlap occurred between Upper Oligocene to Lower Miocene clusters 3 and 5–8, and the four Middle to Upper Miocene clusters. Therefore, a separate analysis was run with only Upper Oligocene to Lower Miocene clusters 1, 2 and 4 and the four Middle to Upper Miocene clusters. A total of 78 colonies and seven characters (NS, CD-MIN, CD-RAT, NND, T1, T2, CL2) was used in the analysis. The results showed that differences between cluster 1 in level 1 and cluster 3 in level 2 are insignificant, and differences between cluster 4 in level 1 and cluster 2 in level 2 are insignificant (Text-fig. 9). These clusters were therefore linked.

The results of the final statistical analyses suggest that a total of 10 morphometric species of *Tarbellastraea* lived in the investigated basins during the Late Oligocene to Late Miocene. For the remainder of our discussion, these statistically recognized morphometric species will be referred to as ‘A’ to ‘J’. The relationships between the ten morphometric species and the statistically recognized clusters are: morphometric species A = cluster 1 in level 1 and cluster 3 in level 2; morphometric species B = cluster 2 in level 1; morphometric species C = cluster 3 in level 1; morphometric species D = cluster 4 in level 1 and cluster 2 in level 2; morphometric species E = cluster 5 in level 1; morphometric species F = cluster 6 in level 1; morphometric species G = cluster 7 in level 1; morphometric species H = cluster 8 in level 1; morphometric species I = cluster 1 in level 2; morphometric species J = cluster 4 in level 2. Means and standard deviations for the 12 measured characters (Text-fig. 3), NS, CD-RAT, and ST-RAT in the ten statistically recognized morphometric species are given in Appendix 1.

COMPARISON WITH TYPE SPECIMENS

Selection of type specimens

In order to assign names to the statistically recognized morphometric species, information was assembled about the primary types of all species and varieties that have previously been assigned to the genus *Tarbellastraea*. Primary types of species of the other seven genera in Table 1 were also considered, if they were collected in the regions that we considered in our study and if they strongly resembled *Tarbellastraea*. The final list of species is given in Table 4.

The calical surfaces of the type specimens of all species and varieties in Table 4 were first examined to determine if they possessed the diagnostic characteristics of *Tarbellastraea* given in Table 1. Two type specimens in Table 4 (*Leptastraea anomala* and *Orbicella eggenburgensis*) had a spongy columella (Text-fig. 10) and therefore clearly did not belong to *Tarbellastraea*. Another (*T. bliosi*) had paliform lobes, and therefore also did not belong. Three others (*Astrea astroites* = *T. organalis* Barta-Calmus, 1973, *Phyllocoenia ovalis* and *T. ukrainica*) had very large calices (> 5 mm) and four or more cycles of septa, and thus also did not belong. The remaining 25 species in Table 4 possessed the diagnostic characteristics of *Tarbellastraea*, and were therefore considered when determining names for the statistically recognized species.

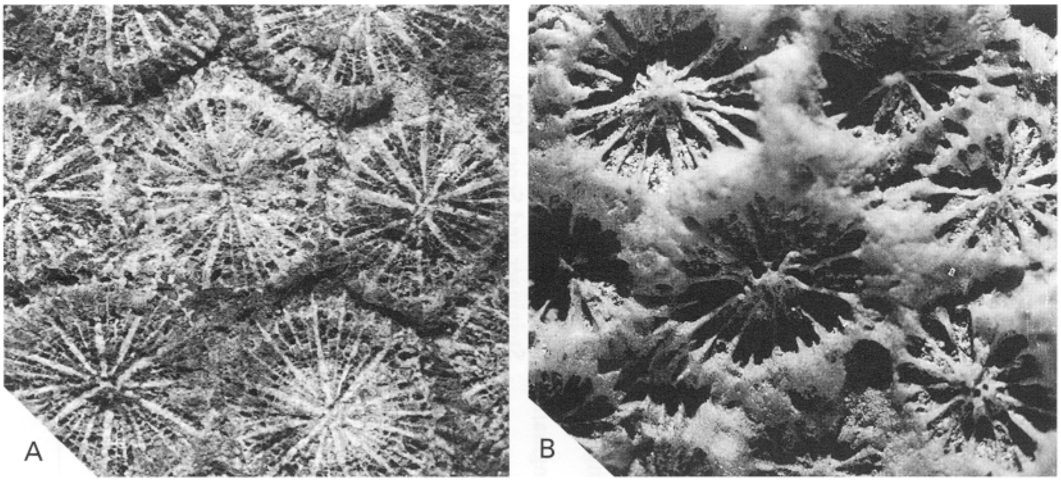
Synonymies

Where possible, three measurements (NS, CD-MIN, NND) were made on calical surfaces of the types of the 25 species and varieties (Appendix 2). In two cases (*P. carryana* and *T. aquitaniensis*), thin sections were available of the holotype, so measurements were made directly from these and included in the original canonical discriminant analysis (Text-fig. 4). In one case (*Explanaria crassa*), the preservation was extremely poor, so no measurements could be made. In four other cases (*T. distans*, *A. ellisiana*, *T. edwardsi*, *T. ellisiana* var. *manthelanensis*), the type specimens were either lost or unavailable for measurement. For *T. distans*, measurements of the holotype were taken from Barta-Calmus (1973). For *T. edwardsi* and *T. ellisiana* var. *manthelanensis*, no measurements of the holotype exist in the literature; therefore, only a qualitative assessment could be made (see species descriptions of *T. profundata* and *T. bragai* below). For *A. ellisiana*, the holotype is lost, and the neotype designated by Alloiteau (1957, pl. 8, figs 4, 15; MNHN, I. P. R10933) could not be located. Therefore, measurements were made directly on thin sections of ten 'topotype' specimens in the general collections in Paris (MNHN, I. P., AFB # 129, 131, 133–140) labelled as '*Tarbellastraea ellisiana* (Defrance, 1826)' from Mérignac, Gironde (Aquitaine, France), and included in the original canonical discriminant analysis (Text-fig. 4). These specimens were amongst the material studied by Alloiteau (1957) in designating his neotype, and were also studied by Chevalier (1962). We hesitate to designate another neotype for *T. ellisiana*, as long as the potential exists for Alloiteau's (1957) neotype to be found.

In the remaining 18 types, the three measurements (NS, CD-MIN, NND) were made on the calical surfaces of holotypes. As with the 13 localities (Table 2), one of us (FRB) determined the geological age dates for the type locality of each of the 25 species and varieties of *Tarbellastraea* by consulting with specialists on the local geology of the area, and by conducting a thorough review of the most recent literature (Table 5). As mentioned earlier, problems in age determination are to be discussed in fuller detail in a second paper.

TABLE 4. List of type specimens examined. Types of underlined species were found not to be belong to *Tarbellastraea*. Measurements were made on types of species with code numbers. *, holotype lost; **, holotype not seen; ***, holotype not seen, but recent photograph examined.

	Species	Code	Reference	Repository and catalogue number
	Tarbellastraea abditaxis Chevalier, 1962	1	p. 204, pl. 6, fig. 10; pl. 23, fig. 8	MNHN, I.P.-R10525
	Leptastraea anomala Michelotti, 1871	—	p. 306, pl. 8, fig. 7	MPUR-3302
	Tarbellastraea aquitaniensis Chevalier, 1962	2	p. 201, pl. 9, fig. 12; pl. 23, fig. 2	MNHN, I.P.-R10518
	Tarbellastraea aquitaniensis var. *termofurae* Chevalier, 1962	3	p. 202, pl. 8, figs 17–18	MNHN, I.P.-R10575
	Astrea astroites Catullo, 1856	—	p. 59, pl. 12, fig. 4	MPUP-8261
	Tarbellastraea bliosi Barta-Calmus, 1973	—	p. 280, pl. 15, figs 6–8	MNHN, I.P.-R55164
	Phyllocoenia carryana d'Orbigny, 1852	4	p. 147	MNHN, I.P.-R10521
	Tarbellastraea carryensis var. *major* Chevalier, 1962	5	p. 198, pl. 7, fig. 8	MNHN, I.P.-R10523
	Tarbellastraea carryensis var. *minor* Chevalier, 1962	6	p. 198, pl. 10, figs 3, 9–10	MNHN, I.P.-R10522
	Heliastraea conoidea Reuss, 1872	7	p. 240, pl. 10, fig. 3	NHMW-1854.XXXV.500
	Explanaria crassa Reuss, 1847	—	p. 18, pl. 3, fig. 1	NHMW-1832.I.1358
***	*Tarbellastraea distans* Chevalier, 1962	8	p. 208, pl. 5, fig. 9	MNHN, I.P.-R55165
***	*Tarbellastraea edwardsi* Chevalier, 1955	—	p. 390, pl. 3, fig. 4	MNHN, I.P.-M00787 (= *P. archiaci*)
	Orbicella eggenburgensis Kühn, 1925	—	p. 5, pl. 1, figs 1–2	KME
	Tarbellastraea cf. *eggenburgensis* (Kühn); Chevalier, 1962	9	p. 202, pl. 6, fig. 3; pl. 24, fig. 9	MNHN, I.P.
	Orbicella eggenburgensis var. *formosa* Kühn, 1925	10	p. 7, pl. 1, fig. 3	KME
	Tarbellastraea eggenburgensis var. *andalousiensis* Chevalier, 1962	11	p. 203, pl. 9, fig. 13; pl. 23, fig. 9	MNHN, I.P.-R10528
*	*Astrea ellisiana* Defrance, 1826	—	p. 382	—
**	*Tarbellastraea ellisiana* var. *manthelanensis* Chevalier, 1962	—	p. 195, pl. 5, fig. 4	MNHN, I.P.-R10509
	Solenastraea manipulata Reuss, 1872	12	p. 243, pl. 8, fig. 2	NHMW-1984/61
	Tarbellastraea minbastensis Chevalier, 1962	13	p. 199, pl. 5, fig. 3; pl. 23, fig. 1	MNHN, I.P.-R10529
***	*Phyllocoenia ovalis* Gümbel, 1861	—	p. 666	BSPHGM-AS-38
	Astraea prevostiana Milne Edwards and Haime, 1850	14	p. 110	MNHN, I.P.-M01184
	Astrea profundata Catullo, 1856	15	p. 56, pl. 11, fig. 6	MPUP-8142
	Astraea raulini Milne Edwards and Haime, 1850	16	p. 110	MNHN, I.P.-M01281
	Astraea reussiana Milne-Edwards and Haime, 1850	17	p. 110	MHMW-1846.37.967 (= *E. astroites*)
	Tarbellastraea reussiana var. *echinulata* Chevalier, 1962	18	p. 206, pl. 5, fig. 18; pl. 24, fig. 7	MNHN, I.P.-R10510
	Tarbellastraea siciliae Chevalier, 1962	19	p. 207, pl. 7, fig. 10; pl. 23, fig. 7	MNHN, I.P.-R10527
	Explanaria tenera Reuss, 1847	20	p. 18, pl. 3, fig. 2	NHMW-1872.XIII.61
	Orbicella transsylvanica Kühn, 1925	21	p. 4	NHMW-1872.XIII.56
**	*Tarbellastraea ukrainica* Kuzmicheva, 1987	—	p. 105, pl. 16, figs 1–2	MGU-N185/507



TEXT-FIG. 10. Calical surfaces of holotypes of two species that have been previously assigned to *Tarbellastraea* but do not belong in this genus. A, *Astrea astroites* Catullo, 1856 (= *Tarbellastraea organalis* Barta-Calmus, 1973); MPUP-8261. B, *Leptastraea anomala* Michelotti, 1871; MPUR-3302. Both ×5.

In the three cases where thin section measurements were made (*T. aquitaniensis*, *P. carryana*, *A. ellisiana*), the type specimens for these species were assigned to the statistically recognized species as part of the canonical discriminant analyses, and synonymies between the statistical species and these type specimens were determined on the basis of the results of this analysis (Text-fig. 4). In this procedure, *T. aquitaniensis* was only synonymized questionably with statistical species D, because of the large distance of its holotype from the centre of that cluster. The type specimen for *P. carryana* clearly lay in the centre of statistical species C, and the topotypes for *A. ellisiana* definitely belonged to statistical species E. Therefore, synonymies for these two species were made without question.

In the remaining 19 cases (including *T. distans*) where measurements were made on calical surfaces of holotypes (Appendix 2), bivariate plots were constructed for number of septa (NS) *vs* distance between corallites (NND), and for corallite diameter (CD) *vs* distance between corallites (NND) using the same two major stratigraphical levels as in the canonical discriminant analyses: (1) Upper Oligocene to Lower Miocene and (2) Middle to Upper Miocene (Text-fig. 11). On each plot, type specimens (labelled 1–21) were considered to be synonymous with a given statistically recognized morphometric species (labelled A–J), if they lay near the statistical species on both of the two plots. In two cases (type 13 with morphometric species E in the Upper Oligocene to Lower Miocene; type 21 with morphometric species I in the Middle to Upper Miocene), only questionable synonymies were made because of the large distance between the type specimen and the statistical species. A questionable synonymy was also made for type 6 with morphometric species F, because of difference in structure of the columella and wall. Two groups of types (1, 3, 9, 11 in the Upper Oligocene to Lower Miocene; 5, 15 in the Middle to Upper Miocene) formed clusters separate from any of the statistical species, and therefore were considered to be distinct morphometric species unrepresented in the statistical analyses. A summary of the results of these comparisons is given in Table 6.

