

**A HISTORY OF THE CLASSIFICATION OF
FORAMINIFERA (1826-1933)**

**PART I
FORAMINIFERAL CLASSIFICATION FROM
D'ORBIGNY TO GALLOWAY**

by

RICHARD CIFELLI

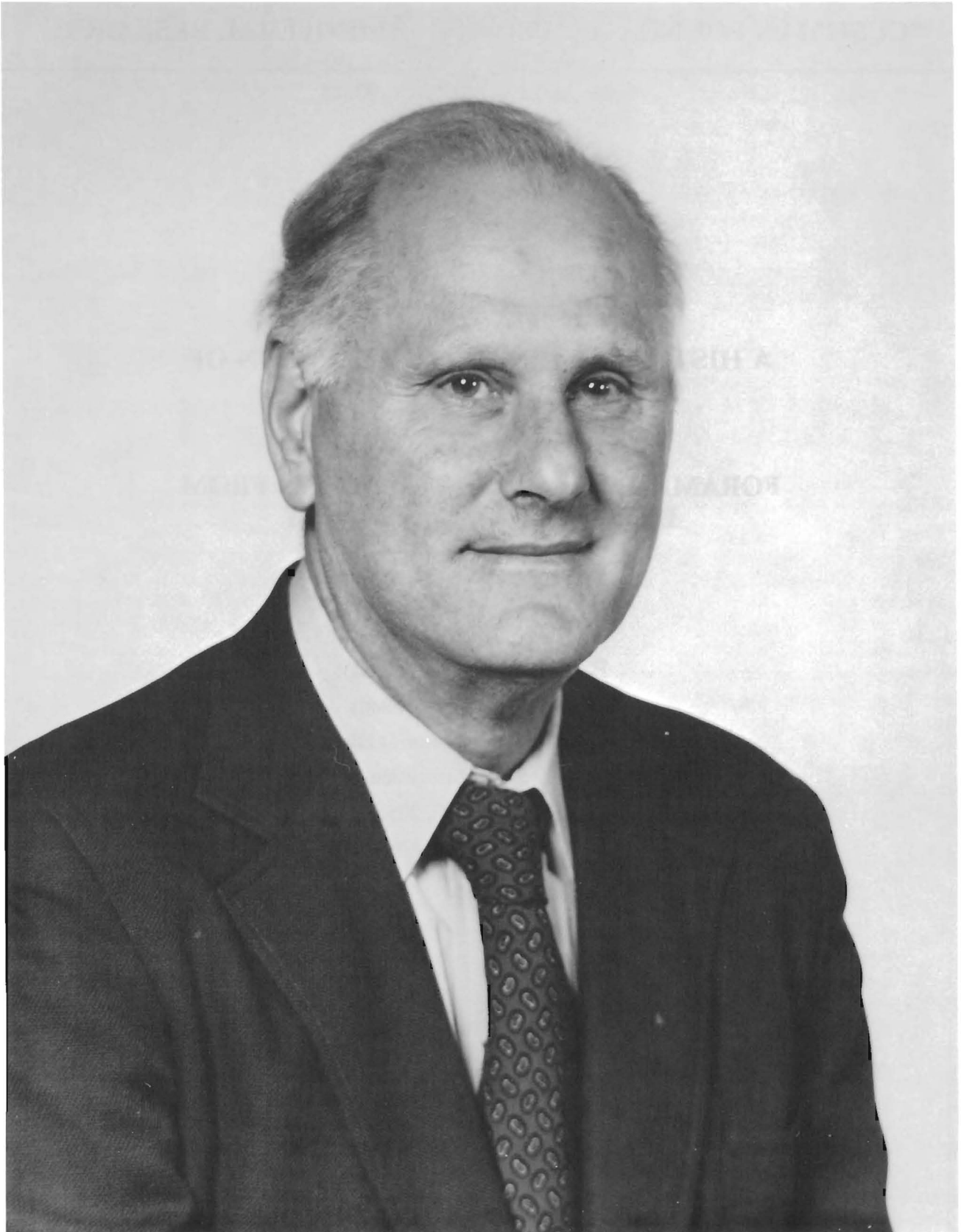
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RICHARD CIFELLI

FOREWORD

This is the final scientific work of Dick Cifelli. I expect it will be of considerable interest because it spans over 150 years of foraminiferal research. It is not just an historical account, but delves into the philosophy of classifications and reveals a good deal about the people who made them. Over the 20 years that we were curators together of the U.S. National Museum's foraminiferal collection, we discussed the philosophy of classification and the resulting schemes many times. His mind had an ability to grasp the "big picture," an asset which is truly rare.

Cifelli had intended to bring his analysis up to the present day, but as he became more ill, he realized that this was not to be. So his account ends rather abruptly with the end of the Cushman era.

A draft of his manuscript was given to Susan Richardson by me to complete. She did extensive library research and took copious notes. These notes are so interesting and add so much insight that they are published here as a separate paper. I thank her for her considerable contribution.

Although Richardson made some revisions, the paper is essentially as Dick wrote it. On behalf of our scientific community, I would like to add, Thank you, Dick.

MARTIN A. BUZAS

PREFACE

"In every scientific discipline, the prevalent ideas and even the questions asked are the products of a historical development. Thus to understand the concerns of modern evolutionary biology, it is essential to know something of the history of the subject." (Futuyama, 1982)

Dick Cifelli perceived that to better understand the concerns of modern foraminiferal systematics, it was essential to know something of the history of this subject. His own words best describe his goal, "I have been working on a kind of overview of foraminiferal classification—trying to trace the development of thought that had led to our present outlooks."¹ The following paper was a result of this ambition which absorbed his interest during the last few years of his life. Cifelli examined in detail the development of thought about foraminiferans not only as fossils, but also as living organisms, and analyzed how these ideas influenced the classifications proposed in the nineteenth and early twentieth centuries. That Cifelli had planned to extend his analysis to the classifications proposed by modern systematists is evidenced by a collection of his hand-written notes on their assorted works. Unfortunately, he was never able to synthesize that information into this manuscript. What he has bequeathed to us, however, is a fascinating account of the early evolution of foraminiferal classification.

Some may find the chapter on "Natural Classification and Evolution" to be tedious reading. Cifelli's decision to include this section is best explained in the following excerpt from a letter to Ruth Todd,

"I was interested in your reaction to the 'Pre-Darwinian Theories of Classification' section. . . . In doing something like this it is hard to know if you are being too elementary or taking too much for granted. Actually it took quite awhile before I finally decided to include that section, because I know that it is of little or no interest to most people in this line of work. Finally, I concluded that it had to be there because classification is so closely rooted to philosophy. . . . The philosophic connection is undoubtedly the most overlooked aspect of classification."²

¹ Cifelli to Resig, 16 February 1982, Cifelli Correspondence, Department of Paleobiology, Smithsonian Institution, Washington, D.C.

² Cifelli to Todd, 14 January 1982, Courtesy of Doris Low, Vineyard Haven, MA.

Others agreed with his assessment, "As for your view that philosophy is at the roots of foram classification, I certainly agree, since I think philosophy is, in the final analysis, at the bottom of science."³

Another important consideration to keep in mind when reading this paper is that Cifelli himself had definite ideas on classification and phylogenetic reconstruction. These ideas had a discernible influence on his interpretations of other workers' classifications and their portrayals of evolutionary relationships. It will be obvious that Cifelli thought that a "natural" classification should reflect the evolutionary relationships of the organisms being classified, and most, but not all, modern taxonomists would agree with this view. As for his preferred method of phylogenetic reconstruction, Cifelli advocated a biostratigraphic approach to the assessment of phylogeny. This approach was clearly outlined in his paper, co-authored with George Scott, on the Neogene globorotalid radiation,

"Ideally, this is done by identifying sequences of populations in which variation fields overlap but, because of the small amount of biometric mapping, most estimates of continuity between samples are qualitative. However, the latter method is assisted by the density of the record and the relatively slow progress of character trends. Effectively we are suggesting a version of phenetic linkage as outline by Gingerich (1976). Evaluations of character polarities are used only when stratigraphic evidence is inadequate." (Cifelli and Scott, 1986, p. 3)

Cifelli believed that the geologic "record is often adequate to provide evidence of taxonomic transitions," and that although phylogeny cannot "be literally read from the rocks," the "gross form of the phyletic tree can be estimated from the stratigraphic record" (Cifelli and Scott, 1986, p. 3). There are many modern systematists who question the validity of the stratophenetic approach to the reconstruction of phylogeny.

³ Kleinpell to Cifelli, 23 February 1983, Cifelli Correspondence, Smithsonian Institution, Washington, D.C.

However, much as Cifelli may have disagreed with alternate approaches, he acknowledged an "emotional" aspect to classification and once commented that "one can feel his whole way of thinking threatened by a scheme he disapproves of."⁴

ACKNOWLEDGMENTS

Many people contributed generously to the evolution of Cifelli's final manuscript into this Special Publication, and provided invaluable editorial advice, technical assistance, and financial and emotional support.

I am particularly grateful to Martin A. Buzas, Gail Knisely and Kenneth M. Towe of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. for their respective editorial and philosophical contributions. I also thank C. Geoffrey Adams of the British Museum (Natural History) for providing a duplicate copy of the comments and suggestions he had sent to Cifelli regarding the manuscript, and also for kindly providing photographs of T. Rupert Jones, William C. Williamson, William B. Carpenter, Henry B. Brady and Joseph J. Lister. I would like to thank Marie-Thérèse Vénec-Peyré of the Muséum National d'Histoire Naturelle in Paris, for her generous offer of a reproduction of an original plate from d'Orbigny's "Planches Inédites" and for her kind assistance in arranging for the photograph of the d'Orbigny plaster models; Jean-Claude Fischer and Herve Lelievre of the Muséum National d'Histoire Naturelle provided the negative of the photograph of d'Orbigny's plaster models of foraminiferans; Graham F. Elliot of the British Museum (Natural History) provided the photograph of Charles Davies Sherborn; O. Prof. Dr. Steininger of the Institut für Paläontologie der Universität Wien provided the photograph of Melchior Neumayr;

Prof. Dr. Brabander, Dean of the Forstwissenschaftlichen Fachbereichs der Georg-August-Universität in Göttingen provided the photograph of Ludwig Rhumbler; Tim White of the Peabody Museum of Natural History, Yale University, provided the photograph of Charles Schuchert; and Alan Horowitz of the Department of Geology, Indiana University provided the photograph of Jesse J. Galloway.

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I am indebted to Mary Parrish and Patrice Suggs, National Museum of Natural History, Washington, D.C., for their advice and technical expertise as illustrators. My thanks also go to Bill Sacco, photographer for the Department of Biology, Yale University, for reproducing several of the old photographs used to illustrate the text.

The manuscript was reviewed by C. G. Adams, D. Haman, J. Lipps, A. R. Loeblich, Jr., B. Sen Gupta and R. Todd.

Susan L. Richardson
New Haven, CT

⁴ Cifelli to Lipps, 13 May 1983, Cifelli Correspondence, Department of Paleobiology, Smithsonian Institution, Washington, D.C.

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FORAMINIFERAL CLASSIFICATION FROM D'ORBIGNY TO GALLOWAY

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I. EARLY VIEWS OF FORAMINIFERA

(Superscripts refer to numbered notes in Part II)

Accounts of foraminifera date back to classical times. Herodotus (5th century B.C.) and Pliny the Elder (23-79 A.D.) made references to the *Nummulites* composing the rocks of the pyramids (see Lipps, 1981). The first illustration of a foraminiferan is found in Robert Hooke's *Micrographia* (1665), in which a figure of a rotaliform species was included (Fig. 1). An earlier record of a possible foraminiferan is the illustration of "Ammonis cornu" figured by Conrad Gesner (1565) and later queried by Sherborn (1893, 1955)¹ as either a *Nummulites* or a gastropod (Fig. 2).

By 1758, the year Linnaeus first introduced his method of binomial nomenclature as applied to the animal kingdom (in the tenth edition of *Systema Naturae*), ten papers containing descriptions and figures of foraminifera had been published.² The earliest writers treated foraminifera mainly as objects of curiosity and made no serious attempt to arrange them in an orderly fashion. It was on the descriptions and figures of foraminifera in some of these earlier works, however, that later authors based their species.³ Linnaeus founded the "fifteen species which he admitted into the twelfth edition of his 'Systema Naturae'" on forms that had been previously figured and described by Plancus (1739, 1760),⁴ Gualtieri (1742) and Leder-müller (1761) (Carpenter, 1862, p. 2) (see Figs. 3 and 4).

With the appearance of the later editions of Linnaeus' *Systema Naturae*, the modernized science of classification was born and foraminifera found a place in the scheme of nature. In the twelfth edition of *Systema Naturae*, Linnaeus (1766) recognized fifteen species and placed fourteen of them in the cephalopod genus *Nautilus*. The remaining species, *Quinqueloculina seminula*, he placed in the genus *Serpula*. The idea

that most foraminiferans were tiny cephalopods, while others might be algae or some form of metazoan, not only predated Linnaeus, but persisted for a long time afterwards. It was not until Dujardin demonstrated the protozoan nature of foraminifera (1835a-d) that ideas of cephalopodal or other metazoan affinities were abandoned.

By recognizing only fifteen species and assigning all but one of them to the cephalopod genus *Nautilus*, Linnaeus (1758) clearly demonstrated a very broad view of species limits. He was well aware of the diversity of foraminiferal morphology, but rather than establish additional species, he expressed their variation by designating a number of varieties. Not all of Linnaeus' immediate successors shared his broad view of species limits, nor did they receive his binomial system of designating species with an immediate, universal following. Fichtel and Moll (1798, 1803) were among his closest disciples. They not only grouped their foraminiferal species in the genus *Nautilus*, but also used just a few specific names to which they appended varietal designations. Although the hand-colored figures of Fichtel and Moll are among the most elegant illustrations of foraminifera in existence, their species concepts were met with opposing reactions. The later English workers praised the Fichtel and Moll work and expressed admiration for their restraint in naming species—a reflection of the predominant English belief that the visible diversity among foraminifera was mostly representative of variation around a few central types, a view held in accordance with Linnean principles. But Montagu, a contemporary of Fichtel and Moll, was more doubtful. In reference to the numerous varieties of *Nautilus calcar* delineated by Fichtel and Moll,⁵ Montagu (1808, p. 77) remarked: "If these can be admitted as the same species, . . . we may bid defiance to specific definition." This difference in opinion on species limits was to be an early fore-

Fig. x.

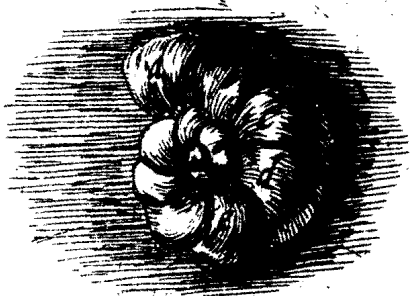


FIGURE 1. This first published illustration of a foraminiferan was accompanied by the following excerpt from the text of the *Micrographia*, in which Hooke recounted his discovery of a "small Shell-fish": "I was trying several small and single Magnifying Glasses, and casually viewing a parcel of white Sand, when I perceiv'd one of the grains exactly shap'd and wreath'd like a Shell, but endeavoring to distinguish it with my naked eye, it was so very small, that I was fain again to make use of the Glass to find it; then, whilst I thus look'd on it, with a Pin I separated all the rest of the granules of Sand, and found it afterwards to appear to the naked eye an exceeding small white spot, no bigger than the point of a Pin. Afterwards I view'd it every way with a better *Microscope*, and found it on both sides, and edge-ways, to resemble the Shell of a small Water-Snail with a flat spiral shell: it had twelve wreathings, *a, b, c, d, e, &c.* all very proportionately growing one less than another toward the middle or center of the Shell, where there was a very small round white spot. I could not certainly discover whether the Shell were hollow or not, but it seem'd fill'd with somewhat, and 'tis probable that it might be *petrify'd* as other larger Shells often are" (Hooke, 1665, p. 80). (Photo courtesy of The Beinecke Rare Book and Manuscript Library, Yale University.)

shadowing of the irreconcilable philosophical viewpoints that still persist today, between "splitters" and "lumpers."

Soldani did not follow the Linnean example at all. In his monographs of the fossil foraminiferal faunas of the Italian mountain and Mediterranean regions he distinguished, and profusely illustrated, a seemingly countless number of forms (Soldani, 1780, 1789, 1791, 1795, 1798). Although he referred many of these forms to "*Nautilus*," he did not attach to them formalized Linnean names. Instead of specific designations he used descriptive differentials, or descriptive phrases, such as "*N. conico-rotundata*." Reaction to Soldani's work was mixed. Because Soldani did not employ binomial nomenclature, none of the forms he had described are considered valid species. Nevertheless, his illustrations (see Fig. 5), were sufficiently accurate to serve as the basis of many new species and genera described by

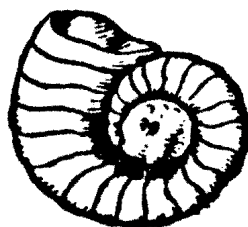


FIGURE 2. Illustration of "*Ammonis cornu*" figured by Gesner (1565, p. 159), and questionably identified by Sherborn (1893, 1955) as either a *Nummulites* or a gastropod. (Reproduction courtesy of the Yale Medical Historical Library, New Haven, CT.)

later workers, most notably by d'Orbigny. Fornasini (1886) made a careful study of Soldani's work and recognized 391 forms that were later given taxonomic names, listing 45 publications in which the Soldani figures were cited. The later English workers, however, who objected to the practice of fine splitting, were less than enthusiastic about Soldani's work and accused him of promoting the proliferation of spurious species. Williamson (1858, p. viii) had this to say about Soldani, "Nothing can be worse than his attempts at the discrimination of species. Plate after plate is crowded with figures merely representing varieties of one protean form, every modification in the diversified arrangements of segments entitling the specimen, in the Abbé's [Soldani's] opinion, to the immortality conferred by pen and pencil" (Fig. 5).

Workers were at first slow to separate foraminifera from *Nautilus*, and this cephalopod genus continued to have some usage as late as 1827.⁶ In the eighteenth century the genera *Ammonia* Brünnich, 1772, and *Lagena* Walker and Boys, 1784 (as a subgenus of *Serpula*),⁷ were introduced; both of these genera remain valid today. Very early in the nineteenth century, inhibitions about proposing new genera were relaxed as it became increasingly clear that many foraminifera had practically nothing in common with *Nautilus*. By 1826, the year d'Orbigny's classification was published, approximately eighty-seven valid generic names had been proposed.⁸ Most of these genera were introduced by three workers—de Montfort (1808), Lamarck (1801–1822) and DeFrance (1816–1825)—forty-four of them can be attributed to de Montfort (Fig. 6). Some of these genera were of a dubious nature—they were not always well-conceived and were often based on trivial differences, or inadequate descriptions and figures—and many of them have long since passed into synonymy.⁹ Nevertheless, a number of these generic names remain valid today. The mere fact that genera had been established shows that the early workers were aware of the different degrees of relationship that exist

among species of foraminifera. The way was paved for a higher order of classification.

II. THE BEGINNING OF CLASSIFICATION

ALCIDE D'ORBIGNY

The earliest classification in which foraminiferans were unequivocally treated as a distinct group is to be found in the *Tableau Méthodique* (d'Orbigny, 1826). Its author, Alcide Dessalines d'Orbigny (Fig. 7), a most extraordinary man even for an age of "megathinkers," had a passion for "great works." His goals knew no bounds, and, when barely more than 20 years of age, he aimed to provide a complete synthesis of the foraminifera. While he was to remain the dominant figure in foraminifera throughout most of his life, he pursued other interests with even more vigor.

In his later years, d'Orbigny became increasingly preoccupied with much broader aspects of natural history, producing a number of works which embraced the entire animal kingdom. From 1840 until the time of his death in 1857, he supervised the publication of eight volumes, illustrated by 1,000 plates, of the *Paléontologie Française* (d'Orbigny, 1840–1860; 1842–1862). In the *Prodrome de Paléontologie* (1850–1852), he catalogued 18,000 species of fossil invertebrates, arranging them in their chronological order of appearance within the global stratigraphic record. He also included an alphabetically arranged table of the 40,000 generic and specific names and their synonymies contained within the *Prodrome*.¹ It is in these two works that d'Orbigny proceeded to make faunal divisions of the stratigraphic column with the purpose of unraveling the whole of earth history. He saw absolutely no continuity of fauna between these successive divisions; he considered it a fact that the stratigraphic record revealed twenty-seven separate acts of creation, each terminated by an intervening catastrophe. Having thus firmly established his "doctrine of successive creations," d'Orbigny became the principal spokesman for Cuvier's theory of catastrophism. Untenable as this theory proved to be, it resulted in what was undoubtedly d'Orbigny's best known contribution to the geological sciences—the subdivision of the Jurassic and Cretaceous systems into stages.

Heron-Allen's (1917) thorough analysis of the life and work of d'Orbigny provides a valuable perspective on d'Orbigny's foraminiferal classification and his legacy. In a "verdict of posterity" Heron-Allen concluded that d'Orbigny could be regarded as both a genius and lunatic.²

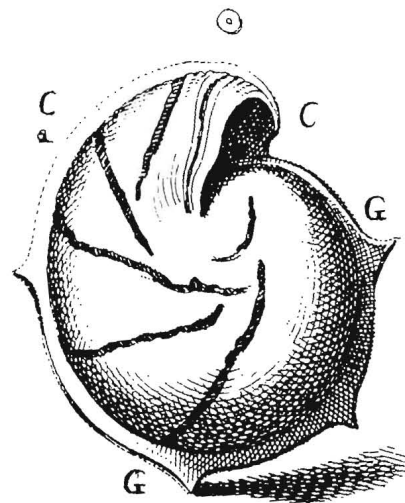


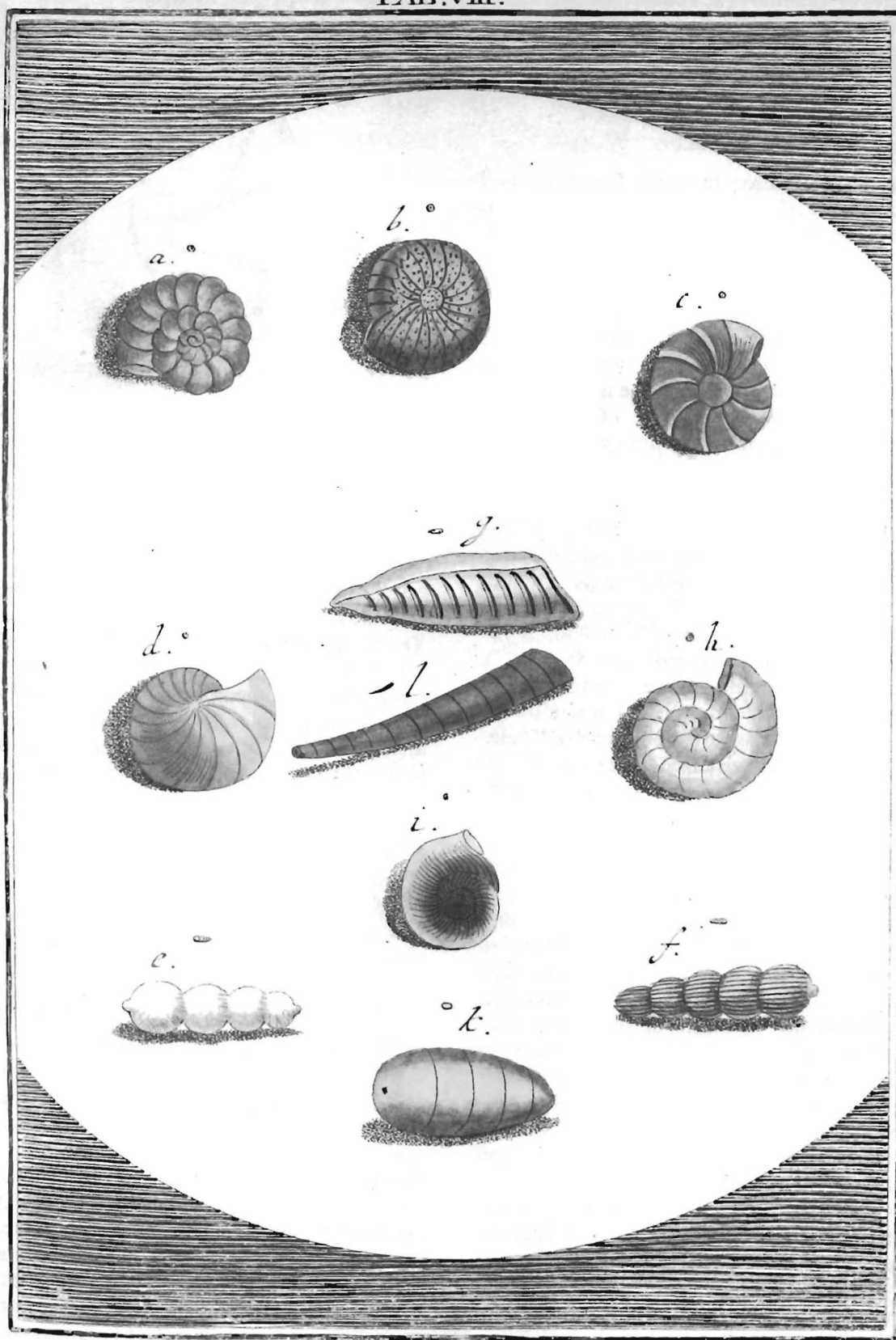
FIGURE 3. Illustration of "Nautilus" figured by Gualtieri (1742, pl. 19, fig. C), upon which Linnaeus (1758) based his species *Nautilus calcar*. Actual size of specimen designated by small figure to upper left of illustration. (Reproduction courtesy of the Mollusk Library, Smithsonian Institution.)

Certainly, he was a creative man, equipped with a keen sense of observation and boundless enthusiasm. Yet, the projects which d'Orbigny undertook were so vast that he could never possibly have achieved his goals. The phenomena with which he dealt became so increasingly complex that he was bound to reduce them to gross oversimplifications and was sometimes forced into inconsistencies. By recognizing twenty-seven living foraminiferal species among the 228 species he had identified in the Miocene strata of the Vienna Basin (1846), d'Orbigny had, by implication, renounced total catastrophism (Blow, 1979).³ In classifying the foraminifera, he never finished the complete synthesis he had planned, and left to his successors a host of nomenclatural problems.

BACKGROUND OF THE *TABLEAU MÉTHODIQUE*

D'Orbigny began his studies of foraminifera at a very early age under the tutelage of his father (d'Orbigny, 1835).⁴ The d'Orbigny family lived on the coast of France in the village of Esnandes, later settling in the town of La Rochelle. D'Orbigny was able to collect Recent and living specimens from the nearby beaches and shores, as well as fossil forms from the Upper Jurassic strata of the surrounding countryside. Through a very active correspondence with collectors and museums, he received a considerable amount of additional material, both Recent and fossil, from various parts of the world, and built up an outstanding collec-

TAB. VIII.



tion. In 1824, at the age of 22, he travelled to Paris, with the bulk of his collection, to verify his identifications (Lys, 1950), and to complete a comprehensive work on the subject of his research. D'Orbigny was already well known in the scientific community through his extensive correspondence with the "leading naturalists of France." The Baron de Ferrusac had invited him to contribute a special section for a planned series of volumes on the "Cephalopod Mollusca." At the time foraminifera were still considered to be "microscopic cephalopods," although a few naturalists had apparently begun to realize that these minute, shelled organisms formed a distinct enough group to warrant special treatment. The age of micropaleontological specialization had begun.

Upon his arrival in Paris, d'Orbigny greatly impressed the members of the Academy of Sciences with the seventy-three completed plates of figures which were intended to accompany his work (Lys, 1950) (see Fig. 8). These figures were beautifully drawn and delicately hand-colored, recalling the figures of Fichtel and Moll.⁵ In addition to the above-mentioned completed plates, d'Orbigny left approximately eighty additional plates in various stages of completion, and the original sketches of the plate figures. In later years, d'Orbigny became so preoccupied with his other endeavors that he was never able to find the time to complete the unfinished plates or to publish the plates that he had finished. For many years the plates lay in obscurity, later to become known as the "Planches Inédites." G. Berthelin was to carefully study the plates and make tracings of the original sketches for his own use. Upon his death in 1887, Berthelin bequeathed the tracings to Carlo Fornasini who reproduced and published them in a series of papers between 1897 and 1908.⁶ These papers constitute the first publication of figures of many of the species mentioned in the *Tableau Méthodique* (Fig. 9).

In addition to the "Planches Inédites," d'Orbigny had constructed a set of 100 models of foraminifera, and had issued plaster casts of them to private subscribers (Fig. 10).⁷ The purpose of these models was to illustrate the features of all of his "genera and subgenera, and even the principle species of the order of Foraminifera" (d'Orbigny, 1826, p. 248). The models were numbered consecutively from one to one hundred and issued in four lots of twenty-five each in the years between 1823 and 1826.

THE *TABLEAU MÉTHODIQUE*

The *Tableau Méthodique* was presented to the Academy of Sciences on November 7, 1825, and published the following year (d'Orbigny, 1826). It was not the totally comprehensive work that d'Orbigny had originally envisioned, but rather comprised an introductory publication, or "Prodrome," as he called it. The comprehensive "special work," which was to have been accompanied by over 150 plates, never came about. The *Tableau Méthodique*, itself, was a rather sketchy work and was presented mostly in the form of an outline with brief diagnoses of families and genera, but none for species. It had been hurriedly put together because d'Orbigny had accepted a post as naturalist on a voyage to South America. He left France on July 29, 1826, and did not return again until 1834.

In having settled for a "Prodrome" and never having successfully completed a final work, d'Orbigny bequeathed a number of nomenclatural problems to posterity. According to a tabulation made by Heron-Allen (1917), 552 species were contained in the *Tableau Méthodique*. Only twenty-six of them were figured on the eight plates that accompanied the work and none of them were described. Many of the species were accounted for by references to the works of earlier authors, especially Soldani, and one hundred others were documented by references to the models d'Orbigny had issued. The species documented by the models, however, were later considered to be invalid because the models had been issued to a limited, private subscription. In addition, 193 of the species received no documentation whatsoever and became *nomina nuda*. A few of these species were later figured by d'Orbigny in subsequent publications (e.g., d'Orbigny, 1846). Parker, Jones and Brady (1865) later figured the models so that the one hundred species documented by the models became valid. Many more species became validated through Fornasini's publication of Berthelin's tracings of d'Orbigny's original drawings from the "Planches Inédites."

As Banner and Blow (1960) discovered, however, when they established lectotypes of d'Orbigny's planktonic species, these later validations resulted in some complicated nomenclatural changes with regard to authorship and date of publication. What Banner and Blow learned was that under the rules of the International Code of Zoological Nomenclature, changes of

FIGURE 4. Plate VIII from Ledermüller (1761), illustrating "Ten different kinds of 'Horns of Ammon' ["Ammonis cornu"] from beach sands." (Photo courtesy of The Beinecke Rare Book and Manuscript Library, Yale University.)

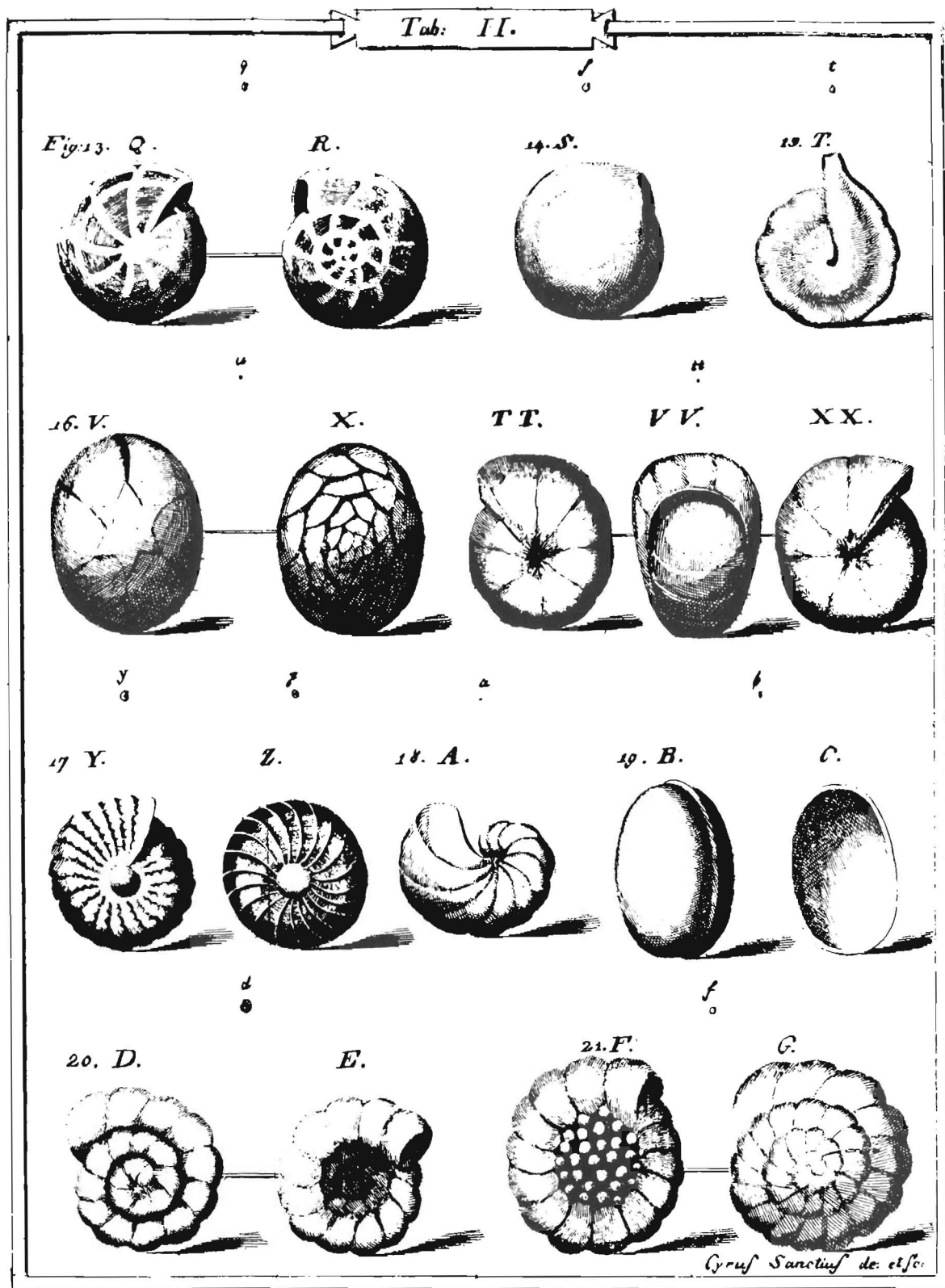


FIGURE 5. Plate accompanying text of Soldani's (1780) work on fossil foraminifera from Tuscany. 13 Q, R, *Nautilus Ammoniformes*, sive trochiformes; 14-16, *Nautili cum Ammonis admixti*; 17 Y, *Nautilus Striati vulgatissimi subflavi*; 17 Z, *Nautilus Striati (Crispi)* ut supra in

authorship and/or date of publication were required for the later validated species. The species based on the one hundred models had to be attributed to Parker, Jones and Brady (1865), because they were the first to produce figures of the models and publish them. On the other hand, the species based on the figures published by Fornasini between 1897 and 1908 remained under the authorship of d'Orbigny because d'Orbigny had drawn the original figures, but their dates of publication had to be changed to the dates when they appeared in Fornasini's works. Some of d'Orbigny's species, therefore, lost priority. Banner and Blow (1960) also found that the planktonic species *Globigerina punctulata* was first figured in 1832 by Deshayes, who changed the spelling to *G. puncticulata*. As a result, *Globigerina punctulata* d'Orbigny, 1826, has now become *G. puncticulata* Deshayes, 1832. In addition, some of the errors and omissions incorporated into d'Orbigny's citations of species described by earlier workers were later clarified by Parker and Jones (1863b) and Parker, Jones and Brady (1865).

The changes required by the rules of nomenclature are often perplexing and sometimes controversial. Anyone using species names from the *Tableau Méthodique* should proceed cautiously.

THE D'ORBIGNY CLASSIFICATION

One of d'Orbigny's principal achievements was the establishment of the "Foraminifères" as a separate order within the Class Cephalopoda. The essential characters upon which he separated the foraminifera from other cephalopods were: their perceived internal shell; their lack of a siphon; the presence of a final, closed chamber; and the one or many apertures which provided the means of communication between chambers. The realization that foraminifera were non-siphonate must have occurred to d'Orbigny not long before he presented his paper to the Academy of Sciences in 1825. Just two years earlier, in 1823, he had mentioned in the brochure which accompanied the issue of the first set of plaster models that: "The place and shape of the siphuncles are indicated by marks or black spots" (Parker, Jones and Brady, 1865).⁸

D'Orbigny believed that the foraminiferal animal had an internal shell and very small head, and he re-

garded the pseudopodia which he had actually observed himself on live specimens as numerous minute tentacles.⁹ It was this interpretation of the pseudopodia that was responsible for d'Orbigny's retention of the Order Foraminifera in the Class Cephalopoda.

A compilation of the classification that appeared in the *Tableau Méthodique* is shown in Table 1. D'Orbigny used latinized names for species and genera, but adopted French modifications of Greek words for familial names. The classification was very simple; families were defined on the single character of plan of growth, or chamber arrangement. It might appear that d'Orbigny had adopted this simple scheme purely as a matter of convenience, since at the time he was in a hurry to complete his classification. D'Orbigny (1826, p. 249) emphasized, however, that he had arrived at the decision to base his families on plan of growth "only after painful and repeated observations, comparing many genera." He believed plan of growth to be the most natural method of grouping genera, and was confident that this system would be followed in the future.

D'Orbigny's classification was attacked soon after its publication by Deshayes, who declared it a "vicious," "unnatural," and "defective" plan (Heron-Allen, 1917, p. 31). D'Orbigny replied sharply, expressing ["his regret that Deshayes could not understand the Models, and that he had gone beyond his province of the Mollusca which he did understand, that if he had not done so 'he would not have tried to upset in one day the result of six years' work upon animals quite different to any he knew'"] (Heron-Allen, 1917, p. 31).

D'Orbigny's system of classification, of course, has not been followed and the idea of grouping genera into families on the basis of plan of growth was later severely criticized (Williamson, 1858; Carpenter, Parker and Jones, 1862; Brady, 1884). An examination of the genera included by d'Orbigny in the various families will uncover many deficiencies of the classification in revealing generic relationships. However, two families remain essentially natural: the Agasthistègues and the Stichostègues. A foundation for the modern Miliolidae can be seen in the Agasthistègues, and, except for the exclusion of distinctly coiled forms and the inclusion of the genus *Pavonia*, the Stichostègues correspond to the modern Nodosariidae. In principle, plan of growth

quibus cellarum divisio apparet, et intima fabrica; 18 A, Nautilus prorsus microscopici quos Gibbosus, seu papyraceos minimos voco, etc.; 19 B, C, Musculi minimi; 20 D, E, Hammoniae Beccarii vulgatissimae, sive utrinque cochleatae depressiusculae, etc.; 21 F, G, Ammoniae cochleatae globoso-rotundatae. Actual size of specimens designated by small figures labelled with lower-case letters. Note also the use of bars to connect different views of same specimen. (Reproduction courtesy of the Todd Library for Foraminiferal Research, Smithsonian Institution.)

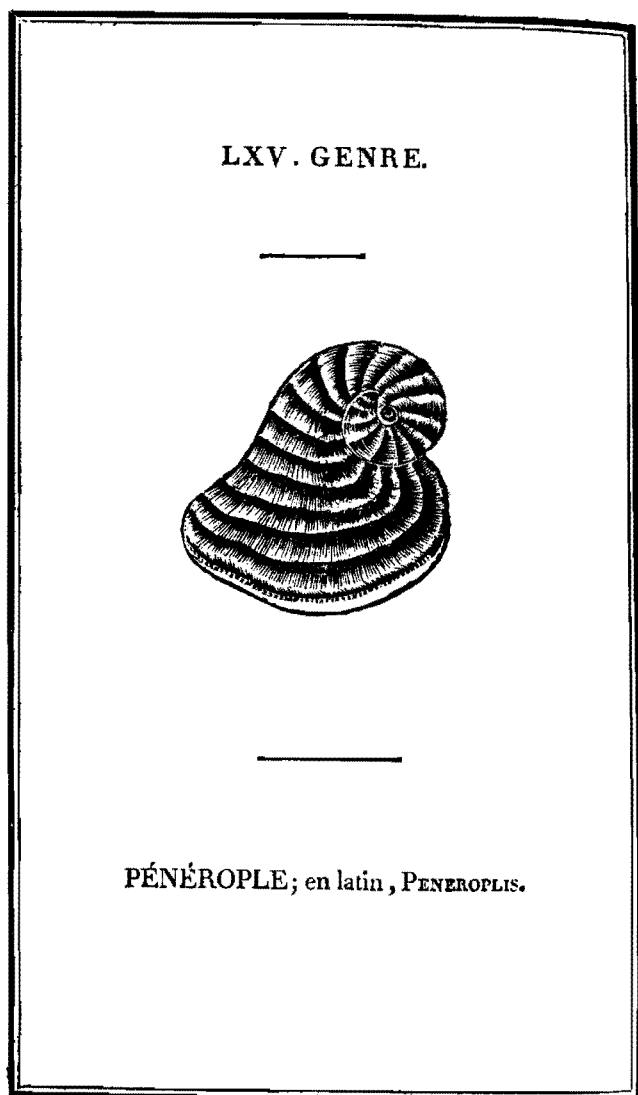


FIGURE 6. Illustration of the genus *Peneroplis* from de Monfort's *Conchyliologie Systematique* (1808). (Reproduction courtesy of the Todd Library for Foraminiferal Research, Smithsonian Institution.)

seems like a reasonable character choice upon which to initiate a classification. Plan of growth, or chamber arrangement, is not only a basic character, but is also the most visible feature of the foraminiferan test. And, despite later malignment, plan of growth remains a character of taxonomic importance. What d'Orbigny

overlooked was the fact that growth plan could be a more important character in some groups than others.

D'Orbigny also grouped together in the same family genera with very different plans of growth. For example, in the Helicostègues, we find the elongate spiral or serial *Bulimina* grouped together with the trocho-spiral *Rotalia* and the planispiral *Nonionina*. The classification also made no accommodation for the fact that plan of growth might change during ontogeny, even though it is obvious that d'Orbigny was well aware of this fact, as is attested to by some of his generic descriptions and illustrations of species.

An omission in the 1826 classification was that it failed to provide for the single-chambered forms, although the family Monostègues was later introduced to accommodate them (d'Orbigny, 1839a). At first, d'Orbigny apparently believed that single-chambered calcareous specimens were the juvenile forms of nodosarids (d'Orbigny, 1839b).¹⁰ The family Monostègues initially included only two genera: the genus *Orbulina* and the newly erected chitinous genus *Gromia* of Dujardin. Shortly thereafter, d'Orbigny (1839b) introduced the genus *Oolina*, using it in place of *Lagena* Walker and Boys, 1792, a genus he never recognized. In the *Cours Élémentaire de Paléontologie*, d'Orbigny (1852) instituted one more family, the Cyclostègues, in which he included the genera *Orbitolites*, *Orbitolina*, *Orbitoides* and *Cyclolina*.

Along with the addition of the above families, d'Orbigny (1839a, 1852) made minor changes in some of the definitions and alterations in some of the families. Essentially, however, his classification remained unchanged (Table 2). Throughout his life d'Orbigny remained convinced that he had achieved a natural system of classification.

DUJARDIN'S DISCOVERY

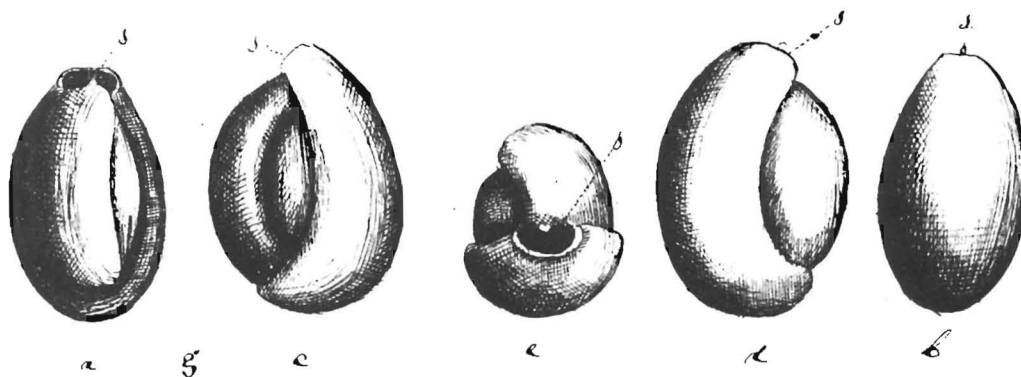
Up until the time of publication of the *Tableau Méthodique* most observations made of living foraminifera, including those of d'Orbigny, were very superficial, probably because of the inadequacy of the optical equipment available at the time. Felix Dujardin (1835a–d) (Fig. 11) was the first worker to critically examine live specimens. His results created enough impact to receive notice in the Paris press (Heron-Allen, 1917).

FIGURE 7. Alcide Dessalines d'Orbigny (1802–1857). Frontispiece from Volume I, *Partie Historique du Voyage dans l'Amérique Méridionale* (d'Orbigny, 1835). (Photo courtesy of The Beinecke Rare Book and Manuscript Library, Yale University.)

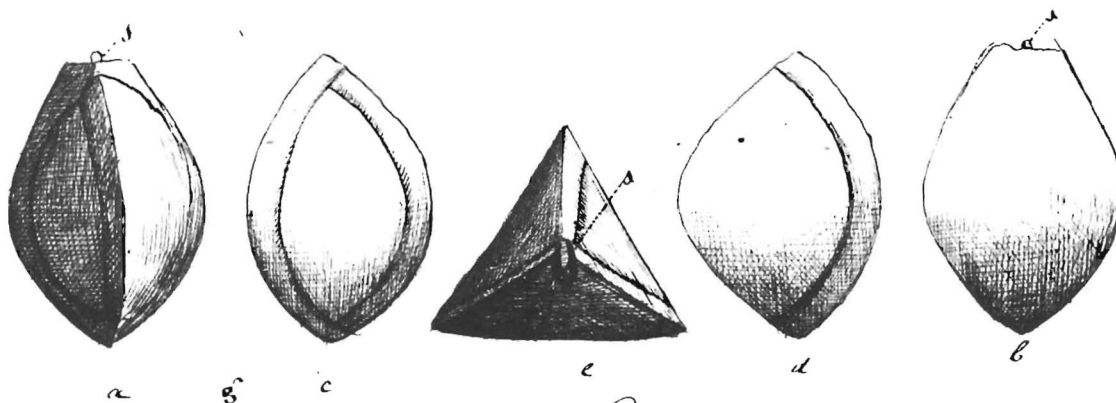


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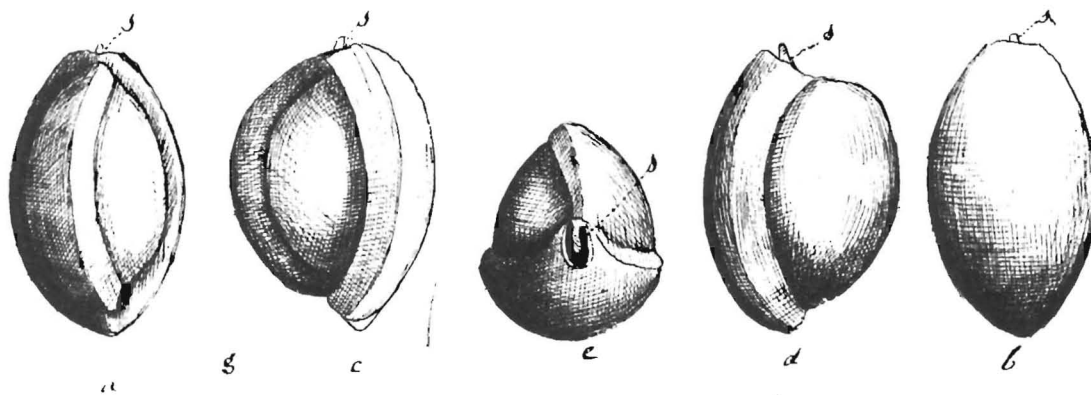
311. *R. mure*



312. *Folicle Supérieur de Bordeaux.*



313. *Folicle Grignon*



Couverture Liban

Dujardin examined a wide variety of calcareous foraminifera, as well as a shell-less "chitinous" form which he named *Gromia oviformis*. In crushing the tests of live specimens, he saw that the substance of the animal was simple, and, in decalcifying the test with weak nitric acid, he obtained the entire animal body which formed a "suite of segments" occupying all of the chambers (1835a). The apparently simple and homogenous substance of the animal, which Dujardin named sarcodite,¹¹ was observed to lack locomotive and digestive organs, and respiratory, circulatory and nervous systems.¹² Dujardin made detailed observations of the movement and structure of the tenuous extensions of the sarcodite (Fig. 12) and definitively concluded that these filamentous prolongations did not represent true tentacles, but on the contrary were analogous to the sarcodite extensions seen in forms like the amoebas. As a result of his investigations, Dujardin concluded that the Foraminifères bore no relation to more advanced organisms such as the Céphalopodes, nor to any other established class in the animal kingdom, but must instead be relegated to the "lowest forms of life."¹³

D'Orbigny completely accepted Dujardin's observations and conclusions and removed the Foraminifères from the Céphalopodes, and elevated the group to the rank of a class and his families to orders. Once the research of Dujardin had established the low degree of organization of foraminifera, attitudes toward these animals underwent an important change.

III. THE ENGLISH SCHOOL AND THE QUESTION OF VARIATION

In view of the great rivalries that existed among the naturalists of the late nineteenth century, one would hardly have expected to find a group of individuals that had built on each other's work so closely or championed a philosophic view so harmoniously that they came to be regarded collectively as a "school." Yet, a group of English workers did band together, in a loosely knit fashion, and together expressed a common opinion on the nature of foraminifera, a point of view that clearly set them apart from their contemporaries on the continent. This group included William K. Parker, T. Rupert Jones (Fig. 13), William C. Williamson (Fig. 14), William B. Carpenter (Fig. 15), and culminated with Henry Bowman Brady (Fig. 16).

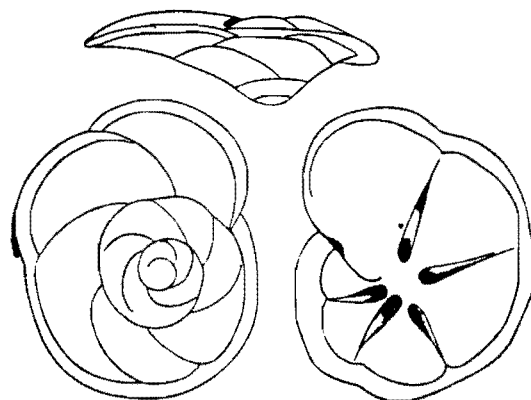


FIGURE 9. Tracing of *Rotalia pileus* made by Berthelin from d'Orbigny's "Planches inédites" and published by Fornasini (1902c, fig. 54, p. 57) as *Discorbina pileus* d'Orbigny. (Reproduction courtesy of the Todd Library for Foraminiferal Research, Smithsonian Institution.)

In reviewing the work of the English School, there appears to have existed among them an apparent "singular unity" of purpose.¹ It seems almost as if the group had worked together as a team, according to an organized plan, to further the understanding of foraminifera. Of course, nothing could have been further from the truth. Each member of the group worked independently—there existed no central facility where their efforts might have been combined. The present British Museum (Natural History), in South Kensington, was not built until 1881, and did not receive specimens from Brady's *Challenger Report* until four years after its publications.² Acquaintances must have been made and views exchanged through the numerous natural history societies and clubs that were so popular in Victorian England.³ Some organizations, in particular the British Association, the Royal Society, and the Geological, Linnaean, and Zoological societies, were influential in the dissemination of ideas and in fostering collaboration between specialists.

The "complete harmony"⁴ in their general results and the lack of rivalry that existed among the group may, in part, be attributed to the opinion, predominant at that time, that foraminifera as a group were considered to be of little or no significance. In the introduction to his monograph on the British Foraminifera, Williamson referred to foraminifera as "this class of objects"⁵ and, probably, he did not regard them as much more than that. The commercial importance of

FIGURE 8. Reproduction of Plate U of d'Orbigny's "Planches inédites." (Photo courtesy of Denis Serrette, Muséum National d'Histoire Naturelle, Paris.)

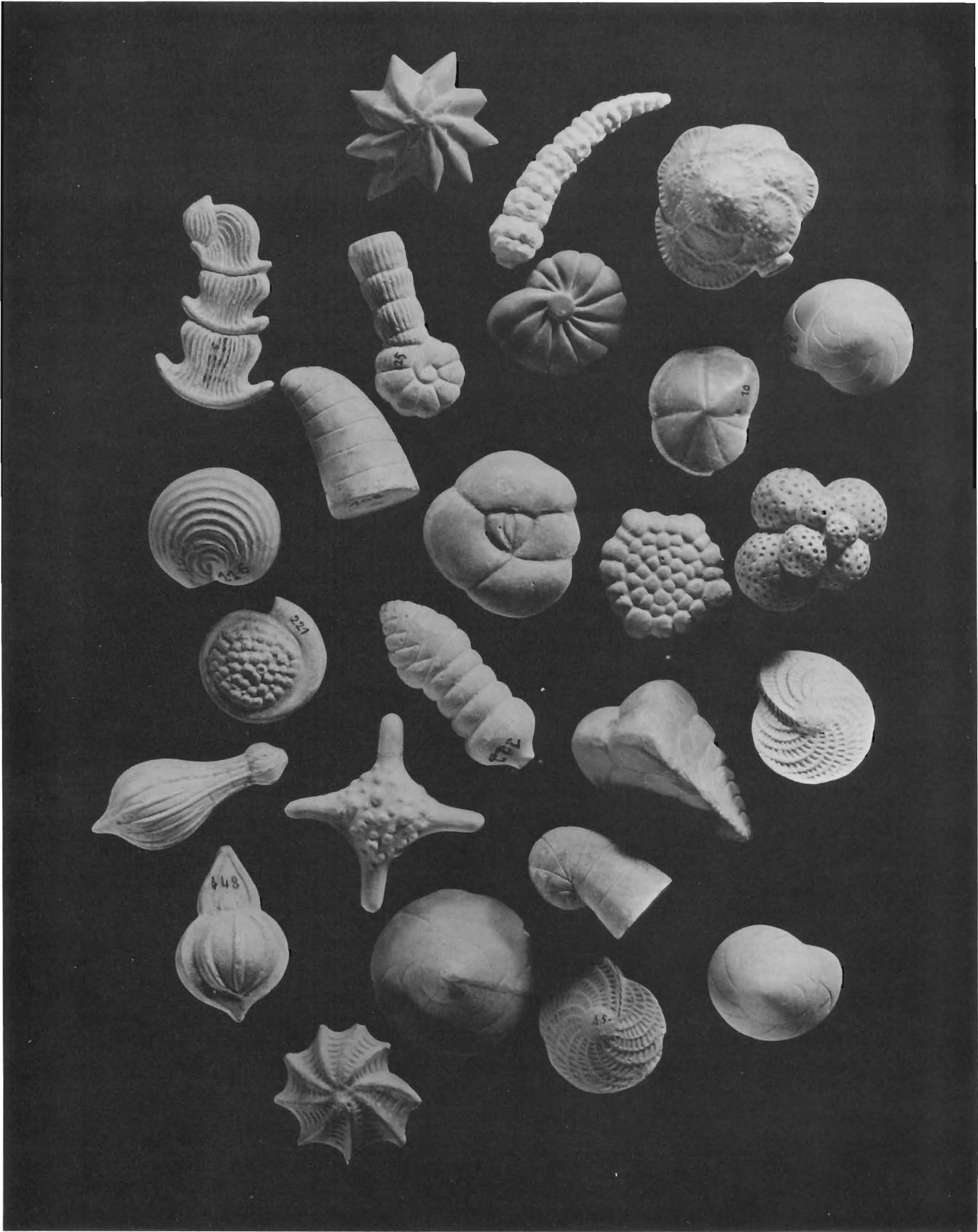


TABLE 1. D'Orbigny's 1826 Classification.

Family I. STICHOSTÈGUES— <i>Nodosaria</i> Lamarck (<i>Glandulina</i> nov., <i>Nodosaria</i> proper, <i>Dentalina</i> nov., <i>Orthocerina</i> nov.); <i>Fron-dicularia</i> Defrance; <i>Lingulina</i> nov.; <i>Rimulina</i> nov.; <i>Vaginulina</i> nov.; <i>Marginulina</i> nov.; <i>Planularia</i> Defrance; <i>Pavonina</i> nov.
Family II. ENALLOSTÈGUES— <i>Bigenerina</i> nov. (<i>Bigenerina</i> proper, <i>Gemmulina</i> nov.); <i>Textularia</i> Defrance; <i>Vulvulina</i> nov.; <i>Dimorphina</i> nov. <i>Polymorphina</i> nov. (<i>Polymorphina</i> proper, <i>Gut-tulina</i> nov., <i>Globulina</i> nov., <i>Pyrulina</i>); <i>Virgulina</i> nov.; <i>Sphae-roidina</i> nov.
Family III. HELICOSTÈGUES
Subfamily Tubinoides — <i>Clavulina</i> nov.; <i>Uvigerina</i> nov.; <i>Bulimina</i> nov.; <i>Valvulina</i> nov.; <i>Rosalina</i> nov.; <i>Rotalia</i> Lamarck (<i>Rotalia</i> proper, <i>Discorbis</i> Lamarck, <i>Trochulina</i> nov., <i>Turbinulina</i> nov.); <i>Calcarina</i> nov.; <i>Globigerina</i> nov.; <i>Gyroidina</i> nov.; <i>Truncatulina</i> nov.
Subfamily Ammonoides — <i>Planulina</i> nov.; <i>Planorbulina</i> nov.; <i>Operculina</i> nov.; <i>Soldania</i> nov.
Subfamily Nautiloides — <i>Cassidulina</i> nov.; <i>Anomalina</i> nov.; <i>Ver-tebralina</i> nov.; <i>Polystomella</i> Lamarck; <i>Dendritina</i> nov.; <i>Pene-ropis</i> Montfort; <i>Spirolina</i> Lamarck; <i>Robulina</i> nov.; <i>Cristellaria</i> Lamarck (<i>Cristellaria</i> , <i>Saracenaria</i> Defrance); <i>Nonionina</i> nov.; <i>Nummulina</i> nov. (<i>Nummulina</i> , <i>Assilina</i>); <i>Siderolina</i> Lamarck
Family IV. AGATHISTÈGUES— <i>Biloculina</i> nov.; <i>Spiroloculina</i> nov.; <i>Triloculina</i> nov.; <i>Articulina</i> nov.; <i>Quinqueloculina</i> nov.; <i>Adel-osina</i> nov.
Family V. ENTOMOSTÈGUES— <i>Amphistegina</i> nov.; <i>Heterostegina</i> nov.; <i>Orbiculina</i> Lamarck; <i>Alveolina</i> Deshayes; <i>Fabularia</i> De-france

foraminifera had not yet been established so there was no cause for competition. The English workers were amateurs, members of the upper middle class who were highly successful in other professions. They possessed a Victorian sense of self-assurance that is often reflected in their writings. The study of foraminifera was a subject to which they devoted their leisure hours, as a means of satisfying their intellectual curiosity about natural history.⁶

The English group made in-depth studies of virtually all aspects of foraminifera and through their collective efforts laid much of the groundwork for modern clas-sification. They examined, in detail, wall textures, in-ternal structures, and shell forms. They recognized the need to put in order the chaotic state of nomenclature and attempted to update species named by earlier workers. In a series of papers, they analyzed and emended the species of Linnaeus, Walker, Montagu, de Montfort, Lamarck, Fichtel and Moll, de Blainville, Defrance, and d'Orbigny (Parker and Jones, 1859a, b, 1860a–c, 1863a, b; Parker, Jones and Brady, 1865). An additional important contribution of the English

TABLE 2. D'Orbigny's 1852 Classification.

Order I. MONOSTÈGUES— <i>Gromia</i> Dujardin; <i>Orbulina</i> d'Orbigny; <i>Oolina</i> d'Orbigny; <i>Ovulites</i> Lamarck; <i>Dactylopora</i> Lamarck; <i>Conodictyum</i> Munster; <i>Goniolina</i> d'Orbigny
Order II. CYCLOSTÈGUES— <i>Cyclolina</i> d'Orbigny; <i>Orbitolites</i> Lamarck; <i>Orbitolina</i> d'Orbigny; <i>Orbitoides</i> d'Orbigny
Order III. STICHOSTÈGUES
Family AEQUILATERALIDAE — <i>Glandulina</i> d'Orbigny; <i>Nodosaria</i> Lamarck; <i>Orthocerina</i> d'Orbigny; <i>Dentalina</i> d'Orbigny; <i>Fron-dicularia</i> Defrance; <i>Lingulina</i> d'Orbigny; <i>Vaginulina</i> d'Orbigny; <i>Marginulina</i> d'Orbigny
Family INAEQUILATERALIDAE — <i>Webbina</i> d'Orbigny
Order IV. HELICOSTÈGUES
Family NAUTILOIDAE — <i>Cristellaria</i> Lamarck; <i>Flabellina</i> d'Orbig-ny; <i>Robulina</i> d'Orbigny; <i>Fusulina</i> Fischer; <i>Nummulites</i> La-marck; <i>Assilina</i> d'Orbigny; <i>Siderolina</i> Lamarck; <i>Hauerina</i> d'Or-bigny; <i>Operculina</i> d'Orbigny; <i>Polystomella</i> Lamarck; <i>Peneroplis</i> Montfort; <i>Dendritina</i> d'Orbigny; <i>Spirolina</i> Lamarck; <i>Lituola</i> Lamarck; <i>Orbiculina</i> Lamarck; <i>Alveolina</i> d'Orbigny
Family TURBINOIDAE — <i>Rotalia</i> Lamarck; <i>Globigerina</i> d'Orbigny; <i>Planorbulina</i> d'Orbigny; <i>Truncatulina</i> d'Orbigny; <i>Placopsilina</i> d'Orbigny; <i>Anomalina</i> d'Orbigny; <i>Rosalina</i> d'Orbigny; <i>Valvu-lina</i> d'Orbigny; <i>Verneuilina</i> d'Orbigny; <i>Bulimina</i> d'Orbigny; <i>Uvigerina</i> d'Orbigny; <i>Pyrulina</i> d'Orbigny; <i>Faujasina</i> d'Orbigny; <i>Chrys-alidina</i> d'Orbigny; <i>Clavulina</i> d'Orbigny; <i>Gaudryina</i> d'Or-bigny
Order V. ENTOMOSTÈGUES
Family ASTERIGINIDAE — <i>Astigerina</i> d'Orbigny; <i>Amphistegina</i> d'Orbigny; <i>Heterostegina</i> d'Orbigny
Order VI. ENALLOSTÈGUES
Family POLYMORPHINIDAE — <i>Dimorphina</i> d'Orbigny; <i>Guttulina</i> d'Orbigny; <i>Globulina</i> d'Orbigny; <i>Polymorphina</i> d'Orbigny
Family TEXTULARIDAE — <i>Bigenerina</i> d'Orbigny; <i>Textularia</i> De-france; <i>Bolivina</i> d'Orbigny; <i>Sagrina</i> d'Orbigny; <i>Cuneolina</i> d'Or-bigny
Order VII. AGATHISTÈGUES
Family MILIOLIDAE — <i>Biloculina</i> d'Orbigny; <i>Fabularia</i> Defrance; <i>Spiroloculina</i> d'Orbigny
Family MULTILOCUUIDAE — <i>Triloculina</i> d'Orbigny; <i>Articulina</i> d'Or-bigny; <i>Sphaeroidina</i> d'Orbigny; <i>Quinqueloculina</i> d'Orbigny; <i>Adelosina</i> d'Orbigny

School came from the exhaustive library work of Charles Davies Sherborn (Fig. 17) who compiled a bibliography of all known references, published from the year 1565 up to 1888, on Recent and fossil fora-minifera, and an index of all described genera and species of foraminifera published up to the year 1889 (Sherborn, 1888, 1893, 1896, 1955).

The philosophical idea which served to unite the group and justified their being labelled a school concerned the subject of variation. The English took an extremely broad view of variation and their concern with it nearly reached the point of obsession. In almost every paper there is some comment on the variability

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FIGURE 10. Some of the original plaster models of d'Orbigny now contained in the collections of the Muséum National d'Histoire Naturelle in Paris. (Photo courtesy of the Muséum National d'Histoire Naturelle, Paris, © Denis Serrette, M.N.H.N.)



FIGURE 11. Felix Dujardin (1801–1860). Photographic reproduction of the frontispiece in *The Protozoa, Sarcodina* by Margaret W. Jepps (1956). The original painting is a miniature portrait of Dujardin made by his daughter Louise in 1847.

of foraminiferal form and the artificiality of the foraminiferal species. Even Sherborn, whose concerns were purely bibliographic, felt compelled in the introduction to his *Index* to point out the “impossibility of defining a ‘species’ in a group where every individual may be regarded as a ‘variety’” (Sherborn, 1950, p. vii). Williamson (1858) was almost apologetic about his use of specific names,⁷ and Carpenter (1862) discussed at length the transitional nature of foraminifera.⁸

The English, especially Carpenter, were the severest critics of d’Orbigny. They regarded most of his species as mere variants of a few types, and considered his classification to be totally unnatural because it was based on plan of growth, an exceptionally variable character. Another interesting view introduced at the time was the idea that species and genera comprised environmentally controlled expressions of a common type.^{9,10}

The English School made important contributions to the development of classification by recognizing

variation and by emphasizing the necessity for “ascertaining the range of variation by an extensive comparison of individual forms” (Carpenter, 1862, p. ix). Yet they cannot by any means be regarded as the precursors of the new systematics. They did not expect that studies of variation would lead to better defined species limits because, in fact, they refused to admit to the existence of such limits. Metazoans could have definable species limits, but not foraminifera. Like Linnaeus, their view of variation was strongly rooted in essentialism, and what they had expected to demonstrate was the existence of a limited number of central types surrounded by diverse, connecting forms. Carpenter carried this view to an extreme. He considered the notion of discrete species to be totally inapplicable to foraminifera and thought that even genera were gradational. Carpenter believed the only way to arrive at a natural classification was to arrange these diverse forms according to their degree of divergence from a few familial types. Williamson was somewhat more moderate in his views and acknowledged that some species probably had a real existence. Brady generally upheld the central type concept, but he recognized that variability might be greater in some groups than in others,¹¹ and launched a new, empirical approach to classification.

The English view of variation was clearly influenced by Dujardin’s discovery of the protozoan nature of foraminifera. Because foraminifera belonged among the lowest forms of life, it seemed to follow that a foraminiferal species could not have the same meaning as a species in a higher organism.¹²

The strongest arguments given by Williamson and Carpenter for “the extreme latitude of the range of variation in this group,”¹³ were based on examples of miliolids and nodosarids. In many instances, in both of these exceptionally variable groups, it is difficult if not impossible to separate species or even genera in a way that is generally satisfactory. One either recognizes a multitude of scarcely distinguishable species or a very few species that essentially amount to central types. Throughout the years the dilemma of these groups has remained unresolved and, as in the nineteenth century, the approach to them follows one of two courses—fine splitting, in the fashion of d’Orbigny, or broad lumping, in the tradition of the English School.¹⁴

Looking at the group as a whole, it is difficult to conceive of foraminifera, in all their diversity, as being centered around a few central types. Yet, the English were vindicated in their grouping together of the coiled and the serial nodosarids into a single family. This approach constituted a major change in outlook on

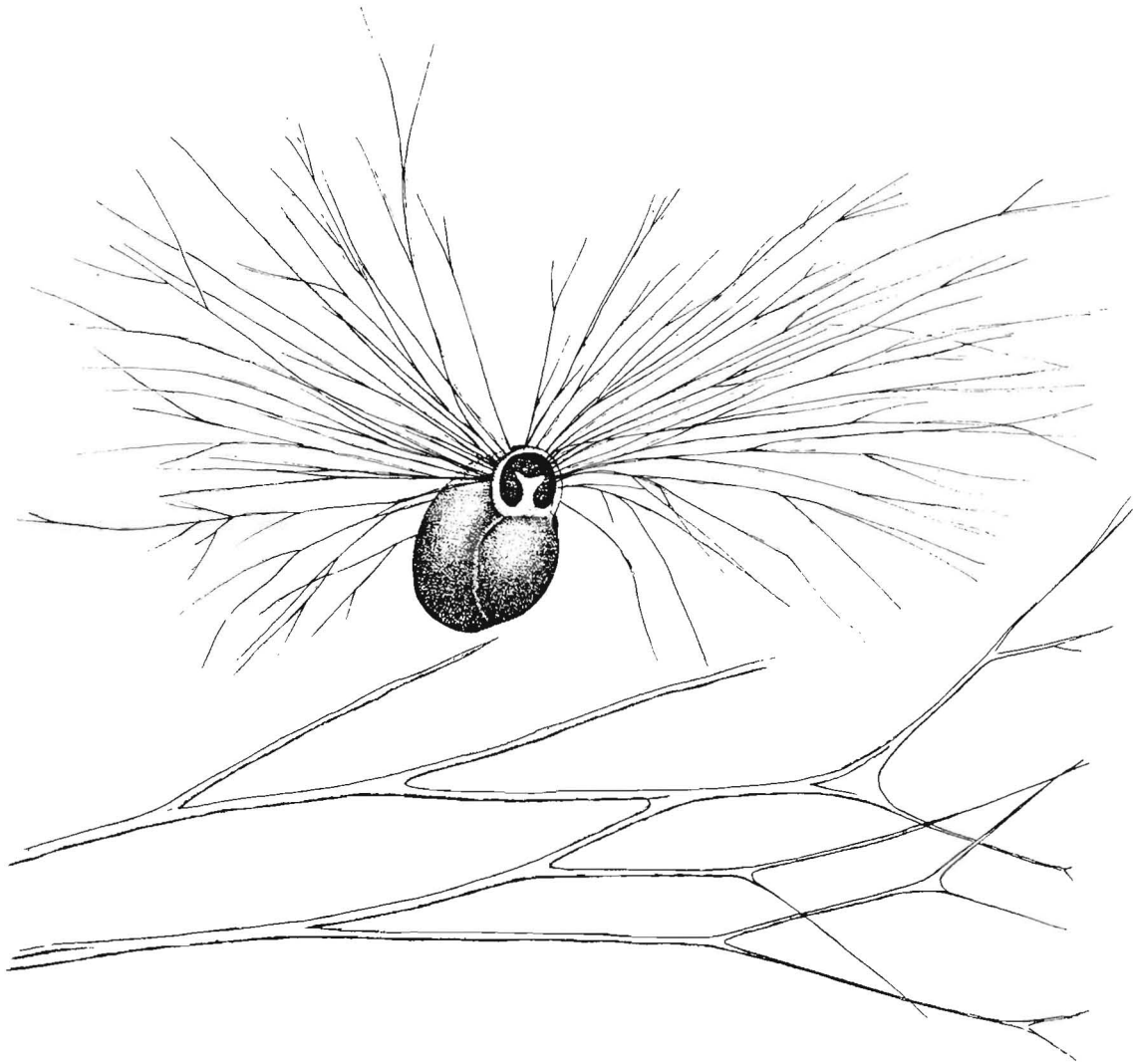


FIGURE 12. Illustrations of a miliolid with its pseudopodia extended and a detail of the branching and anastomosing pseudopodia, as observed by Dujardin (1835d). Figure redrawn from Dujardin (1835d, pl. 9, figs. 3 and 4).

classification, a change that their continental colleagues were slow to accept.

IV. LATE NINETEENTH CENTURY ADVANCES

THE CONTRIBUTION OF WILLIAMSON

Williamson (1858) stated that his monograph on British Recent Foraminifera had been completed under difficult circumstances. Located as he was in Manchester, or in the provinces as he described it, he had no direct access to the London library facilities. William Crawford Williamson, by trade a practicing physician and professor of Natural History, worked on foraminifera only during his spare hours as a means of relaxation.¹

Although Williamson (1858, p. xix) "made no attempt to group the genera into classes or orders" (Table 3), his work was influential in setting the foundation of modern classification. He considered d'Orbigny's familial categories to be worthless as they were based on plan of growth which, like other external features, he considered to be a highly variable character. Williamson thought that many so-called species represented different ontogenetic stages.² Other species he felt were merely variants of a single form. D'Orbigny's classification required that these variants be placed in separate families, an idea which Williamson found unacceptable. Williamson adopted a binomial nomenclature, but mainly as a "useful mode of indicating special types of form" (Williamson, 1858, p. xi).

While Williamson considered plan of growth to be



FIGURE 13. T. Rupert Jones (1819–1911). (Photo courtesy of the British Museum (Natural History), London.)

of little or no importance, he nevertheless studied it carefully and contributed to the development of this aspect of shell form into a more usable taxonomic character. As mentioned earlier, perhaps the chief problem of d'Orbigny's classification was that the various modes of growth upon which he based his families were inadequately defined. Williamson was much more rigorous in his approach and clearly distinguished the several major forms of shell growth. He was precise in his descriptive terminology of shell parts and their dimensions. Where d'Orbigny more or less left the student to fend for himself in learning the various shell forms from his models or plate illustrations, Williamson provided "illustrative diagrams" of shells accompanied by careful descriptions of the shell parts (Fig. 18).

Williamson perceived that foraminifera reproduce sexually as well as asexually and believed that the "repetition of identical types" was maintained by the asexual phases (fission), and diversity achieved by the

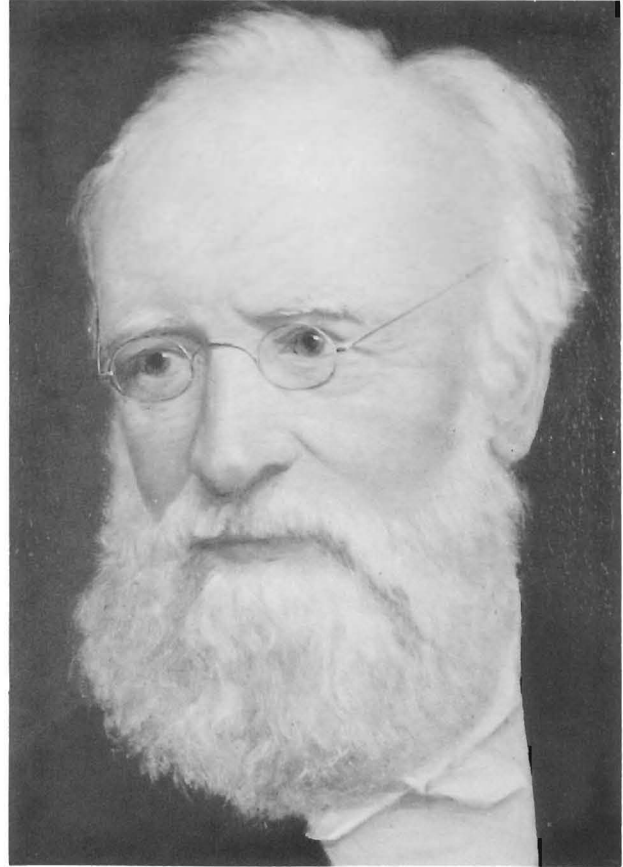


FIGURE 14. William Crawford Williamson (1816–1895). Photographic reproduction of an oil painting by A. Brothers, 1887, now in the University Library, Manchester. (Photo courtesy of the British Museum (Natural History), London.)

sexual phases (Williamson, 1858, p. xi). He was impressed with the permanence of form, as many Recent types could be found in ancient strata, and also by the almost endless diversity that was coupled to this persistence of form.