In general, a total of 12 species of *Tarbellastraea* was found to have lived in the investigated European and Mediterranean regions during the Late Oligocene to Late Miocene. The distinguishing characteristics for these 12 species are summarized in Table 7, and formal descriptions are provided in the section below on systematic palaeontology. Although the overall number of species is similar to that recognized by Chevalier (1962), nine of his 19 species and

TABLE 5. List of localities for type specimens of *Tarbellastraea* with current interpretations of their geological age.

Species	Type locality	Age	Age reference
1. *Tarbellastraea abditaxis*	Sciolze (Torino, Italy)	Burdigalian-Langhian	Bonsignore *et al.* 1969
2. *Tarbellastraea aquitaniensis*	Le Peloua (Gironde, France)	Early Burdigalian	Cahuzac and Chaix 1993
3. *Tarbellastraea aquitaniensis* var. *termofurae*	Termô Fôrà (Torino, Italy)	Burdigalian–Langhian	Bonsignore *et al.* 1969
4. *Phyllocoenia carryana*	Carry-le-Rouet (Bouches-du-Rhône, France)	Late Chattian	Monleau *et al.* 1988
5. *Tarbellastraea carryensis* var. *major*	Carry-le-Rouet (Bouches-du-Rhône, France)	Late Chattian	Monleau *et al.* 1988
6. *Tarbellastraea carryensis* var. *minor*	Carry-le-Rouet (Bouches-du-Rhône, France)	Late Chattian	Monleau *et al.* 1988
7. *Heliastraea conoidea*	Enzesfeld (Vienna, Austria)	Badenian	Piller and Kleemann 1991
— *Explanaria crassa*	Vienna Basin (Austria)	Badenian	Piller and Kleemann 1991
8. *Tarbellastraea distans*	Albugnano (Torino, Italy)	Burdigalian–Langhian	Bonsignore *et al.* 1969
— *Tarbellastraea edwardsi*	Gaas (Landes, France)	Stampian	Chevalier 1955
9. *Tarbellastraea* cf. *eggenburgensis*	Sciolze, Albugnano (Torino, Italy)	Burdigalian–Langhian	Bonsignore *et al.* 1969
10. *Orbicella eggenburgensis* var. *formosa*	Eggenburg (Vienna, Austria)	Eggenburghian	Steininger and Senes 1971
11. *Tarbellastraea eggenburgensis* var. *andalousiensis*	Quentar (Granada, Spain)	Late Tortonian	Braga *et al.* 1990
— *Tarbellastraea ellisiana*	Mérignac (Gironde, France)	Early Burdigalian	Cahuzac and Chaix 1993
— *Tarbellastraea ellisiana* var. *manthelanensis*	Manthelan (Indre-et-Loire, France)	Langhian	Cavelier *et al.* 1980
12. *Solenastraea manipulata*	Enzesfeld (Vienna, Austria)	Badenian	Piller and Kleemann 1991
13. *Tarbellastraea mimbastensis*	Mimbaste (Landes, France)	Early Burdigalian	Cahuzac 1984
14. *Astraea prevostiana*	Malta	Late Toronian–Early Messinian	Giannelli and Salvatorini 1975; Pedley 1989
15. *Astrea profundata*	Montecchio (Vicenza, Italy)	Rupelian	Bosellini 1988
16. *Astraea raulini*	Le Peloua (Gironde, France)	Early Burdigalian	Poignant and Pujol 1978
17. *Astraea reussiana*	Vienna Basin (Austria)	Badenian	Piller and Kleemann 1991
18. *Tarbellastraea reussiana* var. *echinulata*	Mérignac (Gironde, France)	Early Burdigalian	Cahuzac and Chaix 1993
19. *Tarbellastraea siciliae*	Landro (Sicily, Italy)	Late Tortonian	Catalano 1979
20. *Explanaria tenera*	Vienna Basin (Austria)	Badenian	Piller and Kleemann 1991
21. *Orbicella transsylvanica*	Enzesfeld (Vienna, Austria)	Badenian	Piller and Kleemann 1991

TABLE 6. List of species found to be synonymous by examination of measurements made on type specimens, as shown in Text-figure 11.

Code	Species found to be synonymous	Name assigned
	Statistical species A	
20	*Explanaria tenera* Reuss, 1847	*Tarbellastraea tenera* (Reuss, 1847)
7	*Heliastraea conoidea* Reuss, 1872	
19	*Tarbellastraea siciliae* Chevalier, 1962	
	Statistical species B	
8	*Tarbellastraea distans* Chevalier, 1962	*Tarbellastraea distans* (Chevalier, 1962)
	Statistical species C	
4	*Phyllocoenia carryana* d'Orbigny, 1852	*Tarbellastraea carryensis* (d'Orbigny, 1852)
	Statistical species D	
16	*Astraea raulini* Milne Edwards and Haime, 1850	*Tarbellastraea raulini* (Milne Edwards and Haime, 1850)
14	*Astraea prevostiana* Milne Edwards and Haime, 1850	
2	?*Tarbellastraea aquitaniensis* Chevalier, 1962	
18	*Tarbellastraea reussiana* var. *echinulata* Chevalier, 1962	
	Statistical species E	
—	*Astrea ellisiana* Defrance, 1826	*Tarbellastraea ellisiana* (Defrance, 1826)
13	?*Tarbellastraea mimbastensis* Chevalier, 1962	
	Statistical species F	
6	?*Tarbellastraea carryensis* var. *minor* Chevalier, 1962	*Tarbellastraea chevalieri* sp. nov.
	Statistical species G	*Tarbellastraea russoi* sp. nov.
	Statistical species H	*Tarbellastraea salentinensis* sp. nov.
	Statistical species I	
17	*Astraea reussiana* Milne Edwards and Haime, 1850	*Tarbellastraea reussiana* (Milne Edwards and Haime, 1850)
12	*Solenastraea manipulata* Reuss, 1872	
21	?*Orbicella transsylvanica* Kühn, 1925	
	Statistical species J	*Tarbellastraea bragai* sp. nov.
10	*Tarbellastraea eggenburgensis* var. *formosa* Kühn, 1925	*Tarbellastraea abditaxis* (Chevalier, 1962)
1	*Tarbellastraea abditaxis* Chevalier, 1962	
3	*Tarbellastraea aquitaniensis* var. *termofurae* Chevalier, 1962	
9	*Tarbellastraea* cf. *eggenburgensis* Chevalier, 1962	
11	*Tarbellastraea eggenburgensis* var. *andalousiensis* Chevalier, 1962	
15	*Astrea profundata* Catullo, 1856	*Tarbellastraea profundata* (Catullo, 1856)
5	*Tarbellastraea carryensis* var. *major* Chevalier, 1962	

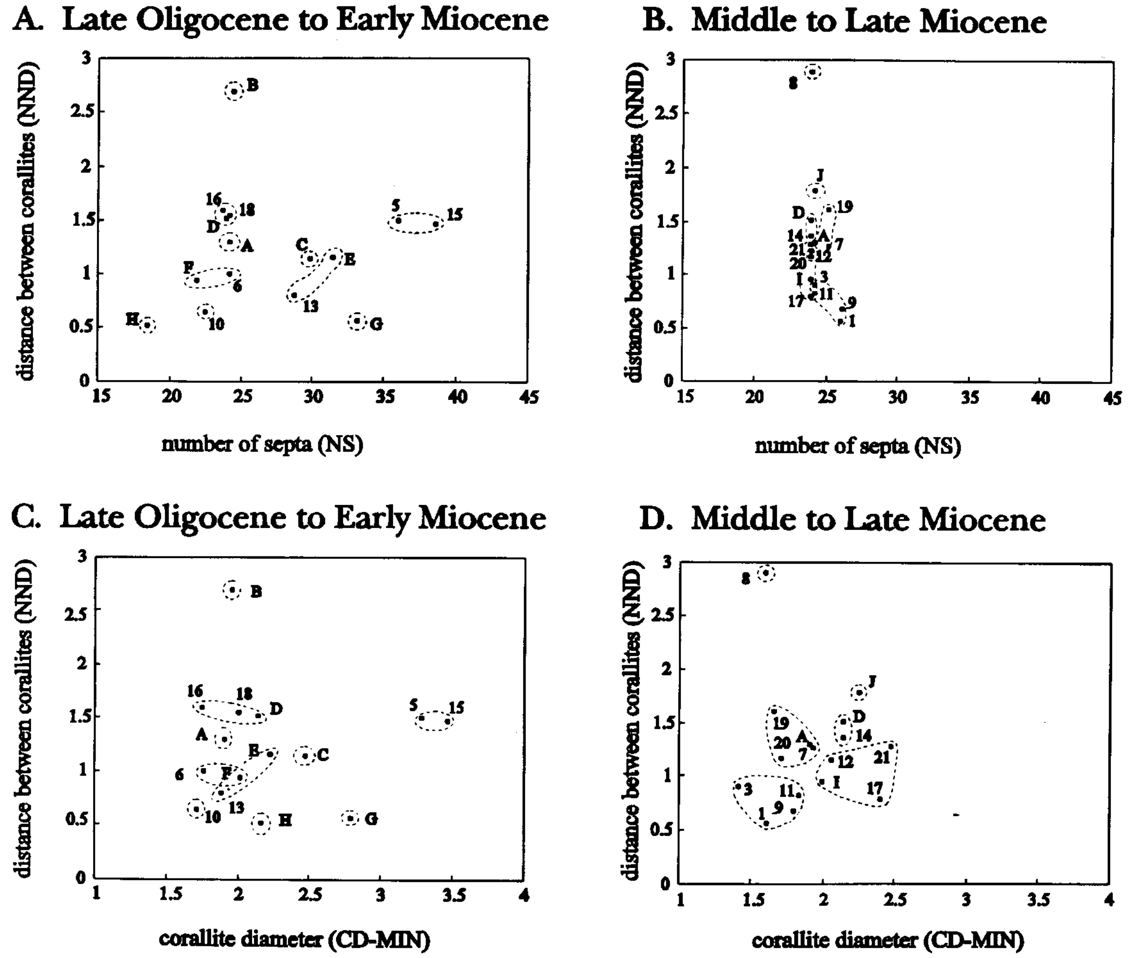
varieties are synonymized, and two new species are recognized from the Oligocene of Italy. Thus, our results suggest that some of Chevalier's (1962) species and varieties can be synonymized, but certainly not all, as advocated by Best *et al.* (1984).

In general, early during the evolution of the genus (Late Oligocene to Early Miocene), species exhibited a wider range of morphologies (Text-fig. 11). Number of septa per corallite (NS) ranged from 18 to 38, and corallite diameter (CD–MIN) ranged from 1·7 mm to 3·5 mm. In contrast, during the Mid to Late Miocene, number of septa per corallite (NS) ranged from 24 to 26, and corallite diameter (CD–MIN) ranged from 1·4 mm to 2·5 mm. Therefore, *Tarbellastraea* exhibited a striking decrease in overall morphological disparity through geological time.

TABLE 7. Distinguishing morphological characteristics of 12 species of *Tarbellastraea* that were found to have lived in the investigated regions during the Late Oligocene to Late Miocene. *, 'corallite spacing' refers to the distance between centres of adjacent calices.

Species	Colony form	Corallite shape	Corallite size (mm)	Corallite spacing* (mm)	Septal number	1st septal cycle length (mm)	Costae length (mm)
T. abditaxis	Massive	Round	1·5–2·3	2·2–3·0	23–25	< 1·1	Moderately long
T. bragai	Laminar, columnar or branched	Irregular	1·8–2·3	3·4–4·7	23–25	0·87–1·11	0·39–0·53
T. carryensis	Massive–columnar	Irregular	2·1–2·9	3·1–4·1	26–33	0·86–1·16	0·42–0·62
T. chevalieri	Massive	Round–irregular	1·6–2·4	2·5–3·4	19–25	0·66–0·94	Relatively short
T. distans	Massive	Round	1·7–2·1	4·1–5·2	23–26	0·68–0·84	0·49–0·79
T. ellisiana	Massive	Irregular	1·9–2·5	2·9–3·9	27–35	0·69–1·01	0·47–0·77
T. profundata	Massive–digitate	Round	3·3–3·5	4·8–5·0	36–39	1·2–1·6	Moderately long
T. raulini	Massive	Regular	1·6–2·3	3·0–4·2	23–25	0·75–0·97	0·39–0·63
T. reussiana	Massive	Round–irregular	1·7–2·1	2·5–3·3	23–25	0·67–0·87	0·32–0·47
T. russoi	Massive, knobby	Round–irregular	2·3–3·3	2·7–4·1	30–37	0·88–1·24	Moderately long
T. salentinensis	Massive–digitate	Irregular	1·8–2·5	2·6–2·8	15–22	0·70–0·86	Relatively short
T. tenera	Columnar	Round	1·6–2·0	2·7–3·7	23–25	0·63–0·79	0·42–0·78

Species	Wall structure	Wall thickness (mm)	Columella development	Columella form	Columella thickness (mm)	Endothecal dissepiments	Exotheca
T. abditaxis	Septothecal	0·15–0·25	Strong or weak	?Tied to septa	< 0·08	Weak or absent	No distinct banding
T. bragai	Septothecal	0·09–0·19	Strong or weak	Tied to septa	0·05–0·13	Weak or absent	Dense, horizontal layering
T. carryensis	Septothecal or partially parathecal	0·02–0·16	Strong or weak	Tied to septa	< 0·14	Well-developed; 1–3 rings	No distinct banding
T. chevalieri	Septothecal	0·09–0·29	Weak or absent	Tied to septa	0·05–0·09	Weak or absent	No distinct banding
T. distans	Septothecal	0·05–0·21	Weak	Free or tied to septa	< 0·08	Well-developed; 1 ring	Strong density banding
T. ellisiana	Septothecal or partially parathecal	0·01–0·20	Strong	Tied to septa	0·1–0·2	Well-developed; 1–3 rings	Strong banding and dense coenosteum
T. profundata	Septothecal	< 0·1	Strong	Tied to septa	< 0·13	Well-developed; 1–2 rings	No distinct banding
T. raulini	Septothecal	0·04–0·12	Weak	Tied to septa	0·05	Well-developed; 1–2 rings	Sparse density banding
T. reussiana	Septothecal	0·04–0·14	Weak	Free or tied to septa	0·08	Weak; 1 ring	No distinct banding
T. russoi	Septothecal	0·05–0·13	Strong	Tied to septa or free	< 0·15	Well-developed; 2 rings	Strong density banding
T. salentinensis	Septothecal	0·04–0·07	Weak or absent	Free or tied to septa	Not available	Absent	Dense horizontal layering
T. tenera	Septothecal	0·08–0·26	Strong	Tied to septa	0·06–0·15	Weak; 1 ring	Some density banding



A. Late Oligocene to Early Miocene

B. Middle to Late Miocene

C. Late Oligocene to Early Miocene

D. Middle to Late Miocene

TEXT-FIG. 11. Plots of mean measurements made on type specimens and statistically recognized species. Dashed lines enclose species that are interpreted to be synonymous. Numbers refer to codes given in Table 8; letters refer to statistically recognized species shown in Text-figures 4, 6 and 8–9. Measurement data for statistically recognized species are given in Appendix 1; measurement data for type specimens are given in Appendix 2.