The foraminiferal test seemed to be an unreliable guide for the separation of species. Williamson (1858), however, conceded that species of foraminifera must have at least some real existence.³ And moreover, he thought "the materials of which the shells are composed" might prove to be a reliable criterion for the discrimination of species (Williamson, 1858, p. xi). In his own words, "Such differences in the chemical and histological composition of these shells probably indicate correlative physiological differences in the living sarcodae, or secreting animal substance, that have at least a specific value. I have not met with one fact contravening this idea. No examples have occurred to me in which the same *form* of shell has indifferently

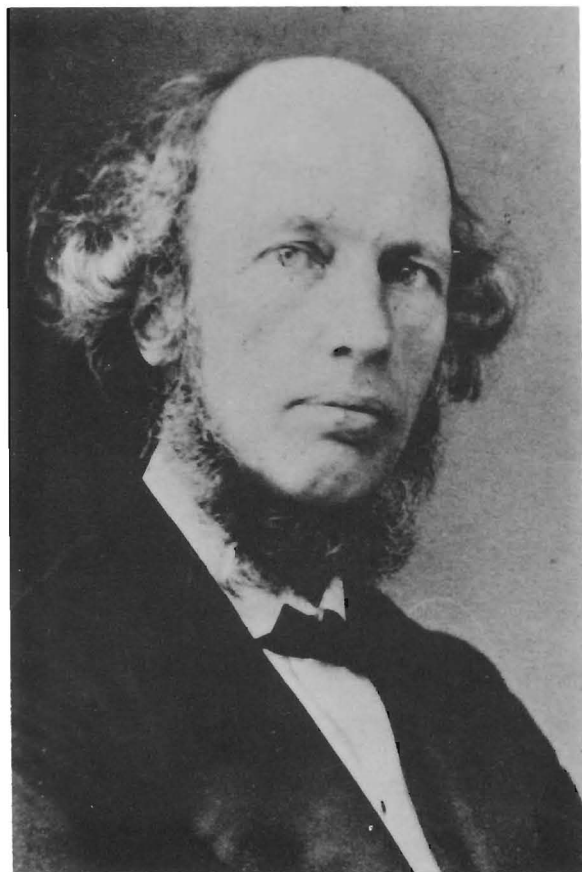


FIGURE 15. William Benjamin Carpenter (1813–1885). (Photo courtesy of the British Museum (Natural History), London.)

presented the arenaceous, porcelainous, and hyaline textures” (Williamson, 1858, p. xi). Williamson (1858, p. xi) recognized three kinds of distinctive wall compositions, “opaque calcareous . . . having a porcelainous aspect . . . rarely if ever foraminiferated”; calcareous having a “transparent and glassy (hyaline)” shell; and shells consisting of “agglutinated grains of sand, but little, if any lime entering into their composition.” However, in spite of his emphasis on wall texture, he grouped calcareous and arenaceous species together in several of his genera.

Williamson’s suggestion that wall texture might have value as a means of separating foraminiferal species in a natural way gained an immediate acceptance. Moreover, his successors carried this suggestion much further than he dared himself. Immediately following the publication of Williamson’s monograph, porosity and wall composition came to be regarded as characters of fundamental importance and thus became entrenched in the higher levels of classification. The modern suborders Textulariina, Miliolina, and Rotaliina all cor-

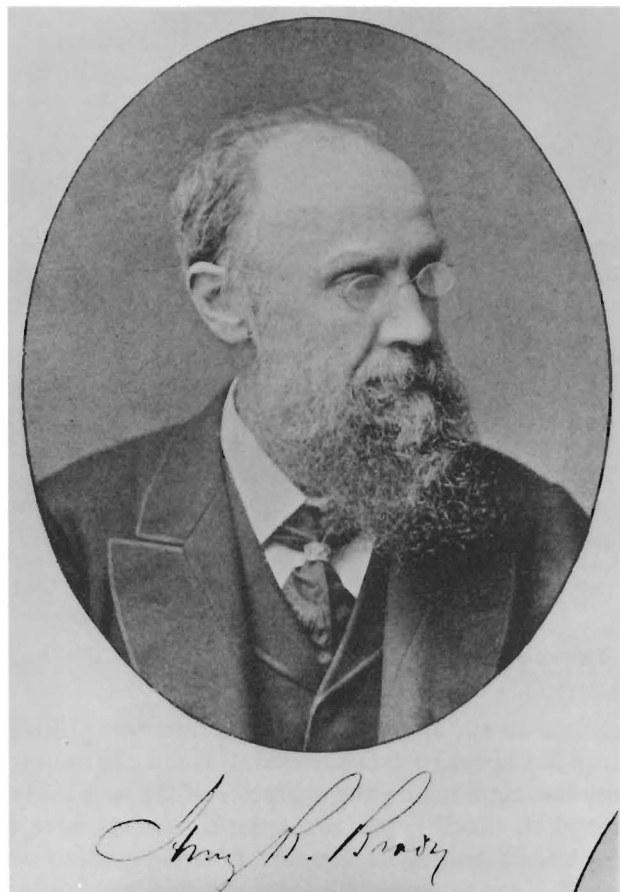


FIGURE 16. Henry Bowman Brady (1835–1891). (Photo courtesy of the British Museum (Natural History), London.)

respond to Williamson’s arenaceous, calcareous imperforate and calcareous perforate divisions.

Two other classifications using wall texture as the basis for the subdivision of families appeared almost simultaneously: one by the Viennese, Reuss (1862), and the other by the British, Carpenter (1862). There is no evidence that Reuss and Carpenter had corresponded with each other or discussed their views on the importance of wall texture; their ideas appear to have developed independently. Acknowledgments to Williamson were made so casually in both of these works that it seems likely that within three years of the publication of Williamson’s monograph the significance of wall texture had come to be regarded as common knowledge.

The introduction of wall texture as a means of separating higher categories marked the greatest turning point in the history of foraminiferal classification. No future development would rival its impact and, except for dissent by Brady (1884), who refused to place total

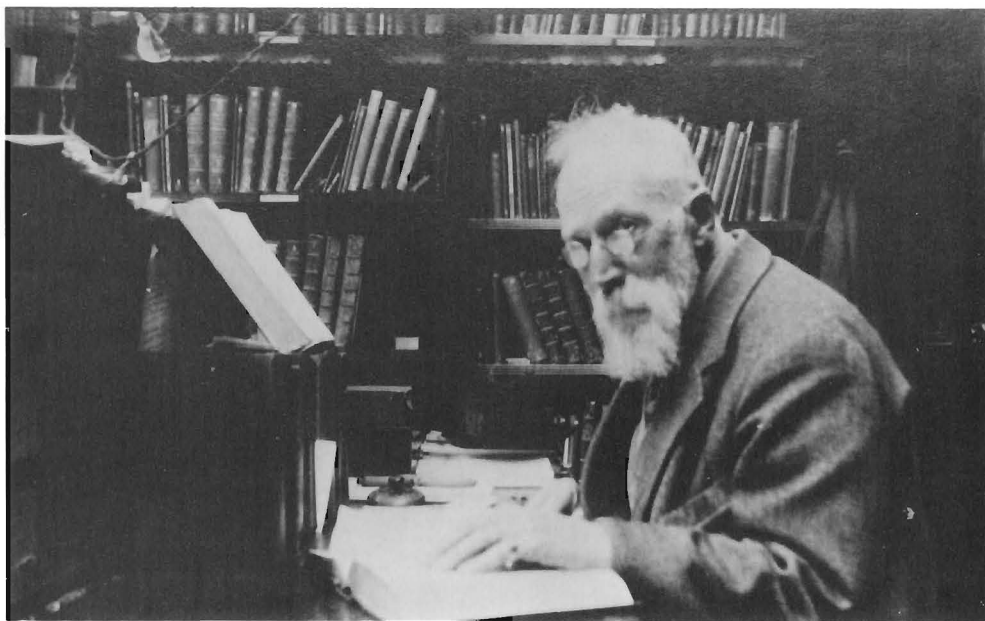


FIGURE 17. Charles Davies Sherborn (1861–1942). (Photo courtesy of the British Museum (Natural History), London.)

reliance on any single character, its overriding importance has never been challenged. It is not clear how or why this thinking on the character of the wall materialized so quickly, but perhaps the reasons were as much philosophical as scientific. D'Orbigny surely was aware of the differences in porosity and wall composition among foraminifera, but did not consider these to be of much importance in classification. Williamson clearly had reservations about using wall texture for more than distinguishing otherwise similar species. As it would turn out, there would be reason for Williamson's reservation. The importance of wall texture remains undeniable, but the philosophical basis of its usage in classification may eventually have to be reconsidered.⁴

THE REUSS CLASSIFICATION

The initial classification proposed by August E. Reuss (1861) (Fig. 19) was contained in a modest-sized publication of forty-two pages in which is included description of the twenty-one families, seven subfamilies and approximately eighty genera that he recognized (Table 4). His descriptions were concise and presented as diagnoses in the modern telegraphic style. Reuss's outlook on classification is revealed in the introductory part of this work. He had a very strong sense of order and believed that species were distinct and immutable. Reuss felt his sense of order threatened by the English notions on variation and by evolutionary theory. This

sense of order probably accounts for the fine splitting of species for which Reuss is known. Although Reuss admired d'Orbigny, he believed that d'Orbigny had not produced as good a classification as might have been accomplished, and criticized d'Orbigny for not recognizing the importance of wall texture. It was very clear to Reuss that the composition of the wall and the presence or absence of pores revealed the fundamental nature of foraminifera.

In his original classification, Reuss divided his twenty-one foraminiferal families into two major groups: the single-chambered Monomera and the multichambered Polymera. Both the Monomera and Polymera were then subdivided into superfamilial groupings on the basis of wall texture. Reuss included seven families in the Monomera: the chitinous Gromidea; the single-chambered, hyaline Lagenidea; the coiled, tubular families Spirillinidea, Ammodiscinea and Cornuspiridea; and the families Squamulinidea and Ovulitidea. The fact that each of the three tubular families was monotypic demonstrates the great emphasis Reuss placed on wall texture for the separation of simple, otherwise identical forms.

Reuss's primary division of foraminifera into the Monomera and the Polymera suggests that he may not have been quite ready to break completely with the chamber arrangement tradition. Seven years earlier, Schultze (1854) had published a classification, in which he also proposed a two-fold breakdown of the "testaceous rhizopods," into single-chambered and mul-

TABLE 3. Williamson's 1858 Classification.

Genus <i>Protonina</i> nov.
Genus <i>Orbulina</i> d'Orbigny
Genus <i>Lagena</i> Walker
Genus <i>Entosolenia</i> Ehrenberg
Genus <i>Lingulina</i> d'Orbigny
Genus <i>Nodosaria</i> Lamarck
Genus <i>Dentalina</i> d'Orbigny
Genus <i>Fronicularia</i> Defrance
Genus <i>Cristellaria</i> Lamarck
Genus <i>Nonionina</i> d'Orbigny
Genus <i>Nummulina</i> d'Orbigny
Genus <i>Polystomella</i> Lamarck
Genus <i>Peneroplis</i> Montfort
Genus <i>Patellina</i> nov.
Genus <i>Rotalina</i> d'Orbigny
Genus <i>Globigerina</i> d'Orbigny
Genus <i>Planorbulina</i> d'Orbigny
Genus <i>Truncatulina</i> d'Orbigny
Genus <i>Bulimina</i> d'Orbigny
Genus <i>Uvigerina</i> d'Orbigny
Genus <i>Cassidulina</i> d'Orbigny
Genus <i>Polymorphina</i> d'Orbigny
Genus <i>Textularia</i> Defrance
Genus <i>Biloculina</i> d'Orbigny
Genus <i>Spiroloculina</i> d'Orbigny
Genus <i>Miliolina</i> nov.
Genus <i>Vertebralina</i> d'Orbigny
Genus <i>Spirillina</i> Ehrenberg

tichambered forms (the Monothalamia and Polythalamia, respectively).⁵ Reuss revised his classification immediately after the manuscript had gone to press and consequently the final form of his classificatory scheme appears as a postscript at the end of the text of his 1861 paper (Table 5). In this final revision, Reuss discarded the Monomera and Polymera, but continued to employ a two-fold major subdivision, grouping his families into imperforate and perforate suborders. He separated the imperforate group into arenaceous and calcareous porcellaneous subdivisions and divided the perforate group into hyaline, finely perforate and hyaline, heavily perforate subdivisions. Both of his perforate divisions were described as calcareous. In addition to the above-mentioned changes he excluded the family Gromidea completely from his final scheme.

The structure of Reuss's final classification, therefore, closely paralleled the structure of Williamson's classification, except for the distinction Reuss made between the finely perforate and coarsely perforate forms. Reuss grouped genera into families largely, though not completely, according to plan of growth, in the manner of d'Orbigny. Reuss's family Rhabdoidea corresponded to the Stichostegues of d'Orbigny and contained six subfamilies of linear nodosarids. Coiled nodosarids were contained in the monotypic

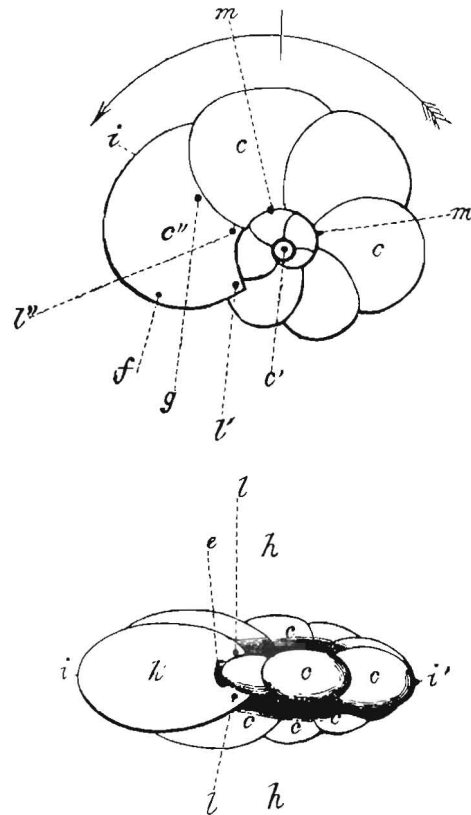


FIGURE 18. Two examples of the carefully labelled diagrams Williamson (1858) used to illustrate the "spiral nautiloid form." Upper figure, Lateral view. Lower figure, Apertural view. *c*, chamber; *c'*, primordial chamber ("being the immediate product of the gemmule or ovum from which the individual originated, and from which all the succeeding segments are gemmations"); *c''*, last-formed chamber; *e*, septal aperture; *f*, anterior margin of last-formed chamber; *g*, posterior margin of last-formed chamber; *h*, lateral surface; *ii'*, peripheral margin; *k*, apertural face of last-formed chamber; *ll*, umbilical angles of septal plane; *l'*, anterior umbilical angle; *l''*, posterior umbilical angle; *m*, spiral suture ("the spiral line marking the external junction of contiguous convolutions"). Arrow indicates "axis of growth."

Cristellaridea. On the other hand, the two arenaceous families included genera with different growth plans. *Ammodiscus*, which Reuss had earlier regarded as belonging to a separate family, was now placed in the Lituolidea, along with the trochospiral *Lituola* and the uniserial *Haplostiche*. Reuss incorrectly described the porcellaneous genus *Nubecularia* as having an arenaceous wall and included this genus in the Lituolidea.⁶ Interestingly, Reuss, like Carpenter, distinguished two of his calcareous, coarsely perforate families (Polystomellidea and Nummulitidea) on the basis of canal systems.

Glaessner (1947) rightly observed that Reuss had



FIGURE 19. August Emanuel Reuss (1811–1873). (Photo courtesy of the Todd Library for Foraminiferal Research, Smithsonian Institution.)

established the framework for modern classification, and that “had these suggestions been followed more closely by later workers, many obvious errors could have been avoided” (Glaessner, 1947, p. 85). A two-fold problem, however, surfaced with the idea of establishing perforate/imperforate primary subdivisions and secondary groupings based on wall texture: some arenaceous foraminifera are perforate, and also many arenaceous forms emulate calcareous forms in virtually all features of their morphology.⁷ In dealing with this problem, Reuss was forced into making inconsistent groupings in his classification. For example, not only did he include both calcareous and arenaceous genera within the family Textilaridea, but he grouped this family with the “glassy, finely perforate, calcareous” families (Reuss, 1861, p. 365). Glaessner (1947) believed that the genus *Textilaria* of Reuss to be equiv-

alent to the calcareous form *Gümbelina*. This idea, however, seems unlikely, as it does not account for the fact that Reuss also included in the Textilaridea the arenaceous genus *Vulvulina*. Reuss was by no means the only worker to group the “textilarids” together with the bolivinids—this later became a common practice.⁸ The serial forms, regardless of wall composition, remained locked together for a long time. One rationale for the reluctance to separate the “textilarids” and the bolivinids may have been the belief that the porous arenaceous forms were basically calcareous. The arenaceous wall was thought to consist of either an “arenaceous incrustation” on a calcareous wall, or a thicker arenaceous layer over an inner calcareous lining. This view of the arenaceous wall texture was further elaborated by Carpenter (Carpenter, 1862).

THE WORK OF CARPENTER

Background

The “introduction” meant to complement Williamson’s (1858) *Recent Foraminifera of Great Britain* resulted in a work of 319 quarto-sized pages—a foraminiferal monument of English Victorian verbalism. Although authorship of the *Introduction to the Study of Foraminifera* is usually cited in bibliographies as Carpenter, Parker and Jones, 1862, Carpenter clearly stated in the preface to the *Introduction* that the work had been primarily his responsibility, and acknowledged Parker and Jones for their contributions in the appropriate sections. Only Carpenter’s name appeared on the cover; Parker and Jones, however, were listed as assistants on the title page.

William B. Carpenter, an eminent physiologist and influential figure in natural history during the nineteenth century, produced an important work that has remained a powerful influence on foraminiferal taxonomy right up to the present generation. Many modern ideas concerning internal structures, canal systems, shell construction and wall texture can be recognized as having originated with Carpenter. Carpenter, unlike Williamson, introduced in his work a scheme of classification, which, except for his use of textural divisions, became the most quickly forgotten part of his work. Nevertheless, because of his eminence, Carpenter’s views carried great authority.

Contributions

Carpenter confirmed and expanded upon Williamson’s observations of the three basic types of wall texture. The imperforate porcellaneous texture, Carpenter

TABLE 4. Reuss's 1861 Classification (from text).

I. FORAMINIFERA MONOMERA	
A. With flexible tests	Family GROMIDEA — <i>Gromia</i> Dujardin; ? <i>Plagiophrys</i> Claparède; <i>Corycia</i> Dujardin
B. With calcareous porous tests	Family LAGENIDEA — <i>Lagena</i> Walker and Boys; <i>Fissurina</i> Reuss
	Family SPIRILLINIDEA — <i>Spirillina</i> (Ehrenberg) Jones
	Family SQUAMULINIDEA — <i>Squamulina</i> Schultze
	Family OVULITIDEA
C. With calcareous compact porcellaneous test	Family CORNUSPIRIDEA — <i>Cornuspira</i> Schultze
D. With arenaceous-siliceous tests	Family AMMODISCINEA — <i>Ammodiscus</i> nov.
II. FORAMINIFERA POLYMERA	
A. With calcareous hyaline finely porous tests	Family RHABDOIDEA Schultze
	Subfamily Nodosaridea — <i>Nodosaria</i> d'Orbigny; <i>Dentalina</i> d'Orbigny; <i>Orthocerina</i> d'Orbigny
	Subfamily Vaginulinidea — <i>Vaginulina</i> d'Orbigny; <i>Rimulina</i> d'Orbigny
	Subfamily Frondicularidea — <i>Frondicularia</i> Defrance; <i>Rhabdogonium</i> Reuss; <i>Amphimorphina</i> Neugeboren; <i>Dentalinopsis</i> Reuss; <i>Flabellina</i> d'Orbigny
	Subfamily Glandulinidea — <i>Glandulina</i> d'Orbigny; <i>Pseudidium</i> Reuss; <i>Lingulina</i> d'Orbigny; <i>Lingulinopsis</i> Reuss
	Subfamily Pleurostomellidea — <i>Pleurostomella</i> Reuss
	Family CRISTELLARIDEA — <i>Cristellaria</i> Lamarck (<i>Marginulina</i> d'Orbigny; <i>Cristellaria</i> d'Orbigny; <i>Robulina</i> d'Orbigny)
	Family POLYMORPHINIDEA — <i>Bulimina</i> d'Orbigny; <i>Virgulina</i> d'Orbigny; <i>Uvigerina</i> d'Orbigny; <i>Polymorphina</i> d'Orbigny (<i>Pyrulina</i> d'Orbigny; <i>Globulina</i> d'Orbigny; <i>Guttulina</i> d'Orbigny; <i>Polymorphina</i> d'Orbigny); ? <i>Strophoconus</i> Ehrenberg; <i>Robertina</i> d'Orbigny; <i>Sphaeroidina</i> d'Orbigny; <i>Dimorphina</i> d'Orbigny
	Family CRYPTOSTEGIA — <i>Chilostomella</i> Reuss; <i>Allomorphina</i> Reuss
	Family TEXTILARIDEA — <i>Textilaria</i> Defrance; <i>Proporus</i> Ehrenberg; <i>Sagraina</i> d'Orbigny; <i>Vulvulina</i> d'Orbigny; <i>Bolivina</i> d'Orbigny; ? <i>Cuneolina</i> d'Orbigny; <i>Gemmulina</i> d'Orbigny; <i>Schizophora</i> Reuss
	Family CASSIDULINIDEA — <i>Cassidulina</i> d'Orbigny; <i>Ehrenbergina</i> Reuss
B. With porcellaneous calcareous tests	Family MILIOLIDEA
	Subfamily Miliolidea genuina— <i>Uniloculina</i> d'Orbigny; <i>Biloculina</i> d'Orbigny; <i>Spiroloculina</i> d'Orbigny; <i>Triloculina</i> d'Orbigny; <i>Quinqueloculina</i> d'Orbigny
	Subfamily Fabularidea — <i>Fabularia</i> Defrance
	Family ORBITULITIDEA — <i>Cyclolina</i> d'Orbigny; <i>Orbitulites</i> Lamarck; <i>Orbitulina</i> d'Orbigny; <i>Orbiculina</i> Lamarck; <i>Alveolina</i> d'Orbigny
	Family PENEROPLIDEA — <i>Peneroplis</i> Montfort (<i>Peneroplis</i> Montfort; <i>Dendritina</i> d'Orbigny; <i>Spirolina</i> Lamarck); <i>Vertebralina</i> d'Orbigny; <i>Hauerina</i> d'Orbigny; <i>Pavonina</i> d'Orbigny
C. With agglutinated tests	Family LITUOLIDEA — <i>Lituola</i> Lamarck (<i>Haplophragmium</i> Reuss; <i>Lituola</i> Lamarck s.s.); <i>Haplostiche</i> Reuss; <i>Nubecularia</i> Defrance
	Family UVELLIDEA — <i>Trochammina</i> Parker and Jones; <i>Valvulina</i> d'Orbigny; <i>Verneuilina</i> d'Orbigny; <i>Tritaxia</i> Reuss; <i>Ataxophragmium</i> Reuss; <i>Plecanium</i> ; <i>Clavulina</i> d'Orbigny; <i>Gaudryina</i> d'Orbigny; <i>Bigenerina</i> d'Orbigny
	Family ROTALIDEA — <i>Rotalia</i> Lamarck (<i>Siphonina</i> Reuss; <i>Asterigerina</i> d'Orbigny; <i>Calcarina</i> d'Orbigny); <i>Patellina</i>

TABLE 4. Continued.

Williamson; <i>Rosalina</i> d'Orbigny; <i>Truncatulina</i> d'Orbigny; <i>Planorbulina</i> d'Orbigny; <i>Globigerina</i> d'Orbigny; ? <i>Spirobotrys</i> Ehrenberg
Family POLYSTOMELLIDEA — <i>Polystomella</i> d'Orbigny; <i>Nonionina</i> d'Orbigny; <i>Fusulina</i> d'Orbigny
Family NUMMULITIDEA — <i>Nummulites</i> Lamarck; <i>Amphistegina</i> d'Orbigny; <i>Operculina</i> d'Orbigny; <i>Heterostegina</i> d'Orbigny; <i>Cycloclypeus</i> Carpenter; <i>Orbitoides</i> d'Orbigny; <i>Conulites</i> Carter

noted, had an opaque white color in reflected light, but an amber color when viewed in thin section under transmitted light. This amber color, he inferred, was due to the presence of organic matter. Shells of the "vitreous or hyaline type" were characterized by an "almost glassy transparency," were usually colorless, while the pores showed considerable variation in size and density (Carpenter, 1862, p. 45). Carpenter did not elaborate on the porosity of the arenaceous shell, but recognized that although it was usually imperforate it could also be perforate. Carpenter (1862, p. 47) described the arenaceous shell as "being formed . . . of particles of sand obtained from without, the cement with which they are attached together being all that is furnished by the animal." The particles could be of variable shape and size, their composition dependent on the nature of the substrate. Carpenter's understanding of wall texture remained essentially unmodified until Wood (1949) introduced a radial-granular division for the hyaline wall, and Cummings (1955, 1956) recognized the microgranular calcareous wall in Paleozoic forms.

Carpenter's chief contribution to foraminiferal classification was his careful analysis of shell architecture. He did a great deal of sectioning and studied the details of internal structure (Fig. 20). Most of this sectioning work was performed on "larger" foraminifera; his observations of canal systems were later elaborated and used as the basis of classification of the larger forms. At the same time, his observations on the architecture of the smaller hyaline foraminifera laid the groundwork for modern studies and views of the shell. Carpenter observed that in the "simpler" coiled forms, chambers were added much in the same manner as in the uncoiled nodosarid. A new chamber formed around the margins of the last-formed chamber, resulting in two chambers separated by only a single septum, the anterior wall of the preceding chamber (Fig. 21). In other coiled forms Carpenter observed that each new chamber which developed had a "complete shelly envelope of its own," the new segment forming a pos-

TABLE 5. Reuss's 1861 Classification (from postscript).

I. FORAMINIFERA WITH IMPERFORATE SHELLS	
A. Agglutinated tests	
Family	LITUOLIDEA — <i>Ammodiscus</i> nov.; <i>Nubecularia</i> De-france; <i>Haplostiche</i> Reuss; <i>Lituola</i> Lamarck
Family	UVELLIDEA — <i>Trochammina</i> Parker and Jones; <i>Val-vulina</i> d'Orbigny; <i>Verneulina</i> d'Orbigny; <i>Tritaxia</i> Reuss; <i>Ataxophragmium</i> Reuss; <i>Plecanium</i> nov.; <i>Clavulina</i> d'Or-bigny; <i>Gaudryina</i> d'Orbigny; <i>Bigenerina</i> d'Orbigny
B. Porcellaneous calcareous tests	
Family	SQUAMULINIDEA — <i>Squamulina</i> Schultze
Family	MILIOLIDEA
Subfamily	CORNUSPIRIDEA — <i>Cornuspira</i> Schultze
Subfamily	MILIOLIDEA genuina— <i>Uniloculina</i> d'Orbigny; <i>Biloculina</i> d'Orbigny; <i>Spiroloculina</i> d'Orbigny; <i>Trilocu-lina</i> d'Orbigny; <i>Quinqueloculina</i> d'Orbigny
Subfamily	FABULARIDEA — <i>Fabularia</i> DeFrance
Family	PENEROPLIDEA — <i>Peneroplis</i> Montfort; <i>Vertebralina</i> d'Orbigny; <i>Hauerina</i> d'Orbigny
Family	ORBITULITIDEA — <i>Cyclolina</i> d'Orbigny; <i>Orbitulites</i> La-marck; <i>Orbitulina</i> d'Orbigny; <i>Orbiculina</i> Lamarck; <i>Alveo-lina</i> d'Orbigny
II. FORAMINIFERA WITH POROUS SHELLS	
A. Glassy, finely porous calcareous tests	
Family	SPIRILLINIDEA — <i>Spirillina</i> Jones
Family	OVULITIDEA — <i>Ovulites</i> Lamarck
Family	RHABDOIDEA
Subfamily	Lagenidea — <i>Lagenia</i> Walker and Boys; <i>Fissurina</i> Reuss
Subfamily	Nodosaridea — <i>Nodosaria</i> Lamarck
Subfamily	Vaginulinidea — <i>Vaginulina</i> d'Orbigny
Subfamily	FRONDICULARIDEA — <i>Fronicularia</i> DeFrance; <i>Rhab-dogonium</i> Reuss; <i>Amphimorphina</i> Neugeboren; <i>Dentali-nopsis</i> Reuss; <i>Flabellina</i> d'Orbigny
Subfamily	Glandulinidea — <i>Glandulina</i> d'Orbigny; <i>Pseca-dium</i> Reuss; <i>Lingulina</i> d'Orbigny; <i>Lingulinopsis</i> Reuss
Subfamily	Pleurostomellidea — <i>Pleurostomella</i> Reuss
Family	CRISTELLARIDEA — <i>Cristellaria</i> Lamarck
Family	POLYMORPHINIDEA — <i>Bulimina</i> d'Orbigny; <i>Virgulina</i> d'Orbigny; <i>Polymorphina</i> d'Orbigny; <i>Uvigerina</i> d'Orbig-ny; <i>Strophoconus</i> Ehrenberg; <i>Robertina</i> d'Orbigny; <i>Sphae-roidina</i> d'Orbigny; <i>Dimorphina</i> Reuss
Family	CRYPTOSTEGIA — <i>Chilostomella</i> Reuss; <i>Allomorphina</i> Reuss
Family	TEXTILARIDEA — <i>Textilaria</i> DeFrance; <i>Proroporus</i> Eh-renberg; <i>Sagraina</i> d'Orbigny; <i>Vulvulina</i> d'Orbigny; <i>Boli-vina</i> d'Orbigny; <i>?Cuneolina</i> d'Orbigny; <i>Gemmulina</i> d'Or-bigny; <i>Schizophora</i> Reuss
Family	CASSIDULINIDEA — <i>Cassidulina</i> d'Orbigny; <i>Ehrenber-gina</i> Reuss
B. Very finely perforate calcareous tests	
Family	ROTALIDEA — <i>Rotalia</i> Lamarck; <i>Patellina</i> Williamson; <i>Rosalina</i> d'Orbigny; <i>Truncatulina</i> d'Orbigny; <i>Planor-bulina</i> d'Orbigny; <i>Globigerina</i> d'Orbigny; <i>Spirobotrys</i> Eh-renberg
C. Calcareous tests with canal systems	
Family	POLYSTOMELLIDEA — <i>Polystomella</i> d'Orbigny; <i>No-nionina</i> d'Orbigny; <i>Fusulina</i> d'Orbigny
Family	NUMMULITIDEA — <i>Nummulites</i> Lamarck; <i>Amphiste-gina</i> d'Orbigny; <i>Operculina</i> d'Orbigny; <i>Heterostegina</i> d'Orbigny; <i>Cyclopeus</i> Carpenter; <i>Orbitoides</i> d'Orbigny; <i>Conulites</i> Carter

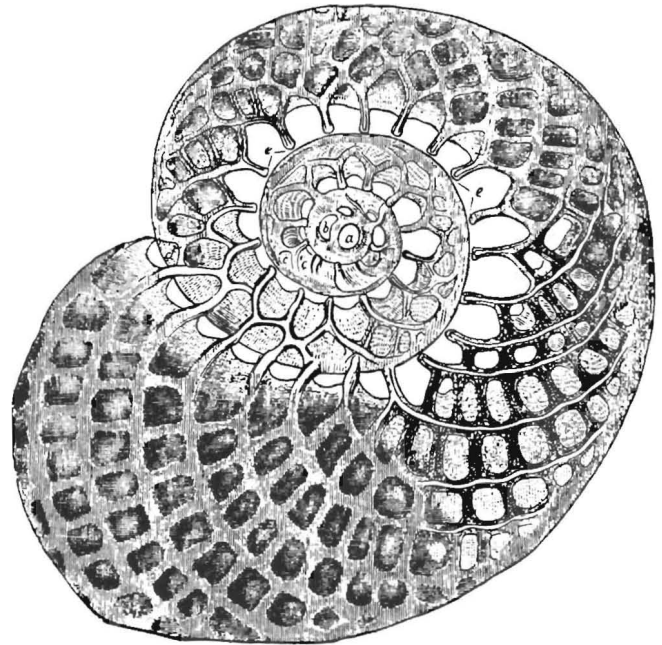


FIGURE 20. Section of *Heterostegina* through the median plane illustrated by Carpenter (1862, Fig. XLV). *a*, first-formed chamber; *b*, second chamber; *c*, *d*, chamberlets; *e*, "free aperture between one row of chamberlets and the next at the inner margin of each spire" (p. 289).

terior wall, which was joined to the anterior wall of the preceding chamber, thus doubling the septum (Fig. 22). In addition, he observed a secondary thickening or deposit extending around the chambers of the test that separated each whorl and attenuated towards the final chambers. This thickened layer, termed an "intermediate skeleton" or "supplementary skeleton," Carpenter believed, was traversed by a system of "minute canals." Much later, other workers (Smout, 1955; Reiss, 1958) would pursue studies of wall construction and develop models of lamellar structure, ideas which have become incorporated into the modern classification of the hyaline foraminifera.

Philosophic Views

Carpenter undoubtedly was d'Orbigny's severest critic (Heron-Allen, 1917). Carpenter, like Williamson, criticized d'Orbigny's reliance on plan of growth as a character of primary importance, and believed that a natural system of classification should be based on all features of the test, instead of "on a single feature which affords no reliable indication of their real affinities" (Carpenter, 1862, p. 43). Yet despite these assertions, Carpenter acknowledged that such a system

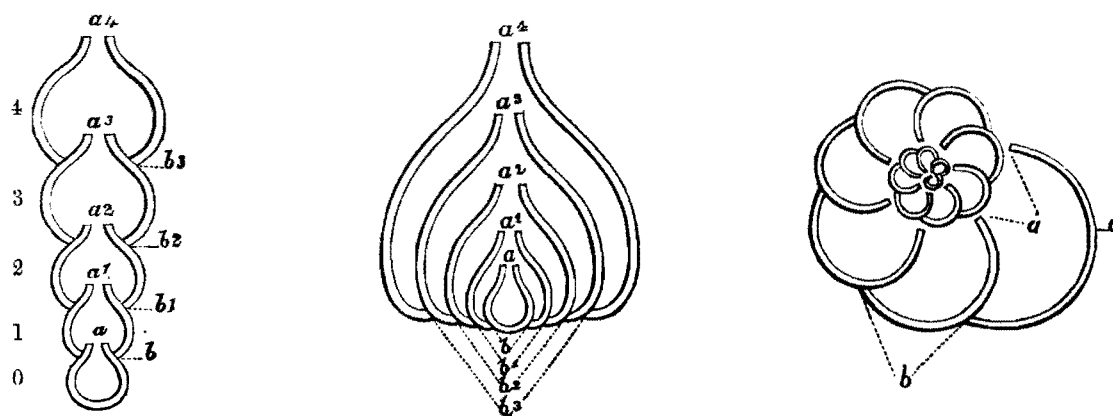


FIGURE 21. Carpenter's (1862) diagrams illustrating addition of chambers in the rectilinear and "simpler" coiled forms. Left, "Nodosarian" form of *Nodosarina* in which "the apertural portion of one segment is completely embraced by the walls of the next chamber" (p. 49). Center, "Fronicularian" form of *Nodosarina*. Right, Spiral form. *a*, apertures between chambers; *b*, sutures between chambers; *c*, chamber; 0-4, number of chamber, "0" being the "primordial chamber."

sometimes did "bring together types which have a real affinity to each other," but he attributed these occasions to coincidence (Carpenter, 1862, p. 42). Plan of growth actually predominates in parts of Carpenter's classification scheme, particularly with regard to the subfamily Textularinae of the family Globigerinida (Fig. 23). Carpenter's suborders (Imperforata and Perforata), like d'Orbigny's families, were defined on a single character (presence or absence of pores), not on a combination of characters.

The English view of variation found its strongest expression through Carpenter. In reading his text one almost senses an ambivalent feeling towards foraminifera, as his view of their virtually ceaseless variation seems to contradict his dedicated study of their structure and form. One aspect of foraminifera he seemed to appreciate was their small size and abundance, which allowed him to arrange numerous specimens in rows within a compact space and observe them under the microscope.⁹ This enabled him to discover (to his own satisfaction at least) the intermediaries that connected many diverse forms.