STRATIGRAPHICAL AND GEOGRAPHICAL DISTRIBUTIONS OF SPECIES

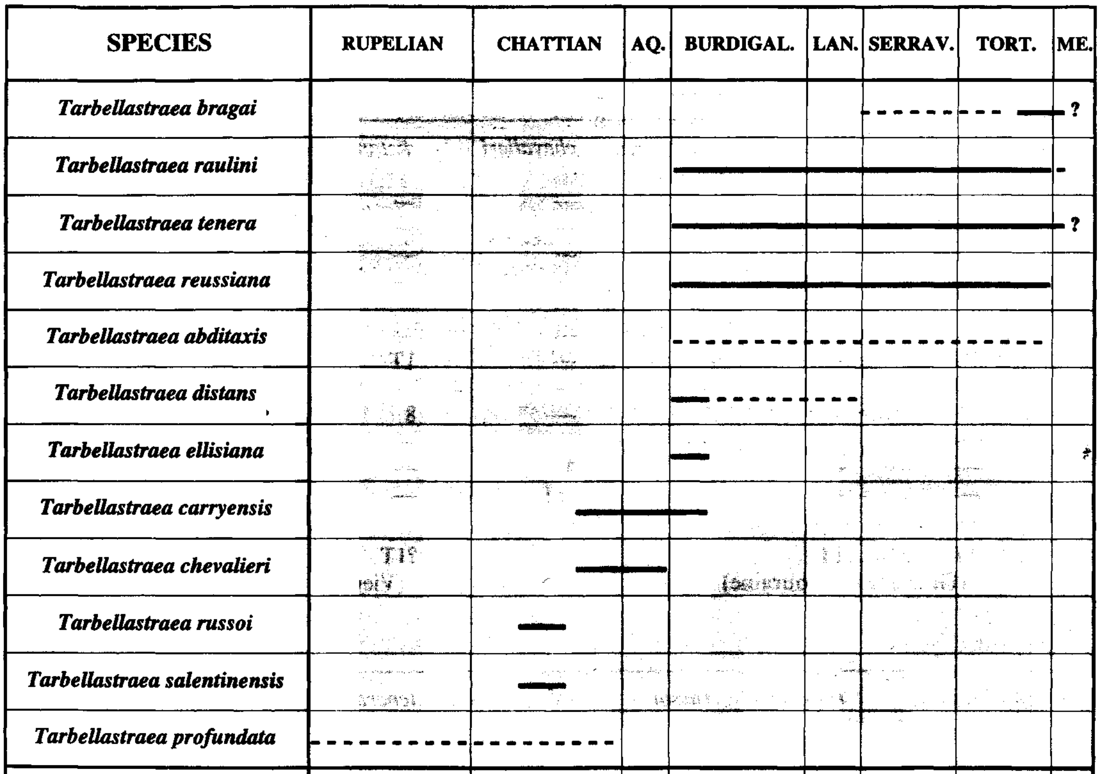
To examine evolutionary patterns within *Tarbellastraea*, we tabulated numbers of colonies of the 12 species occurring in the 13 collecting localities (Table 2) and other type localities (Table 5), and used the results (Table 8) to determine the stratigraphical ranges of species (Text-fig. 12). The genus as a whole appears to have ranged from the Oligocene (Rupelian) to the Early Messinian. Although some authors have suggested that the genus may have originated in the Eocene (e.g. Barta-Calmus 1973; Kuzmicheva 1987), our work clearly shows these earlier occurrences do not belong to the genus *Tarbellastraea* and that the genus most probably originated in the Early Oligocene, as suggested by Chevalier (1962). However, the ranges of most species extend between two or more stages of geological time, and they therefore cannot be considered diagnostic of any one stage (Text-fig. 12; cf. Chevalier 1962). Three possible exceptions are *Tarbellastraea russoi* and *T. salentinensis* which are restricted to the Middle Chattian, and *T. ellisiana* which is restricted to the Lower Burdigalian.

TABLE 8. Occurrences of species of *Tarbellastraea* in the 13 collecting localities used in the morphometric analysis. Locality abbreviations are given in Table 2. Numbers indicate number of non-type colonies examined (Including topotypes). Numbers with 'T's indicate number of primary types examined. E., Early; M., Mid; L., Late.

Locality	*abditaxis*	*bragai*	*carryensis*	*chevalieri*	*distans*	*ellisiana*	*profundata*
MA	—	1	—	—	—	—	—
AL	—	3	—	—	—	—	—
SI	—	—	—	—	—	—	—
LD	—	—	—	—	—	—	—
BL	—	—	—	—	—	—	—
GR	—	—	—	—	—	—	—
TO	3T	—	—	—	1T	—	—
EG	1T	—	—	—	—	—	—
LP	—	—	2	—	8	10, 1T	—
DX	—	—	—	—	—	10	—
SR	—	—	—	4	—	—	—
NE	—	—	15, 1T	?1T	—	—	1T
SP	—	—	—	—	—	—	—
Other	1T (Granada)	1T (Touraine)	—	—	?1T (Vienna)	—	1T (Vicentin), ?1T (Gaas)

Locality	*raulini*	*reussiana*	*russoi*	*salentinensis*	*tenera*	*Geological age*
MA	—	—	—	—	4	L. Tortonian–?Messinian
AL	—	6	—	—	—	L. Tortonian
SI	1	—	—	—	1, 1T	L. Tortonian
LD	1	12	—	—	—	Langhian
BL	6	4	—	—	1	Langhian
GR	—	5	—	—	—	Langhian
TO	—	1	—	—	4	Burdigalian–Langhian
EG	—	—	—	—	10	E.-M. Burdigalian
LP	7, 2T, ?1T	—	—	—	—	E. Burdigalian
DX	—	—	—	—	—	E. Burdigalian
SR	—	—	—	—	—	L. Chattian–Aquitanian
NE	—	—	—	—	—	L. Chattian
SP	—	—	7	1	—	M. Chattian
Other	1T (Malta)	2T, ?1T (Vienna)	—	—	2T (Vienna)	—

Except in the Rupelian, Aquitanian and Messinian, the number of species of *Tarbellastraea* living in the investigated areas during any one time stage ranged from five to seven. Originations of species were concentrated during two time intervals, the Chattian and Burdigalian; while extinctions appear more evenly distributed through time (0–3 species per interval, except the Tortonian). The increase in originations during the Burdigalian was also detected by Chevalier (1962) in his study of the entire reef coral fauna of the western Mediterranean Miocene (86 species, 39 genera), and may have been related to a relatively high global thermal optimum during the Burdigalian (Adams *et al.* 1990; Cahuzac and Chaix 1993; Lauriat-Rage *et al.* 1993; McCall *et al.* 1994). However, unlike Chevalier's (1962) results for the western Mediterranean reef coral fauna as



	RUPELIAN	CHATTIAN	AQ.	BURDIGAL.	LAN.	SERRAV.	TORT.	ME.
total no. of species	1	5	2	7	6	5	5	1
no. of originations	1	4	0	6	1	0	0	0
no. of extinctions	0	3	1	2	1	0	4	1

TEXT-FIG. 12. Stratigraphical range chart summarizing the range interpreted for each species. Solid lines indicate ranges determined by canonical discriminant analysis of thin section measurements. Dashed lines indicate extensions of ranges based on qualitative study of calical surface measurements of primary types. Column width is proportional to the time duration of each stage.

a whole, our study indicates that there was *not* a progressive increase in species extinctions and decline in species diversity within *Tarbellastraea* as a result of progressive cooling between the Burdigalian and Tortonian. Instead, the species extinction rate remained relatively constant until the latest Miocene (Late Tortonian to Messinian), when five of the 12 species in the genus became extinct within a relatively short interval of time, and Mediterranean reefs became dominated by *Porites* (Esteban 1979; Pomar 1991; Riding *et al.* 1991). Thus, the extinction rate increased in *Tarbellastraea* only after a minimum temperature threshold had been reached as cold Atlantic waters entered the Mediterranean (Esteban 1979).

Cursory examination of the geographical distributions of each species suggests that, although possibly restricted during the Oligocene, the distributions of most species included more than one locality within each time interval, and they were therefore relatively widespread. The oldest occurrence of the genus was *Tarbellastraea profundata* in the Early Oligocene (Rupelian) Castelgomerto Limestone of the Vicentin Southern Alps, the rich coral fauna and 200 m thick barrier reef-lagoonal complex of which have been studied intensively by numerous authors (Pfister

1980; Frost 1981; Bosellini 1988; Bosellini and Russo 1988; Bosellini and Trevisani 1992). During the Late Oligocene (Chattian), four new species arose in the central and western Mediterranean. Like *T. profundata*, the geographical distributions of these four species appear to have been restricted. One of the species (*T. carryensis*) spread to the Aquitaine Basin on the Atlantic coast of France by the Burdigalian, where as many as three new species may have originated. One of the three (*T. distans*) also occurred in the Torino region of Italy, which together with the Vienna Basin also contained three or four new species. The two centres of high diversity in the Aquitaine Basin and Torino region during the Burdigalian were also detected in Chevalier's (1962) study of the whole fauna, in which he reported 96 reef coral species in Aquitaine Basin and 91 reef coral species in Torino. However, it should be noted that reefs in neither of these two regions were thick or well-developed.

During the Mid to Late Miocene, many of the species that arose during the Burdigalian expanded their distributions, especially across the Paratethys as it widened. During the latest Miocene, *Tarbellastraea* was concentrated in the central and western Mediterranean. One new species, *T. bragai*, an important reef-framework builder, may have extended from France to southern Spain.

SYSTEMATIC PALAEONTOLOGY

As described in previous sections, species have been distinguished in the present study by performing multivariate statistical analyses on measurements of colonies in thin sections that were collected at 13 scattered localities across the northern Mediterranean region (Table 2). As described earlier, these collections were made by: (1) A. F. Budd (deposited at SUI), (2) F. R. Bosellini (deposited at IPUM), (3) J. C. Braga (deposited at SUI), and (4) A. Russo (deposited at IPUM). Several additional colonies in the collections of Chevalier and d'Orbigny (deposited at MNHN, I.P.) were also measured in thin section. All of these measured colonies are listed in the '*Material*' sections below. Where applicable, localities for colonies listed in the '*Material*' sections are abbreviated as given in Table 2. In some instances, additional unmeasured colonies are also listed in the '*Material*' sections. Type specimens (Table 4) have been assigned qualitatively to statistically distinguished species by visual examination and by consideration of a few cursory measurements on calical surfaces (Appendix 2). In the two cases where thin sections of holotypes were available (i.e. *T. carryensis* (MNHN, I.P.-R10521) and *T. aquitaniensis* (MNHN, I.P.-R10518)), thin section measurements have been used to assign type specimens to statistically distinguished species. Except in a few rare instances, only specimens given in Table 4 are listed in synonymies.

The characters treated in '*Diagnosis*' and '*Description*' sections are summarized in the chart in Table 7. Except in the cases of *T. abditaxis* and *T. profundata*, all descriptions and measurements of corallite level characters are based on examination of thin sections. In general, the range of values given is equal to the overall corallite mean for each species ± one standard deviation. The total number of corallites measured for each species is given in Appendix 1. The range of values given for columella thickness represents an approximate total range of thickness for this feature. In the qualitative description of dissepiments, 'well-developed' is defined as having a ring of dissepiments extending across more than half a corallite as seen in thin section.

Abbreviations of repository institutions. BSPHGM, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany; IPUM, Istituto di Paleontologia, Università di Modena, Italy; KME, Krahnletz Museum, Eggenburg, Austria; MGU, Moscow State University, Russia; MNHN, I.P., Muséum National d'Histoire Naturelle, Institut de Paléontologie, Paris, France; MPUP, Museum dell'Istituto di Geologia e Paleontologia, Università di Padova, Italy; MPUR, Museo di Paleontologia, Università di Roma, Italy; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; SUI, Department of Geology, University of Iowa, Iowa City, USA.

Genus TARBELLASTRAEA Alloiteau, 1950

Type species. Astrea ellisiana Defrance, 1825, p. 382.

Diagnosis. Plocoid colonies with small, cylindrical or subcylindrical corallites. Septothecate, or partially parathecate in larger corallites. Septa in 3–4 cycles; first cycle distinct, lacking paliform lobes. Columella generally lamellar at calicular surface, sublamellar to lamellar below. Weakly costate with tabulo-vesicular endotheca and exotheca. Endotheca consisting of thin dissepiments arranged in one or two concentric circles near wall.

Remarks. Alloiteau (1950) established *Tarbellastraea* and designated *Astrea ellisiana* Defrance as the type species of the genus. Subsequent detailed diagnoses of the genus appeared in Alloiteau (1952, 1957). The diagnosis used in the present study is essentially the same as that given by Alloiteau (1952, 1957), except that the condition of the corallite wall in the genus is predominantly septothecal in the sense of Vaughan and Wells (1943) and Wells (1956). The holotype of *T. ellisiana* (Defrance) was collected at St-Paul-lès-Dax, and was reported by Alloiteau (1957) as lost. Alloiteau (1957, pl. 8, figs 4, 15) designated a neotype (MNHN, I.P.-R10933), which could not be located at the MNHN, I.P. (S. Barta-Calmus, pers. comm. 1994). Because the potential still exists for this neotype to be found, we hesitate to designate another neotype, and thus base our concept of *T. ellisiana* (Defrance) on the study of 10 'topotype' specimens in the general collections in Paris (MNHN, I.P., AFB# 129, 131, 133–140) labelled as '*Tarbellastraea ellisiana* (Defrance, 1826)' from Mérignac, Gironde, France. These specimens were amongst the material studied by Alloiteau (1957) in designating his neotype, and were also studied by Chevalier (1962).

As noted above, species included in *Tarbellastraea* are most similar to those in the genus *Antiguastrea*. They can generally be distinguished by their more clearly plocoid form, their smaller corallite size and fewer septa. Also, in species of *Tarbellastraea* the first cycle of septa is commonly distinctly thicker and longer than the second cycle, while in *Antiguastrea* the first and second cycles of septa are subequal. *Antiguastrea* species also tend to possess a better developed endotheca than species of *Tarbellastraea*, though this is probably a factor of the generally larger corallite size in *Antiguastrea*.

Tarbellastraea abditaxis Chevalier, 1962

Plate 1, figures 1–2; Text-figures 11–12

1925 *Orbicella eggenburgensis* var. *formosa* Kühn, p. 7, pl. 1, fig. 3.
1962 *Tarbellastraea abditaxis* Chevalier, p. 204, pl. 6, fig. 10; pl. 23; fig. 8.
1962 *Tarbellastraea aquitaniensis* var. *termofurae* Chevalier, p. 202, pl. 8, figs 17–18.
1962 *Tarbellastraea* cf. *eggenburgensis* (Kühn); Chevalier, p. 202, pl. 6, fig. 3; pl. 24, fig. 9.
1962 *Tarbellastraea eggenburgensis* var. *andalousiensis* Chevalier, p. 203, pl. 9, fig. 13; pl. 23, fig. 9.

Holotype. MNHN, I.P.-R10525; Sciolze, Torino (Italy); Burdigalian–Langhian.

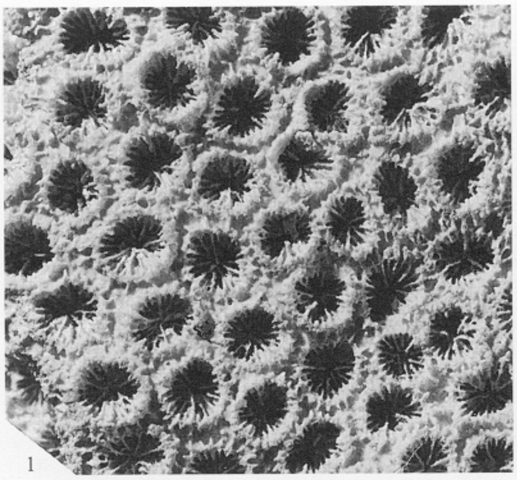
EXPLANATION OF PLATE 1

Figs 1–2. *Tarbellastraea abditaxis* Chevalier, 1962; Burdigalian–Langhian, Sciolze, Torino (Italy), calical surfaces. 1, holotype, MNHN, I.P.-R10525. 2, synonym, MNHN, I. P. (original figured specimen of *Tarbellastraea* cf. *eggenburgensis* Chevalier, 1962, pl. 6, fig. 3, and pl. 24, fig. 9). Both × 5.

Figs 3–4. *Tarbellastraea bragai* Stemann and Budd sp. nov.; holotype, SUI-84664, Upper Tortonian, Purchena, Almería (Spain). 3, calical surface; × 7. 4, transverse thin section; × 11.

Figs 5–6. *Tarbellastraea carryensis* (d'Orbigny, 1852); holotype, MNHN, I.P.-R10521, Upper Chattian, Carry-le-Rouet, La Nerthe, Bouches-du-Rhône (France). 5, calical surface; × 5. 6, transverse thin section; × 11.

PLATE 1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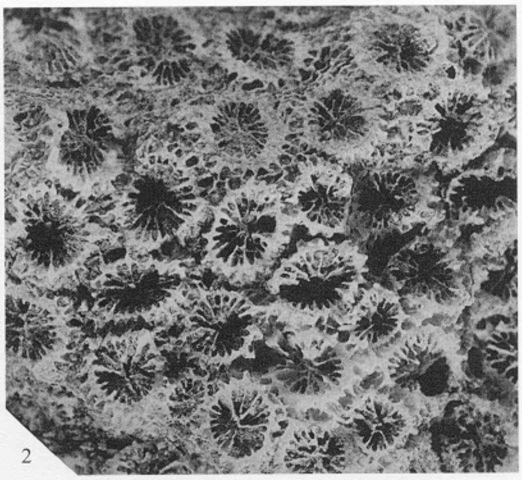
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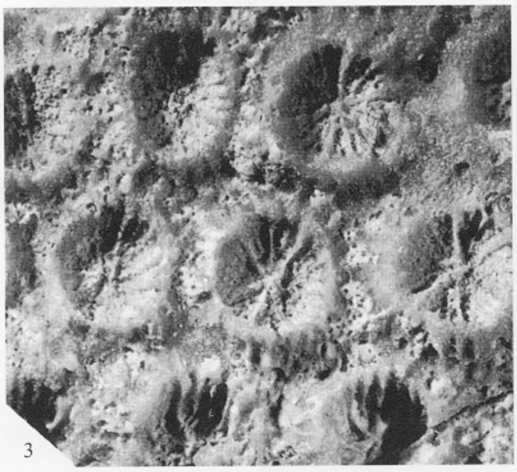
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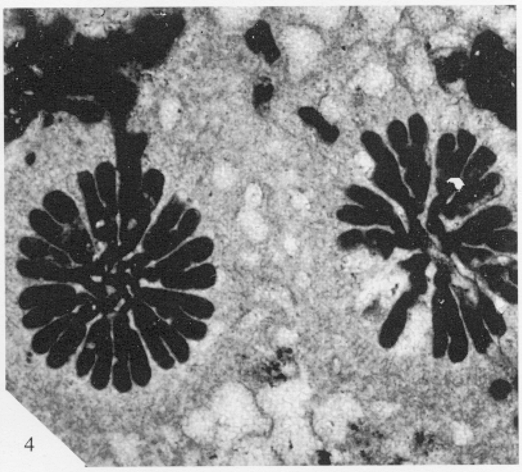
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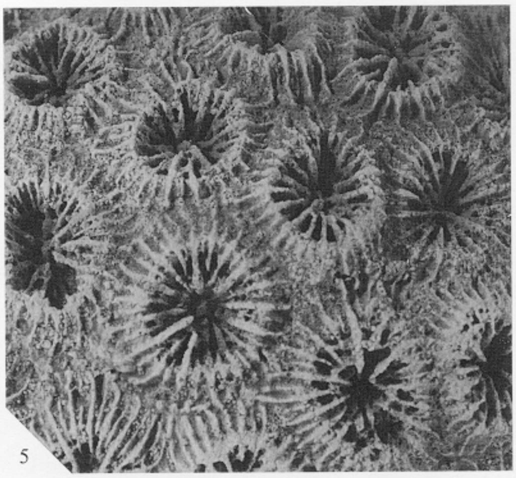
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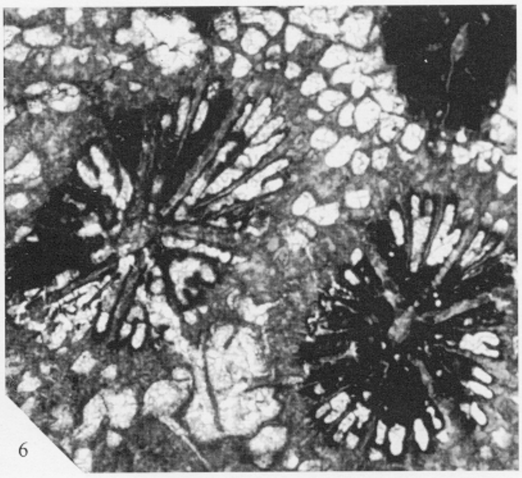
6

BUDD *et al.*, *Tarbellastraea*

Material. None, other than the type specimens for the five species given in the synonymies above (see Table 4 for museum catalogue numbers).

Diagnosis. Massive colonies with intermediate-sized, closely spaced corallites bearing a thick wall.

Description. Colony form massive. Corallite round, diameter 1·5–2·3 mm, centres spaced 2·2–3·0 mm apart with 23–25 septa per centre. Length of first cycle septa < 1·1 mm. Largest costae moderately long. Corallite wall septothecal and 0·15–0·25 mm thick. Columella strong or weak, apparently tied to septa, and < 0·08 mm thick. Endotheca weak or absent. Exotheca exhibits no distinct density banding.

Remarks. None of the collections in our study contains specimens of *T. abditaxis*. This species is closest morphologically to *T. chevalieri* and *T. reussiana* (Text-fig. 6). It can be distinguished from the former by its more closely spaced corallites and from the latter by its smaller corallite diameter and its higher number of septa per corallite. This species appears similar to what has been called '*T. eggenburgensis*' by some past authors (e.g. Chevalier 1962). However, the syntypes of *Orbicella eggenburgensis* Kühn, 1925 (pl. 1, figs 1–2) at the KME have a large, spongy columella and clearly belong to *Solenastrea* as defined in Table 1. We interpret the name *Orbicella eggenburgensis* var. *formosa* to be infrasubspecific, because Kühn (1925) originally described this variety as caused by environmental variation and not by geographical variation. Following Article 45 of the International Code of Zoological Nomenclature (Ride *et al.* 1985, p. 85), the valid name is, therefore, *Tarbellastraea abditaxis* Chevalier, 1962.

Occurrence. Lower–Middle Burdigalian, Eggenburg (Austria); Burdigalian–Langhian, Torino (Italy); Tortonian, Granada (Spain).

Tarbellastraea bragai Stemann and Budd sp. nov.

Plate 1, figures 3–4; Text-figures 6–7, 9, 11–12

?1962 *Tarbellastraea ellisiana* var. *manthelanensis* Chevalier, p. 195, pl. 5, fig. 4 [not seen].

Derivation of name. In honour of Juan C. Braga (Departamento de Estratigrafía y Paleontología, Universidad de Granada, Spain).

Holotype. SUI-84664; Purchena, Almería (Spain); Upper Tortonian.

Paratypes. SUI-84658, 84659; Purchena, Almería (Spain); Upper Tortonian.

Material. 9 SUI colonies (AL), 3 measured: SUI-84658–84659, 84664; one measured IPUM specimen (MA): IPUM-24880.

Diagnosis. Laminar, columnar or branched colonies with intermediate-sized, widely spaced corallites.

Description. Colony form laminar, columnar or branched palmately. Corallite shape irregular, diameter 1·8–2·3 mm, centres spaced 3·4–4·7 mm apart with 23–25 septa per centre. Length of first cycle septa 0·87–1·11 mm. Length of largest costae 0·39–0·53 mm. Corallite wall septothecal and 0·09–0·19 mm thick. Columella strong or weak, tied to septa, and 0·05–0·13 mm thick. Endotheca weak or absent. Exotheca exhibits dense, horizontal layering.

Remarks. One specimen of *T. ellisiana* var. *manthelanensis* from Manthelon (France) in the d'Orbigny collection at MNHN, I.P. (R10509) belongs to this species, but it does not match the photograph of the type given by Chevalier (1962, pl. 5, fig. 4), nor do measurements made in the present study match those given for this variety by Chevalier (1962). Therefore, *T. ellisiana* var. *manthelanensis* is only questionably synonymized. *T. bragai* is closest morphologically to *T. raulini* and to *T. reussiana* (Text-fig. 6). It can be readily distinguished from these two species by its more widely spaced corallites, and its growth form.

Occurrence. Langhian, Manthelan, Touraine, Indre-et-Loire (France); Upper Tortonian, Almería (Spain); Upper Tortonian–?Lower Messinian, Mallorca (Spain).

Tarbellastraea carryensis (d'Orbigny, 1852)

Plate 1, figures 5–6; Text-figures 4–5, 8, 11–12

1852 *Phyllocoenia carryana* d'Orbigny, p. 147.

Holotype. MNHN, I.P.-R10521. Carry-le-Rouet, La Nerthe, Bouches-du-Rhône (France); Upper Chattian. Thin section measured.