Carpenter summarized his conclusions about foraminifera in a set of eight general "propositions."¹⁰ These conclusions were strongly drawn and because of Carpenter's eminent authority, they had a lasting influence, even though he later appears to have tempered his views. Carpenter did not think that foraminifera could be classified in the same manner as higher organisms or that the variations of the several types were of any significance other than to demonstrate the futility of refined subdivision. He recognized a few central types surrounded by innumerable, intergrading variants. He believed that the geologic record of fo-

raminifera was of a continuous rather than a catastrophic nature and that foraminifera had diversified to a certain degree through descent. Carpenter, however, firmly believed that there was "no evidence of any fundamental modification or advance in the Foraminiferous type from the Palaeozoic period to the present time" (Carpenter, 1862, p. xi). This concept initially disturbed Darwin because according to his theory of natural selection, the modified descendants of species should be more improved and better suited to their environment.¹¹ To deal with this problem Darwin made special allowances for the foraminifera and other "lowly organised Protozoa"¹²—such accommodations virtually eliminated foraminifera from serious consideration in evolutionary studies for many years (Lipps, 1981).

Much later, Carpenter (1883) modified his views and

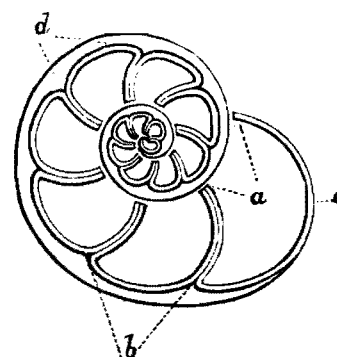


FIGURE 22. Carpenter's (1862) diagram illustrating the addition of chambers in the "highest types" of spiral foraminiferans. *a*, apertures between chambers; *b*, sutures between chambers; *c*, chamber; *d*, "intermediate" or "supplemental" skeleton.

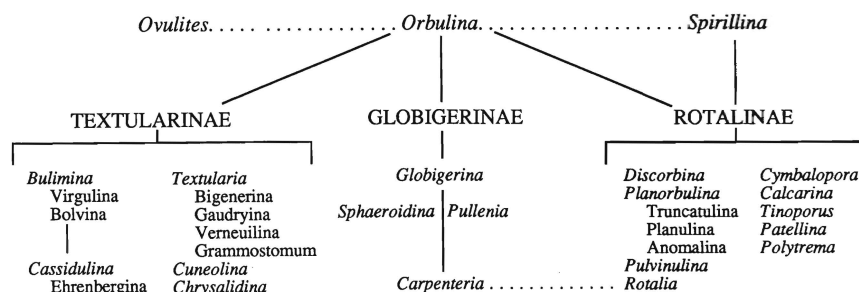


FIGURE 23. Carpenter's (1862) schematic arrangement of his family Globigerinida.

from a morphoserries leading to *Orbitolites* he enthusiastically presented a case for a progression towards a "highly specialised type of structure" through recapitulation (Fig. 24). He even recognized the existence of discrete species or "distinct races," as he preferred to call them. However, he emphasized that the "evolutionary history of the Orbitoline type" which he had presented, demonstrated very clearly that the more specialized types had had no selective advantage over the simpler types—both "complex" and "simple" types seemed to prosper equally well under the "very same conditions" (Carpenter, 1883, p. 570).¹³ Moreover, specialization in structure did not seem to be accompanied by any advancement whatsoever in physiological condition—all of the types of foraminiferal shells, no matter how complex, contained the same kind of undifferentiated protoplasm.¹⁴ Carpenter did not find natural selection to be an "all-sufficient explanation" of the origin of species and used his "remarkable case of 'descent with modification'" as a direct attack on Darwin's theory (Carpenter, 1883, p. 569).¹⁵

The Classification

It was a remarkable coincidence that Carpenter, simultaneously and independently, should produce a classification (Table 6) essentially the same in its major features as the classification of Reuss (1861). Like Reuss, Carpenter subdivided his "Order Reticularia" into two primary groups, the "Sub-Orders" Imperforata and Perforata, on the basis of the presence or absence of "pseudopodial" pores in the test wall. Carpenter considered porosity to be of greater systematic value than plan of growth, because he believed porosity represented a fundamental physiological condition of the organism. Also like Reuss, Carpenter recognized in his imperforate suborder a calcareous group, which he placed in the family Miliolida, and an arenaceous group, which he placed in the family Lituolida. Carpenter considered the "Foraminifera" to be coextensive with

the Order Rhizopoda Reticularia (Carpenter, 1862, p. 40).¹⁶ He believed the gromids, characterized by their "membranous tests" and root-like pseudopodia, showed closer affinities to foraminifera,¹⁷ and retained the family Gromida within his classificatory scheme.

The only real difference between Reuss's system of major division and Carpenter's was the fact that Reuss had excluded the gromids from the final version of his classification. Otherwise, there was total agreement between the two on a major, two-fold breakdown based on the presence or absence of pores and an additional subdivision based on wall composition. Reuss had provided for a clearer separation between the arenaceous and imperforate forms, but the idea was the same. The textural character of the test was considered fundamental and invariant. Carpenter was unable to deal with the porous arenaceous forms any better than Reuss, but this was not a serious enough obstacle to question the framework of his classification.

Aside from the textural characters of the wall, Carpenter did not find any of the other characters of the foraminiferal test to be of real value for taxonomic purposes. He thought that the "nature and position of the *septal apertures*," were often reliable characters for distinguishing genera but warned that these too were sometimes variable (Carpenter, 1862, p. 55). In principle, Carpenter considered plan of growth to be an essentially worthless character for "separating the great primary divisions of Foraminifera," and that "no constant reliance" could be placed on it "as a means of differentiating even" genera (Carpenter, 1862, p. 55). Consequently, within the main frameworks of their classifications, Reuss and Carpenter departed radically. Reuss used conventional morphological descriptions throughout his classification and emphasized plan of growth in his familial definitions. Carpenter had essentially abandoned a conventional morphologic basis for classification and did not think it possible to give definition to families or even genera. Where Reuss was inclined to make increasingly fine taxonomic di-

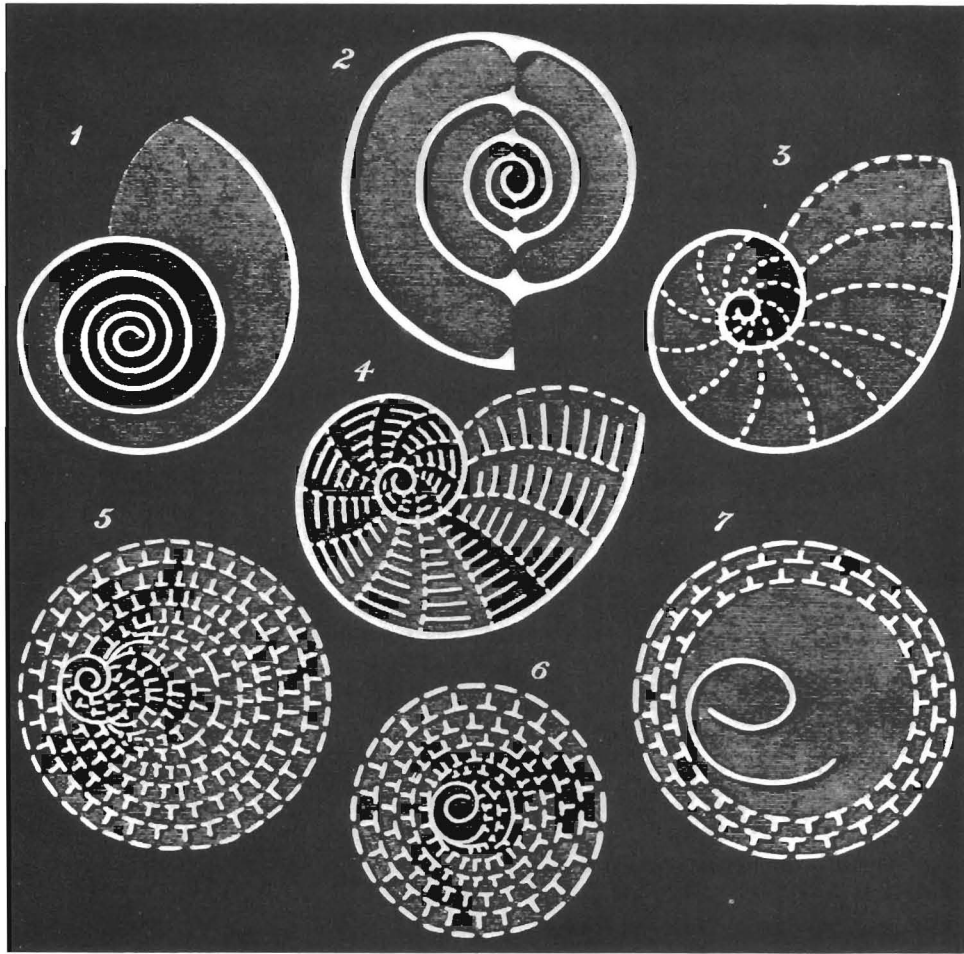


FIGURE 24. Carpenter's (1883) "Diagram illustrating the Pedigree of the Complex type of *Orbitolite*." 1, Simple undivided spire of *Cornuspira*; 2, Partially constricted spire of *Spiroloculina*; 3, Spire divided into chambers by transverse partitions, illustrated by *Peneroplis*; 4, Spirally arranged chambers divided by longitudinal partitions into chamberlets, illustrated by *Orbiculina*; 5, Spiral plan of growth "gives place" to cyclical chamber arrangement, illustrated by the "simple" type of *Orbitolites*; 6, Spiral plan of growth greatly reduced in an intermediate type of "duplex" *Orbitolite*; 7, The "complex" type of *Orbitolite* in which the chambered nucleus alone shows an abbreviated spire, the very first row of chamberlets forming a complete ring.

visions, Carpenter attempted to show the artificiality of fine division.

The eight general propositions expounded by Carpenter, with their emphasis on variation, central types (typology) and simplicity of expression, were applied fully to his scheme of classification. Carpenter's classification was a model of parsimony, containing only six families, three subfamilies and fifty-four genera. It clearly had been Carpenter's intention not only to stem the tide of taxonomic proliferation, but to reverse it. The arenaceous Lituolida were treated especially curtly, with only three genera included in the family. Carpenter, however, emphasized the unity of the group and called attention to the frequent isomorphy observed between lituolid genera and miliolid and "vit-

reous" forms. Carpenter's largest family, the Globigerinida, encompassed twenty-one genera divided into two subfamilies. Interestingly, Carpenter, like Reuss, also recognized a family of "larger" foraminifera, the Nummulinida, characterized by their internal structure and "canal systems."

Carpenter based his six families on central types, which he considered to be fundamental, natural units. He did not think that there were any real connections between the families, although he regarded the family Lituolida as being more closely related to the family Miliolida than to their hyaline isomorphs and he also considered the family Globigerinida to hold "an intermediate rank" between the Lagenida and the Nummulinida (Carpenter, 1862, p. 172).

TABLE 6. Carpenter's 1862 Classification.

I. Suborder IMPERFORATA	
Family	GROMIDA — <i>Lieberkuhnia</i> ; <i>Gromia</i> Dujardin; <i>Lagynia</i> Schultze
Family	MILIOLIDA — <i>Squamulina</i> Schultze; <i>Cornuspira</i> Schultze; <i>Nubecularia</i> DeFrance; <i>Vertebralina</i> d'Orbigny; <i>Miliola</i> Lamarck; <i>Fabularia</i> DeFrance; <i>Peneroplis</i> Montfort; <i>Orbiculina</i> Lamarck; <i>Alveolina</i> Deshayes; <i>Orbitolites</i> Lamarck; <i>Dactylopora</i> Lamarck; <i>Acicularia</i> d'Archiac
Family	LITUOLIDA — <i>Trochammina</i> Parker and Jones; <i>Lituola</i> Lamarck; <i>Valvulina</i> d'Orbigny
II. Suborder PERFORATA	
Family	LAGENIDAE — <i>Lagena</i> Walker; <i>Nodosarina</i> d'Orbigny; <i>Orthocera</i> d'Orbigny; <i>Polymorphina</i> d'Orbigny; <i>Uvigerina</i> d'Orbigny
Family	GLOBIGERINIDA — <i>Orbulina</i> d'Orbigny; <i>Ovulites</i> Lamarck; <i>Spirillina</i> Ehrenberg
Subfamily	Globigerinae — <i>Globigerina</i> d'Orbigny; <i>Pullenia</i> Parker and Jones; <i>Sphaeroidina</i> d'Orbigny; <i>Carpenteria</i> Gray
Subfamily	Textularinae — <i>Textularia</i> DeFrance; <i>Chrysalidina</i> d'Orbigny; <i>Cuneolina</i> d'Orbigny; <i>Bulimina</i> d'Orbigny; <i>Cassidulina</i> d'Orbigny
Subfamily	Rotalinae — <i>Discorbina</i> nov.; <i>Planorbulina</i> d'Orbigny; <i>Pulvinulina</i> nov.; <i>Rotalia</i> Lamarck; <i>Cymbalopora</i> Hagenow; <i>Calcarina</i> d'Orbigny; <i>Tinoporos</i> Montfort; <i>Patellina</i> Williamson; <i>Polytrema</i> Blainville
Family	NUMMULINIDA — <i>Amphistegina</i> d'Orbigny; <i>Operculina</i> d'Orbigny; <i>Nummulina</i> d'Orbigny; <i>Polystomella</i> Lamarck; <i>Heterostegina</i> d'Orbigny; <i>Cyloclypeus</i> Carpenter; <i>Orbitoides</i> d'Orbigny; <i>Fusulina</i> Waldheim

That Carpenter's families can be considered archetypes or essences is shown by the fact that for each family he defined, he selected a form which represented "the fundamental or essential 'idea' of [the] group under its simplest aspect" (Carpenter, 1862, p. 172). Carpenter then attempted to demonstrate how, starting with this simplest form, it was possible to develop all of the diverse forms of a family, with genera forming the connecting links.¹⁸ He developed the Lituolida¹⁹ and Miliolida (Fig. 25) from undivided, "monothalamous" types, while he derived the Lagenida (Fig. 26) and the Globigerinida (Fig. 23) from single-chambered, globular forms. He was unable to outline a developmental sequence for the family Nummulinida (Fig. 27) and was somewhat bothered by its apparent overlapping relationship with the Globigerinida. Carpenter was most successful in outlining a linear series of development in the Lagenida. Starting with the single-chambered *Lagena*, he derived all of the diverse forms of the family through the addition of chambers in a single straight series, curved series or coiled series.²⁰

On the other hand, Carpenter included a hodgepodge of genera in the Globigerinida and argued for a series of developmental relationships that even from the outset must have seemed most unlikely, except perhaps

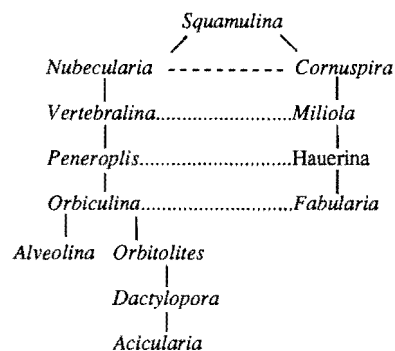


FIGURE 25. Carpenter's (1862) tabular arrangement of the members of his family Miliolida.

to some of his closest colleagues. Although Carpenter disallowed speciation and advancement of type among foraminifera, his schematic arrangement of relationships among genera bears a close resemblance to a family tree (Fig. 23). The series starts with the supposedly single-chambered, spherical genus *Orbulina* which is connected by dotted lines to the compressed genus *Ovulites* and the coiled, tubular genus *Spirillina*. However, even if *Orbulina* was single-chambered, as Carpenter erroneously had assumed, a change from a spherical to a tubular form (or vice versa) clearly poses a formidable mechanical problem. Carpenter connected the Rotalinae with both *Orbulina* and *Spirillina*, but did not explain this ambiguity. In the text, he had derived the Rotalinae from *Spirillina*, pointing out that the intermediate stages in the series were shown by the partially septate spirillinids.²¹ The simplest trochoid state is represented by the genus *Discorbina*. (The unitalicized names in this arrangement are forms which Carpenter considered intermediates, not worthy of generic status.) Although he considered the most advanced form of the Rotalinae to be the genus *Rotalia*, this posed a problem in Carpenter's scheme because its doubled septum and canal system suggested a relationship with the Nummulinida.²²

Carpenter derived the Globigerinae in much the same way as he had the Lagenida. He developed the genus *Globigerina*, characterized by rounded chambers similar in morphology to the genus *Orbulina*, by the addition of a series of orbuline chambers into a simple, trochoid spire. From *Globigerina* he derived the genera, *Sphaeroidina* and *Pullenia* by the development of a more complex trochospire. Between these genera and *Carpenteria*, the end member of the subfamily, there was a serious gap.²³

It is difficult to comprehend Carpenter's rationale for his inclusion of the textularids as a subfamily in the Globigerinida, and he gave no explanation as to

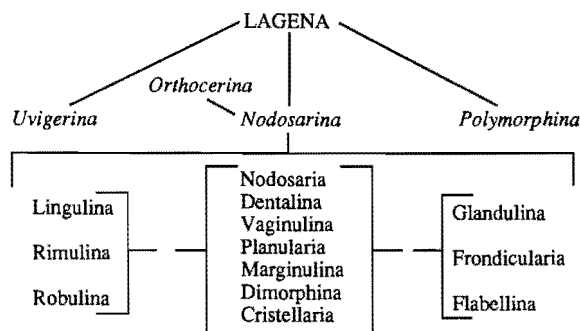


FIGURE 26. Carpenter's (1862) schematic arrangement of genera he included in his family Lagenida.

how he thought these serial forms had developed from *Orbulina*.²⁴ Brady mildly criticized Carpenter for his placement of the Textularinae alongside the Globigerinae and the Rotalinae.²⁵ Like Reuss (1861), Carpenter included arenaceous textularids with the hyaline bolivinids in the Textularinae. Carpenter handled this thorny inconsistency, which threatened to undermine the whole textural basis of his classification, in the same manner as Reuss. He pointed out that, in the first place, the textularids were porous, and even though forms like *Textularia* may appear arenaceous, he thought they were basically hyaline with an inner calcareous lining. In view of the importance of this outlook which was prevalent at the time, it is worth quoting from Carpenter's (1862) description of *Textularia*.

"The proper substance of the shell is hyaline, with large pores usually not very closely set, though in some varieties more minute and more nearly approximated; it is occasionally to be observed that the pores open at the surface into deep hexagonal pits. It very commonly happens, however, that the shell, as it increases in size, becomes incrustated with arenaceous particles, which are commonly large and coarse, and which may entirely conceal the pores from superficial observation; and in some of the smallest examples from deep water, the shell-substance appears externally to be almost as completely replaced by an aggregation of fine sand grains as it is in *Lituola* or *Valvulina*. In the coarsest *Textulariae*, however, I have never failed to bring the pores distinctly into view by examining the shell by transmitted light when rendered sufficiently transparent by the removal of the wall on one side; and in the smallest and finest I have been able to distinguish the pores in the interspaces between the sand-grains, when I have made use of a sufficient magnifying power.—It is in some of the large fossil *Textulariae* that the arenaceous incrustation is the coarsest in its

	<i>Amphistegina</i>
<i>Polystomella</i>	<i>Nummulina</i>
<i>Nonionina</i>	<i>Operculina</i>
<i>Fusulina</i> ?.....	<i>Heterostegina</i> .. <i>Cyclocypeus</i> .. <i>Orbitoides</i>

FIGURE 27. Carpenter's (1862) representation of the affinities of the genera he included in his family Nummulinida.

texture, so as to give the greatest roughness to the surface" (Carpenter, 1862, p. 191).

It will be noticed that while Carpenter asserted that pores were always visible in *Textularia* (= *Textulariae*) when fully examined, he made no such similar claim about the hyaline inner lining. He was no more able than Reuss to prove the existence of a hyaline inner lining—he had to assume it. Carpenter was also aware that *Miliolina* appeared arenaceous, but he regarded that genus as having a calcareous wall with a surficial coating of sand grains, and without hesitation he placed it in the family Miliolida.

While the textural framework that Carpenter had developed, became rooted in foraminiferal taxonomy, the other aspects of his classification never received serious attention and quickly faded into obscurity. There is much to be said for Carpenter's emphasis on variation. No doubt many genera proposed before and after his time have been no more than variant forms of particular species. The idea of containing the vast multitude of foraminiferal shell forms within the framework of a limited number of central types (the fewer the better), however, was too much for even his English contemporaries to accept. As for Carpenter's own attitude towards his classification, he realized that it was imperfect and knew that modifications would follow with increased knowledge.²⁶ He was also aware that his own observations did not fully support his concept of series of intergrading genera around the central family types, and that the family types might not be totally exclusive of each other. Still, he did not doubt that he had embarked on the right track and, like d'Orbigny, felt confident that his system was basically the most natural one.

A MODIFIED CLASSIFICATION BY JONES

Carpenter's classification scheme was later elaborated by his collaborator Rupert Jones (1876) (Table 7).²⁷ Jones excluded the "chitinous" gromids from the Foraminifera, and employed a three-fold textural breakdown of suborders instead of the two-fold subdivisions used by Carpenter and Reuss. He compromised appreciably with Carpenter's extreme parsimonious principle by increasing the number of families

TABLE 7. Jones's 1876 Classification.

I. IMPERFORATE OR PORCELLANEOUS FORAMINIFERA	
Family NUBECULARIDA — <i>Squamulina</i> Schultze; <i>Nubecularia</i> Defrance	
Family MILIOLIDA — <i>Vertebralina</i> d'Orbigny (<i>Articulina</i> d'Orbigny); <i>Cornuspira</i> Schultze; <i>Miliola</i> Lamarck (<i>Uniloculina</i> d'Orbigny, <i>Biloculina</i> d'Orbigny, <i>Triloculina</i> d'Orbigny, <i>Quinqueloculina</i> d'Orbigny, <i>Cruciloculina</i> d'Orbigny, <i>Spiroloculina</i> d'Orbigny, <i>Ceratospirulina</i> Ehrenberg); <i>Hauerina</i> d'Orbigny; <i>Fabularia</i> Defrance	
Family PENEROPLIDA — <i>Peneroplis</i> de Montfort (<i>Spirolina</i> Lamarck, <i>Dendritina</i> d'Orbigny)	
Family ORBICULINIDA — <i>Orbiculina</i> Lamarck; <i>Orbitolites</i> Lamarck (<i>Pavonia</i> d'Orbigny); <i>Alveolina</i> d'Orbigny	
Family DACTYLOPORIDA — <i>Haploporella</i> Gümbel; <i>Dactyloporella</i> Gümbel; <i>Thyrsoporella</i> Gümbel; <i>Gyroporella</i> Gümbel; <i>Cylindrella</i> Gümbel; <i>Uteria</i> Michelin; <i>Acicularia</i> d'Archiac; <i>Verticillipora</i> (?) Mantell; <i>Receptaculites</i> Defrance; <i>Archaeocyathus</i> Billings	
II. ARENACEOUS FORAMINIFERA	
Family PARKERIADA — <i>Parkeria</i> Carpenter; <i>Loftusia</i> Brady	
Family LITUOLIDA — <i>Endothyra</i> Phillips; <i>Involutina</i> Terquem; <i>Trochammmina</i> Parker and Jones (<i>Webbina</i> d'Orbigny); <i>Valvulina</i> d'Orbigny; <i>Textraxis</i> Ehrenberg; <i>Ataxophragmium</i> Reuss (sandy <i>Bulimina</i>); <i>Plecanium</i> Reuss (sandy <i>Textularia</i>); <i>Saccammmina</i> Sars (<i>Psammospaera</i> F. E. Schulze, <i>Storhosphaera</i> F. E. Schulze); <i>Pilulina</i> Carpenter; <i>Astrorhiza</i> Sandahl (<i>Astrodiscus</i> F. E. Schultze); <i>Rhabdammina</i> Carpenter; <i>Botellina</i> Carpenter; <i>Proteonina</i> Williamson; <i>Lituola</i> Lamarck (<i>Placopsilina</i> d'Orbigny, <i>Haplophragmium</i> Reuss, <i>Haplostiche</i> Reuss, <i>Hippocrepina</i> Parker, <i>Polyphragma</i> Reuss, <i>Conulina</i> (?) d'Orbigny)	
III. PERFORATE OR HYALINE FORAMINIFERA	
Family LAGENIDA — <i>Ellipsoidina</i> Seguenza; <i>Lagena</i> Walker and Jacob (<i>Entosolenia</i> Ehrenberg, <i>Fissurina</i> Reuss); <i>Ramulina</i> Jones; <i>Nodosarina</i> Parker and Jones (<i>Glandulina</i> d'Orbigny, <i>Nodosaria</i> Lamarck, <i>Dentalina</i> d'Orbigny, <i>Lingulina</i> d'Orbigny, <i>Lingulinopsis</i> Reuss, <i>Rimulina</i> d'Orbigny, <i>Vaginulina</i> d'Orbigny, <i>Marginulina</i> d'Orbigny, <i>Pseudium</i> Reuss, <i>Cristellaria</i> Lamarck, <i>Planularia</i> Defrance, <i>Flabellina</i> d'Orbigny, <i>Fronculularia</i> Defrance, <i>Amphimorphina</i> Neugeboren); <i>Orthocerinina</i> d'Orbigny (<i>Dentalinopsis</i> Reuss)	
Family POLYMORPHINIDA — <i>Polymorphina</i> d'Orbigny (<i>Dimorphina</i> d'Orbigny); <i>Uvigerina</i> d'Orbigny (<i>Sagrina</i> d'Orbigny)	
Family BULIMINIDA — <i>Bulimina</i> d'Orbigny (<i>Ataxophragmium</i> (sandy) Reuss, <i>Bolivina</i> d'Orbigny, <i>Virgulina</i> d'Orbigny, <i>Bifarina</i> Parker and Jones, <i>Robertina</i> d'Orbigny); <i>Cassidulina</i> d'Orbigny (<i>Ehrenbergina</i> Reuss)	
Family TEXTULARIDA — <i>Textularia</i> Defrance (<i>Plecanium</i> (sandy) Reuss, <i>Bigenerina</i> d'Orbigny, <i>Spiroplecta</i> Ehrenberg, <i>Gaudryina</i> d'Orbigny, <i>Verneuilina</i> d'Orbigny, <i>Tritaxia</i> Reuss, <i>Clavulina</i> d'Orbigny, <i>Heterostomella</i> Reuss, <i>Vulvulina</i> d'Orbigny, <i>Venilina</i> Gümbel, <i>Candeina</i> d'Orbigny, <i>Cuneolina</i> d'Orbigny)	
Family GLOBIGERINIDA	
Subfamily Globigerina — <i>Ovulites</i> Lamarck; <i>Orbulina</i> d'Orbigny; <i>Globigerina</i> d'Orbigny; <i>Pullenia</i> Parker and Jones; <i>Sphaeroidina</i> d'Orbigny; <i>Carpenteria</i> Gray; <i>Allomorphina</i> Reuss; <i>Chilostomella</i> Reuss	
Subfamily Rotalina — <i>Spirillina</i> Ehrenberg; <i>Discorbina</i> Parker and Jones; <i>Planorbulina</i> d'Orbigny (<i>Planulina</i> d'Orbigny, <i>Truncatulina</i> d'Orbigny); <i>Pulvinulina</i> Parker and Jones; <i>Rotalia</i> Lamarck; <i>Cymbalopora</i> von Hagenow; <i>Thalamopora</i> Reuss; <i>Calcarina</i> d'Orbigny; <i>Tinoporus</i> de Montfort; <i>Patellina</i> Williamson; <i>Conulites</i> Carter; <i>Polytrema</i> Risso	
Subfamily Polystomellina — <i>Polystomella</i> Lamarck (<i>Nonionina</i> d'Orbigny)	

TABLE 7. Continued.

Subfamily Nummulinina — <i>Nummulina</i> d'Orbigny (<i>Operculina</i> d'Orbigny, <i>Assilina</i> d'Orbigny); <i>Amphistegina</i> d'Orbigny; <i>Heterostegina</i> d'Orbigny; <i>Cycloclypeus</i> Carpenter; <i>Orbitoides</i> d'Orbigny; <i>Fusulina</i> Fischer; <i>Archaeosphaerina</i> (?) Dawson; <i>Archaediscus</i> Brady; <i>Eozoon</i> Dawson
The systematic place of the following is not yet determined— <i>Caunopora</i> Phillips; <i>Coenostroma</i> Winchell; <i>Sparsispongia</i> d'Orbigny; <i>Stromatocerium</i> Hall; <i>Stromatopora</i> Goldfuss

from six to twelve. Whereas Carpenter would allow but fifty-two genera and no subgenera, Jones admitted to seventy-seven genera and sixty-three subgenera. Unfortunately, Jones' classification was given only in outline form and was insufficiently detailed to have been of value. The families were accompanied by either vague descriptions in the text or none at all. Possibly he had intended to fill in the details at a later date, but came to realize that whatever he might have done would be superseded by Brady who was at that time working on the extensive material collected on the Challenger Expedition. Nevertheless, some of Jones' modifications and opinions are of interest.

Jones' three suborders—the Imperforata, Arenacea and Perforata—were based on wall texture and represented a reversion to Williamson's porcellaneous, agglutinated and hyaline subdivisions. Jones of course was aware of the "arenaceous problem" and did not believe the Arenacea to be a natural grouping.²⁸ He found it convenient to group together those genera that were totally and unquestionably arenaceous, but there remained an appreciable number of other genera which demonstrated affinities with either calcareous imperforate or perforate forms. Jones believed that in some instances basically calcareous forms became modified during later growth stages by the addition of extraneous particles to a calcareous, shell-forming cement. The ratio of particles to cement could vary considerably, so that the difference between an arenaceous wall and a calcareous wall texture might be more a matter of degree than of kind. This belief became a common view and much later Wood (1949) was to speculate that the granular hyaline wall might be the end form of certain calcareous cemented arenaceous types. Jones upheld the English philosophy of the "variability of form" in foraminifera and believed in central types, but he was somewhat more egalitarian in his views than Carpenter. In an earlier paper Jones (1872) had expressed the view that genera of foraminifera had about the same status as species in other organisms.²⁹ In his 1876 classification, Jones recognized that the

Textularida had been misplaced among the Globigerinida and separated them into different families, the Textularida and the Bolivinida. He also separated the polymorphinids from the Lagenida and placed them in the family Polymorphinida.³⁰ On the other hand, he felt it necessary to reduce Carpenter's family Nummulinida to a subfamily (the Nummulinina) of the Globigerinida. He removed *Polystomella* from the Nummulinina and erected the subfamily Polystomellina. Some of the changes that Jones made among the Perforata were changes that Carpenter might have anticipated. The textularids were obviously misplaced and the Nummulinida did not comprise a totally distinct family. Carpenter, however, may have been disappointed with the finely split families of the Imperforata erected by his former collaborator. Where Carpenter had delineated three families Jones erected seven; five of them split from the Miliolida, two from the Lituolida. This difference was emphasized much more by the increase in genera. For example, Carpenter recognized only three genera among the Lituolida, whereas Jones included in that family 14 genera and ten subgenera. Carpenter, therefore, had had no success at all in stemming the tide of taxonomic proliferation. Indeed, that tide had barely begun to rise.

THE SCHWAGER CLASSIFICATION

Schwager's classification was very brief and concise (Table 8). It originally appeared as two separate articles (1876, 1877), but later reprints consist of a single, continuous article paged from 1–24. Conrad Schwager (Fig. 28), a German, published his classification in an Italian journal, in the Italian language.

The format of Schwager's classification was very simple and formalistic, with brief diagnoses—it reads like a key designed to be a practical guide to the families and genera of foraminifera. However, Schwager had intended his classification to provide more than just a key. While he realized that his scheme was provisional, he meant it to be "closest to nature as possible" (Schwager, 1876, p. 475). The text, unfortunately, is garbled in places, and Schwager's ideas are not clearly presented. According to P. Ascoli (written communication, 1981), the text had obviously been written in German and then rather poorly translated into Italian. Translation problems may have also been compounded by Schwager's indecisiveness and ambiguity of thought; it is in the section dealing with the the difficult "arenaceous problem" that the text becomes the most garbled.

In any case, it is difficult to follow Schwager's lines



FIGURE 28. Conrad Schwager. (Photo courtesy of the Todd Library for Foraminiferal Research, Smithsonian Institution.)

of reasoning. He thought that Reuss' classification was a more natural and preferable system than Carpenter's classification, because Reuss had established an arenaceous group equal in rank to the calcareous imperforate group. However, in apparent contradiction, he allowed that recognition of a separate arenaceous group was difficult to justify theoretically, because many arenaceous forms demonstrated close relationships to perforate forms. At the same time, Schwager thought that it was immediately evident that natural relationships were interfered with if morphologically similar forms with different wall textures were grouped together. In other words, arenaceous forms could be distinguished from their perforate, calcareous isomorphs on other test features. Schwager also recognized that the arenaceous miliolids remained a problem but made no provision for them in his classification.

The classifications of Schwager (1876, 1877) and Jones (1876) appeared almost simultaneously. Just as

TABLE 8. Schwager's 1877 Classification.

I. FORAMINIFERA WITH PURELY CALCAREOUS PERFORATED TESTS	
A. Chambers arranged in a single line and plane	
Family LAGENOIDEA — <i>Lagena</i> Walk. and subgenera; <i>Fissurina</i> Reuss; <i>Rhabdoidea</i> Schultze, in part; <i>Nodosaria</i> d'Orbigny; <i>Orthocerina</i> d'Orbigny; <i>Rhabdogonium</i> Reuss; <i>Glandulina</i> d'Orbigny; <i>Lingulina</i> d'Orbigny; <i>Frondicularia</i> Defrance; <i>Amphimorphina</i> Neugeboren	
Family DENTALINOIDEA	
Subfamily Dentalinidae — <i>Dentalinopsis</i> Reuss; <i>Dentalina</i> d'Orbigny; <i>Placopsilina</i> (d'Orbigny) Terquem pars; <i>Citharina</i> d'Orbigny (<i>Vaginulina</i> pars)	
Subfamily Pullenidae — <i>Pullenia</i> Parker and Jones; <i>Nonionina</i> d'Orbigny; <i>Polystomella</i> d'Orbigny; <i>Fusulina</i> Fischer <i>sensu stricto</i> ; <i>Melonia</i> (Blainville) Ehrenberg pars	
Subfamily Nummulitidae — <i>Amphistegina</i> d'Orbigny; <i>Nummulites</i> Lamarck <i>sensu stricto</i> ; (<i>Assilina</i>) d'Orbigny; (<i>Operculina</i>) d'Orbigny; <i>Heterostegina</i> d'Orbigny	
Family CRISTELLAROIDEA — <i>Marginulina</i> d'Orbigny; <i>Vaginulina</i> d'Orbigny; <i>Cristellaria</i> d'Orbigny; (<i>Planularia</i>) Defrance; <i>Robulina</i> d'Orbigny charact. emend.; <i>Lingulinopsis</i> Reuss; <i>Flabellina</i> d'Orbigny	
B. Chambers arranged in a single line and turbinate	
Family POLYMORPHINIDEA — <i>Polymorphina</i> d'Orbigny; <i>Ellipsoidina</i> Brady; <i>Proroporus</i> Ehrenberg; <i>Uvigerina</i> d'Orbigny; <i>Sagraina</i> d'Orbigny; <i>Dimorphina</i> d'Orbigny	
Family BULIMINIDEA	
Subfamily Bulimididae — <i>Pleurostomella</i> Reuss; <i>Bulimina</i> d'Orbigny; <i>Virgulina</i> d'Orbigny; (<i>Bifarina</i>) Parker and Jones; <i>Sphaeroidina</i> d'Orbigny	
Subfamily Rotalidae — <i>Pulvinulina</i> Williamson; <i>Rotalia</i> Lamarck; <i>Archaeodiscus</i> Brady	
Family GLOBIGERINIDEA	
Subfamily Globigerinidae — <i>Orbulina</i> d'Orbigny; <i>Ovulites</i> Lamarck; <i>Globigerina</i> d'Orbigny; <i>Discorbina</i> Parker and Jones <i>sensu stricto</i> ; (<i>Truncatulina</i>) d'Orbigny; (<i>Anomalina</i>) d'Orbigny; (<i>Planulina</i>) d'Orbigny	
Subfamily Planorbulinidae — <i>Carpenteria</i> Gray; <i>Spirillina</i> Jones; (<i>Involulina</i>) Terquem; <i>Planorbulina</i> d'Orbigny; <i>Cymbalopora</i> Hagenow; <i>Asterigerina</i> d'Orbigny; <i>Patellina</i> Williamson; <i>Siphonina</i> Reuss	
C. With two or more rows of chambers	
Family TEXTILARIDEA	
Subfamily Textilaridae — <i>Textilaria</i> Defrance; <i>Cuneolina</i> d'Orbigny; <i>Vulvulina</i> d'Orbigny; <i>Bolivina</i> d'Orbigny; <i>Schizopora</i> Reuss; <i>Gemmulina</i> d'Orbigny; <i>Reussia</i> nov.; (<i>Verneuulina</i> aut.); <i>Cassidulina</i> d'Orbigny; <i>Ehrenbergina</i> Reuss; <i>Robertina</i> d'Orbigny	
Subfamily Cryptostegia — <i>Chilostomella</i> Reuss; <i>Allomorphina</i> Reuss	
D. Concameration more or less complex	
Family TINOPORIDEA — <i>Polytrema</i> Blainville; <i>Tinoporus</i> Montfort; <i>Calcarina</i> d'Orbigny; <i>Conalites</i> Carter; <i>Cycloclypeus</i> Carpenter; <i>Orbitoides</i> d'Orbigny	
II. AGGLUTINATED FORAMINIFERA	
A. Constructed in a single line	
Family TROCHAMMINIDEA — <i>Trochammina</i> Parker and Jones; (<i>Ammodiscus</i>) Reuss; (<i>Silicina</i>) Bornemann; <i>Saccamina</i> Sars; <i>Haplostiche</i> Reuss (<i>Reophax</i> Montfort); <i>Nodosinella</i> Brady; <i>Webbina</i> d'Orbigny; <i>Haplophragmium</i> Reuss; <i>Coskinolina</i> Stache; <i>Lituola</i> Lamarck; <i>Polyphragma</i> Reuss	
Family ATAXOPHRAGMIDEA — <i>Ataxophragmium</i> Reuss; <i>Clavulina</i> d'Orbigny; <i>Valvulina</i> d'Orbigny; <i>Climacammina</i> Brady; <i>Endothyra</i> Phillips; ? <i>Stachea</i> Brady; ? <i>Loftusia</i> Brady	

TABLE 8. Continued.