Material. 69 SUI colonies (NE), 14 measured; SUI-84764–84765, 84767–84768, 84782, 84786, 84788–84790, 84795, 84797, 84804, 84807–84808. Two non-type specimens (Mérignac, Gironde, France) at MNHN, I.P. measured (AFB # 130, 132). One topotype (La Nerthe, Bouches-du-Rhône, France) in the Chevalier collection at MNHN, I.P. measured (AFB # 171).

Diagnosis. Irregularly shaped colonies with large, widely spaced corallites.

Description. Colony form massive–columnar. Corallite shape irregular, diameter 2·1–2·9 mm, centres spaced 3·1–4·1 mm apart with 26–33 septa per centre. Length of first cycle septa 0·86–1·16 mm. Length of largest costae 0·42–0·62 mm. Corallite wall septothecal or partially parathecal and 0·02–0·16 mm thick. Columella strong or weak, tied to septa, and < 0·14 mm thick. Endotheca well-developed forming 1–3 rings. Exotheca exhibits no distinct density banding.

Remarks. T. carryensis is closest morphologically to *T. raulini* and *T. ellisiana* (Text-fig. 4). It can be distinguished from the former primarily by its higher number of septa per corallite and from the latter by its larger corallite size, its reduced costae, and its slightly fewer number of septa per corallite.

Occurrence. Upper Chattian, La Nerthe, Bouches-du-Rhône (France); Lower Burdigalian, Bordeaux (France).

Tarbellastraea chevalieri Bosellini sp. nov.

Plate 2, figures 1–2; Text-figures 8, 11–12

?1962 *Tarbellastraea carryensis* var. *minor* Chevalier, p. 198, pl. 10, figs 3, 9–10.

Derivation of name. In honour of the late J. P. Chevalier (MNHN, I.P.).

Holotype. IPUM-24876; Dolianova, Sardinia (Italy); Upper Chattian–Aquitanian.

Paratypes. IPUM-24877–24879; Dolianova, Sardinia (Italy); Upper Chattian–Aquitanian.

Material. 4 IPUM colonies (SR), 4 measured: IPUM-24876–24879; plus type specimen of *T. carryensis* var. *minor* (MNHN, I.P.-R10522).

Diagnosis. Massive colonies with small, intermediately spaced corallites bearing a thick wall.

Description. Colony form massive. Corallite shape round–irregular, diameter 1·6–2·4 mm, centres spaced 2·5–3·4 mm apart with 19–25 septa per centre. Length of first cycle septa 0·66–0·94 mm. Largest costae relatively short. Corallite wall septothecal and 0·09–0·29 mm thick. Columella weak or absent, tied to septa, and 0·05–0·09 mm thick. Endotheca weak or absent. Exotheca exhibits no distinct density banding.

Remarks. The specimens from Sardinia have a distinctively thicker wall and more reduced columella than *Tarbellastraea carryensis* var. *minor* Chevalier, 1962. Thus, the Sardinian specimens and *T. carryensis* var. *minor* are only questionably synonymized. Furthermore, following Article 16 of the International Code of Zoological Nomenclature (Ride *et al.* 1985, p. 38), a scientific name proposed for a variety after 1960 is excluded from zoological nomenclature. A new name is therefore assigned to the species. The reduced costae of the Sardinian specimens suggest that this species may be allied with *Solenastrea*. However, because of its reduced columella, the species is assigned to *Tarbellastraea*, until a more thorough phylogenetic study can be performed.

T. chevalieri is extremely close morphologically to *T. abditaxis* and is distinguished primarily by its more widely spaced corallites (Text-fig. 11). More samples from the Torino region of Italy need to be evaluated in order to determine whether *T. chevalieri* and *T. abditaxis* are truly distinct. *T. chevalieri* is also close morphologically to *T. tenera* (Text-fig. 8) from which it differs primarily in its larger, more narrowly spaced corallites.

Occurrence. ?Upper Chattian, La Nerthe, Bouches-du-Rhône (France); Upper Chattian–Aquitanian, Sardinia (Italy).

Tarbellastraea distans Chevalier, 1962

Plate 2, figure 6; Text-figures 4–5, 9, 11–12

?1847 *Explanaria crassa* Reuss, p. 18, pl. 3, fig. 1.
1962 *Tarbellastraea distans* Chevalier, p. 208, pl. 5, fig. 9 [not seen].

Holotype. MNHN, I.P.-R55165; Albugnano, Torino (Italy); Burdigalian–Langhian (could not be found).

Material. 7 SUI colonies (LP), 6 measured: SUI-51236, 51243, 51251, 51255, 51257–51258. Two non-type specimens (Le Peloua, Gironde, France) in the Chevalier collection at MNHN, I.P. measured (AFB# 117, 160). Holotype of *Explanaria crassa* (NHMW-1832.I.1368).

Diagnosis. Massive colonies with small, very widely spaced corallites bearing long costae.

Description. Colony form massive. Corallite round, diameter 1·7–2·1 mm, centres spaced 4·1–5·2 mm apart with 23–26 septa per centre. Length of first cycle septa 0·68–0·84 mm. Length of largest costae 0·49–0·79 mm. Corallite wall septothecal and 0·05–0·21 mm thick. Columella weak, free or tied to septa, and < 0·08 mm thick. Endotheca well-developed forming one ring. Exotheca exhibits strong density banding.

Remarks. *Explanaria crassa* is only questionably synonymized with this species, because of the poor preservation of its holotype (NHMW-1832.I.1368). *T. distans* differs from all other members of

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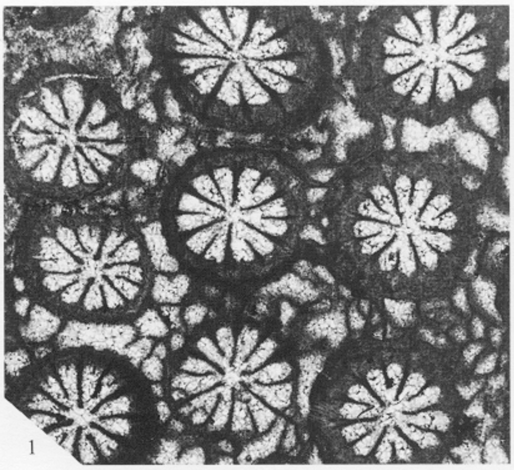
EXPLANATION OF PLATE 2

Figs 1–2. *Tarbellastraea chevalieri* Bosellini sp. nov. 1, holotype, IPUM-24876; Upper Chattian–Aquitanian, Dolianova, Sardinia (Italy); transverse thin section; × 10. 2, possible synonym, MNHN, I.P.-R10522 (holotype of *Tarbellastraea carryensis* var. *minor* Chevalier, 1962); Upper Chattian, Carry-le-Rouet, La Nerthe, Bouches-du-Rhône (France); calical surface; × 5.

Figs 3–5. *Tarbellastraea tenera* (Reuss, 1847); calical surfaces. 3, synonym, NHMW-1854.XXXV.500 (holotype of *Heliastraea conoidea* Reuss, 1872); Badenian (Langhian), Enzesfeld (Austria); × 5. 4, synonym, MNHN, I.P.-R10522 (holotype of *Tarbellastraea siciliae* Chevalier, 1962); Upper Tortonian, Landro, Sicily (Italy); × 5. 5, holotype, NHMW-1872.XIII.61; Badenian (Langhian), Kostel, Vienna Basin (Austria); × 6.

Fig. 6. *Tarbellastraea distans* Chevalier, 1962; non-type, MNHN, I.P., AFB# 117; Lower Burdigalian, Le Peloua, Bordeaux (France); transverse thin section; × 11.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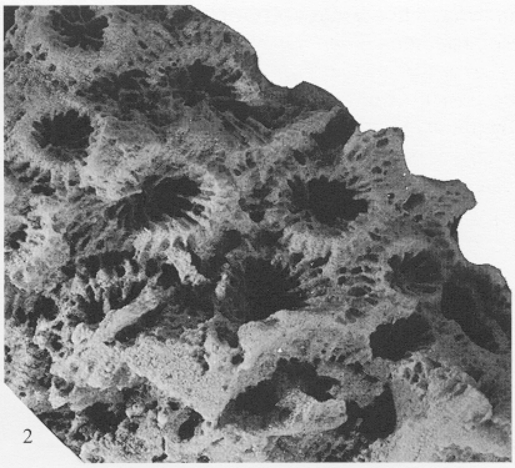
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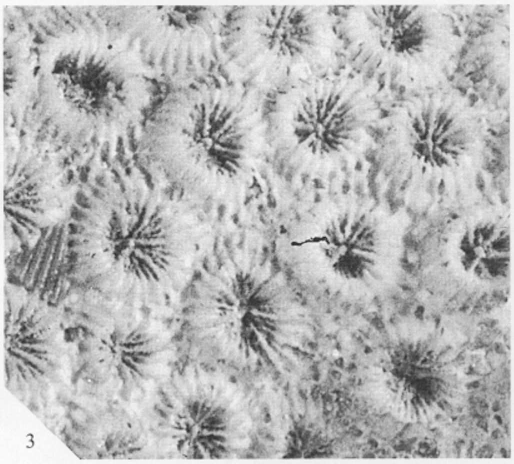
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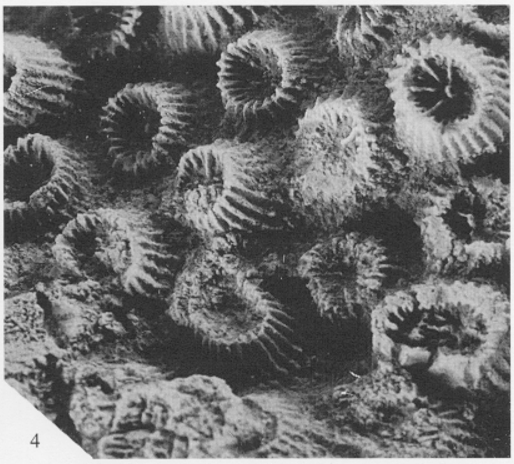
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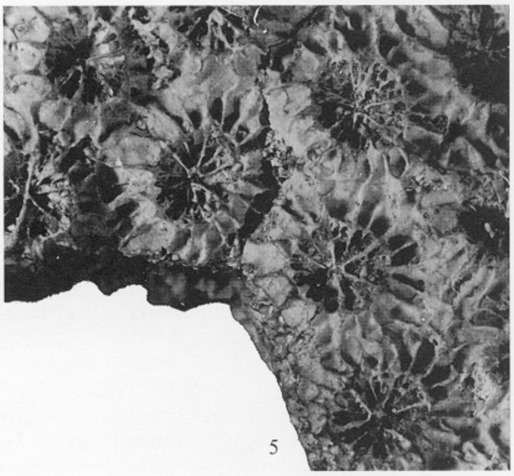
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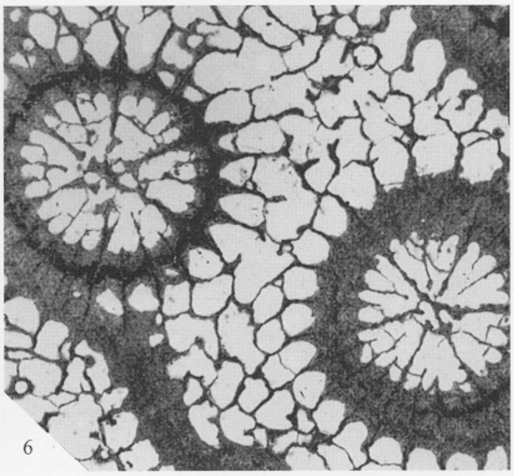
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Tarbellastraea in its extremely widely spaced corallites (Text-fig. 5). It is closest morphologically to *T. raulini*.

Occurrence. Lower Burdigalian, Bordeaux (Gironde, France); Burdigalian–Langhian, Torino (Italy); ?Langhian, Vienna (Austria).

Tarbellastraea ellisiana (Defrance, 1826)

Plate 3, figures 1–2; Text-figures 1, 4–5, 8, 11–12

1826 *Astrea ellisiana* Defrance, p. 382 [holotype lost].
1957 *Tarbellastraea ellisi* (Defrance, 1926); Alloiteau, p. 128, pl. 8, fig. 4, 15 [neotype designated, not seen].
?1962 *Tarbellastraea mimbastensis* Chevalier, p. 199, pl. 5, fig. 3; pl. 23, fig. 1.

Neotype. MNHN I.P.-R10933; Mérignac, Gironde, Bordeaux (France); Lower Burdigalian (could not be found).

Material. 10 SUI colonies (DX), all measured: SUI-84734–84743. Ten topotypes (Mérignac, Gironde, France) at MNHN, I.P. measured (AFB # 129, 131, 133–140). Holotype of *T. mimbastensis* (MNHN, I.P.-R10529).

Diagnosis. Massive colonies with intermediate-sized to large, intermediately spaced, irregularly shaped corallites bearing numerous septa.

Description. Colony form massive. Corallite shape irregular, diameter 1·9–2·5 mm, centres spaced 2·9–3·9 mm apart with 27–35 septa per centre. Length of first cycle septa 0·69–1·01 mm. Length of largest costae 0·47–0·77 mm. Corallite wall septothecal or partially parathecal and 0·01–0·20 mm thick. Columella strong, tied to septa, and 0·1–0·2 mm thick. Endotheca well-developed forming 1–3 rings. Exotheca exhibits strong density banding and dense coenosteum.

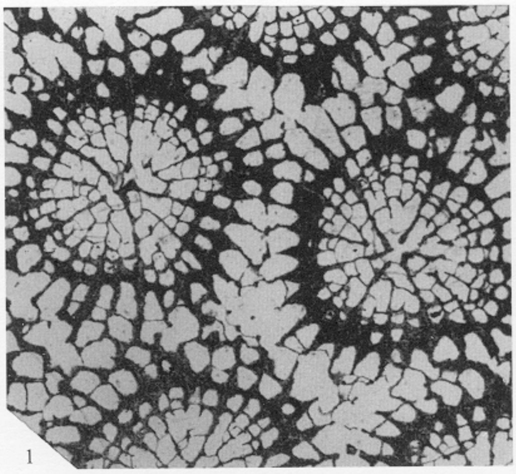
Remarks. The holotype is lost, and the specimen that was figured in Alloiteau (1957, pl. 8, fig. 4, 15) and used in Alloiteau's original description of the genus *Tarbellastraea* is considered to be the neotype [S. Barta-Calmus, pers. comm. 1994). The neotype could not be found at the MNHN, I.P. for our study; however, ten topotypes that are morphologically similar to Alloiteau's (1957) description and photograph were measured in thin section and included in the statistical analyses. As explained in the main text, *T. mimbastensis* is only questionably synonymized because of its slightly smaller corallite diameter and fewer number of septa. *T. ellisiana* is very close morphologically to *T. carryensis* (Text-fig. 4), but can be distinguished by its smaller corallite size, more numerous septa per corallite, and better developed costae.

Occurrence. Lower Burdigalian, Saint-Paul-les-Dax, Landes and Bordeaux, Gironde (France).

EXPLANATION OF PLATE 3

Figs 1–2. *Tarbellastraea ellisiana* (Defrance, 1826); Lower Burdigalian. 1, topotype, MNHN, I.P.; Mérignac, Gironde, Bordeaux (France); transverse thin section; × 11. 2, possible synonym, MNHN, I.P.-R10529 (holotype of *Tarbellastraea mimbastensis* Chevalier, 1962); Mimbaste, Bordeaux (France); calical surface; × 5.

Figs 3–6. *Tarbellastraea profundata* (Catullo, 1856); calical surfaces. 3–4, holotype, MPUP-8142, Rupelian, Montecchio, Vicenza (Italy). 5, synonym, MNHN, I.P.-R10523 (holotype of *Tarbellastraea carryensis* var. *major* Chevalier, 1962); Upper Chattian, Carry-le-Rouet, La Nerthe, Bouches-du-Rhône (France). 6, possible synonym, MNHN, I.P.-M00787 (non-type specimen of *Tarbellastraea edwardsi* Chevalier, 1956 (= *Phyllocoenia archiaci* Milne Edwards and Haime, 1848)), Stampian, Gaas, Landes (France). All × 5.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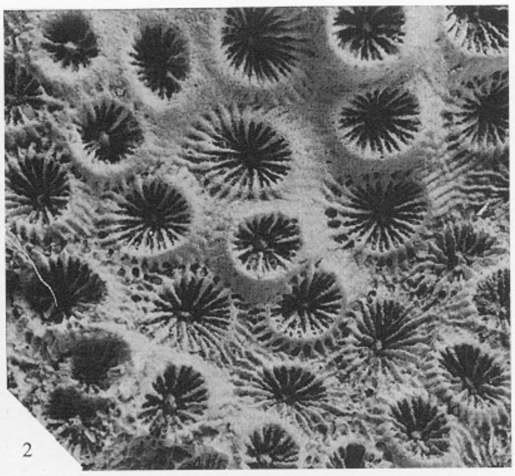
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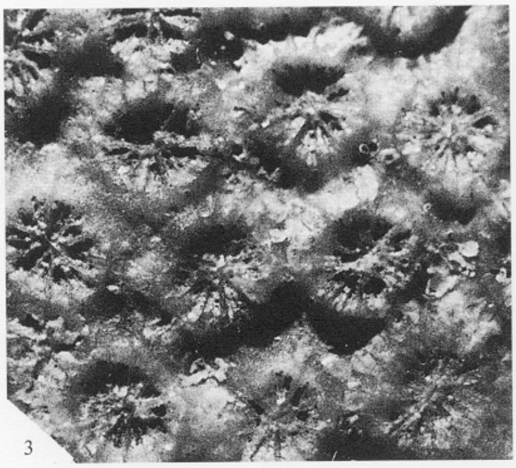
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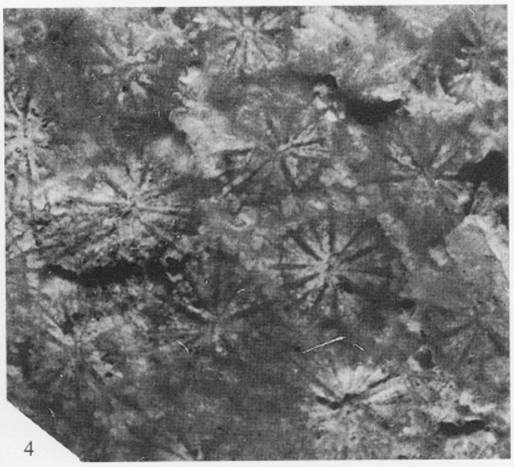
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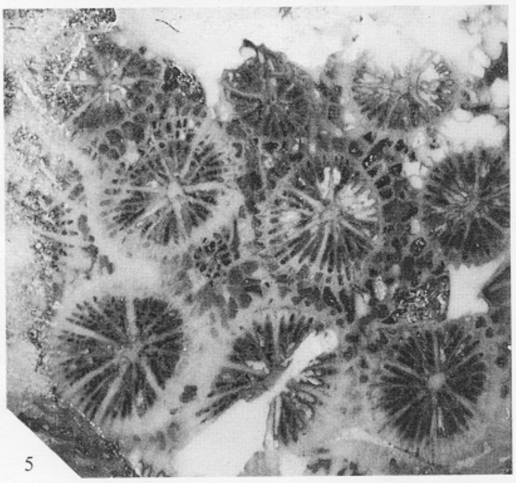
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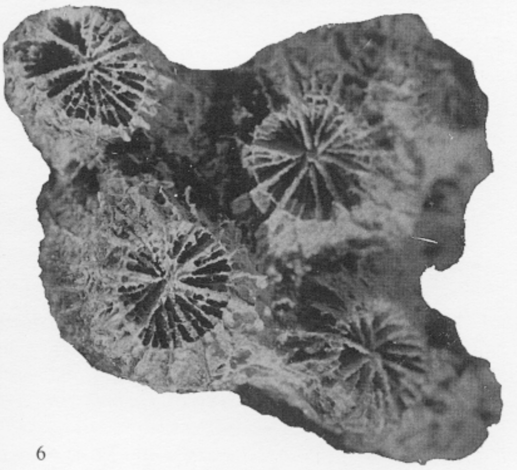
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BUDD *et al.*, *Tarbellastraea*

Tarbellastraea profundata (Catullo, 1856)

Plate 3, figures 3–6; Text-figures 11–12

1856	*Astrea profundata* Catullo, p. 56, pl. 11, fig. 6.
?1955	*Tarbellastraea edwardsi* Chevalier, p. 390, pl. 3, fig. 4 [= *Phyllocoenia archiaci* Milne Edwards and Haime 1848, p. 303].
1962	*Tarbellastraea carryensis* var. *major* Chevalier, p. 198, pl. 7, fig. 8.
1980	*Tarbellastraea anomala* (Michelotti); Pfister, p. 78, pl. 12, figs 1–2.
?1985	*Tarbellastraea* cf. *profundata* (Catullo); Pfister, p. 197 [not seen].

Holotype. MPUP-8142; Montecchio, Vicenza (Italy); Rupelian.

Material. None other than the type specimens for the first three species given in the synonymies above (see Table 4 for museum catalogue numbers), and Pfister's (1980) specimen of '*T. anomala*' (Pfister collection, Naturhistorisches Museum Bern, Switzerland, Pf-SL 12/1-2).

Diagnosis. Irregularly shaped colonies with very large, widely spaced corallites bearing numerous septa.

Description. Colony form massive–digitate. Corallite shape round, diameter 3·3–3·5 mm, centres spaced 4·8–5·0 mm apart with 36–39 septa per centre. Length of first cycle septa 1·2–1·6 mm. Largest costae moderately long. Corallite wall septothecal and < 0·1 mm thick. Columella strong, tied to septa, and < 0·13 mm thick. Endotheca well-developed forming 1–2 rings. Exotheca exhibits no distinct density banding.

Remarks. None of the collections in our study contains specimens of *T. profundata*. This species can be distinguished easily from all other members of the genus by its extremely large corallite diameters and extremely high number of septa per corallite (Text-fig. 11). A photograph of one type specimen (Pl. 3, fig. 6) of *T. edwardsi* from the Stampian of Gaas (Landes, France) has been examined (S. Barta-Calmus, pers. comm. 1993), but it does not match the photograph given in Chevalier (1955, pl. 3, fig. 4), nor does the photo correspond with measurements given by Chevalier (1955). Therefore, *T. edwardsi* is only questionably synonymized pending examination of more material from Gaas.

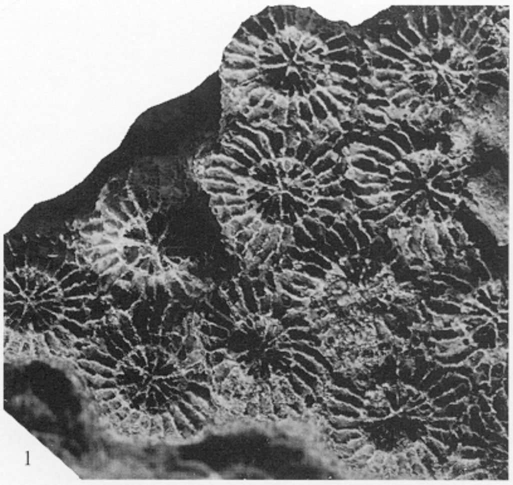
Pfister's (1980) specimen of '*T. anomala*' from San Luca (Vicenza, Italy) has a sublamellar columella and weakly developed paliform lobes, two diagnostic features of *Tarbellastraea* (Table 1), and differs considerably from the holotype of *Leptastraea anomala* Michelotti, 1871 (MPUR 3302), which has a well-developed spongy columella (Text-fig. 10). It has a corallite size and spacing similar to those of *T. profundata*. Therefore, we synonymize it with *T. profundata*. Pfister (1985) also described one colony of *T.* cf. *profundata* from the Rupelian near Cairo Montenotte (Liguria, Italy); however, this specimen is reported to have significantly smaller calices (2–2·5 mm) and can therefore only be questionably assigned to *T. profundata*.

Occurrence. Rupelian, Vicenza (Italy); Upper Chattian, La Nerthe, Bouches-du-Rhône (France).

EXPLANATION OF PLATE 4

Figs 1–4. *Tarbellastraea raulini* (Milne Edwards and Haime, 1850); Lower Burdigalian, Le Peloua, Bordeaux (France). 1, holotype, MNHN, I.P.-M01281; calical surface; × 5. 2, possible synonym, MNHN, I.P.-R10518 (holotype of *Tarbellastraea aquitaniensis* Chevalier, 1962); calical surface; × 5. 3–4, synonym, MNHN, I.P.-M01184 (holotype of *Tarbellastraea prevostiana* (Milne Edwards and Haime, 1850)). 3, calical surface; × 5. 4, transverse thin section; × 11.