B. With two or more rows of chambers	
Family PLECANIOIDEA — <i>Plecanium</i> Reuss; <i>Verneuulina</i> d'Orbigny; <i>Gaudryina</i> d'Orbigny; <i>Heterostomella</i> Reuss; <i>Bigenerina</i> d'Orbigny; <i>Venilina</i> Gumbel	
III. CALCAREOUS FORAMINIFERA WITH IMPERFORATE TESTS	
A. Chambers either disposed in a single continuous series or cyclically	
Family CORNUSPIRIDEA — <i>Nubecularia</i> Defrance; <i>Cornuspira</i> Hauerina d'Orbigny; <i>Vertebralina</i> (<i>Articulina</i>) d'Orbigny	
Family PENEROPLIDEA — <i>Peneroplis</i> Montfort; (<i>Spirolina</i>) d'Orbigny; <i>Orbiculina</i> Lamarck; <i>Orbitulites</i> Lamarck; <i>Alveolina</i> d'Orbigny	
B. Chambers disposed in more series than one	
Family MILIOLIDEA — <i>Biloculina</i> d'Orbigny; <i>Spiroloculina</i> d'Orbigny; <i>Triloculina</i> d'Orbigny; <i>Quinqueloculina</i> d'Orbigny; <i>Fabularia</i> Defrance	
C. Shells with complex structure	
Family DACTYLOPORIDEA — <i>Petrascula</i> Gumbel; <i>Uteria</i> Michelin; <i>Gyroporella</i> Gumbel; (<i>Haploporella</i>); (<i>Dactyloporella</i>) Gumbel; (<i>Thyrsoporella</i>) Gumbel	
Family RECEPTACULITIDEA — <i>Receptaculites</i> Defrance	
IV. Foraminifera with chitinous test	
Family GROMIDEA — <i>Gromia</i> Dujardin	

fifteen years earlier Reuss (1861) and Carpenter (1862) had produced classifications virtually identical in their major features, so now did Schwager and Jones. Within the major frameworks of both Schwager's and Jones' classifications there was a radical difference in their respective approaches to taxonomy, a difference which reflected the continuing discord in thought between the English and Europeans. Schwager believed in central types, but in no way was he converted to the English school of variation; nor was he impressed with the debunking of plan of growth by the English. Schwager gave tight definitions to all of his groups and retained great faith in plan of growth. His classification was a model of the formalistic, single-character approach to taxonomy—a rigid combination of wall texture at the top of the hierarchy and growth plan at the next level.

Schwager also included a "chitinous" group in his classification, in addition to the imperforate, perforate and arenaceous groups. He did not attach subordinal or superfamilial names to these four major divisions, possibly because he considered the system to be provisional. Schwager not only subdivided the texturally established major categories solely on the basis of plan of growth, but defined many of the families and genera in the same way. He revived, therefore, d'Orbigny's first principle of classification (plan of growth) and ignored the English arguments on variation. Schwager's position was so unbending that he distributed the nodosarids, a group that the English used as one of the

prime examples of growth-plan variability, into several different families.

In spite of his rigid application of principles to classification, Schwager was still unable to avoid creating the same inconsistencies as his predecessors. For example, his calcareous, perforate family Textularidea included arenaceous, as well as calcareous genera. Curiously, Schwager placed the genus *Bigenerina* in the arenaceous family Plecanioidea, but placed the genus *Gemmulina*, now universally regarded as synonymous with *Bigenerina*, in the Textularidea. The idea that certain arenaceous foraminifera were basically both calcareous and perforate had become firmly established in nineteenth century foraminiferal thought, even though it lacked adequate supporting evidence. Justifications had appeared occasionally,³¹ but in retrospect the arguments do not seem all that convincing. The appeal of a texturally based classification was very strong, and students of foraminifera may have found this rationalization about arenaceous forms as the only possible way to ensure its survival. The arenaceous problem would later be treated quite differently, nevertheless it remains a problem which has never been resolved satisfactorily (Banner and Pereira, 1981).

H. B. BRADY AND THE CHALLENGER REPORT

Background

Adams (1978) rightly stated that Henry Bowman Brady (Fig. 16), along with Alcide d'Orbigny and Joseph Cushman, remains one of the three most familiar names in the field of foraminiferal research. Brady's greatest achievement would be his report on the foraminifera collected during the world-wide expedition of the H.M.S. *Challenger*—a report that materialized as a monograph of 814 pages and 115 plates. Almost 100 years after its publication, this report (Brady, 1884) remains a most important scientific reference and the collection it described is consulted more frequently than any other in the extensive foraminiferal collections housed in the British Museum (Natural History) (Adams, 1978). The classification that Brady established to deal with the huge, world-wide fauna at his disposal, would be generally followed for probably a more extended period of time than any other classification before or since. His notes on the geographic and bathymetric distribution of species allowed for insight into the ecology of benthic foraminifera and his study of tow-net material brought planktonic foraminifera into focus for the first time.

In itself, the monumental *Challenger Report* would have served as the culmination of a professional career. The study of foraminifera, however, was just an avocation that Brady pursued while he earned his living as a highly successful pharmacist (Adams, 1978). He ran a profitable wholesale and retail pharmaceutical business which included the export of scientific instruments. In addition to his commercial enterprises, Brady was very active scientifically and contributed articles to pharmaceutical journals. He tutored botany at Durham College and was elected to membership in a number of pharmaceutical societies. In 1874, he was elected a fellow of the Royal Society. Brady began his association with T. Rupert Jones and W. K. Parker in 1865, and simultaneously with his pharmaceutical career, managed to publish 20 papers on foraminifera.

Brady retired in 1876 at the age of 42 to devote full time to the study of foraminifera, and began work on the *Challenger* collection in 1878 (Adams, 1978). He had approximately 200 bottom samples (soundings and dredgings) and about 100 plankton tows at his disposal—not an impressive number by modern standards, especially since the expedition had lasted three and a half years (1872–1876). Yet, most of the world's oceanic regions had been sampled during the expedition, with the exception of the Indian Ocean, the eastern Pacific and the high latitudes of the northern hemisphere. (The track of the *Challenger* and station localities are shown in Figure 29.) Samples collected on the *Knight Errant* Expedition of 1880, the *Porcupine* Expedition of 1869, and British (1875–1876) and Austro-Hungarian (1872–1874) North Polar expeditions provided additional material to fill gaps left in the northern high latitudes. Habitats “of widely representative character, whether as to locality, depth of water, chemical composition or physical aspect” (Brady, 1884, p. ii), had been sampled during the *Challenger* Expedition, and Brady, therefore, had the opportunity to observe the range in diversity afforded by the total modern fauna. As a result of this opportunity, Brady was able to perceive, more clearly than his predecessors, the variety of form that a foraminiferal classification must encompass.

Perspective

Carpenter (1862) had already exhausted all there was to be said on the subjects of the variability of foraminifera and the inapplicability of the species concept to organisms of so low an organizational level. Brady generally agreed with the views of Carpenter and his other English colleagues, and thus regarded forami-

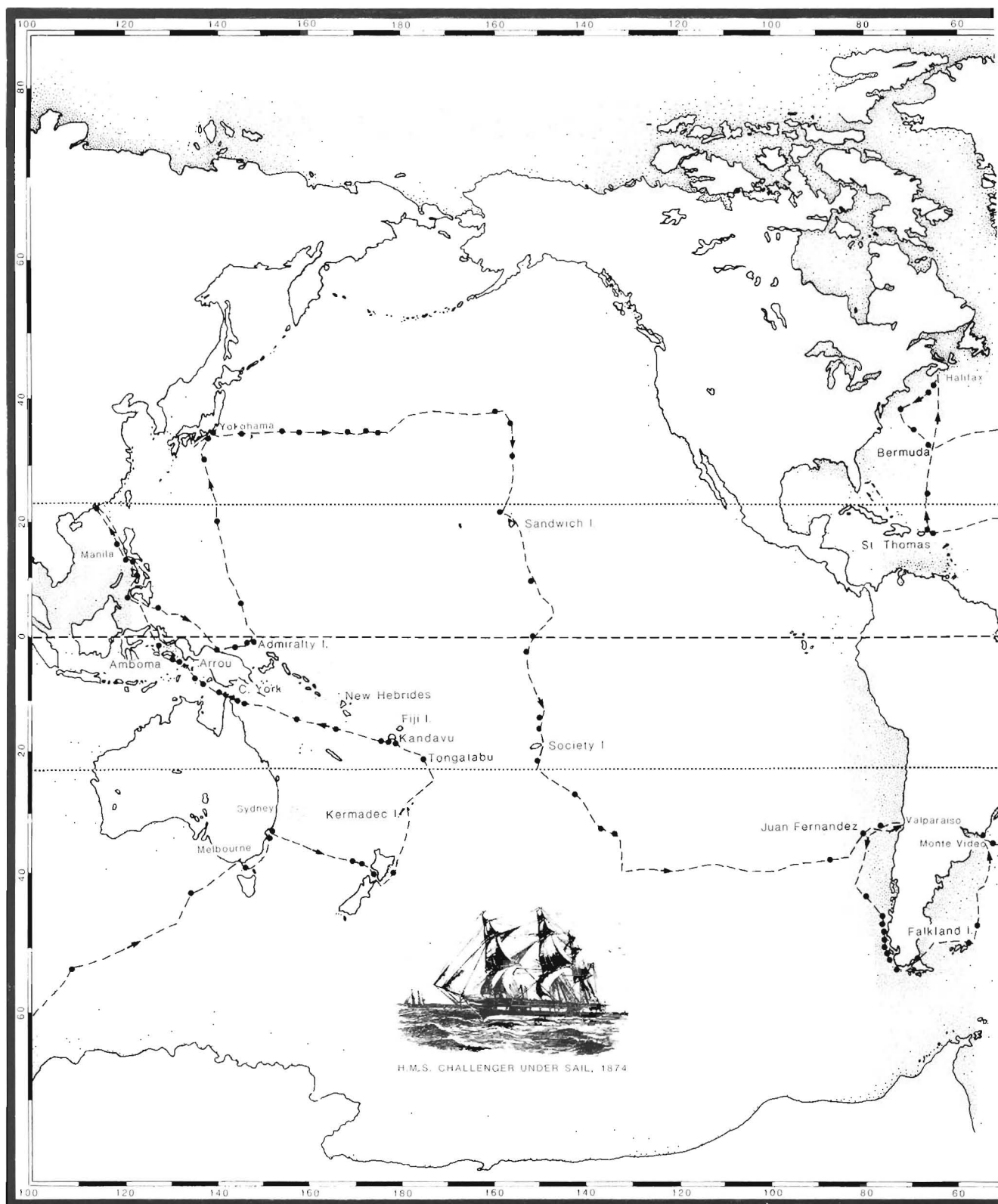
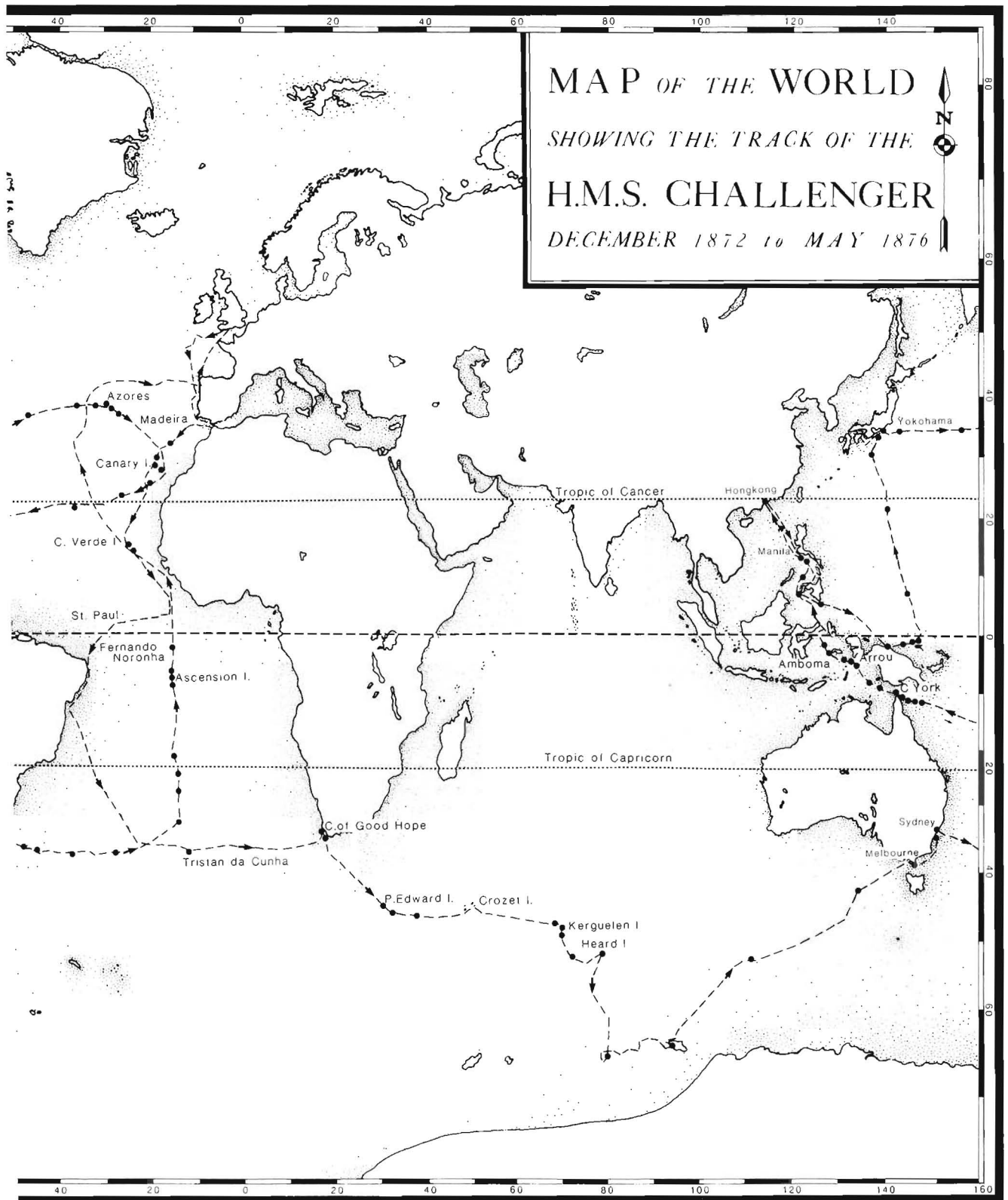


FIGURE 29. Map of the world showing the track of the H.M.S. *Challenger*. Black dots mark the dredging and trawling stations which yielded foraminiferal specimens. Map modified from supplementary map included in Brady's (1884) volume.



nifera as consisting of central types surrounded by intermediaries. However, Brady was above all a practical person.³² Whether or not "true species" existed "amongst the lower Protozoa, and especially amongst the Foraminifera," was an abstract question that had little relevance in actual practice (Brady, 1884, p. vi). Importantly, Brady recognized that while, in some families, many species and even genera seemed to be connected by "a close array of intermediate modifications" (Brady, 1884, p. vi), there were other groups in which the species possessed clearly defined limits. Furthermore, Brady observed that the "various modifications" of a series differed not only in details of morphology, but also "in habit."³³ "Whether 'species' or not," Brady observed that many of these forms could be easily identified and that it was "obviously necessary that they should be provided with distinctive names" (Brady, 1884, p. vii). The only question remaining was, therefore, what system of nomenclature was to be pursued?

Brady believed that strict adherence to the central type concept had sometimes led his colleagues to nomenclatural excess. He gave as an example the case of a form that Parker and Jones (1865) had called "*Pulvinulina repanda*, var. *menardii*, subvar. *pauperata*" (Brady, 1884, p. vii). Brady argued that such designations were "something more than names," and resembled "too much the descriptive sentences" employed in pre-Linnean nomenclature (Brady, 1884, p. vii). To "speak of *Pulvinulina pauperata* as a sub-variety of *Pulvinulina menardii*" involved an "assumption . . . founded on inference rather than on observed facts" (Brady, 1884, p. vii). Brady's own observations indicated that *Pulvinulina pauperata* and *P. menardii* were distinct forms and that there was no evidence for a connection between the two. Thus, while Brady recognized the value of "grouping the almost endless varieties of Foraminifera round a small number of typical and subtypical species," he found himself unable to make such a practice "a basis of nomenclature" (Brady, 1884, p. vii).

Brady thought that no scheme could match the Linnean system for its simplicity and convenience, whether or not a genus or a species of an organism with such "low organisation and extreme variability" as a foraminiferan, might have an equivalent meaning as the same in any of the "higher divisions of the animal kingdom" (Brady, 1884, p. vii). He pointed out that species and generic concepts had changed considerably since the time of Linnaeus and would probably continue to change, and then summarized his conclusions pragmatically as follows,

"The Linnean method is too simple and convenient to be abandoned without some better reason than the different value of these terms, as employed in different zoological groups. The practical point upon which we all agree is that it is impossible to deal satisfactorily with the multifarious varieties of the Foraminifera without a much freer use of distinctive names than is needful or indeed permissible amongst animals endowed with more stable characters" (Brady, 1884, p. vii).

Although Brady maintained the central type concept throughout his classification, he never committed himself to its implications.³⁴ As a result, his method of comparative morphology comprised a distinct advance over the methods of his predecessors. Brady did not lay aside the intermediaries between generic types as variants, important only in the sense that they showed the futility of applying the species concept to foraminifera. Rather, he used these intermediate forms to establish connections between genera and to demonstrate developments in shell form. Brady was particularly interested in the phenomenon of "dimorphism," a term which he used to refer to those forms which exhibited "two modes of growth in the individual shell" (Brady, 1884, p. viii). Through the examination of the ontogenetic patterns of "dimorphous forms" he was able to establish connections between genera having different plans of growth. Brady (1884) freely admitted that in some families, such as the Miliolidae and the Lagenidae, the generic types were connected by a continuous series of intermediate forms and that no limits could be placed between them.³⁵ However, he also pointed out that the genera of other families, such as the Globigerinidae and the Rotalidae, formed discontinuous, "collateral groups," which could not be arranged in a continuous series (Brady, 1884, p. 589).³⁶ Although Brady produced a strictly two-dimensional classification, nearly devoid of any evolutionary implications, his analytical methods were not unlike some more modern methods used to establish phyletic lineages.

In spite of his pragmatic approach, Brady aimed to achieve as natural a classification as possible. No matter what system of arrangement systematists might adopt, "every attempt to arrange in a single series a class of organisms of which the constituent groups are apt to run in parallel lines" would be "of necessity open to objection at one point or another" (Brady, 1884, p. 58). The goal of the systematist, Brady believed, was to reduce to a minimum these anomalies and inconsistencies.

Brady respected the efforts of his predecessors and viewed his own scheme of classification as merely an elaboration of what had come before. He gave d'Orbigny full credit for having first recognized the "Foraminifera as a distinct zoological group" and for having provided a "fair attempt to deal with a great mass of facts" (Brady, 1884, p. 48). Brady, unlike his English colleagues, had not criticized d'Orbigny for his use of plan of growth in classification, but rather criticized him for having relied entirely on "a single set of characters—the arrangement of the segments" (Brady, 1884, p. 49) for the definition of his family groups. By doing so, d'Orbigny had produced an artificial system which separated closely related genera while bringing together genera that had nothing in common but plan of growth. Brady firmly believed that "in any artificial arrangement of the Foraminifera, closely allied genera" were "often separated whilst others with no immediate affinity" were "thrown into juxtaposition" (Brady, 1884, p. 57). For example, he thought Reuss' introduction of wall texture into classification a significant advance, but believed that Reuss, like d'Orbigny, had also been forced to split natural groups "in order to meet the exigencies of an artificial distinction" (Brady, 1884, p. 56). Carpenter's classification (1862) and its later revision by Jones (1876) also suffered from the same failings. Schwager's method of classification "would leave little to be desired were the sole aim of the systematist the easy determination of doubtful specimens," and Brady considered its "precise definitions" and rigid structure totally unsuitable for showing any kind of meaningful relationships "in the treatment of forms as variable as the Rhizopoda" (Brady, 1884, p. 57).

Probably no one before or since has addressed the "arenaceous problem" so squarely as Brady. In a criticism of Reuss' inclusion of the arenaceous types in the suborder Imperforata, Brady pointed out that examples of arenaceous forms with porous tests were too numerous and varied to be disregarded as mere exceptions. To illustrate his point, he cited as examples the primitive genera *Psammosphaera* and *Sorosphaera* both of which have no apertures but only "interstitial orifices," and the genus *Thurammina* which is characterized by "numerous small mammillate orifices" (Brady, 1884, p. 55). Brady also focussed attention on the serial forms, exemplified by members of the family Textularidae. To Brady these forms appeared to comprise a totally natural group and he considered invalid attempts to split "the Textularian and Bulimine types" on the basis of "shell-texture" (Brady, 1884, p. 56). Brady objected to the fact that Reuss had divided cer-

tain genera and placed "the two halves in different Sub-Orders." Reuss had erected the genera *Plecanium* and *Ataxophragmium* as the arenaceous counterparts of the calcareous genera *Textularia* and *Bulimina*, respectively, thereby "cutting the knot rather than untying it" (Brady, 1884, p. 56). Among the Textularidae, Brady believed the difference between the calcareous, hyaline and totally arenaceous wall was one of degree rather than kind, with gradations present from "truly arenaceous" to "hyaline and perforate" to "externally sandy . . . with an inner perforate shell." Brady agreed with his contemporaries that the wall texture of the genus *Textularia* was basically calcareous with an arenaceous aspect sometimes superimposed in later development. He also observed that for arenaceous representatives of Miliolidae "in all cases, however thick the sandy incrustation, there is a distinct imperforate, calcareous shell, of the typical porcellaneous structure underneath, immediately surrounding the animal" (Brady, 1884, p. 31).

In view of the dilemma posed by the "arenaceous problem," Brady rejected wall texture as an overriding first principle of classification and "in the absence of any simple and easily recognised characters to serve the same end," divided the "entire Order . . . directly into Families without the interposition of Sub-Orders" (Brady, 1884, p. 59). He thought that no single character could be thought of as fundamental and inviolate. Brady believed very strongly that only a consideration of a combination of characters would allow a natural arrangement of genera, and also that particular characters could have more weight among some groups than others. He completely disallowed overriding generalizations about any particular features of the foraminiferal shell. Just as Schwager stood as a model of fundamental formalism, Brady was undoubtedly the strongest spokesman for a whole organism approach to systematics. His influence was strong, and over forty years passed before wall texture again surfaced as a cardinal factor in the subdivision of the Foraminifera.

The Classification

While Brady was concerned primarily with the classification of the modern foraminiferal fauna, he made provision for the consideration of fossil genera as well. However, like his predecessors and contemporaries, Brady did not take into account the stratigraphic disjunctions between genera, consequently his classification remained purely two-dimensional and devoid of evolutionary implications. For example, he grouped the later Paleozoic Fusulininae and the Precambrian(?)

TABLE 9. Brady's 1884 Classification.

Family I. GROMIDAE — <i>Lieberkuehnia</i> Clarapède and Lachmann; <i>Mikrogromia</i> R. Hertwig; <i>Gromia</i> Dujardin; <i>Diaphoropodon</i> Archer; <i>Shepherdella</i> Siddall
Family II. MILIOLIDAE
Subfamily Nubecularinae — <i>Squamulina</i> Schultze; <i>Nubecularia</i> DeFrance
Subfamily Miliolininae — <i>Biloculina</i> d'Orbigny; <i>Fabularia</i> De- France; <i>Spiroloculina</i> d'Orbigny; <i>Miliolina</i> Williamson
Subfamily Hauerininae — <i>Articulina</i> d'Orbigny; <i>Vertebralina</i> d'Or- bigny; <i>Ophthalmidium</i> Kübler; <i>Hauerina</i> d'Orbigny; <i>Planispi- rina</i> Seguenza
Subfamily Peneroplidinae — <i>Cornuspira</i> Schultze; <i>Peneroplis</i> Montfort; <i>Orbiculina</i> Lamarck; <i>Orbitolites</i> Lamarck
Subfamily Alveolininae — <i>Alveolina</i> d'Orbigny
Subfamily Keramosphaerinae — <i>Keramosphaera</i> Brady
Family III. ASTORRHIZIDAE
Subfamily Astrorhizinae — <i>Astrorhiza</i> Sandahl; <i>Pelosina</i> Brady; <i>Storthosphaera</i> Schultze; <i>Dendrophyra</i> Str. Wright; <i>Syringam- mina</i> Brady
Subfamily Pilulininae — <i>Pilulina</i> Carpenter; <i>Technitella</i> Norman; <i>Bathysiphon</i> Sars
Subfamily Saccamininae — <i>Psammospaera</i> Schultze; <i>Soro- sphaera</i> Brady; <i>Saccamina</i> M. Sars
Subfamily Rhabdammininae — <i>Jaculella</i> Brady; <i>Hyperammina</i> Brady; <i>Marsipella</i> Norman; <i>Rhabdammina</i> M. Sars; <i>Asche- monella</i> Brady; <i>Rhizammina</i> Brady; <i>Sagenella</i> Brady; <i>Botellina</i> Carpenter; <i>Haliphysema</i> Bowerbank
Family IV. LITUOLIDAE
Subfamily Lituolinae — <i>Reophax</i> Montfort; <i>Haplophragmium</i> Reuss; <i>Coskinolina</i> Stache; <i>Placopsilina</i> d'Orbigny; <i>Haplostiche</i> Reuss; <i>Lituola</i> Lamarck; <i>Bdeloidina</i> Carter
Subfamily Trochammininae — <i>Thurammina</i> Brady; <i>Hippocrepina</i> Parker; <i>Hormosina</i> Brady; <i>Ammodiscus</i> Reuss; <i>Trochammina</i> Parker and Jones; <i>Carterina</i> Brady; <i>Webbina</i> d'Orbigny
Subfamily Endothyridinae — <i>Nodosinella</i> Brady; <i>Polyphragma</i> Reuss; <i>Involutina</i> Terquem; <i>Endothyra</i> Phillips; <i>Bradyina</i> Möller; <i>Stacheia</i> Brady
Subfamily Loftusinae — <i>Cyclammina</i> Brady; <i>Loftusia</i> Brady; <i>Par- keria</i> Carpenter
Family V. TEXTULARIDAE
Subfamily Textularinae — <i>Textularia</i> DeFrance; <i>Cuneolina</i> d'Or- bigny; <i>Verneulina</i> d'Orbigny; <i>Tritaxia</i> Reuss; <i>Chrysalidina</i> d'Orbigny; <i>Bigenerina</i> d'Orbigny; <i>Pavonina</i> d'Orbigny; <i>Spiro- plecta</i> Ehrenberg; <i>Gaudryina</i> d'Orbigny; <i>Valvulina</i> d'Orbigny; <i>Clavulina</i> d'Orbigny
Subfamily Bulimininae — <i>Bulimina</i> d'Orbigny; <i>Virgulina</i> d'Orbig- ny; <i>Bifarina</i> Parker and Jones; <i>Bolivina</i> d'Orbigny; <i>Pleurosto- mella</i> Reuss
Subfamily Cassidulininae — <i>Cassidulina</i> d'Orbigny; <i>Ehrenbergina</i> Reuss
Family VI. CHILOSTOMELLIDAE — <i>Ellipsoidina</i> Seguenza; <i>Chilosto- mella</i> Reuss; <i>Allomorphina</i> Reuss
Family VII. LAGENIDAE
Subfamily Lageninae — <i>Lagena</i> Walker and Boys
Subfamily Nodosarinae — <i>Nodosaria</i> Lamarck; <i>Lingulina</i> d'Orbig- ny; <i>Fronicularia</i> DeFrance; <i>Rhabdogonium</i> Reuss; <i>Marginulina</i> d'Orbigny; <i>Vaginulina</i> d'Orbigny; <i>Rimulina</i> d'Orbigny; <i>Cris- tellaria</i> Lamarck; <i>Amphicoryne</i> Schlumberger; <i>Lingulinopsis</i> Reuss; <i>Flabellina</i> d'Orbigny; <i>Amphimorphina</i> Neugeboren; <i>Dentalinopsis</i> Reuss
Subfamily Polymorphininae — <i>Polymorphina</i> d'Orbigny; <i>Dimor- phina</i> d'Orbigny; <i>Uvigerina</i> d'Orbigny; <i>Sagrina</i> Parker and Jones (d'Orbigny?)
Subfamily Ramulininae — <i>Ramulina</i> Rupert Jones
Family VIII. GLOBIGERINIDAE — <i>Globigerina</i> d'Orbigny; <i>Orbulina</i> d'Orbigny; <i>Hastigerina</i> Wy. Thomson; <i>Pullenia</i> Parker and Jones; <i>Sphaeroidina</i> d'Orbigny; <i>Candeina</i> d'Orbigny

TABLE 9. Continued.

Family IX. ROTALIDAE
Subfamily Spirillininae — <i>Spirillina</i> Ehrenberg
Subfamily Rotalinae — <i>Patellina</i> Williamson; <i>Cymbalopora</i> Hage- now; <i>Discorbina</i> Parker and Jones; <i>Planorbulina</i> d'Orbigny; <i>Truncatulina</i> d'Orbigny; <i>Anomalina</i> Parker and Jones; <i>Carpenteria</i> Gray; <i>Rupertia</i> Wallich; <i>Pulvinulina</i> Parker and Jones; <i>Rotalia</i> Lamarck; <i>Calcarina</i> d'Orbigny
Subfamily Tinoporinae — <i>Tinoporus</i> Carpenter (Montfort?); <i>Gyp- sina</i> Carter; <i>Aphrosina</i> Carter; <i>Thalamopora</i> Roemer; <i>Polytre- ma</i> Risso
Family X. NUMMULINIDAE
Subfamily Fusulininae — <i>Fusulina</i> Fischer; <i>Schwagerina</i> Möller
Subfamily Polystomellinae — <i>Nonionina</i> d'Orbigny; <i>Polystomella</i> Lamarck
Subfamily Nummulitinae — <i>Archaediscus</i> Brady; <i>Amphistegina</i> d'Orbigny; <i>Operculina</i> d'Orbigny; <i>Heterostegina</i> d'Orbigny; <i>Nummulites</i> Lamarck; <i>Assilina</i> d'Orbigny
Subfamily Cycloclypeinae — <i>Cycloclypeus</i> Carpenter; <i>Orbitoides</i> d'Orbigny
Subfamily (?) Eozooninae — <i>Eozoon</i> Dawson

Eozooninae together with the Late Cretaceous-Ceno-
zoic Nummulitinae in the Nummulinidae.

Yet, Brady's classification marked a significant ad-
vance over the classificatory schemes of his predeces-
sors and proved to be essentially modern in much of
its structure (Table 9).³⁷ Although his classification
contained only ten families, it also included twenty-
nine subfamilies that were important taxonomic cat-
egories. Many of Brady's subfamilies have since been
elevated to familial or higher ranks. More than any of
his predecessors Brady was able to present reasonable
arguments based on comparative morphology and to
uphold his interpretations of generic relationships. His
species concepts were unquestionably overly broad and
many of his interpretations have since been revised.
Nevertheless, his classification had the advantage of
the "elasticity which gives to a system of classification
the element of permanence" (Brady, 1884, p. 49) so
that even with subsequent changes and modifications,
much of the original structure of his classification would
be retained without major disruption.

Since Brady recognized no groupings of subordinal
or superfamilial rank, he arranged his families in nu-
merical order, grading them from the most primitive
family (Gromidae) to the most structurally advanced
family (Nummulinidae) (Table 9). Cushman (1927b),
used this same procedure for his original classification
and later revisions (1928, 1933, 1940, 1948). Brady
recognized the "chitinous" forms as primitive fora-
minifera and placed them in the family Gromidae. He
did not subdivide the Gromidae into subfamilies, but
rather distinguished two categories defined on the pres-
ence of a single, terminal aperture or a double aperture

["a mouth at each end of the test" (Brady, 1884, p. 61)].

Brady regarded the porcellaneous forms as more primitive than the arenaceous forms and consequently, the Miliolidae appeared as the second family in his classification. Although Brady described his family Miliolidae as being "coextensive with Dr. Carpenter's *Miliolida*, with Von Reuss's *Porenlose Foraminiferen*, and with Professor Rupert Jones' *Imperforata vel Porcellana*," he recognized, however, "numerous modifications of the typical structure," some of which were "hereditary and characteristic of species" and others dependent "in part upon external influences" (Brady, 1884, p. 131). The most important of these modifications arose from the "tendency evinced under certain conditions to incorporate sand with the calcareous matter of the shell-wall, and the construction in such cases of a composite or arenaceous test in place of the normal homogenous shell" (Brady, 1884, p. 131).

Brady divided the Miliolidae into six subfamilies based largely on plan of growth. The Nubecularinae included the single-chambered and spiral coiled forms, the Miliolininae the forms that were coiled in alternating planes, the Hauerininae the "dimorphous" forms (that is, forms which display change in growth plan during their ontogeny), and the Peneroplinae for the planispiral and cyclical forms. Following English tradition, Brady naturally treated this family very broadly and recognized only seventeen genera with only two among the Nubecularinae and four among the Miliolininae. The other two subfamilies, the Alveolininae and Keramosphaerinae, are monotypic. He regarded *Quinqueloculina* and *Triloculina* as totally transitional forms and placed both genera in synonymy with *Miliolina*. Nomenclaturally, however, Brady was incorrect, because *Miliolina* Williamson, 1858, is junior to *Triloculina* and *Quinqueloculina* d'Orbigny, 1826. The species that Brady included in *Miliolina* have subsequently been distributed among nine separate genera (Barker, 1960).

The families Astrorhizidae and Lituolidae follow the Miliolidae in Brady's scheme of classification. Both of these families are described as being totally arenaceous, and no mention is made of the presence or absence of pores in their descriptions. He believed that the question of porosity was irresolvable and therefore he disregarded it.³⁸ Because Brady based his classification on a combination of characters rather than on any single character, no harm was done to its structure. By disregarding porosity among arenaceous foraminifera, Brady set a precedent that has been followed continuously ever since and he unknowingly left the door

open for a return to a superfamilial, three-fold breakdown of foraminifera on a textural basis. Only recently has the question of porosity in arenaceous walls been revived (Banner and Pereira, 1981). Brady treated the arenaceous forms rather elaborately and forty-three of the total 141 genera he described were placed in these two arenaceous families. Many of the astrorhizid and lituolid forms occupy deep-water habitats and were poorly known or unknown before they were collected in the deep-sea dredgings of the *Challenger* and other expeditions. Of these forty-three arenaceous genera, fifteen were introduced by Brady in the *Challenger Report*. He considered the family Astrorhizidae, mostly comprised of deep-water inhabitants, to be structurally primitive and distinguished four subfamilies on the basis of wall composition and test shape. In the family Lituolidae he included the septate and structurally more advanced arenaceous forms. Brady's remark that "no hard line of separation can be drawn between the two Families" (Brady, 1884, p. 285), is illustrated by the fact that he placed the coiled tubular non-septate *Ammodiscus* in the Lituolidae. The reason for this is not completely clear, except that Brady probably considered *Ammodiscus* to be a connecting link with the coiled septate *Trochammina*. Although Brady described the family as being comprised of "sandy isomorphs of the simple porcellaneous and hyaline types (*Cornuspira*, *Miliolina*, *Peneroplis*, *Lagena*, *Nodosaria*, *Cristellaria*, *Globigerina*, *Rotalia*, *Nonionina*, &c.)" (Brady, 1884, p. 65), he did not include any of the arenaceous milioline genera in the Lituolidae. This apparent discrepancy may suggest that Brady was unsure about the relationship between the calcareous and arenaceous miliolines. Brady distinguished four subfamilies in the Lituolidae mainly on details of wall composition and to a lesser extent on shape and chamber arrangement. He divided the Lituolininae into two groups, one with non-labyrinthic chambers, the other with labyrinthic chambers. For the Endothyrinae, Brady leaned heavily on the calcareous, fine-textured nature of the arenaceous wall and included such diverse forms as the uniserial *Nodosinella*, the coiled, tubular *Involutina* and the coiled, septate *Endothyra*.³⁹

From a historical point of view, the Textularidae is probably the most interesting family in Brady's classification, because here, arenaceous and hyaline serial forms are freely grouped together. Unlike Reuss, Brady did not separate the serial forms into a strictly arenaceous, imperforate group and a basically calcareous, perforate family—he placed all of the serial forms in the Textularidae. Brady described the Textularidae as follows, "Tests of the larger species arenaceous, either

with or without a perforate calcareous basis; smaller forms hyaline and conspicuously perforated. Chambers arranged in two or more alternating series, or spiral, or confused; often dimorphous" (Brady, 1884, p. 67). As is implied in this description, Brady retained the belief that certain totally arenaceous forms were basically calcareous. It is odd that he followed the thinking of his generation in this respect because he was not committed to the fundamental nature of wall texture. Brady thought that agglutination in the Textularidae was essentially an ontogenetic, environmentally induced phenomenon and that traces of a calcareous inner lining could be found almost always, even in the most coarsely arenaceous forms. To illustrate this concept, he cited the drawings of a sectioned specimen of *Textularia agglutinans* figured by Moebius (1880) (Fig. 30). Actually, the figure only shows a wall with well-developed pores that are covered and invisible at the surface. The "inner layer" is certainly finer textured than the rest of the wall, but there is no evidence that it is crystalline rather than finely arenaceous in structure.