Figs 5–6. *Tarbellastraea reussiana* (Milne Edwards and Haime, 1850); calical surfaces. 5, holotype, NHMW-1846.37.967; Badenian (Langhian), Mattersdorf, Vienna Basin (Austria). 6, figured specimen (Reuss 1872, pl. 9, fig. 2), NHMW-1863.XV.A; Badenian (Langhian), Niederleis, Vienna Basin (Austria). Both × 5.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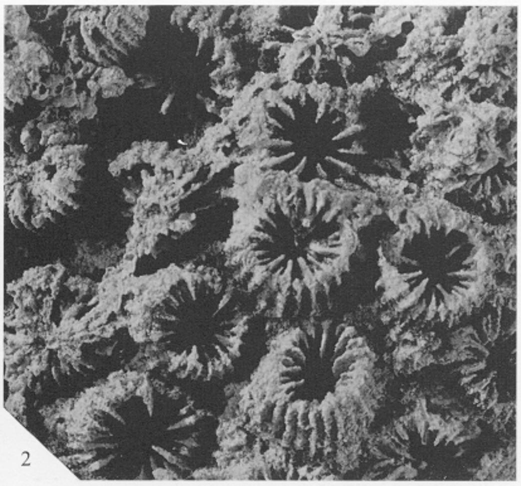
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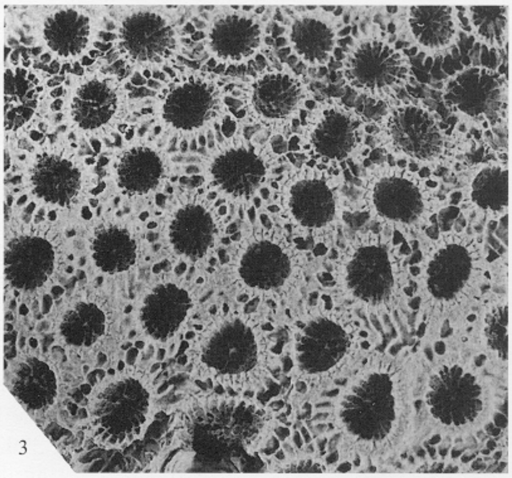
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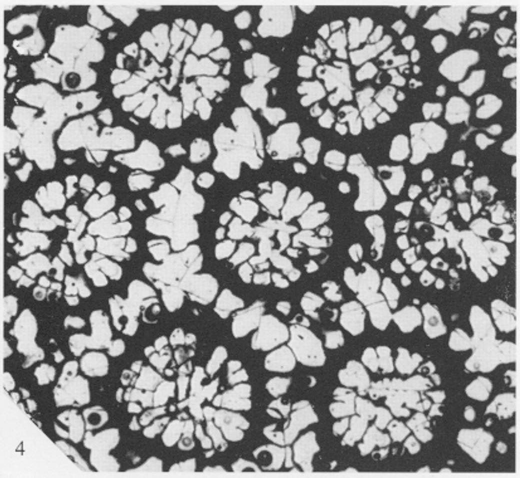
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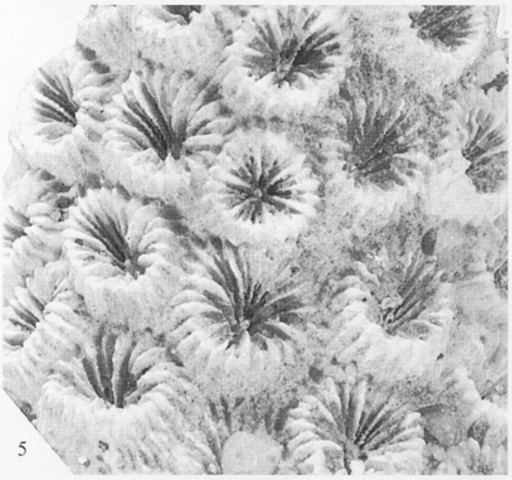
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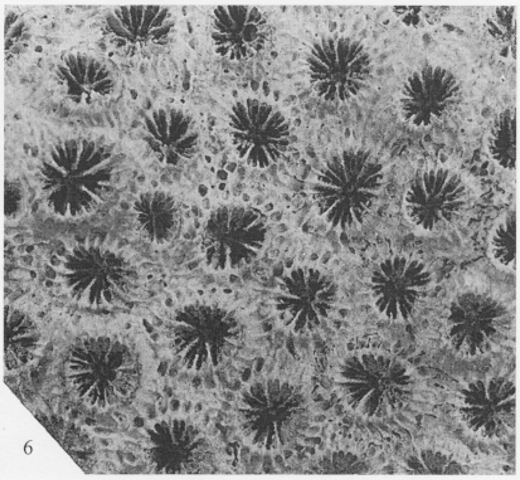
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Tarbellastraea raulini (Milne Edwards and Haime, 1850)

Plate 4, figures 1–4; Text-figures 4, 6–9, 11–12

1850 *Astrea raulini* Milne Edwards and Haime, p. 110.
1850 *Astrea prevostiana* Milne Edwards and Haime, p. 110.
?1962 *Tarbellastraea aquitaniensis* Chevalier, p. 201, pl. 9, fig. 12; pl. 23, fig. 2.
1962 *Tarbellastraea reussiana* var. *echinulata* Chevalier, p. 206, pl. 5, fig. 18; pl. 24, fig. 7.

Holotype. MNHN, I.P.-M01281; Le Peloua, Gironde (France); Lower Burdigalian.

Material. 12 SUI colonies, 10 measured (4LP, 6BL): SUI-51234, 51247–51248, 51253, 84667–84668, 84670–84672, 84674. Three topotypes (Le Peloua, Gironde, France) in the Chevalier collection at MNHN, I.P. measured (AFB# 116, 169, 177). Three non-type specimens (two from Sicily; one from Seriège, France) in the Chevalier collection at MNHN, I.P. measured (AFB# 127, 164, 111). Type specimens for the four species given in the synonymies above (see Table 4 for museum catalogue numbers).

Diagnosis. Massive colonies with small to intermediate-sized, widely corallites bearing a thin wall.

Description. Colony form massive. Corallite shape regular, diameter 1·6–2·3 mm, centres spaced 3·0–4·2 mm apart with 23–25 septa per centre. Length of first cycle septa 0·75–0·97 mm. Length of largest costae 0·39–0·63 mm. Corallite wall septothecal and 0·04–0·12 mm thick. Columella weak, tied to septa, and 0·05 mm thick. Endotheca well-developed forming 1–2 rings. Exotheca exhibits sparse density banding.

Remarks. *T. aquitaniensis* is only questionably synonymized because of its more closely spaced corallites with high numbers of septa. *T. raulini* is closest morphologically to *T. tenera* and *T. carryensis* (Text-fig. 4). It can be distinguished from the former by its more widely spaced corallites, and from the latter by its smaller corallites and fewer septa per corallite. *T. aquitaniensis* is only questionably indicated in synonymy with *T. raulini* because its holotype lies within the margin of overlap between *T. raulini* and *T. carryensis*. Because the holotype of *T. aquitaniensis* lies closer to the centre of the *T. raulini* cluster (Text-fig. 4), it more probably belongs to *T. raulini* than to *T. carryensis*.

Occurrence. Lower Burdigalian, Bordeaux, Gironde (France); Langhian, Pleven (Bulgaria), Languedoc (France); Upper Tortonian, Sicily (Italy); Upper Tortonian–Lower Messinian, Malta.

Tarbellastraea reussiana (Milne Edwards and Haime, 1850)

Plate 4, figures 5–6; Plate 5, figures 1–12; Text-figures 6–7, 9, 11–12

1847 *Explanaria astroites* (Goldfuss, 1826); Reuss, p. 17, pl. 2, figs 7–8.
1850 *Astraea reussiana* Milne Edwards and Haime, p. 110.
1872 *Solenastraea manipulata* Reuss, p. 243, pl. 8, fig. 2.
1872 *Heliastraea reussana* Milne Edwards and Haime; Reuss, p. 240, pl. 9, fig. 2; pl. 18, fig. 4.
?1925 *Orbicella transsylvanica* Kühn, p. 4.

Holotype. NHMW-1846.37.967; Mattersdorf (Austria); Badenian (Langhian).

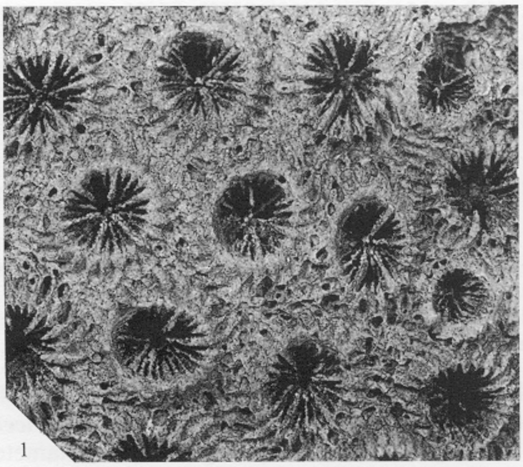
EXPLANATION OF PLATE 5

Figs 1–2. *Tarbellastraea reussiana* (Milne Edwards and Haime, 1850); calical surfaces. 1, synonym, NHMW-1872.XIII.56 (holotype of *Orbicella transsylvanica* Kühn, 1925); Badenian (Langhian), Lapugy, Vienna Basin (Austria). 2, figured specimen (Chevalier, 1962, pl. 10, fig. 1; pl. 24, fig. 4); MNHN, I.P., Langhian, Autignac, Languedoc (France). Both × 5.

Figs 3–4. *Tarbellastraea russoi* Bosellini sp. nov.; holotype, IPUM-24869; Middle Chattian, Castro Limestone, Vitigliano, Salento (Italy); transverse thin sections; × 10.

Figs 5–6. *Tarbellastraea salentinensis* Bosellini sp. nov.; holotype, IPUM-24868; Middle Chattian, Castro Limestone, Vitigliano, Salento (Italy); transverse thin sections; × 10.

PLATE 5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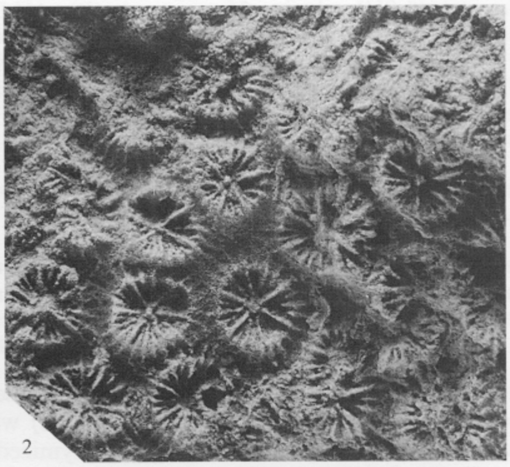
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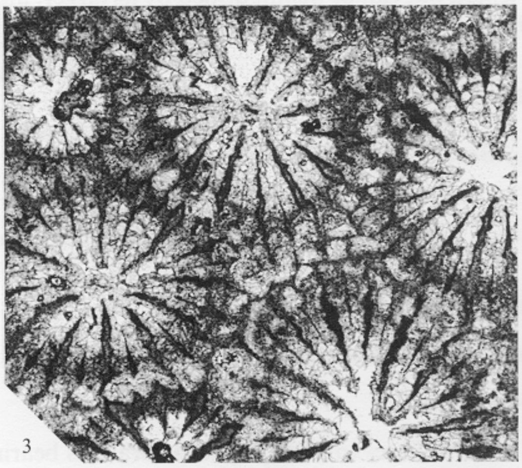
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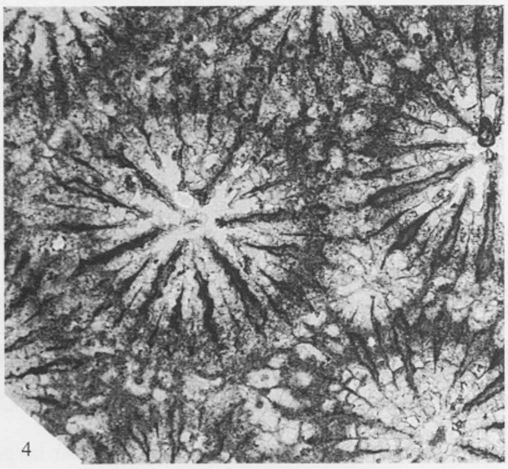
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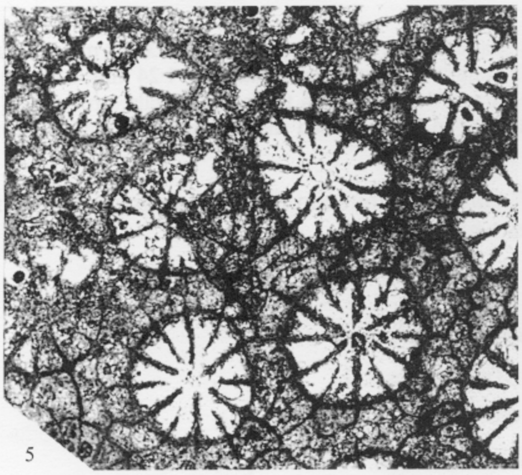
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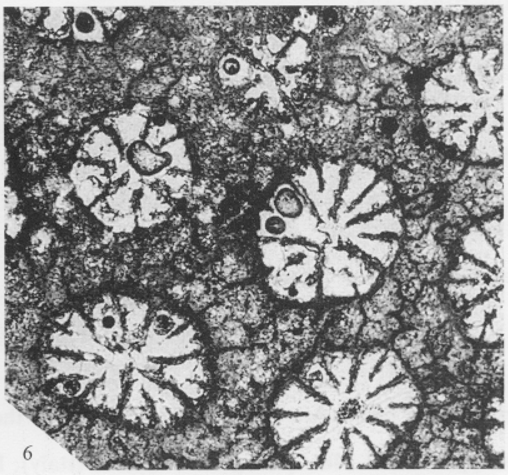
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BUDD *et al.*, *Tarbellastraea*

Material. 48 SUI colonies, 26 measured (4BL, 11LD, 5GR, 6AL): SUI-84651–84652, 84655, 84662–84663, 84665–84666, 84675, 84677–84680, 84683, 84687–84688, 84690–84691, 84696, 84702–84706, 84709, 84711, 84715. Two non-type specimens (one Autignac, France; one Sciolze, Italy) in the Chevalier collection at MNHN, I.P. measured (AFB # 100, 179). Type specimens for the four species given in the synonymies above (see Table 4 for museum catalogue numbers) and a specimen figured by Reuss (1872, pl. 9, fig. 2, NHMW-1863.XV.A).

Diagnosis. Irregularly shaped colonies with small, closely spaced corallites bearing a thin wall and short costae.

Description. Colony form massive, knobby. Corallite shape round–irregular, diameter 1·7–2·1 mm, centres spaced 2·5–3·3 mm apart with 23–25 septa per centre. Length of first cycle septa 0·67–0·87 mm. Length of largest costae 0·32–0·47 mm. Corallite wall septothecal and 0·04–0·14 mm thick. Columella weak, free or tied to septa, and 0·08 mm thick. Endotheca weak. Exotheca exhibits no distinct density banding.

Remarks. Milne Edwards and Haime (1850) based their description of *T. reussiana* on Reuss' (1847) specimen of *Explanaria astroites* (Goldfuss) which is currently deposited at NHMW. *Orbicella transylvanica* is only questionably synonymized because of its relatively large corallite diameter. *T. reussiana* is most similar morphologically to *T. tenera* but can be distinguished by its larger, more closely spaced, thin walled corallites (Text-fig. 6).