The Textularidae was one of the smaller families Brady described, containing eighteen genera distributed among three subfamilies, largely according to plan of growth. The subfamily Textularinae included the straight, biserial and triserial genera while the Bulimininae contained the elongate spiral genera with loop-shaped apertures and the Cassidulininae the biserial, coiled genera. However, Brady placed the biserial genus *Bolivina* in the Bulimininae because he interpreted the aperture to be asymmetrical and homologous to the loop-shaped aperture of that family. Cushman (1911) later pointed out the error of this interpretation.⁴⁰ Totally disregarding wall composition or texture, Brady described many hyaline, biserial species as *Textularia* which clearly belong to *Bolivina*. The mixture of distinctly hyaline and coarsely arenaceous species in the same genus may now look like a bad misplacement although in Brady's time and for many years afterwards, it seemed like the most natural arrangement possible.

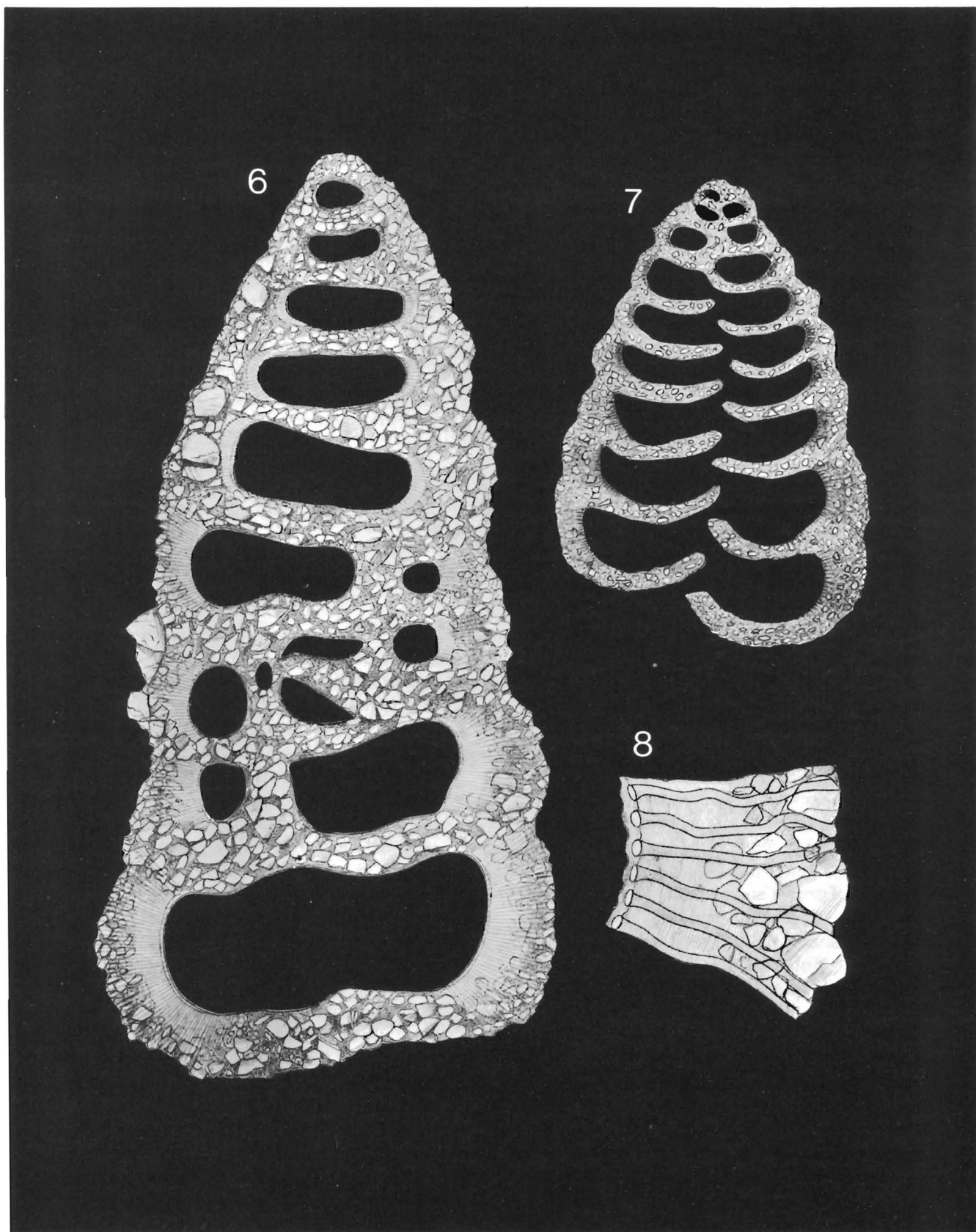
The family Chilostomellidae consisted of only three genera, all having different growth plans, and corresponded to Reuss's family Cryptostegia. Brady understood the family to include rare forms with mostly thin shells and curved, slit-like apertures. This family has

been retained ever since, in one way or another, but it has always been difficult to adequately describe its morphologic characters and to appropriately assign genera to it.

Brady's Lagenidae closely followed Carpenter's original designation and conception of this family. Brady recognized four subfamilies: the Lageninae (single-chambered), the Nodosarinae (multichambered, linear or coiled) and the Polymorphininae (chambers arranged spirally or irregularly around the long axis) and Ramulininae (irregular, branching). In his definition of the family, he also noted the lack of an "interseptal skeleton" or "canal system" (Brady, 1884, p. 69). He grouped together the single-chambered, linear and coiled forms ("*Cristellaria*") in the Lagenida and once and for all settled the question of the natural relationships of this group. Except for the inclusion of the genus *Uvigerina* (Polymorphininae), his treatment of the Lagenidae has been accepted although his family has since been raised to superfamilial status and the name changed to Nodosariacea because of priority (Loeblich and Tappan, 1961, 1964). *Uvigerina*, of course, has since been made the basis of a separate family (Loeblich and Tappan, 1961, 1964). Many more genera have since been added to the nineteen Brady included in the Lagenidae,⁴¹ but Brady no doubt, and with some justification, would have considered many of them artificial.

Brady thought that his family Globigerinidae corresponded to Carpenter's subfamily of the Globigerinida, the Globigerinae.⁴² But in fact he totally recast the group and gave it a coherence that it previously had lacked. Brady realized that Carpenter's developmental series from *Globigerina* to *Carpenteria* (Fig. 22) was indefensible, although he excluded the latter genus from his family. However, in spite of the varied, disconnected nature of the eight genera he recognized in the Globigerinidae, Brady recognized in this family a morphologic unity.⁴³ He viewed the Globigerinidae as a structurally simple group with "usually much inflated," spirally arranged chambers. And he also saw in this family "no trace of supplementary skeleton or interseptal canals" (Brady, 1884, p. 588).⁴⁴ Importantly, Brady was able to demonstrate that most of the species of the genera he included in the Globigerinidae occupied a planktonic habitat.⁴⁵ That some species of foraminifera were planktonic had been known since

FIGURE 30. Moebius' (1880, pl. 9, figs. 6-8) figures of *Textularia agglutinans* upon which Brady (1884) based his interpretations of the agglutinated wall.



Major Owen reported their occurrence in net tows of the surface waters of the Atlantic and Indian Oceans (Owen, 1865, 1868), and perhaps even earlier (d'Orbigny, 1839b).⁴⁶ Until Brady, little attention had been paid to the planktonic species. Brady conceived of the Globigerinidae as an essentially planktonic family even though two of the genera, *Pullenia* and *Sphaeroidina* are typically benthonic. However, he understood *Pullenia* to include the planktonic genus *Pulleniatina*, and *Sphaeroidina* the planktonic genus *Sphaeroidinella*. He excluded the genus *Globorotalia* (then included in "*Pulvinulina*") even though he had captured them in net tows.⁴⁷ He understandably believed that forms like *Globorotalia menardii* showed clear morphologic affinities with the Rotalidae. Yet considering Brady's keen eye for variation, it is a little surprising that he missed the connection between *Globorotalia* and other planktonic genera. Even in the modern planktonic faunas there are enough connecting links which point to a relationship between *Globorotalia* and *Globigerina* (Cifelli, 1965, Cifelli and Scott, 1986).

Brady found the rotaliform genera which he placed in the family Rotalidae a "complicated and difficult" group,⁴⁸ and contemporary workers have found them no easier to classify. Yet, Brady (1884) believed that these spirally coiled forms formed a natural grouping and that the tubular *Spirillina* could be linked to this group by weakly septate forms such as *Patellina*. He characterized the Rotalidae as being "typically spiral and 'Rotaliform.'" . . . Some of the higher modifications with double chamber walls, supplemental skeleton, and a system of canals" (Brady, 1884, p. 72). Brady readily admitted that adequate morphologic descriptions could not be given for the seventeen genera and three subfamilies of this family because so many of the genera seemed to him to have been "constructed on lines so nearly identical" (Brady, 1884, p. 628). He selected species as central types of genera and presented a table to show the isomorphism of several genera (Table 10). The subfamily Spirillinae was monotypic, while most of the genera of the Rotalidae are contained in the Rotalinae. The Tinoporinae included the genera with irregularly formed chambers. Subsequently, these rotaliform genera have been split into many additional families, but their treatment, in many cases, remains unsatisfactory.

Brady's tenth and last family, the Nummulinidae, was defined to include both trochospiral and planispiral genera which in the more advanced forms possess a supplementary skeleton and a canal system. Brady recognized twelve genera in this family, distributed among four subfamilies. In addition, he questionably

and with obvious misgivings, included the Pre-Cambrian Eozooninae as a fifth subfamily within the Nummulinidae, although he was fully aware that *Eozoon* Dawson might be of inorganic origin.⁴⁹ The Nummulinidae, more than any other family, reflects the total two-dimensional outlook of Brady's. Structural grade was the sole basis for grouping together the four subfamilies (Fusulininae, Polystomellinae, Nummulitinae, Cycloclypeinae); their discrete geologic ranges were essentially disregarded. He extended the range of the Cretaceous-Cenozoic Nummulitinae back to the Paleozoic, by including the genus *Archaeodiscus* in this subfamily—although Brady had a first-hand knowledge of this genus, he apparently misinterpreted its structure.⁵⁰ Brady recognized that the simple *Nonionina* was fully transitional to the complex *Polystomella* (= *Elphidium*) with its "more or less fully developed" canal system and grouped together the two genera in the subfamily Polystomellinae. Since Brady's time, however, the Nummulitidae have been refined considerably and now comprise a field of several distinct specializations.

V. NATURAL CLASSIFICATION AND EVOLUTION

Today natural classification, with some qualifications, is understood to mean an arrangement of species and genera according to their phylogenetic relationships. There have been dissenters to this view on the grounds that an evolutionary scheme is unrealistic and impractical (see Blow, 1979),¹ but by and large it is hard to find a taxonomist who would knowingly and willingly place polyphyletic species in the same genus. Most taxonomists like to think that their arrangements are at least consistent with a genealogical interpretation. Yet, even before Darwinism became generally accepted, when species were still believed to be immutable, naturalists often held strong opinions about what was natural and what was not in classification. D'Orbigny regarded his method of classifying the foraminifera as the most natural one, although his classification was dismissed shortly after its publication as being totally artificial. Carpenter was equally confident that the scheme he had proposed comprised a "natural arrangement of the group" (Carpenter, 1862, p. 44), but while he discussed his classificatory principles in detail, he never explained the meaning of his achievement. Schwager (1876) too, believed that he had embarked on some kind of natural system, even though his classification reads like a practical guide to the identification of genera. The English School, through their

TABLE 10. Brady's 1884 table illustrating isomorphism.

	DISCORBINA	PLANORBULINA	PULVINULINA	ROTALIA
Superior face conical, inferior flat.	<i>D. tabernacularis</i> , Brady <i>D. turbo</i> , d'Orbigny	<i>T. rosea</i> , d'Orbigny <i>T. conica</i> , Roemer (?)	<i>P. procera</i> , Brady <i>P. trochus</i> , Munster	— <i>R. nitida</i> , Williamson
Superior face more or less convex, inferior flat.	<i>D. globularis</i> , d'Orb. <i>D. parisiensis</i> , d'Orb. <i>D. opercularis</i> , d'Orb.	— <i>T. schloenbachi</i> , Reuss —	— <i>P. hemisphaerica</i> , Reuss —	— — —
Thin, outspread, one or both faces slightly convex.	<i>D. cora</i> , d'Orbigny —	<i>T. wuellerstorfi</i> , Schwager <i>T. ungeriana</i> , d'Orb.	<i>P. concava</i> , Reuss <i>P. menardii</i> , d'Orbigny	— —
Thick, both faces convex.	<i>D. nana</i> , Reuss <i>D. turris</i> , Karrer	<i>T. simplex</i> , d'Orbigny <i>T. haidingerii</i> , d'Orbigny	<i>P. punctulata</i> , d'Orbigny <i>P. repanda</i> , Fichtel & Moll	<i>R. beccarii</i> , Linné <i>R. broeckhiana</i> , Karrer
Complanate, more or less evolute, margin square.	<i>D. biconcava</i> , Parker & Jones	<i>A. ariminensis</i> , d'Orbigny	—	—
Complanate, more or less evolute, margin round.	<i>D. rugosa</i> , d'Orbigny <i>D. polystomelloides</i> , Parker & Jones	<i>A. ammonoides</i> , Reuss <i>A. grosserugosa</i> , Gumbel	— —	<i>R. ammoniformis</i> , d'Orbigny —
Superior face flat, inferior more or less convex.	<i>D. saulcii</i> , d'Orb. <i>D. bertheloti</i> , d'Orb. (?)	<i>T. akneriana</i> , d'Orb. <i>T. lobatula</i> , Walker & Jacob	<i>P. boueana</i> , d'Orbigny <i>P. crassa</i> , d'Orbigny	<i>R. exsculpta</i> , Reuss <i>R. orbicularis</i> , d'Orb.
Superior face flat, inferior highly convex or conical.	—	<i>T. refulgens</i> , Montfort	<i>P. micheliniana</i> , d'Orb.	<i>R. soldanii</i> , d'Orbigny
Thin, evolute, adherent.	—	<i>P. mediterranensis</i> , d'Orbigny	<i>P. vermiculata</i> , d'Orb.	—
Wild-growing, adherent.	—	<i>P. retinaculata</i> , Parker & Jones	<i>P. dispansa</i> , Brady	—
Limbate sutures.	<i>D. binkhorsti</i> , Reuss <i>D. valvulata</i> , d'Orb.	<i>A. calymene</i> , Gumbel <i>T. praecincta</i> , Karrer	<i>P. caracolla</i> , Roemer <i>P. berthelotiana</i> , d'Orb.	<i>R. ornata</i> , d'Orbigny <i>R. annectens</i> , P. & J.
Stellate or spinous margin.	<i>D. stellata</i> , Reuss (?) <i>D. imperatoria</i> , d'Orb. (?)	<i>A. polymorpha</i> , Costa —	<i>P. spinimargo</i> , Reuss —	<i>R. calcar</i> , d'Orbigny <i>R. pulchella</i> , d'Orbigny

studies of variation, thought that they had discovered the key to understanding foraminiferal relationships but their contemporaries on the continent, however, did not share their beliefs.

If genealogy was not the issue, what was?

PRE-DARWINIAN THEORIES OF CLASSIFICATION

Mayr (1969) distinguished five basic theories of taxonomy: essentialism, nominalism, empiricism, cladism, and evolutionary classification. While cladism and evolutionary classification are based on the concept of evolution, essentialism, nominalism, and empiricism hark back to pre-Darwinian times and have their theoretical roots in philosophy. It was, therefore, these three theories that guided early attitudes towards what was natural in classification.

Essentialism

Essentialism, the oldest and in many ways most pervasive theory of classification, dominated biological classification from Aristotle to Linnaeus. The theory derived originally from Plato's theory of Ideas (Popper, 1963), but was developed more especially from Aristotle's doctrine of "essences" and his method of "logical division" (Cain, 1958).

In Plato's view, the only real things are abstractions, which he called universals. Sensible things are regarded as merely imperfect, temporary manifestations of the universals. Because the senses themselves are imperfect, universals can never become known through them. In the analogy of the cave, Plato argued that just as the shadows on the wall cast by the light of a fire give indistinct images of objects, so the individual objects give distorted impressions of forms or universals that

are, in fact, perfect and eternal (de Santillana, 1961).² Because the universals are abstractions, they exist outside of time and space. The nature of universals is revealed by intellectual intuition and reasoning. Plato further assumed universals to be prototypes of the original plan of creation, and sensible objects, both animate and inanimate, to be continually degenerating copies of them. Plato's universals have been debated up through modern times and despite many criticisms and corrections of errors, part of his theory remains seemingly indestructible. This is because, besides the metaphysical aspect of universals, there is also a logical aspect to them. Bertrand Russell clearly explained the distinction as follows,

"The logical part has to do with the meaning of general words. There are many individual animals of whom we can truly say 'this is a cat'! What do we mean by the word 'cat'? Obviously something different from each particular cat. An animal is a cat, it would seem, because it participates in a general nature common to all cats. Language cannot get on without general words such as cat and such words are evidently not meaningless. But if the word 'cat' means anything, it means something which is not this cat or that cat, but some kind of universal cat-yness. This is not born when a particular cat is born, and does not die when it dies. In fact, it has no position in space or time; it is 'eternal'. This is the logical part of the doctrine. The arguments in its favour, whether ultimately valid or not, are strong and quite independent of the metaphysical part of the doctrine.

"According to the metaphysical part of the doctrine, the word 'cat' means a certain ideal cat, '*the cat*,' created by God and unique. Particular cats partake of the nature of *the cat*, but more or less imperfectly; it is only owing to this imperfection that there can be many of them. *The cat* is real; particular cats only apparent" (Russell, 1945, p. 121).

It seems fairly clear that Plato's theory of Ideas could not help but have had a strong influence on the Christian view of nature and the organic world. Plato's doctrine is both rational and harmonious with a Christian idea of a plan of creation. According to Plato, a taxonomic unit becomes a universal type that is manifested by many earthly variants.

Plato's theory of Ideas, however, was found to be generally unsuitable for the study of natural history because it involved the denial of the reality of animate or inanimate objects. It was Aristotle who developed a methodology for biological classification. Aristotle

accepted Plato's universals, but believed that individual things did indeed have a real existence. His solution to the problem of reconciling universals with individual objects was applicable mainly to biology (Brumbaugh, 1964). Aristotle assumed that an individual was a combination of "matter," which was its substance, and "form," which set its boundaries and determined the kind of thing the individual was. Form corresponded to Plato's universal, but here Aristotle introduced "essence"—a term that has become a source of debate not only in philosophy but also in classification. Essence is the "inner nature" of a thing, a property which the thing cannot lose without ceasing to be itself. Species and genera, as well as individuals have an essence. The definition of a species or genus is a statement of its essence. Russell considered Aristotle's notion of essence "a muddle-headed action, incapable of precision" (Russell, 1945, p. 165), yet the historical influence of this concept has been profound and essentialism still (albeit unconsciously) guides some aspects of classification.³

There is more to Aristotle's doctrine than just "form" and "matter," and while his system may appear abstruse it had a definite bearing on nineteenth century classification. According to Russell, Aristotle's doctrine can be viewed as a common-sense interpretation of Plato;⁴ that is, Aristotle tried to reconcile Plato's universals to the fact that our everyday experience dictates that objects do exist.

Aristotle recognized four causes—material, formal, efficient and final—or factors responsible for a thing being what it is (Fig. 31). The material cause of a thing is the matter which makes up the individual; the material causes of biological organisms include substances such as tissues and organs. The formal cause, in the case of an organism, is a species or genus and this determines the essence of the individual. Aristotle's formal cause corresponds to Plato's universal.⁵

The efficient cause⁶ is necessary to join matter and form together. In the total scheme of things, the efficient cause is ascribed to "God," but in the case of an organism it is the parents "that generate a new individual of their species" (Brumbaugh, 1964, p. 191). The fourth cause, called the final cause, is a kind of "vital force" that directs the growth of an individual to achieve the essence of the species to which it belongs. It is a kind of instinct that not only preserves the species but also strives for perfection. This striving, however, is not for an individual to be more than it is, but rather for an attainment of the pure essence of the species to which the individual belongs (Brumbaugh, 1964).⁷

In Aristotle's orderly scheme of nature everything

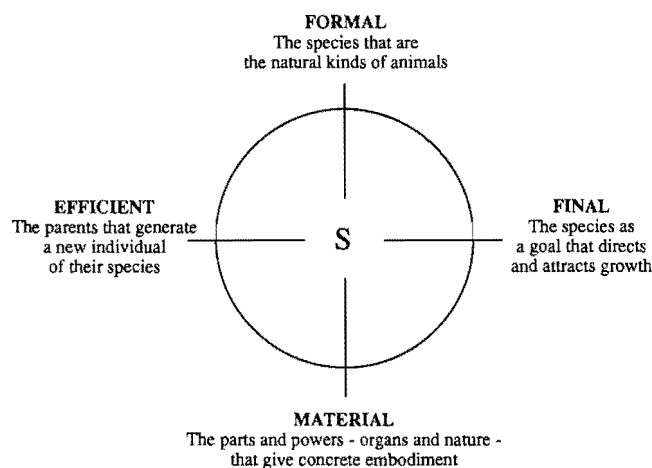


FIGURE 31. Diagram of "Aristotle's Four Causes in Zoology." (Reproduced from *The Philosophers of Greece* by Robert S. Brumbaugh (1964) by permission of the State University of New York Press, © Robert S. Brumbaugh.)

had its own place. The Greeks appeared to have believed in a notion of cosmic justice, according to which everything in a cosmic, as well as a social order "should mind his own business" (Popper, 1963, p. 90). Aristotle regarded species as finite in number, invariable and immortal; the only change that could occur in a species was a change towards a more perfect expression of its essential form.

Unlike Plato, Aristotle believed in specimens and he thought that the examination of numerous specimens could yield important information about species. Russell (1945) listed Aristotle as the first in a series of inductionist philosophers. Nevertheless, Aristotle never made a clear break with Plato's idea of a universal having a reality and an importance greater than an object. As a result he never totally pursued his empirical views (Russell, 1945). Aristotle treated species and genera like universals and defined them by *a priori* and deductive means, rather than by the extraction of information gained from observation. He gave logical definitions to genera and species and treated them like mathematical forms (Cain, 1958). A definition of a genus is a statement of its essence or its fundamental character. A genus also has distinct properties, but these are a consequence of its essence and they are not included in its definition. A species of a genus may be defined as a "particular mode in which the genus may exist" (Cain, 1958, p. 146). Species definitions must be homogeneous in construction and make statements of variation around a central morphologic theme. In pure form, essentialistic taxonomy amounts to search for fundamental constructions and their modifications.

It is a process of discovery that theoretically should ultimately result in a precise cataloguing of all organic form.

An examination of the principle features of Linnean taxonomic theory shows it to be based primarily on Aristotelian principles of classification. These same general principles guided taxonomy up until the publication of *On the Origin of Species* (Darwin, 1859) (Cain, 1958, 1959). Linnaeus closely followed the rules of Aristotle's method of logical division⁹ and attempted to produce a classification founded not on superficial resemblance, but on the real natures of organisms, their essences. According to this method, the genus is considered to be a "general type or plan," the species, a particular mode of that type (Joseph, 1916, p. 83). In a strict sense, this method is only applicable to entities capable of being analyzed.¹⁰ Consequently, logical division cannot be applied to the classification of organic forms because all species of a genus are not known when that genus is described; and thus, their essences can never be determined with certainty.

In order to adapt the method of logical division to biological classification, the characters believed to be the most important, or fundamental, to the existence of a group are taken to be essences. The most fundamental character is taken as the first principle and used to define the top of an hierarchy. The next most important character becomes the second principle and is used to define the next level of the hierarchy. The Linnean method leads to a classification based on a carefully determined pre-weighting of characters, and if totally consistent, such a classification can be considered natural. In order to be consistent, however, the fundamental characters must be totally invariant. Any change implies a denial of essence and, therefore, would violate the rules.

A classification constructed according to the above method is natural only in a formalistic sense. There was always doubt as to whether this method adequately dealt with the problem of "natural affinities." The principle aim of a classification, really, was to group together those organisms that most closely resembled each other. It sometimes happened that a classification based on fundamental characters disrupted groups that common sense would dictate as being natural.¹¹ Linnaeus was aware of this problem, although probably not of its magnitude, and compromised his principles somewhat in his classification of the plants (Cain, 1958). Indeed, the leading essentialist taxonomists of the nineteenth century, such as Cuvier and Lamarck, found themselves unable to determine which characters should be considered the essential characters in a group.

Often the characters that were the most constant in a group were taken to be essential characters, with the reasoning that because they were constant, they must be fundamental.¹² These arguments are tautological, however, because in order to determine constancy the members in a group must first be arranged according to a combination of characters (Cain, 1959).

Nominalism

The doctrine of nominalism overlaps with, and is often difficult to separate from, the philosophical theory of empiricism. In fact, nominalism is no more than an extreme form of empiricism—nominalism tends to challenge the reality of abstractions to a greater degree than empiricism.

Nominalism arose in opposition to essentialism, resulting from medieval debates over the nature of universals and essences. The problem of the reality of a universal remained unresolved, and medieval philosophical arguments became sterile. What could be proved by logic often defied common sense. In the thirteenth century, Thomas Aquinas (c. 1225–1274) attempted to resolve this problem by making a distinction between the logical and metaphysical components of a universal (Russell, 1945). He proposed that arguments in theology and metaphysics should be clearly separated from those belonging to the realm of logic and language. This view was later restated, more explicitly, by William of Ockham (c. 1285–1349), the last of the medieval scholars, who is considered to be the founder of the school of nominalism (Russell, 1945).¹³

According to the doctrine of nominalism, a universal is a purely logical term used in an act of reasoning and can have no real existence. Understanding is of *things*, not *universals*, and knowledge is derived from the senses. The seventeenth century philosopher John Locke (1632–1704) declared that universals and essences were purely verbal. He thought that species were artifacts of language rather than of nature. Species represented “distinct complex ideas with distinct names annexed to them” (cited in Russell, 1945, p. 611). Locke, moreover, thought the differences between species gradational, and the boundaries between them, man-made (Russell, 1945).

Nominalism, therefore, was an outright denial of essentialism and even of natural classification. Only individuals exist; species are man-made abstractions.¹⁴ Because species were not considered to be real, a biological classification was the same as a classification of inanimate objects.¹⁵ Classification thus becomes an

activity of reason; sensory perceptions are grouped together in classes which result in an arrangement of objects according to their similarities.

Nominalism has not had a strong, or at least vociferous, influence on classification, although the nominalist philosophy has also been adopted by the modern pheneticist school of taxonomy (Mayr, 1969). After the Middle Ages, it was the essentialistic outlook of Aristotle that prevailed in both philosophy and natural history. Locke’s strong empirical position during the seventeenth century was an extraordinary viewpoint for the time; other philosophers maintained the belief that most important knowledge was *not* obtained by experience (Russell, 1945).

Empiricism

The theory that guided the taxonomists who classified according to *natural affinity* (as opposed to *natural* in the formalistic sense of the essentialists) is called empiricism. The roots of empiricism pre-date Linnaeus and can be found in the work of the early eighteenth-century botanist John Ray, who wrote “Since from the same essences flow the same qualities, operations, and other things which are accidents, there can be no surer mark of essential, and so of generic, agreement than to have many common attributes, that is, many parts and accidents similar, or to have the whole facies, habit, and structure the same” (Ray, 1703, cited in Cain, 1958, p. 156).

Prior to Darwin, empiricism had no underlying principle. In the post-Linnaean century, prior to the publication of *On the Origin of Species*, taxonomists began to place greater emphasis combinations of characters and overall similarities, as the obscurity of “essential” characters became increasingly apparent. Unlike the nominalists, the empiricists did not take the view that classification was artificial. They believed that the empirical method led to a classification which revealed the orderliness of Nature, resulting in a classification that was much more “natural” than the formal type of system proposed by Linnaeus and his followers. Until *On the Origin of Species* appeared, the empiricists had no explanation for this order.¹⁶

There was not so much a direct conflict between essentialism and empiricism as there was a shift in emphasis, often unconscious, from the placement of less weight on a single, all important character to the consideration of a combination of characters. Very often, taxonomists have used the methods of both philosophies simultaneously; the English School was a peculiar mixture of essentialism and empiricism. Dur-

ing the nineteenth century a "creeping" empiricism infiltrated the attitudes of foraminiferal taxonomists and culminated in the work of Brady. In spite of his essentialistic assertions about central typology,¹⁷ Brady was the first and perhaps the foremost empiricist of all students of foraminifera. Brady's influence did not completely turn the tide, however, as a strong element of essentialism still persists today in modern foraminiferal classification.

DARWIN ON NATURAL CLASSIFICATION

Darwin argued that to some naturalists, a "Natural System" of classification comprised a scheme for "arranging together those living objects which are most alike, and for separating those living objects which are most unlike" (nominalism) (Darwin, 1859, p. 413). To many other naturalists, a "Natural System" meant a scheme which would reveal "the plan of the Creator" (essentialism) (Darwin, 1859, p. 413). Darwin viewed the first approach as an "artificial means for enunciating, as briefly as possible, general propositions," and rejected the second approach as unscientific (Darwin, 1859, p. 413).

Linnaeus is quoted as having said that "the characters do not give the genus, but the genus gives the characters" (Darwin, 1859, p. 413).¹⁸ Darwin used this expression to emphasize that "something more" than just a grouping of resemblances was implied in classification. That something more was "propinquity of descent,—the only known cause of the similarity of organic beings" (Darwin, 1859, p. 413). Taxonomists had always, Darwin observed, placed individuals of "both sexes and of all ages" together in the same species, in spite of their distinct morphological differences (Darwin, 1859, p. 433). This same practice held true for individuals of alternate generations, and also for variants which differed appreciably from other individuals in a species. All of this, Darwin (1859) argued, indicated that taxonomists had always, albeit unconsciously, proposed systems that were genealogical in arrangement.¹⁹ "Community of descent," Darwin believed, was the "hidden bond which naturalists have been unconsciously seeking, and not some unknown plan of creation, or the enunciation of general propositions, and the mere putting together and separating objects more or less alike" (Darwin, 1859, p. 420).

In a discussion of "the rules followed in classification" [and their inherent difficulties], Darwin (1859, p. 414) made the observation that characters not functionally important were usually the most important in classification, and the most adaptive characters the

least important.²⁰ Even the "physiological importance" of a character did not imply a certain classificatory value (Darwin, 1859, p. 415). What mattered was its constancy.²¹ Moreover, a particular character might be highly constant and diagnostic in one group, but more variable and less diagnostic in other groups.²² To illustrate his point, Darwin used as an example the antennae of insects, which are of equal physiological importance to all insect groups but have different classificatory value among the groups. Darwin emphasized that taxonomists should look for uniformity and occurrence common to a large number of forms, before attaching a high value on a character in classification. Also, a combination of characters, even if the characters appeared to be of little significance, was important, particularly if the combination occurred consistently. Darwin regarded no single character as being completely invariable. He pointed out that a species could be lacking in a physiologically important character and yet still be recognized as belonging to a particular genus by a combination of other characters. Moreover, because a particular character might be of greater classificatory value in one group than another, Darwin disapproved of the pre-weighting of characters.

In regard to essentialistic, fundamental character types of classifications, Darwin had this to say, "It has been found, that a classification founded on any single character, however important that may be, has always failed; for no part of the organisation is universally constant" (Darwin, 1859, p. 417). Brady (1884), in his own practical fashion, expressed a virtually identical philosophy towards classification as Darwin, even though he defended the central type concept of his English colleagues. Had Darwin chosen foraminifera rather than barnacles as an avocation it is not unlikely he would have evaluated wall texture in the same context as Brady, that is, as a character of importance but not totally invariant and therefore subject to limitations in classification.

VI. ESSENTIALISM AND EMPIRICISM IN NINETEENTH CENTURY FORAMINIFERAL CLASSIFICATION

The development of foraminiferal classification during the nineteenth century can, in a sense, be viewed as an interplay between essentialism and empiricism. Essentialism totally dominated foraminiferal classification at the outset of the nineteenth century, but progressively became undermined by empiricism. D'Orbigny (1826) followed the methodology of essentialism

hen he used "plan of growth" or chamber arrangement to define his families.¹ This distinction in mode of growth had seemed so important to Schultze (1854) that he divided the foraminifera into the single-chambered Monothalamia and the multi-chambered Polythalamia. Reuss (1861) had been inclined to do the same, but changed his mind in postscript. The Aristotelian influence or outlook on nature can also be seen in one other aspect of d'Orbigny's classification—the rather unlikely combinations of genera that he included in some of his family groups. D'Orbigny attached little importance (low classificatory value) to the ontogenetic changes observed in chamber arrangement, and, indeed, this rather vague treatment of chamber arrangement was perhaps the weakest feature of his classification. His lack of emphasis on the early ontogenetic stages was compatible with an essentialist view, as the essence of a thing cannot be fully achieved until adulthood. The adult form was considered by foraminiferal taxonomists to be of primary importance in establishing relationships, and this is a fact worth considering when evaluating the older literature.

The importance of chamber arrangement as a primary character in foraminiferal classification changed after Dujardin's (1835a–d) discovery.² When it was learned that foraminifera were simple protozoans, far-removed from the cephalopods, the rationale for considering chamber arrangement the primary essence diminished. Dujardin's discovery seems to have affected the English workers in particular, who in it found a justification for the partially empirical approach to classification that they were just beginning to adopt. The English workers found that chamber arrangement could be a highly variable character, particularly when viewed against a combination of characters. They, no doubt, completely overstated their case, however, by rejecting chamber arrangement completely as a character of any use in classification. Nevertheless, they did demonstrate the futility of blindly accepting a single character as the basis of classification.