Occurrence. Burdigalian–Langhian, Torino (Italy); Langhian, Leibnitz and Vienna (Austria), Pleven (Bulgaria), Languedoc (France); Upper Tortonian, Almería (Spain).

Tarbellastraea russoi Bosellini sp. nov.

Plate 5, figures 3–4; Text-figures 8, 11–12

Derivation of name. In honour of Antonio Russo (Istituto di Paleontologia, Università degli Studi di Modena, Italy).

Holotype. IPUM-24869; Vitigliano, Salento (Italy); Middle Chattian.

Paratypes. IPUM-24870–24875; Vitigliano, Salento (Italy); Middle Chattian.

Material. Seven IPUM measured colonies (SP): IPUM-24869–24875.

Diagnosis. Irregularly shaped colonies with large, intermediate- to widely spaced corallites bearing numerous septa.

Description. Colony form massive, knobby. Corallite shape round–irregular, diameter 2·3–3·3 mm, centres spaced 2·7–4·1 mm apart with 30–37 septa per centre. Length of first cycle septa 0·88–1·24 mm. Length of largest costae moderately long. Corallite wall septothecal and 0·05–0·13 mm thick. Columella strong, tied to septa or free, and $< 0·15$ mm thick. Endotheca well-developed forming two rings. Exotheca exhibits strong density banding.

Remarks. *T. russoi* is similar morphologically to *T. carryensis*, but can easily be distinguished by its larger corallites and its more numerous septa (Text-fig. 8).

Occurrence. Middle Chattian, Salento (Italy).

Tarbellastraea salentinensis Bosellini sp. nov.

Plate 5, figures 5–6; Text-figures 8, 11

Derivation of name. After the Salento Penninsula, the type locality.

Holotype. IPUM-24868; Vitigliano, Salento (Italy); Middle Chattian.

Material. One measured colony (SP): the holotype.

Diagnosis. Irregularly shaped colonies with intermediate-sized, closely spaced corallites bearing very few septa.

Description. Colony form massive–digitate. Corallite shape irregular, diameter 1·8–2·5 mm, centres spaced 2·6–2·8 mm apart with 15–22 septa per centre. Length of first cycle septa 0·70–0·86 mm. Length of largest costae relatively short. Corallite wall septothecal and 0·04–0·07 mm thick. Columella weak or absent, free or tied to septa, and 0·06–0·09 mm thick. Endotheca absent. Exotheca exhibits dense, horizontal layering.

Remarks. T. salentinensis is clearly distinct from all other members of the genus in its reduced number of septa per corallite and its more narrowly spaced corallites (Text-figs 8, 11).

Occurrence. Middle Chattian, Salento (Italy).

Tarbellastraea tenera (Reuss, 1847)

Plate 2, figures 3–5; Text-figures 4–9, 11–12

1847 *Explanaria tenera* Reuss, p. 18, pl. 3, fig. 2.
1872 *Heliastraea conoidea* Reuss, p. 240, pl. 10, fig. 3.
1962 *Tarbellastraea siciliae* Chevalier, p. 207, pl. 7, fig. 10; pl. 23, fig. 7.

Holotype. NHMW-1872. XIII.61; Kostel (Austria); Badenian (Langhian).

Material. 19 SUI colonies (EG), 11 measured: SUI-84673, 84716–84720, 84724–84725, 84727, 84731–84732; 4 IPUM specimens (MA), 4 measured: IPUM-24881–24884. Five non-type specimens (four from Torino, Italy; one from Sicily) in the Chevalier collection at MNHN, I.P. measured AFB # 43, 161–163, 165. Type specimens for the three species given in the synonymies above (see Table 4 for museum catalogue numbers).

Diagnosis. Columnar colonies with small, intermediately spaced corallites bearing a thick wall.

Description. Colony form massive columnar. Corallite shape round irregular, diameter 1·6–2·0 mm, centres spaced 2·7–3·7 mm apart with 23–25 septa per centre. Length of first cycle septa 0·63–0·79 mm. Length of largest costae 0·42–0·78 mm. Corallite wall septothecal and 0·08–0·26 mm thick. Columella strong, tied to septa, and 0·06–0·15 mm thick. Endotheca weak to well-developed forming one ring. Exotheca exhibits some density banding.

Remarks. T. tenera is closest morphologically to *T. raulini* and *T. reussiana* (Text-fig. 6). It can readily be distinguished from these two species by its slightly smaller corallites and its thicker wall.

Occurrence. Lower Burdigalian, Eggenburg (Austria); Burdigalian–Langhian, Torino (Italy); Langhian, Pleven (Bulgaria); Upper Tortonian, Sicily (Italy); Upper Tortonian–?Lower Messinian, Mallorca (Spain).

CONCLUSIONS

Our study has shown that:

1. The stratigraphical distribution of *Tarbellastraea* is from the Oligocene (Rupelian) to the Early Messinian. Previously reported pre-Oligocene occurrences of the genus do not belong to *Tarbellastraea*.
2. Of the 25 species and varieties of *Tarbellastraea* previously described, only ten appear to be distinct. Of these ten, two have previously been described only as varieties, and are therefore assigned new names. In addition to these ten, two previously undescribed species have been discovered in the Middle Chattian of the Salento Peninsula of Italy. Thus, a total of 12 species of *Tarbellastraea* appears to have existed in the investigated Mediterranean and European regions during the Oligocene and Miocene.
3. The stratigraphical ranges of nine of the 12 species extend through two or more stages, and they therefore cannot be considered diagnostic of any one stage. However, the two new species from the Salento Peninsula of Italy appear restricted to the Middle Chattian, and *T. ellisiana* is restricted to the Lower Burdigalian of the Aquitaine Basin of France.

4. Although species richness did not change significantly during the evolution of *Tarbellastraea*, overall morphological disparity among species decreased in the genus through time. Early in the evolution of the genus, numbers of septa per corallite ranged from 18–38. Later in its evolution, this range dropped to 24–26. A similar trend can be detected in corallite diameter.
5. Species origination rates appear to have been highest in the genus during the Burdigalian, when high diversity centres may have developed in the Aquitaine basin and Torino regions.
6. Species extinction rates remained relatively constant until the extinction of the entire genus in the latest Miocene. The biggest increase occurred over a relatively short time interval during the latest Tortonian to Messinian, when the genus became extinct and *Porites* dominated the reef-building coral fauna (Esteban, 1979; Pomar, 1991; Riding *et al.* 1991).
7. At the onset of the evolution of *Tarbellastraea*, species had relatively restricted geographical distributions. However, throughout much of the Miocene, all but one species (*T. ellisiana*) were widespread.

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APPENDIX 1

Means (standard deviations) for morphometric species. *, may be biased by preservation.

Character	A (*T. tenera*)	B (*T. distans*)	C (*T. carryensis*)	D (*T. raulini*)	E (*T. ellisiana*)
Number of colonies (number of corallites)	10 (150)	8 (78)	18 (107)	16 (148)	20 (188)
NS	24·19 (0·87)	24·42 (1·38)	29·47 (3·66)	23·95 (0·97)	31·46 (3·72)
CD–MIN	1·822 (0·209)	1·866 (0·172)	2·272 (0·328)	2·032 (0·247)	2·144 (0·350)
CD–MAX	2·014 (0·236)	2·044 (0·200)	2·591 (0·375)	2·247 (0·266)	2·388 (0·382)
CD–RAT	0·906 (0·050)	0·915 (0·048)	0·879 (0·062)	0·905 (0·054)	0·888 (0·070)
NND	1·392 (0·424)	2·788 (0·530)	1·304 (0·399)	1·619 (0·490)	1·299 (0·376)
CL1	0·316 (0·090)	0·290 (0·070)	0·322 (0·082)	0·268 (0·095)	0·280 (0·078)
CL2	0·461 (0·102)	0·414 (0·095)	0·477 (0·099)	0·404 (0·108)	0·442 (0·105)
T1	0·546 (0·132)	0·643 (0·150)	0·517 (0·100)	0·555 (0·132)	0·624 (0·148)
T2	0·188 (0·095)	0·134 (0·082)	0·097 (0·066)	0·097 (0·087)	0·094 (0·102)
L1	0·712 (0·084)	0·762 (0·084)	0·980 (0·134)	0·864 (0·112)	0·863 (0·169)
L2	0·570 (0·093)	0·619 (0·106)	0·815 (0·131)	0·696 (0·152)	0·718 (0·178)
L3	0·304 (0·110)	0·325 (0·077)	0·500 (0·129)	0·430 (0·120)	0·452 (0·143)
ST1	0·059 (0·026)	0·045 (0·011)	0·086 (0·034)	0·046 (0·019)	0·063 (0·027)
ST2	0·038 (0·017)	0·030 (0·009)	0·058 (0·024)	0·030 (0·010)	0·042 (0·017)
ST-RAT	0·702 (0·351)	0·689 (0·234)	0·701 (0·235)	0·720 (0·305)	0·712 (0·254)

Character	F (*T. chevalieri*)	G (*T. russoi*)	H (*T. salentinensis*)	I (*T. reussiana*)	J (*T. bragai*)	Duncan's test results
Number of colonies (number of corallites)	4 (16)	7 (35)	1 (5)	28	4 (24)	—
NS	21·88 (2·96)	33·23 (3·41)	18·40 (3·58)	23·96 (0·89)	24·21 (0·72)	G > E > C > BJAID > F > H
CD–MIN	2·015 (0·390)	2·786 (0·494)	2·160 (0·329)	1·874 (0·201)	2·067 (0·260)	G > CHE ⩾ JDF ⩾ IBA
CD–MAX	—	—	—	2·107 (0·229)	2·429 (0·267)	C > JE > D > IBA
CD–RAT	—	—	—	0·891 (0·051)	0·851 (0·055)	BAD ⩾ IEC > J
NND	0·948 (0·189)	0·575 (0·566)	0·520 (0·205)	1·066 (0·354)	1·974 (0·567)	B > J > DA ⩾ CE ⩾ IF > GH
CL1	—	—	—	0·296 (0·076)	0·248 (0·056)	CAI ⩾ BED ⩾ J*
CL2	0·402 (0·164)	0·664 (0·263)	0·600 (0·245)	0·453 (0·114)	0·424 (0·072)	G > H > CAIEJBDF*
T1	—	—	—	0·398 (0·073)	0·459 (0·072)	BE > DAC > J > I
T2	0·189 (0·096)	0·091 (0·036)	0·054 (0·013)	0·093 (0·055)	0·141 (0·054)	FA > JBDCEIG ⩾ H
L1	0·806 (0·144)	1·061 (0·180)	0·780 (0·084)	0·774 (0·105)	—	G > C > DEF ⩾ HIB ⩾ A
L2	0·614 (0·136)	0·895 (0·160)	0·600 (0·079)	0·589 (0·133)	—	GC > ED ⩾ BFGIA
L3	0·187 (0·098)	0·571 (0·184)	0·190 (0·022)	0·348 (0·092)	—	G > CED > IBA > HF
ST1	—	—	—	0·050 (0·017)	0·071 (0·024)	C > J > EA > IDB*
ST2	—	—	—	0·037 (0·011)	0·043 (0·015)	C > JE ⩾ AI > DB*
ST-RAT	—	—	—	0·762 (0·245)	0·632 (0·177)	I ⩾ DEACB ⩾ J*

APPENDIX 2

Means (standard deviations) for primary types in Table 4. *, measured in thin section. **, holotype not seen; measurements after Barta-Calmus (1973).

Code	Species	Number of corallites	NS	CD-MIN	NND
1	*abditaxis*	7	26·0 (1·9)	1·61 (0·11)	0·56 (0·05)
*2	*aquitaniensis*	5	23·4 (0·9)	1·622 (0·160)	0·817 (0·119)
3	var. *termofurae*	7	24·2 (0·8)	1·41 (0·08)	0·90 (0·10)
*4	*carryensis*	2	31·0 (7·1)	2·391 (0·369)	1·348 (0·184)
5	var. *major*	4	36·0 (1·6)	3·29 (0·11)	1·50 (0·29)
6	var. *minor*	7	24·2 (2·4)	1·76 (0·19)	1·00 (0·35)
7	*conoidea*	10	25·2 (1·9)	1·93 (0·18)	1·26 (0·27)
**8	*distans*	—	24 (—)	1·6 (—)	2·9 (—)
9	cf. *eggenburgensis*	7	26·1 (0·7)	1·80 (0·12)	0·67 (0·16)
10	var. *formosa*	10	22·5 (2·1)	1·71 (0·18)	0·64 (0·11)
11	var. *andalousiensis*	7	24·2 (0·8)	1·83 (0·13)	0·83 (0·14)
12	*manipulata*	10	24·0 (0·0)	2·05 (0·27)	1·19 (0·47)
13	*mimbastensis*	7	28·7 (3·3)	1·88 (0·23)	0·80 (0·18)
14	*prevostina*	7	24·0 (0·0)	2·14 (0·10)	1·36 (0·43)
15	*profundta*	8	38·5 (5·3)	3·46 (0·23)	1·46 (0·53)
16	*raulini*	7	23·7 (1·2)	1·75 (0·12)	1·58 (0·32)
17	*reussiana*	10	24·0 (0·9)	2·40 (0·17)	0·80 (0·34)
18	var. *echinulata*	7	24·2 (0·7)	2·00 (0·10)	1·54 (0·27)
19	*siciliae*	7	25·2 (1·7)	1·66 (0·14)	1·60 (0·36)
20	*tenera*	10	24·0 (0·0)	1·71 (0·11)	1·17 (0·23)
21	*transsylvanica*	10	24·0 (0·0)	2·47 (0·12)	1·29 (0·31)