In other respects, the early English workers remained essentialists. They merely substituted wall texture for chamber arrangement as the first principle of classification. On the continent, English claims about variation were rejected, and an empirical approach to classification, of any kind, was very slow in making an appearance. Reuss, with his tidy sense of order, seems to have set out to establish a precise catalogue of all of the different forms of foraminifera. He was what might today be called a "stamp collector." The prime European essentialist, however, was Schwager who used not one, but two, principles in his classification (that

is, wall texture as the first principle and chamber arrangement as the second principle).³

Wall texture, or the combined character of wall composition and the presence or absence of pores, did not emerge as a first principle in classification until some twenty-five years after Dujardin had revealed the protozoan nature of foraminifera. This delay may have been due to the reluctance on the part of naturalists to attempt the classification of such simply organized forms. Williamson (1858) expressed reservations about the feasibility of classifying the foraminifera in light of the knowledge that existed at the time.⁴ Once introduced as a viable character, wall texture was immediately accepted as a first principle in classification. As pointed out by Williamson, the appeal of using wall texture as a primary character was the relative consistency with which it could be correlated with other characters.⁵ Yet, from the beginning, the application of wall texture to classification has been purely essentialistic, and it has remained so through the years. Wall texture was not introduced into classification as the result of any new discovery; both Reuss (1861) and Carpenter (Carpenter, 1862) wrote about wall texture as if what they had to say was fairly common knowledge. They used wall texture in a totally invariant sense, and almost everyone since has done the same. Used in such a sense, wall texture can be viewed as an essence—something that cannot be changed without changing the entire nature of the individual. For example, a calcareous species of *Haplophragmoides* would be inconceivable because by definition the genus is arenaceous. The chief dissenter to this approach was Brady (1884). Brady appreciated the importance of wall texture, but refused to allow that any one character could be of more importance than a combination of characters. Darwin would have agreed.⁶

THE ORGANIZATIONAL LEVEL OF FORAMINIFERA

Following the publication of the first edition of Darwin's *On the Origin of Species* (1859), most naturalists found a new meaning in their classifications and began to adopt arrangements that would better show lines of descent. Ernst Haeckel (1866) depicted the "phylogeny" of all living organisms as being represented by a monophyletic, branching "Tree of Life" (Fig. 32). The three kingdoms of Plantae, Protista and Animalia comprise the three main branches of Haeckel's phylogenetic tree. Foraminifera ("Polythalamia") emerge as a tiny branchlet of the Rhizopoda, which form a sub-branch of the tree connected to the Protista by the "Archeophyleum protisicum." Beyond this, however,

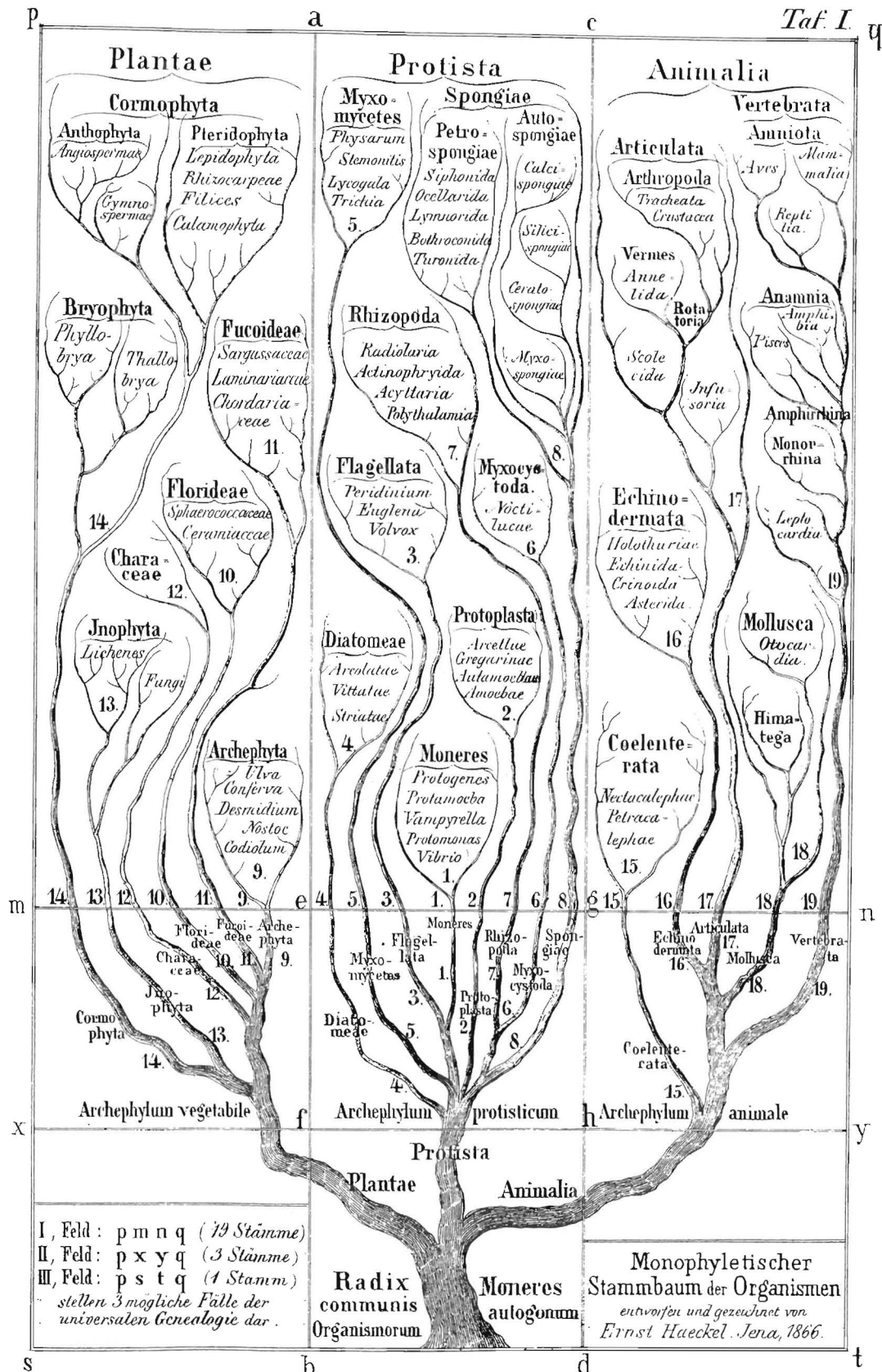


FIGURE 32. Haeckel's (1866) "monophyletic pedigree of organisms." The Foraminifera are represented by the group "Polythalamia."

there was hardly a murmur about foraminiferal evolution, except for an occasional weak reference to possible relationships between specific groups. Brady, for example, in a study of late Paleozoic foraminifera observed that an arenaceous, "quasi-Nodosarian" Carboniferous form (*Nodosinella*), had been replaced by a "more hyaline, true Nodosarian" form in Permian-aged Magnesian limestones, and by a larger, thicker "more arenaceous" form in mid-Permian-aged beds (Brady, 1876, p. 16). Although "direct evidence of continuity" could not be demonstrated, Brady considered it reasonable to assume that these "early quasi-Nodosarians" were the precursors, if not the "lineal ancestors, of two still living, and now widely separated, groups of Foraminifera" (Brady, 1876, p. 16). Brady also suggested that Recent species of *Patellina* might represent degenerate forms of earlier rotalids, which "during the Cretaceous and Nummulitic periods" had been "exemplified by organisms of comparatively large dimensions and complex structure" (Brady, 1884, p. 634).

In the fourth and later editions of *On the Origin of Species*, Darwin (1866, 1869, 1873), influenced by Carpenter's verdict,⁷ dismissed foraminifera from evolutionary consideration in a few brief sentences.⁸ According to Darwin, all organisms should show some advancement over their ancestors,⁹ although there could be exceptions. He rationalized that organisms with such a low organizational level as protozoans, were ideally suited to a simple way of life.¹⁰ Darwin, like so many other naturalists, expressed an ignorance of the "potentialities" of single-celled organisms,¹¹ and ignored not only the structural complexities of shell form that foraminifera have achieved, but the diverse habitats to which they have adapted.¹²

Early naturalists classified foraminifera with the cephalopods, because what they observed was an apparently equivalent level of organization in shell form. This equivalence in shell organization represents one of the more remarkable parallelisms in the organic world, and it is surprising that this parallelism continues to be ignored.¹³ Both Darwin and Carpenter erred in assuming that protozoans necessarily occupied a simple way of life. Foraminifera are found to inhabit every viable marine habitat, from brackish estuaries to abyssal depths. In the benthos they are infaunal, epifaunal, attached or free-living. Foraminifera also have exploited the pelagic realm where they are found throughout all parts of the world's oceans. As a group, they are omnivorous in their feeding habits and can directly contest prey organisms of their own size (Fig. 33).

The fossil record reveals a pattern of development in foraminifera that is fully comparable with that of the invertebrates (Cifelli, 1969; Cifelli and Scott, 1985). In retrospect, it seems that foraminifera with their abundant occurrence, wide-ranging distribution and continuity of descent in the fossil record, might have been considered an ideal group for the study of evolution. There was, however, a persistent skepticism about the evolutionary potential of single-celled organisms. Evolutionary thought about foraminifera was slow in starting and has always lagged behind current ideas and theories (Lipps, 1981). Foraminifera are still largely ignored by evolutionary biologists.¹⁴ The entire blame for the inertia in foraminifera evolutionary thought, however, cannot be placed on Darwin and Carpenter.¹⁵ An empirical approach to classification, which had paved the way for Darwinism, was not adopted in foraminiferal classification until Brady (1884). As late as 1876, Schwager elaborated an outline of classification that strictly adhered to Linnean principles. Even Brady upheld the central type concept. A strong sense of essentialism still permeates modern methodologies of foraminiferal classification in one form or another.

EVOLUTIONARY APPROACHES TO FORAMINIFERAL CLASSIFICATION

The initial impetus to producing an evolutionary classification of foraminifera came from Melchior Neumayr (1887), an ammonite specialist (Fig. 34). Neumayr held no bias against unicellular organisms and was not disturbed by their variability, or by the long-ranging genera and parallel developments observed in the foraminifera. In these respects, foraminifera seemed no more troublesome than multicellular organisms. He also believed that the foraminifera displayed an historical pattern of development. Neumayr was dissatisfied with the pre-existing foraminiferal classifications, partly because of the inconsistencies in their treatment of the arenaceous forms, but mainly because they were strictly two-dimensional and took no account of the fossil record. Although he did not propose a new classification, Neumayr sketched out a scheme of relationships that could serve as a natural basis for grouping genera (Table 11). He arrived at these relationships from a consideration of the succession of developmental stages in the foraminifera as observed in the geologic record. Neumayr rightly concentrated his attention on the Paleozoic record where most of the important developments in shell form and structure were to be found. For a non-specialist, he

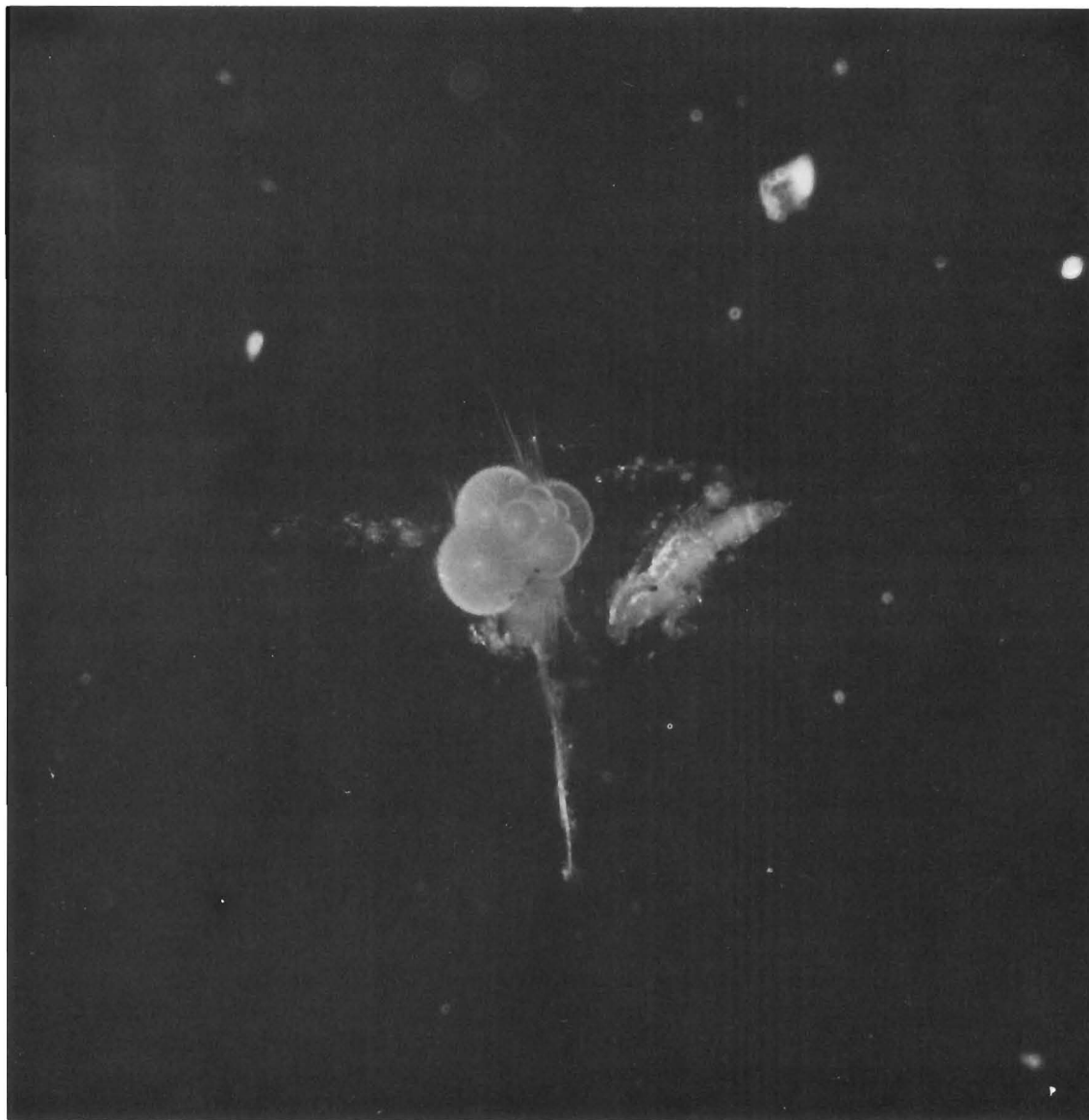


FIGURE 33. Photomicrograph of a living foraminiferan with a copepod entangled in its pseudopodia. Photo by Richard Cifelli.

showed a remarkably good grasp of the complexities of foraminifera. Although at the time he wrote there was a poor understanding of the wall texture of Paleozoic forms, Neumayr believed strongly in an absolute division on the basis of wall texture, except where a transition was indicated, as he thought to be the case with *Fusulinella*. He made a complete and unambiguous separation between the arenaceous and calcareous textularids. Due to the inadequacies of the fossil record, Neumayr thought it impossible to trace individual lines of descent, especially in the lower part of the Paleozoic. On the other hand, he grouped the foraminifera into three major developmental stages which

appeared in successive order in the fossil record (Fig. 35). The most primitive stage is the irregular agglutinated stage of development and is represented by the astrorhizids, single-chambered forms with irregular shapes. These forms make their appearance during the early part of the Paleozoic. Somewhat later in the early Paleozoic this primitive stage is followed by an intermediate, regular agglutinated stage of development. This next stage is characterized by four "types" of arenaceous groups: a cornuspirid-type, comprised of coiled tubular genera, such as *Ammodiscus*; a textularid-type, all non-calcareous textularids; a lituolid-type, all coiled, chambered forms; and a fusulinid-type,



FIGURE 34. Melchior Neumayr (1845–1890). (Photo courtesy of the Institut für Paläontologie der Universität Wien.)

primitive species of *Fusulinella* believed to be arenaceous. The advanced calcareous stage of development is represented by both perforate and imperforate forms which find their morphological counterparts in the regular agglutinated stage of development. Forms at the calcareous stage of development first make their appearance in the Carboniferous.

Neumayr proposed that all of the forms in the calcareous stage of development had been derived directly from arenaceous types displaying similar shell morphologies. The calcareous “cornuspirid-types” include both an imperforate and perforate series. In the imperforate series there are two branches; one branch includes the miliolines and the peneroplins, and the other, the alveolines. The perforate series of the calcareous cornuspirids is very limited, with *Spirillina* as the root, and only two poorly developed relatives. Neumayr believed that the genus *Spirillina* had developed

TABLE 11. Neumayr's 1887 Table of Natural Relationships.

IRREGULAR AGGLUTINATED STAGE OF DEVELOPMENT— <i>Astrorhizida</i>	
REGULAR AGGLUTINATED STAGE OF DEVELOPMENT	
A.	CORNUSPIRIDA-type— <i>Ammodiscus</i> ; <i>Silicina</i> ; <i>Agathammina</i>
B.	TEXTILARIDA-type—Agglutinated Textilarids
C.	LITUOLIDA-type— <i>Lituola</i> s.l. (<i>Haplophragmium</i> , <i>Haplostiche</i> , <i>Reophax</i> , etc.); <i>Trochammina</i> ; <i>Endothyra</i> ; <i>Stacheia</i> ; <i>Nodosinella</i> ; etc.
D.	FUSULINIDA-type— <i>Fusulinella per pro</i> ; Agglutinated forms. (Probably connected to <i>Endothyra</i>)
CALCAREOUS STAGE OF DEVELOPMENT	
A.	CORNUSPIRIDA-type—(Perforate and imperforate)
1.	Imperforate series
a)	Cornuspirine— <i>Cornuspira</i>
b)	Milioline— <i>Ophthalmidium</i> ; <i>Planospirina</i> ; <i>Spiroloculina</i> ; <i>Biloculina</i> ; <i>Triloculina</i> ; <i>Quinqueloculina</i>
c)	Peneroplidine— <i>Hauerina</i> ; <i>Vertebralina</i> ; <i>Peneroplis</i> ; <i>Orbiculina</i> ; <i>Orbitolites</i>
?d)	Alveoline
2.	Perforate series
a)	Spirilline— <i>Spirillina</i> ; <i>Involutina</i> ; <i>Problematica</i>
B.	TEXTILARIDA-type (Perforate)—Calcareous-shelled Textilarids; Chilostomellids?
C.	LITUOLIDA-type (Perforate)
1.	Nodosarian series—Nodosarinae; (Lageninae)
2.	Endothyran series
a)	Polystomellid branch— <i>Nonionina</i> ; <i>Sphaeroidina</i> ; <i>Polystomella</i>
b)	Globigerinid branch— <i>Globigerina</i> ; <i>Pullenia</i> ; <i>Orbulina</i>
c)	Rotalid branch
aa)	Rotalids— <i>Cymbalopora</i> ; <i>Discorbina</i> ; <i>Planorbulina</i> ; <i>Truncatulina</i> ; <i>Pulvulina</i> ; <i>Rotalia</i> ; <i>Calcarina</i> ; <i>Amphistegina</i> ; <i>Tinoporus</i> ; <i>Carpenteria</i> ?
?bb)	Cyclocypeids— <i>Cyclocypeus</i> ; <i>Orbitoides</i>
?)	Nummulitid branch— <i>Operculina</i> ; <i>Nummulites</i>
D.	FUSULINIDA-type (Perforate and imperforate)
1.	Imperforate series— <i>Fusulinella</i>
2.	Perforate series— <i>Fusulina</i> ; <i>Hemifusulina</i> ; <i>Schwagerina</i>

from the same arenaceous ancestor as had the genus *Cornuspira* and, therefore, grouped the spirillinids separately from the other calcareous perforate groups. The calcareous “textularid-types” include all of the calcareous biserial forms, sharply separated from the arenaceous biserial forms. The genus *Chilostomella* is tentatively placed in this group. The calcareous perforate “lituolid-types” include a uniserial “nodosarian-series” and a coiled “endothyran-series.” Neumayr linked these series to their arenaceous ancestors through the finely arenaceous, uniserial genus *Nodosinella* and the planispiral genus *Endothyra*, respectively. Neumayr did not consider the single-chambered genus *Lagena*, to be the ancestral taxon of either series because *Lagena* was preceded in the fossil record by *Nodosaria*. The endothyrid series is developed into a planispiral branch (polystomellid) and two trochospiral branches (globigerinid and rotalid); the cyclocypeids are tentatively placed with the rotalids. Neumayr's arrangement of the lituolids closely parallels Brady's scheme of clas-

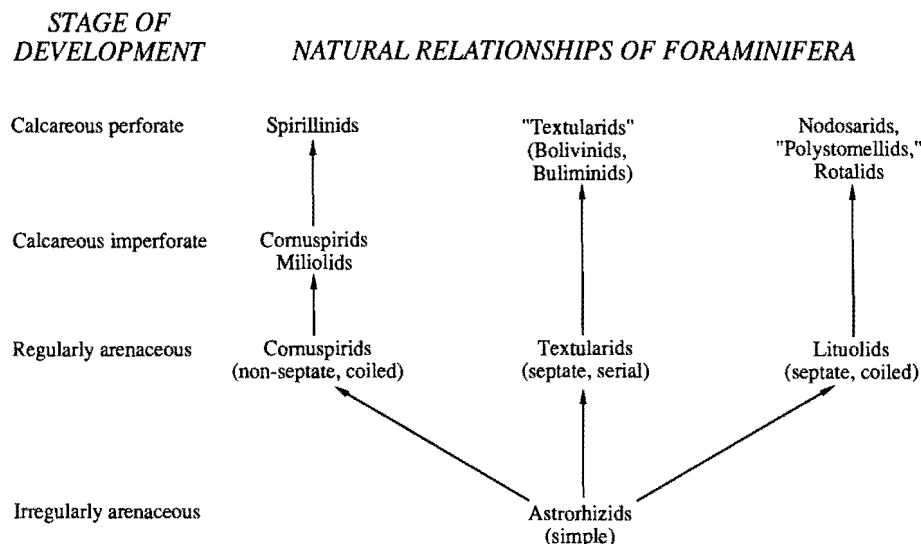


FIGURE 35. Simplified diagram of Neumayr's stages of development (fusulinids not shown) in the Foraminifera. Figure adapted from Neumayr's (1887) "Table of Natural Relationships."

sification. The fusulinids consist of an imperforate series (*Fusulinella*) and a perforate series (*Fusulina*, *Hemifusulina*, and *Schwagerina*). Neumayr connected the calcareous fusulinids with the primitive, supposedly arenaceous species of *Fusulinella*. In turn, he saw a probable connection between these primitive fusulinid species and the planispiral genus *Endothyra* which he also believed to have an arenaceous wall. At the time when Neumayr wrote, arenaceous walls were often confused with calcareous, microgranular walls.

While Neumayr is usually given a passing mention in most micropaleontology courses and textbooks, his ideas made relatively little impact on foraminiferal classification. Nevertheless, his contribution was most significant. He successfully refuted Carpenter's verdict and demonstrated that indeed there was a succession of shell forms observed in the fossil record of foraminifera. Importantly, too, he pointed out that the difficulties with variation and parallelisms observed in the foraminifera were really no different from those encountered in other groups of organisms. As an eminent specialist in ammonites, he could speak with authority on this subject.

ONTOGENY AND PHYLOGENY

The biogenetic law of recapitulation—"ontogeny recapitulates phylogeny"—dominated evolutionary thought in the last two decades of the nineteenth century. This law, a modification of the more generalized law of von Baer,¹⁶ and always more popularly held

among paleontologists than biologists, seemed to provide a simple key to natural classification and phylogenetic relationships. Character modifications were believed to have occurred through palingenesis.¹⁷ In order to determine the ancestry of a particular form, all one had to do was to compare the early developmental stages with the adult stages of geologically earlier forms. Cenogenesis,¹⁸ the opposite of palingenesis, was not generally considered to be a major factor in evolution. Not surprisingly, ammonite specialists were among the first leading spokesmen for recapitulation.¹⁹ The morphological features of the ammonite shell preserve an intact, readily visible record of its growth stages which makes the ammonite well suited to demonstrate the parallels between ontogeny and phylogeny.²⁰ Although the foraminiferal test retains an equally good record of growth, foraminifera were essentially ignored during the heyday of recapitulation. Application of the recapitulatory law to foraminifera had a slow beginning and never actually became well established until after the law had been discredited scientifically.

Carpenter (1883) essentially employed the law of recapitulation when he proposed to show the development of "*Orbitolites*" by relating the early stages of this form to the adult stages of simpler forms (Fig. 24). His work, however, received very little notice. Rumbler (1897), as will be seen, boldly proposed that cenogenesis was a more common form of character modification than palingenesis, but his ideas were ignored by most workers. Lister (1903) expressed the opinion that foraminifera may have developed by recapitula-

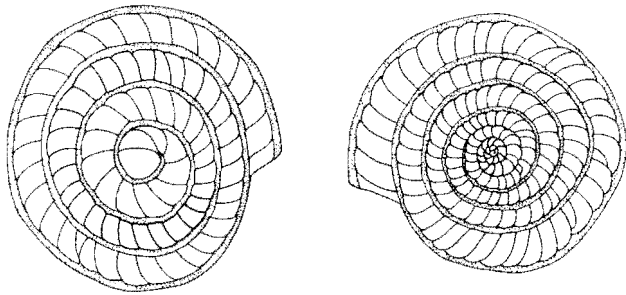


FIGURE 36. Two figures of the species *Nummulites laevigata* Lamarck which illustrate the phenomenon of dimorphism as recognized by Munier-Chalmas (1880). Left, Microspheric form. Right, Megalospheric form. Figures redrawn from de la Harpe (1881, Figs. 1 and 2).

tion and encouraged further research. Cushman (1905) analyzed the ontogenetic stages in species of the Lagenidae (Nodosariidae) and inferred a development of that family by recapitulation. The first really definitive statements concerning recapitulation in foraminifera were made independently by Schubert in his 1907 paper, and by Cushman in 1909, in his unpublished doctoral thesis. Recapitulation did not really become established in the study of foraminifera, however, until 1927 when Cushman introduced it into his preliminary classification.

The discovery of the morphologic dimorphism of the foraminiferal test greatly contributed to the understanding of the ontogenetic development of foraminifera, and was an impetus to studies relating ontogeny to phylogeny. It had long been noted that fossil species of *Nummulites* were represented by pairs of species which, although given separate names, were superficially similar and always occurred together in the same beds. One species, much more common than the other, was of a moderately large size and, in section, had a larger prolocular area. The other species was of a larger size and had more numerous chambers and a small prolocular area (Fig. 36). Munier-Chalmas (1880) proposed that these two forms belonged to the same species and thus that species of *Nummulites* were dimorphic.²¹ Although Munier-Chalmas did not comprehend the biological meaning of dimorphism, he felt sure that the embryonic apparatus of a single species could occur in two forms and that the phenomenon was a common one. Munier-Chalmas and Schlumberger (1883, 1885), and Schlumberger (1891), demonstrated dimorphism for a number of miliolid species. They showed that in the megalospheric form (with a large prolocular area), the early stages of development are often skipped, but the full ontogeny of a species is

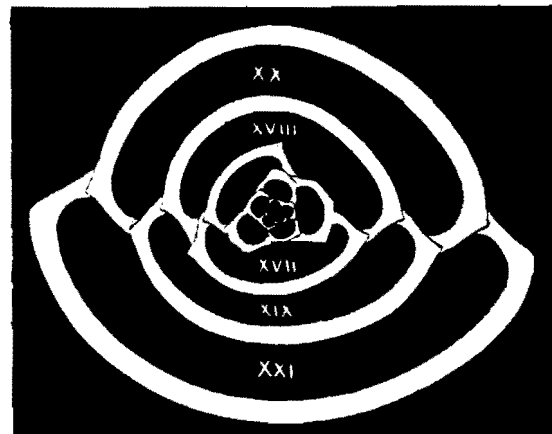
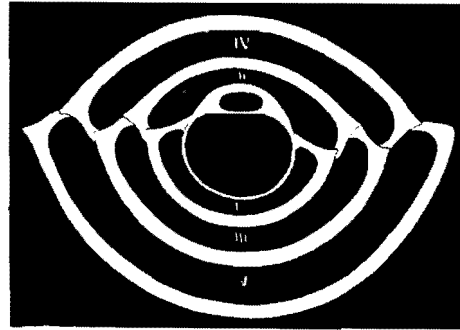


FIGURE 37. Schlumberger's (1891) figures illustrating dimorphism in the species *Biloculina* [= *Pyrgo*] *sarsi*. Upper, Megalospheric form. Lower, Microspheric form.

revealed in the microspheric form (Fig. 37). They defined their genera on the basis of ontogenetic development which they studied from carefully sectioned specimens. The biological significance of dimorphism was described from independent studies of *Elphidium crispum* by Lister (1895) and Schaudinn (1895), who found the microspheric and megalospheric forms to result from alternating generations in the foraminiferal life cycle.

THE RHUMBLER CLASSIFICATION

Ludwig Rhumbler (Fig. 38) was a thoughtful and innovative worker whose theoretical contributions are undoubtedly worth more attention than they have received.²² He also had ideas that were perhaps far ahead of his time. Glaessner (1947) dismissed him as a mechanist, yet Rhumbler's view of adaptations of the foraminiferal test to resist shell breakage, today seems like a reasonable and acceptable interpretation of shell design strategy.

Rhumbler (1895, 1897) was one of the very few workers who, before World War I, had followed the

lead of Neumayr in attempting to place the foraminifera in a phylogenetic framework. He accepted Neumayr's sketch of the relationships between the arenaceous and calcareous forms and went on to show how further relationships could be interpreted from ontogenetic development. He concluded that there were enough analogies between foraminifera and metazoans to establish that their development was governed by the same laws of palingenesis and cenogenesis (even though it might not at first seem that way). He showed that there were many examples of variations in the ontogenies of foraminifera; similar adult forms could have different developmental stages. These differences, he believed, represented morphological changes, that is, abbreviations or additions to the "normal" developmental cycle that did not affect other stages of development. Therefore, even though modifications might appear in the early ontogenetic stages, a normal shape could be achieved in the adult form. All of these variations in the stages of development of foraminifera provide the material for selection, as in the metazoans. Rhumbler's views, however, were out of step with the dominant recapitulationist views of his time. Rhumbler argued that the foraminifera developed both palingenetically and cenogenetically, but that cenogenesis was the rule rather than the exception. According to Rhumbler, evolutionary development in foraminifera was the reverse of recapitulation, with the early part of the test representing the descendent rather than the ancestral stage, except for the prolocular area. The distal end of the test represented the most primitive stage of development and eventually becomes discarded in the course of phylogeny. One reason he gave for this conclusion is that in the course of ontogeny, a change in growth plan proceeds from more complex to simple and not the reverse. In Rhumbler's view, the chief factor in foraminiferal development was adaptation to resist mechanical stress through selection of more compact test forms. He regarded the biserial, triserial and spiral forms as increasingly more resistant to breakage than the uniserial forms. The reversal of the usual order of ontogenetic development was attributed to the greater delicacy of the small chambers in the early part of the test. In the later stages of growth, the greater bulk of protoplasm present in the expanded chambers could compensate for a weaker type of chamber form. Rhumbler used a number of examples to illustrate his point, including the development of the coiled genus *Cristellaria* (= *Lenticulina*) from the uniserial *Nodosaria*, and the development of the biserial genus *Textularia* from the uniserial *Nodosinella* and the biserial-uniserial *Bigenerina*. One of his more interesting examples

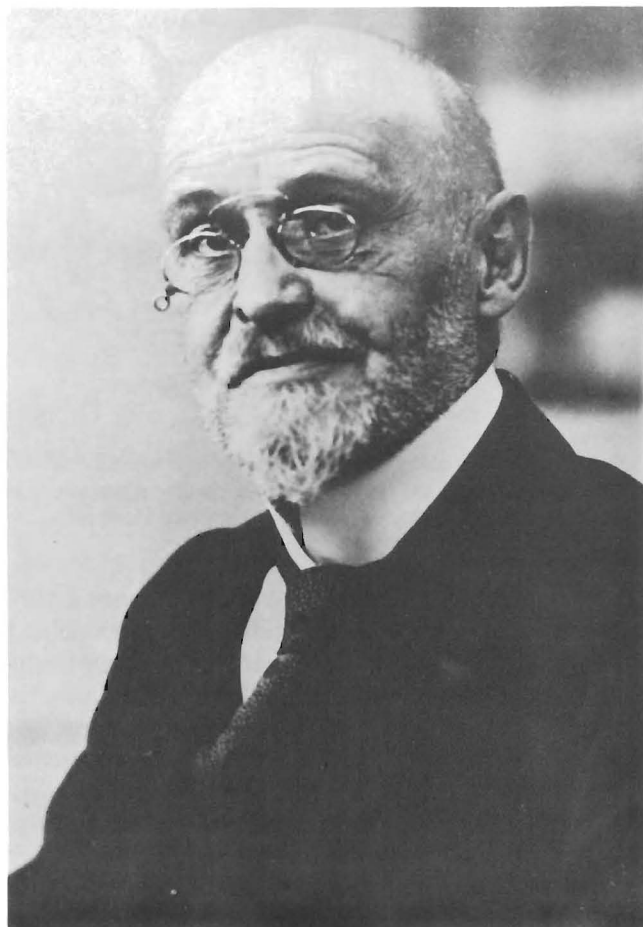


FIGURE 38. Johann Ludwig Rhumbler (1864–1939). (Photo courtesy of Georg-August-Universität Göttingen.)

is the development of the genus *Spiroloculina* through the uniserial *Nubecularia* and the non-septate and septate forms of *Ophthalmidium* (Fig. 39). Rhumbler had a similar explanation for the different modes of growth in the microspheric and megalospheric generations and argued that there was less need in the megalospheric form for a compact arrangement of initial chambers.

Rhumbler did not believe, however, that cenogenesis extended back to the earliest or prolocular chamber. Because of its spherical shape, he regarded the proloculus as a very early, primitive stage, that was commonly disseminated and retained among the foraminifera. Rhumbler observed that a number of coarsely perforate calcareous forms had prolocular chambers that were much less perforate in contrast to the imperforate *Peneropolis* which has a perforate proloculus. He emphatically stated that it would be a serious error to assume on this basis that imperforate genera were derived from perforate genera because, in

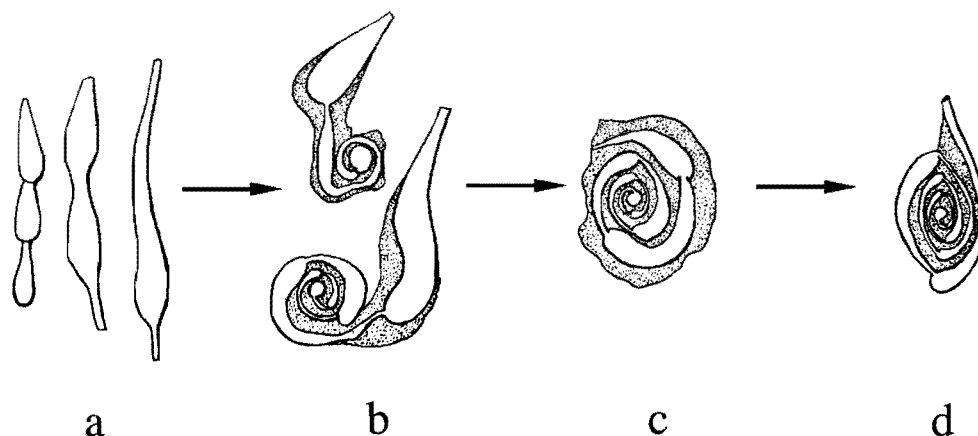


FIGURE 39. Case of the transformation of the genus *Nubecularia* into the genus *Spiroloculina* proposed by Haeusler (1887), which Rhumbler (1897) used as one of the main pieces of evidence in support of his ideas on the cenogenetic evolution of the Foraminifera. **a**, *Nubecularia tibia* Jones and Parker; **b**, *Ophthalmidium walfordi* Haeusler; **c**, *Ophthalmidium nubeculariformis* Haeusler; and **d**, *Spiroloculina* sp.

his view, it was not possible to progress from a perforate to an imperforate condition. Rhumbler upheld the view of Neumayr that the calcareous perforate forms were derived from coarsely perforated arenaceous forms which in turn were derived from less perforate or imperforate arenaceous forms. Therefore, the recurrence of weakly perforate prolocular chambers in coarsely perforate calcareous genera, Rhumbler believed, was fully in accord with the biogenetic law. On the other hand, he removed the genus *Peneroplis* from the imperforate group because of its perforate proloculus. Rhumbler is probably best remembered as the one who applied the biogenetic law in reverse, a contribution for which he usually has received no more than passing notice. Yet, the implications of his ideas were far-reaching and no doubt they could have been profitably pursued. Rhumbler's paper was published by the German Zoological Society and it was addressed, therefore, to a general audience of evolutionary biologists rather than a group of paleontological specialists. In order to appreciate his perception, it is necessary to consider several ideas that were prevalent at the time he wrote. First of all, foraminifera were still generally considered of no evolutionary importance; the work of Neumayr had little impact. Second, the question of the relationship between ontogeny and phylogeny was being debated but, by and large, the authorities, led by the influential vertebrate specialist Cope and the ammonite specialist Hyatt, held firm to a palingenetic interpretation of the biogenetic law (Gould, 1977). That is, evolutionary developments occurred at the adult, terminal stage of development with the result that a descendant, through acceleration, recapitulates the ancestral adult stages in the course of its ontogeny. It was

admitted that cenogenetic reversals could occur, but these reversals were regarded as exceptions and falsifications of the true phylogeny. Third, by the end of the nineteenth century natural selection had fallen into disfavor and Lamarckism was undergoing a revival. Recapitulation, through palingenesis, provided a new justification for Lamarckism because it was implicit in the theory of recapitulation that modifications occur by addition in the adult stage (Gould, 1977). And last of all, the Mendelian laws of heredity had not yet been rediscovered.

Rhumbler not only supported the views of Neumayr (1887) and defended an orderly evolutionary process for the foraminifera, but he also proposed that the examples provided by the foraminifera could be applied to metazoans.²³ This, indeed, was an audacious view since Darwin earlier had restricted the foraminifera to a simple, unchanging way of life. That foraminifera had evolved largely through cenogenesis was only secondary to the larger point that Rhumbler wanted to get across. He used the foraminifera to demonstrate that modifications could and did occur at early stages of development without affecting either the initial or adult stages. He did not, by any means, deny palingenesis, but rather pointed out that it was an overly narrow interpretation of development. Even if Rhumbler's interpretations did not prove to be totally correct, his general outlook is in accord with some modern views on development which favor heterochrony (Gould, 1977),²⁴ or the displacement of characters during ontogeny. In addition, Rhumbler strongly emphasized that phylogenetic transformation could not occur without variation and selection in the breeding population. Therefore, although he did not say it

TABLE 12. Rhumbler's 1895 Classification.

- I. Family **RHABDAMMINIDAE**
 Subfamily **Myxothecinae**—*Myxotheca* Schaudinn; *Hyalopus* Schaudinn; *Gromia* Dujardin; *Craterina* Gruber; *Rynchogromia* Rhumbler; *Dendrotuba* Rhumbler; *Dactylosaccus* Rhumbler; *Shepherdella* Siddall; *Rhynchosaccus* Rhumbler
 Subfamily **Astrorhizinae**—*Astrorhiza*
 Subfamily **Saccammininae**—*Pelosina* Brady; *Saccamina* M. Sars; *Storthosphaera* F. E. Schultze; *Thuramina* Brady; *Sorosphaera* Brady; *Pilulina* Carpenter; *Reophax* (Montfort) emend. Rhumbler; *Tholosina* nov.
 Subfamily **Rhizammininae**—*Rhizammina* Brady
 Subfamily **Rhabdammininae**—*Technitella* Normann; *Marsipella* Normann; *Bathysiphon* Sars; *Botellina* Carpenter; *Webbina* d'Orbigny; *Rhabdammina* M. Sars; *Dendrophrya* Str. Wright; *Haliphysema* Bowerbank; *Ophiotuba* Rhumbler?; *Hyperamina* Brady
 Subfamily **Hippocrepininae**—*Hippocrepina* Parker; *Jaculella* Brady
 Subfamily **Girvanellinae**—*Girvanella* Nicholson and Etheridge; *Tolypamina* nov.; *Syringamina* Brady
- II. Family **AMMODISCIDAE**
 Arenaceous tests—*Lituotuba* nov.; *Ammodiscus* (Reuss) emend. Rhumbler; *Psammonyx* Doderlein; *Gordiamina* nov.; *Turitelopsis* nov.
 Calcareous tests—*Cornuspira* M. Schultze
- III. Family **SPIRILLINIDAE**—*Spirillina* Ehrenberg; *Involutina* Terquem; ?*Archaeodiscus* Brady; *Patellina* Williamson
- IV. Family **NODOSINELLIDAE**—*Nodosinella* Brady; *Nodulina* nov.; *Hormosina* Brady; *Bdelloidina* Carter; *Haplostiche* Reuss; *Polyphragma* Reuss; *Aschemonella* Brady
- V. Family **MILIOLINIDAE**
 Subfamily **Nubecularinae**—*Nodobacularia* nov.; *Nubecularia* DeFrance; *Calcituba* Roboz
 Subfamily **Miliolinae**—*Agathammina* Neumayr; *Biloculina* d'Orbigny; *Fabularia* DeFrance; *Triloculina* d'Orbigny; *Articulina* d'Orbigny; *Quinqueloculina* d'Orbigny; *Ophthalmidium* Kubler; *Spiroloculina* d'Orbigny; *Sigmoilina* Schlumberger
 Subfamily **Hauerininae**—*Vertebralina* d'Orbigny; *Peneropolis* Forskal; *Hauerina* d'Orbigny; *Planispirina* Seguenza
- VI. Family **ORBITOLITIDAE**
 Arenaceous preliminary stage—*Neusina* Goes
 Calcareous imperforate stage of development—*Orbitolites* Lamarck; *Orbiculina* Lamarck; *Keramosphaera* Brady
 Calcareous perforate stage of development—*Orbitoides* d'Orbigny; *Cyclocypeus* Carpenter
- VII. Family **TEXTULARINAE**
 Subfamily **Textularinae**—*Bigenerina* d'Orbigny; *Textularia* DeFrance; *Pavonina* d'Orbigny; *Cuneolina* d'Orbigny; *Spiroplecta* Ehrenberg; *Gaudryina* d'Orbigny; *Verneuilina* d'Orbigny; *Tritaxia* Reuss; *Chrysalidina* d'Orbigny; *Valvulina* d'Orbigny; *Clavulina* d'Orbigny
 Subfamily **Buliminae**—*Bolivina* d'Orbigny; *Chilostomella* Reuss; *Pleurostomella* Reuss; *Bifarina* Parker and Jones; *Bulimina* d'Orbigny; *Allomorphina* Reuss; *Virgulina* d'Orbigny
 Subfamily **Cassidulinae**—*Ehrenbergina* Reuss; *Cassidulina* d'Orbigny
- VIII. Family **NODOSARIDAE**
 Subfamily **Nodosarinae**—*Nodosaria* Lamarck; *Glandulina* d'Orbigny; *Ellipsoidina* d'Orbigny; *Lingulina* d'Orbigny; *Amphimorphina* Neugeboren; *Frondicularia* DeFrance; *Dentalinopsis* Reuss; *Rhabdogonium* Reuss; *Marginulina* d'Orbigny; *Vaginulina* d'Orbigny; *Rimulina* d'Orbigny

TABLE 12. Continued.

- Subfamily **Lageninae**—*Lagena* Walker and Jacob
 Subfamily **Cristellarinae**—*Amphicoryne* Schlumberger; *Lingulinopsis* Reuss; *Flabellina* d'Orbigny; *Cristellaria* Lamarck
 Subfamily **Polymorphininae**—*Dimorphina* d'Orbigny; *Polymorphina* d'Orbigny; *Sagrina* Parker and Jones; *Uvigerina* d'Orbigny
 Subfamily—*Ramulina* Jones
- IX. Family **ENDOTHYRINAE**
 Subfamily **Endothyridae**—*Placopsilina* d'Orbigny, excl. *Tholosina*; *Haplophragmium* Reuss; *Endothyra* Phillips; *Bradyina* Möller; *Stacheia* Brady; *Trochammina* (Parker and Jones) Neumayr; *Carterina* Brady; *Cyclammina* Brady
 Subfamily **Fusulininae**—*Fusulina* Fischer; *Schwagerina* Möller; *Hemifusulina* Möller; *Loftusia* Brady; *Alveolina* d'Orbigny
- X. Family **ROTALIDAE**
 Subfamily **Rotalinae**—*Truncatulina* d'Orbigny; *Planorbulina* d'Orbigny; *Anomalina* Parker and Jones; *Pulvinulina* Parker and Jones; *Rotalia* Lamarck; *Discorbina* Parker and Jones; *Cymbalopora* Hagenow; *Carpenteria* Gray; *Polytrema* Risso; *Calcarina* d'Orbigny
 Subfamily **Tinoporinae**—*Tinoporus* Carpenter; *Gypsina* Carter; *Aphrosina* Carter; *Thalamopora* Reuss
 Subfamily **Globigerininae**
 Spiny form—*Globigerina* d'Orbigny; *Orbulina* d'Orbigny; *Hastigerina* Wy. Thomson
 Spineless form—*Pullenia* Parker and Jones; *Sphaeroidina* d'Orbigny; *Candeina* d'Orbigny
 Subfamily **Polystomellinae**—*Nonionina* d'Orbigny; *Polystomella* Lamarck; *Operculina* d'Orbigny
 Subfamily **Nummulitinae**—*Amphistegina* d'Orbigny; *Heterostegina* d'Orbigny; *Nummulites* Lamarck; *Assilina* d'Orbigny

in so many words, he appears to have been pleading for a return to Darwinism in opposition to the resurgent Lamarckism. Moreover, Rhumbler's idea on adaptations resulting in an increase in mechanical strength now seems like a reasonable interpretation of adaptive strategy in shell design. His principle failing was that he could not support his phylogenies with stratigraphic evidence. Nevertheless, with a few changes, one would be hard put to recognize that his ideas were presented over eighty-five years ago.

In most respects, Rhumbler's classification (Table 12) follows Brady's, although Rhumbler did propose several important changes. Rhumbler recognized the same number of families, ten, and also refrained from grouping the families into superfamilies. He split the arenaceous forms somewhat more finely, but reduced Brady's families Globigerinidae, Rotalidae and Nummulinidae to subfamilies and combined them into the Globigerinidae.

The major change that Rhumbler introduced was an application of Neumayr's foresighted ideas about relationships (Fig. 40). Rhumbler removed the hyaline

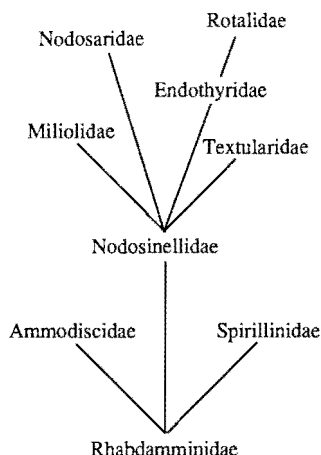


FIGURE 40. Rhumbler's (1895) scheme of evolution of the families of Foraminifera.

spirillinids from the Rotalidae and made them a separate family which he placed alongside the arenaceous Ammodiscidae, following Neumayr's suggestion that there was a close connection between these two groups. In a similar fashion, he removed the Fusulinidae from the Nummulinidae and the Endothyridinae from the Lituolidae, and combined them into the single family the Fusulinidae. Again following Neumayr, Rhumbler proposed the family Nodosinellidae as a primitive group ancestral to the Nodosariidae. Rhumbler's important emendations to classification were virtually ignored for many years, but they have since been incorporated into the modern foraminiferal classification (Loeblich and Tappan, 1964).

VII. EARLY TWENTIETH CENTURY STATUS OF FORAMINIFERAL CLASSIFICATION

In an attempt to determine natural affinities, Brady had rejected the sanctity of fundamental characters and focussed his attention instead on a combination of characters. As a consequence, he had produced a classification that was both logical and workable. Yet, in spite of its merits, Brady's classification was far behind the times, as it comprised a strictly two-dimensional scheme which ignored ancestor-descendent relationships and made no provision for the temporal distribution of taxa. Brady, moreover, retained the English philosophy of broad species limits and tended to ignore details of morphology; he sometimes combined in the same species Recent and ancient forms of distinct morphology. These practices, as well as the total lack of a stratigraphic focus in his classification was a source of

annoyance to the Europeans. Schlumberger (1891) commended Brady for his *Challenger Report* but could not refrain from commenting that the influence of Carpenter on Brady was all too evident.¹ Yet, in spite of this complaint and others (Neumayr, 1887),² no reasonable alternative to Brady's scheme emerged. Consequently, foraminiferologists continued to use a scheme of classification, totally devoid of any evolutionary implications, throughout the first quarter of this century. In part, the longevity of Brady's classification may be attributed to its overall workability, in spite of its lack of a time perspective. And in part, its longevity may have been a result of the disruption of scientific activities from 1914 to 1918 caused by World War I. The emergence of micropaleontology as an applied science during the first quarter of this century, perhaps also contributed to the continued use of Brady's classification (Lipps, 1981).

Joseph J. Lister's (Fig. 41) interest in foraminifera was predominantly biological. He was particularly interested in their life histories, especially their alternating megalospheric and microspheric cycles of development, a field in which he made important contributions (Lister, 1895, 1903; Heron-Allen, 1930). In his chapter on "Foraminifera" in Lankester's *Treatise on Zoology*, Lister (1903) presented a virtually unmodified version of Brady's classification, in which he elevated the rank of Foraminifera to a class and Brady's ten family groupings to orders (Table 13). Importantly, he rejected outright Carpenter's views on the "variation of the Foraminifera,"³ thereby terminating once and for all the tradition of the English school. Variation was no longer to be the philosophical issue it had been, and it became generally agreed upon that species could be recognized in foraminifera.

While Lister treated the stratigraphic distribution of foraminifera very superficially, he believed that the further study of the early stages of development would prove important in the future and might "throw light on the complicated problems of phylogeny" (Lister, 1903, p. 140). Lister was clearly attracted to the theory of recapitulation, and saw evidence supporting this view in "the case of '*Polytrema*'" (= *Homotrema rubrum*) in which it seemed "clear that the arrangement of the chambers formed early in life repeats that of the rotaline stock from which it sprang, while the later chambers are disposed on a plan acquired as it has diverged from that stock" (Lister, 1903, p. 135). Lister also found Carpenter's (1883) proposed paligenetic development of *Orbitolites* (Fig. 25) a convincing example of recapitulation.⁴ On the other hand he rejected the cenogenetic views of Rhumbler, not on any par-

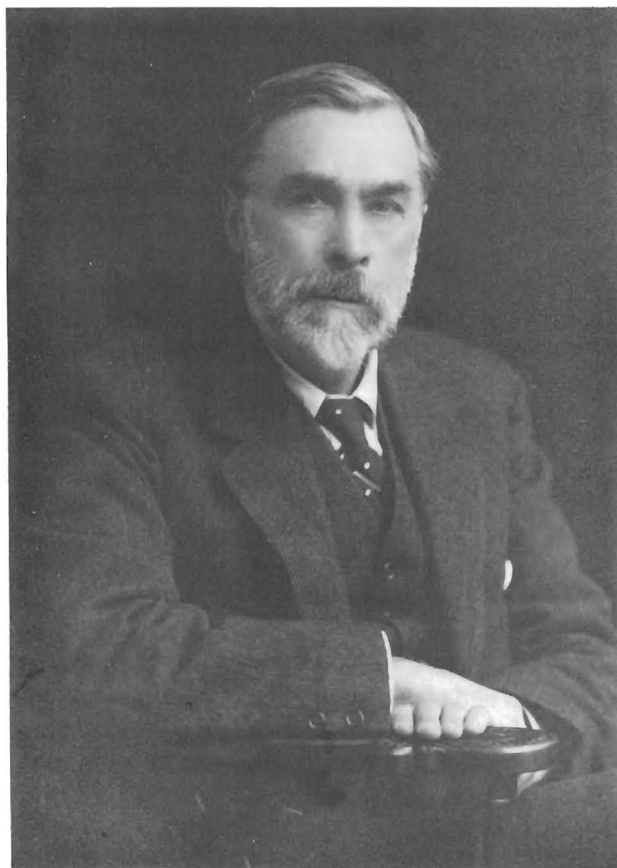


FIGURE 41. Joseph Jackson Lister (1857–1927). (Photo courtesy of the British Museum (Natural History), London.)

ticular grounds, but merely because he thought that Rhumbler's arguments were insufficient for discarding the "view of Carpenter."⁵

Henri Douvillé explored the evolutionary trends of a few morphologic types of foraminifera in his 1906 paper on the "Evolution et Enchaînements des Foraminifères." He made the astute observation that a particular morphotype will recur in the fossil record associated with a particular ecological niche.⁶ He recognized that the fusiform shell architecture characteristic of Paleozoic fusulinids, the Cretaceous genus *Loftusia*, and Cenozoic alveolinids, was associated with shallow-water facies. Douvillé also defined a *forme fondamentale*—a symmetrical spiral, coiled around an initial embryonic chamber—which he regarded as the shell form basic to all others. Many numerous and diverse forms could be derived from this ancestral type through uncoiling, change in coiling axis, loss of symmetry, or increase in size and number of chambers. The idea of a symmetrically coiled prototype would later be adopted by many workers—Cushman became

TABLE 13. Lister's 1903 Classification.

Order 1. GROMIIDEA
Family POLYSTOMATIDAE
Family MONOSTOMATIDAE
Family AMPHISTOMATIDAE
Order 2. ASTRORHIZIDEA
Family ASTRORHIZIDAE
Family PILULINIDAE
Family SACCAMMINIDAE
Family RHABDAMMINIDAE
Order 3. LITUOLIDEA
Family LITUOLIDAE
Family TROCHAMMINIDAE
Family ENDOTHYRIDAE
Family LOFTUSIIDAE
Order 4. MILIOLIDEA
Family MILIOLINIDAE
Family HAUERINIDAE
Family PENEROPLIDAE
Family ALVEOLINIDAE
Family KERAMOSPHAERIDAE
Family NUBECULARIDAE
Order 5. TEXTULARIDEA
Family TEXTULARIDAE
Family BULIMINIDAE
Family CASSIDULINIDAE
Order 6. CHILOSTOMELLIDEA
Order 7. LAGENIDEA
Family LAGENIDAE
Family NODOSARIIDAE
Family POLYMORPHINIDAE
Family RAMULINIDAE
Order 8. GLOBIGERINIDEA
Order 9. ROTALIDEA
Family SPIRILLINIDAE
Family ROTALIDAE
Family TINOPORIDAE
Order 10. NUMMULITIDEA
Family FUSULINIDAE
Family POLYSTOMELLIDAE
Family NUMMULITIDAE

totally committed to it and habitually derived his genera from a series of increasingly complex modifications of a simple, coiled ancestral form.

Joseph A. Cushman (1905), while still a student at Harvard, published a paper entitled "Developmental stages in the Lagenidae." Although, it now appears naive in its evolutionary outlook, the paper remains of historical interest. Cushman (Fig. 42), seldom committal or explicit in his views, here proposed that the same evolutionary laws which had previously only been applied to metazoans, were "equally applicable" to protozoans.⁷ The laws he referred to were the developmental laws formulated by Alpheus Hyatt, the nineteenth century invertebrate paleontologist responsible for many of the major concepts of recapitulation (Hyatt, 1889, 1894; Jackson, 1913).⁸ Following Hyatt's example, Cushman recognized in foraminifera, *embryonic*, *nepionic*, *neanic* and *ephebic* stages of develop-



FIGURE 42. Joseph Augustine Cushman (1881–1949). (Photo courtesy of the Todd Library for Foraminiferal Research, Smithsonian Institution.)

ment (Fig. 43), with development proceeding by palingenesis and the acceleration of earlier stages.⁹ He regarded the single-chambered *Lagena* as the primitive radicle of the family Lagenidae—its simple form retained in the embryonic stage (proloculus) of all other genera in the family. “Straight Nodosarian growth” characterized the nepionic stage of development (Cushman, 1905, p. 544). Here, Cushman closely paralleled Hyatt’s (1894) interpretations of the ontogenetic stages in the nautiloids, in which he represented the primitive form by a straight shell. Cushman (1905) also maintained that the true generic characters were achieved in the neanic stage of development. And he followed Hyatt’s reasoning in his interpretation of “the uncoiling of forms” as a “decided feature of senescence,” and a reversion to a more youthful stage (Cushman, 1905, p. 547).¹⁰ Thus, Cushman regarded the final chambers of *Marginulina*, *Dimorphina*, and *Nodosaria* as atavistic.¹² In his later works Cushman changed his ideas on development and came to regard the coiled stage as being primitive. Taking into con-

sideration the intellectual climate of the time, Cushman’s developmental model for the Lagenidae was quite reasonable. He probably did not push his data much harder to meet the needs of theory than Hyatt had done likewise with the cephalopods. Cushman, however, made his interpretations on morphoserries which had not been documented by stratigraphic occurrences.⁹

In 1909 Cushman completed his doctoral thesis which was entitled “The Phylogeny of the Miliolidae.” Several aspects of his thesis are of historical interest as they reveal some insight into Cushman’s views on classification—he rarely elaborated his views on this subject in his later works. The title is actually misleading, because his thesis was really no more than an analysis of the developmental stages of twenty miliolid genera. Although there are strong phylogenetic implications throughout the manuscript, an actual scheme of origins was never proposed.

Cushman rejected completely the English School and their extravagant ideas on variation; he thought that the English had actually done harm by misinterpreting some of d’Orbigny’s drawings of miliolids. He made no comment on Brady’s classification, although he criticized Brady himself for having been too influenced by Carpenter, and also for having used variations to unite forms rather than trying to explain their differences. On the other hand, Cushman was clearly influenced by Lister’s views on the importance of the early developmental stages in elucidating phylogenetic relationships.¹³ The studies of Munier-Chalmas and Schlumberger (1883, 1885) on the dimorphism of miliolids as revealed through the careful examination of specimens in thin section, probably also stimulated the direction of Cushman’s research. Here, and in Cushman’s later work, there is found a strong emphasis on dimorphism, probably more so than is found in any contemporary work.

Cushman’s method of achieving a natural classification was expressed clearly and unambiguously in this early work. Very simply, his method involved a comparative analysis of the microspheric forms of species and the grouping together, in the same genus or associated genera, those species which had the same early stages of development—it mattered not if the adult forms of the species were quite different.¹⁴ He determined the relationships between genera by a comparative analysis of their adult and early stages. Cushman believed that the ideal phylogenetic classification could be constructed by comparing the young stages of genera of a particular geologic age with the adult forms of geologically older genera.¹⁵ Although he was never able


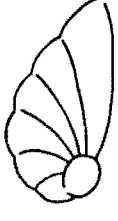



















	<i>Marginulina</i>	<i>Cristellaria</i>	<i>Nodosaria</i>	<i>Polymorphina</i>	<i>Dimorphina</i>
<i>Ephebic</i>	 5	 9	 13	 17	 21
<i>Neanic</i>	 4	 8	 12	 16	 20
<i>Nepionic</i>	 3	 7	 11	 15	 19
<i>Embryonic</i>	 2	 6	 10	 14	 18
 <i>Lagena</i>					

FIGURE 43. Cushman's (1905) table illustrating the "Developmental Stages in the Lagenidae." The figures are arranged to show comparative stages in development. 1, *Lagena*, the primitive radicle; 2-5, *Marginulina*; 6-9, *Cristellaria*; 10-13, *Nodosaria*; 14-17, *Polymorphina*; 18-21, *Dimorphina*. "The embryonic stage, the proloculum, is represented in the lower row and may be compared to *Lagena*. The nepionic [stage], representing the first two chambers in the next row above, may be compared to *Nodosaria*. In the neanic [stage] shown in the third row the true generic characters are definitely taken on at least as regards progressive characters" (p. 543).

to accomplish this with any degree of success, he continued to use this same comparative method throughout his lifetime. The diagrams that Cushman later used to show generic relationships in families illustrate his methodology very well (see Figs. 50, 52). Seldom, however, has the stratigraphic evidence lent support to a phylogenetic interpretation of the relationships shown.¹⁶

While the value of the recapitulatory principles underlying Cushman's methods are certainly disputable, there is no denying the important influence that the method itself has had on classification. In earlier times, attention had been focussed on the adult forms of species and genera, and little significance was attributed to the younger stages of development. Cushman totally reversed this emphasis, and ever since, taxonomists, even those who are not consciously recapitu-

lationists, have considered the early ontogenetic stages of greater classificatory value than the adult stages.¹⁷

The potential importance of the early stages of development in classification had already been perceived by Brady (1884), Douvillé (1906), Lister (1903), and especially Schubert (1907). Schubert (1907) made a preliminary attempt to apply the principle of recapitulation to establish natural, evolutionary relationships among foraminifera. Although a few years earlier, both Carpenter (1883) and Rhumbler (1897) had inferred relationships between ontogeny and phylogeny, they had done so solely on the basis of morphoserries observed among contemporary forms. Schubert (1907) thought it absolutely essential for a natural classification to be consistent with the known stratigraphic ranges of species and genera, although he was well aware that the stratigraphic record seemingly revealed a number

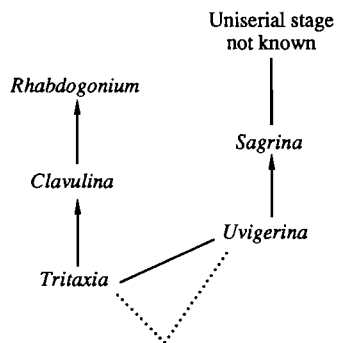


FIGURE 44. Schubert's (1907) diagram depicting the parallel series of development of the triserial genera *Tritaxia* and *Uvigerina* towards totally uniserial end forms.

of ambiguities in their originations. He concluded, therefore, that genera, or at least some of them, represented particular evolutionary stages and were what we would now call morphotypes. A genus might consist of species which had evolved independently; for example, *Textularia* in Schubert's view was not a true genus, but a morphological designation for a heterogeneous group of species that had evolved in the same direction. A natural system should group together the morphological stages of a particular evolutionary series, as determined by their stratigraphic succession. He believed that the evolutionary stages of a series was revealed in the ontogenetic stages of individuals, and that connections between series were revealed by ontogenetic changes in the form of the aperture. Schubert also thought that these modifications occurred palingogenetically; for example, Schubert recognized a sequential developmental series from *Tritaxia* to *Clavulina* to *Rhabdogonium* as involving a change from a totally triserial form, to an initially triserial but uniserial adult form, to a form almost totally uniserial in the adult stage. And he believed that a *Uvigerina* series could be linked to *Tritaxia* by the elongate aperture seen in the early ontogenetic stages of *Uvigerina* (Fig. 44). Schubert admitted that there was no clear evidence in the Mesozoic or Cenozoic record to favor palingenesis over cenogenesis as proposed by Rhumbler, but believed that the Paleozoic record favored palingenesis. He thought that the problem of deciphering phylogenies was made much more difficult by the then current taxonomic practices which lumped together species with different growth plans into the same genus. A good part of Schubert's paper involves an attempt to clarify textularid genera. Schubert's methodology, therefore, involved the constant revision of narrowly defined genera, under stratigraphic control. Clearly, a

TABLE 14. Schubert's 1921 Classification.

I.	PROTAMMIDA
II.	METAMMIDA
III.	BASISTOMA
	Family ENDOTHYRIDAE— <i>Endothyridinae</i> ; <i>Fusulininae</i>
	Family ROTALIDAE— <i>Truncatulinae</i> ; <i>Pulvinulininae</i> ; <i>Globigerininae</i> ; <i>Rotalinae</i> ; <i>Discorbininae</i> ; <i>Patellinae</i>
	Family ORBITOIDIDAE
	Family NUMMULITIDAE
IV.	PORCELLANEA
	Family CORNUSPIRIDAE
	Family MILIOLIDAE
	Family ORBITOLITIDAE— <i>Orbitolitinae</i> ; <i>Orbiculininae</i>
	Family KERAMOSPHAERIDAE
	Family ALVEOLINIDAE
V.	TELOSTOMA
	Family NODOSARIDAE— <i>Nodosarinae</i> ; <i>Cristellarinae</i>
	Family POLYMORPHINIDAE
VI.	SCHIZOSTOMA
	Family VALVULINIDAE— <i>Valvulininae</i> ; <i>Textularinae</i>
	Family BULIMINIDAE— <i>Bulimininae</i>

classification could not be created overnight in this way.

Schubert was a casualty of the war and thus never lived to produce the kind of classification that he had proposed. A classification was published posthumously, but it incorporated none of his earlier ideas (Schubert, 1921) (Table 14). While Schubert's methods have always been highly regarded, they have never been followed. Considering the complexity of the fossil record, one wonders whether his method, requiring as it did the continual revision of genera with the discovery of new isomorphic series, could realistically be applied to a classification of the foraminifera.

VIII. THE AGE OF CUSHMAN

JOSEPH A. CUSHMAN (1881–1949)

For most of the first half of the twentieth century Joseph A. Cushman (Fig. 42) would be the most renowned authority on foraminifera; his influence extended throughout the world. Never was there before, nor probably will there ever again be such a towering figure in the field of foraminiferal research. He modernized classification to the extent that his own classification scheme remains a practical guide for the arrangement of genera, and his methodology has had a strong lasting influence. Cushman introduced professionalism into the study of foraminifera. He was probably the first person to complete a dissertation on this group of organisms and the first to earn a living by their study. He also pioneered the practical application of the study of foraminifera to subsurface stratigraphy. During his lifetime Cushman, either by himself or in

collaboration with others (and always as senior author), published 554 papers with three others in press at the time of his death. Many of these papers were very brief, but others were major monographs on Recent and fossil foraminiferal faunas, as well as definitive revisions of families and genera. Cushman's textbook (1928, 1933, 1940, 1948) has enjoyed a remarkable longevity. First published in 1928, it underwent four editions, and a few copies, even now, are being sold each year.¹ The book greatly facilitated the teaching and use of foraminifera (Henbest, 1952).

In his lifetime Cushman amassed the largest collection of foraminifera in the world. This collection now forms the basis, indeed the bulk, of the foraminiferal collections at the Smithsonian's National Museum of Natural History.

Cushman was a man of inexhaustible energy. He had the extraordinary ability to recognize and exploit the unique opportunities which, at the time, were available to him. He maintained an almost lifetime association with both the Smithsonian Institution and the U.S. Geological Survey. While the Smithsonian could never offer Cushman remuneration for his work, the Institution did make available for his study the very extensive dredgings and hydrographic soundings of the U.S. Bureau of Fisheries' steamer *Albatross*, as well as samples and accumulated material from other oceanographic expeditions from the world's oceans. The Smithsonian also provided an outlet for the publication of his monographs, and financial assistance for the preparation of material. Through the Survey, for whom he served as a foraminiferal specialist for many years, Cushman gained access to the major stratigraphically documented Cretaceous and Tertiary foraminiferal sequences of the United States. His familiarity with fossil faunas was further augmented by his experience as an oil-field consultant. Through all of these opportunities, of which he took the fullest advantage, Cushman was able to gain an unprecedented knowledge of the kinds and varieties of foraminifera and their distributions in space and time. If Cushman's work sometimes appears superficial, the overwhelming magnitude of the vast amount of material available for his study and the limit to which it could be assimilated in any single lifetime, should be borne in mind. Nevertheless, Cushman was never overwhelmed with his projects. He always maintained a strict self discipline and a tight organization. He neither lost sight of his goals nor allowed himself to get bogged down with difficulties and problems (Henbest, 1952). As a result, he was able to bring a good deal of order into a field which was still in a rather chaotic state, and his clas-

sification, like much of his monographic work, became a point of departure for later considerations (Henbest, 1952). Importantly, Cushman recognized the value of studying type specimens and type material, as well as the need of complying with the Rules of Zoological Nomenclature. He was one of the first students of foraminifera to visit the museums of Europe to study their type collections, and also to collect material from the classic European type localities.

Background

Joseph Augustine Cushman was born in Bridgewater, Massachusetts, and died in nearby Sharon. In manner, habits and values Cushman remained rooted to his Yankee heritage throughout his life.²

Cushman entered the Bridgewater Normal School when he was 16 years of age and graduated, after a four-year course of study, in 1901. He received a scholarship to Harvard College and, in the autumn of 1901, entered the Lawrence Scientific School with junior standing. After his graduation from Harvard University in 1903 (*magna cum laude*), Cushman accepted a position as a curator at the Museum of the Boston Society of Natural History. He continued at Harvard on a part-time basis, and received his doctoral degree, just six years later, in 1909.

Initially, Cushman pursued studies in cryptogamic botany,³ but his interests, however, turned to paleontology after a course from the Harvard invertebrate paleontologist Robert Tracy Jackson. Jackson was an important influence on Cushman as he carried on the tradition of the recapitulationist school, first introduced at Harvard by Louis Agassiz, and later firmly established by Alpheus Hyatt. Both Cushman's bachelor's thesis "Developmental stages in the Lagenidae," and his doctoral dissertation "The phylogeny of the Miliolidae," as well as his later outlook on the relationships of foraminifera, closely reflect the strong influence of the recapitulationist school of thought.

Probably more than anything else, the acquaintance he established with Mary Jane Rathbun, during the two summers he spent as a "paid investigator" at the Woods Hole Biological Laboratory of the Bureau of Fisheries, set the course of his career. On an autographed copy of the first edition of his textbook, Cushman wrote, "To Dr. Mary J. Rathbun who more than any other person is responsible for starting my serious work on the foraminifera twenty five years ago with hope that the confidence then shown has not been a source of disappointment and with my very best wishes" (Schmitt, 1950, p. 29).



FIGURE 45. Photograph of the Cushman Laboratory for Foraminiferal Research in Sharon, Massachusetts, taken March 21, 1944. (Photo courtesy of the Todd Library for Foraminiferal Research, Smithsonian Institution.)

Mary Jane Rathbun was an assistant curator in charge of the marine invertebrate collections at the U.S. National Museum. Her brother, Richard Rathbun, was the assistant Secretary of the Smithsonian in charge of the U.S. National Museum. Through her encouragement and influence, Cushman was given a commission to work up the samples of Recent material collected on the expeditions of the U.S. Fisheries Commission steamer *Albatross*. The agreement was that the Museum would send the raw samples to Cushman in installments and the Smithsonian Institution would publish the results of his study.⁴ This most ambitious undertaking involved the preparation and study of a vast number of samples from the North Atlantic, North Pacific and Tropical Pacific, as well as the Philippine Sea. Moreover, at the time that Cushman made this commitment he was simultaneously working as a curator at the Boston Society of Natural History and continuing his studies for a doctoral degree. Yet, all proceeded according to a carefully calculated schedule, and in 1910, just one year after the completion of his dissertation, the first part of *U.S. National Museum Bulletin 71* appeared. At the time of Cushman's death in 1949, all of the monographs on the Recent faunas had been completed (Cushman, 1913–1915, 1917, 1918, 1920, 1922–1924a, 1929–1932, 1933b, 1942) except for the last part of *Bulletin 161* which was to have dealt with the rotalid genera from the tropical Pacific. This last volume was later completed by Ruth Todd (Todd, 1965).

Cushman further expanded the scope of his activities by accepting an appointment with the U.S. Geological Survey in 1912. The employment by the U.S. Geological Survey of a specialist on foraminifera to work as a stratigraphic paleontologist was an “event in itself” (Henbest, 1952). As Cushman's training and previous experience had been largely biological, the experience he gained with the Survey added an “invaluable stratigraphic dimension to his work” (Henbest, 1952, p. 95). Much of his work with the Survey during the first World War involved field mapping and was not related to foraminifera. However, he published a brief report on the foraminifera of a waterwell in South Carolina which was included in a U.S. Geological Survey Professional Paper by Stephenson (1915).⁵ Cushman severed all of his connections with the U.S. Geological Survey in January 1922⁶ because of his industrial commitments, and in May 1923 he resigned his position at the Boston Natural History Society to devote his energies to his consulting work and to the study of foraminifera.

In 1923, Cushman built a laboratory specially designed for the study of foraminifera, located in Sharon, Massachusetts, just 500 yards from his house (Fig. 45). Originally, the laboratory was intended to serve the needs of his commercial interests, but shortly after its completion Cushman decided to sever his connections with the oil industry and devote full time to his research. The laboratory became known as the Cushman Laboratory for Foraminiferal Research with Cushman

serving as its director. In 1925 the laboratory initiated a quarterly publication rather awkwardly entitled *Contributions from the Cushman Laboratory for Foraminiferal Research*. The journal was sent to subscribers at a cost of two dollars and fifty cents a year; a local printshop served as the press. The publication was comprised of short, descriptive articles authored by Cushman himself, or in collaboration with others. Publication of the journal was continued right up until his death in 1949, at which time the Cushman Foundation for Foraminiferal Research was established in order to publish a continuing journal. The Cushman Foundation series was initiated in 1950 under the title *Contributions from the Cushman Foundation for Foraminiferal Research* with A. R. Loeblich, Jr., serving as its original editor. The series still continues today, but in 1971 the format was enlarged and the title changed to the more manageable *Journal of Foraminiferal Research*.

After the laboratory opened, Cushman resumed his association with the U.S. Geological Survey, initially on a part-time basis and in 1930 as a full-time employee. He had a small, full-time and part-time staff, with his eldest daughter serving as secretary. In 1926 Cushman initiated a graduate course at the laboratory which was accredited through Harvard. He was appointed lecturer at the university, but received no remuneration for his services. Almost immediately, students from other parts of the country and from abroad came to study at the laboratory. Cushman gave occasional informal lectures and assigned students projects. He worked very closely with the students and often took pains to point out the particular details by which one species could be distinguished from another (Todd, 1950). Cushman was a great advocate of the "apprenticeship" method of teaching and thought that no one should be allowed to do independent work until thoroughly trained by a recognized specialist.⁷

Perspective

Cushman felt an almost equal commitment to both pure research and applied science. He made the difficult decision to devote full time to research in 1925 and, except for a brief period in 1926, he never again engaged in consulting work. However, Cushman always kept sight of the commercial importance of foraminifera and he continued, through his students, to maintain close ties with industry. Most of the students who studied at the Sharon laboratory were oriented towards the oil industry. Cushman had even entitled his textbook *Foraminifera—Their Classification and*

Economic Use. In 1932, during the depth of the Depression, he wrote in a letter to a former student about how much he had enjoyed his experience in industry and how, except for his age, he might consider going back to the consulting field. It is not difficult to understand the temptation, because 1932 became a particularly difficult year for Cushman when he temporarily lost support from the U.S. Geological Survey. However, 1932 was also the year in which he completed his second tour of Europe to study the primary types (Fig. 46). This tour reinforced his enthusiasm for research and he continued to pursue his career in that direction.

From his student days, Cushman believed that foraminifera had finite species limits, just like other organisms. He became all the more convinced of this in the course of his commercial activities where he was forced to find ways to make finer and finer splits of species for stratigraphic purposes. He was often criticized for oversplitting, but answered that it was because of the recognition of these fine distinctions that he had had more success than others with subsurface stratigraphic correlations (Cushman, 1924). Theoretically, the question of species limits was settled when Lister (1903) rejected Carpenter's views and admitted to the existence of the foraminiferal species. Nevertheless, foraminifera were still generally regarded as a "plastic" group comprised of species having broad limits and long ranges. Cushman, and other workers, had to convince industry of the value of foraminifera in stratigraphic correlation. Oil companies were reluctant to use foraminifera for subsurface correlations; while larger fossils were only rarely encountered and often destroyed in the process, entire shells of foraminifera were commonly recoverable in abundance from well samples.

By about 1920 there was considerable activity in the application of foraminifera to the search for oil. Some of the leading workers included "the ladies"—Helen Plummer, Esther Applin, Alva Ellisor and Hedwig Kniker. Yet, whenever there was a discrepancy between correlations obtained by foraminifera, and other lines of evidence, it was the foraminiferal evidence that came under attack.

In 1924 the matter came to a head when the foraminifera were placed "on trial." T. Wayland Vaughan (1923), in a most curious paper, extolled the larger foraminifera for their utility in correlation, but discounted the "relative value" of the smaller forms. Vaughan argued that the vast majority of smaller foraminiferal species were much too long-ranged for stratigraphic zonation. Vaughan concluded that from



FIGURE 46. Photograph of Joseph Cushman and his assistants (Frances Parker and Margaret Moore) at the Naturhistorisches Staatsmuseum in Vienna, July 1932. (Photo courtesy of the Todd Library for Foraminiferal Research, Smithsonian Institution.)

“available evidence similar faunas of small Foraminifera are indicative rather of similarity in ecologic conditions than of identity in age” (Vaughan, 1923, p. 529).

Max W. Ball, president of the American Association of Petroleum Geologists, called upon Cushman and Charles Schuchert for their opinions. Cushman blamed the English School, and their views on the extreme variability of foraminiferal form, for having given the impression that foraminifera, because of their low organizational level, could not be subjected to the “ordinary terms of systematic treatment.” He went on to state, “It has taken a long time to shake off even in some measure this early interpretation, which, like all false accusations, clings tenaciously” (Cushman, 1924, p. 489). Cushman pointed out that many so-called long-ranging species when examined more closely, could be subdivided into “many species with short ranges” in a manner so as to be useful for correlation. Later, Cushman went so far as to say, “If stages of development are taken into consideration, and differences due to microspheric and megalospheric forms are considered, the actual variation left is less than in most other groups of animals. When specific lines are drawn more sharply than at present, as will be done as more material is studied, the variation will be more apparent than real” (Cushman, 1925, p. 8).

Cushman countered Vaughan by pointing out that the “distinction between larger and smaller foraminifera” was an artificial and “unfortunate one, and one for which” he was “entirely to blame, having published two papers on the foraminifera of the Canal Zone some years ago [Cushman, 1918a, b] under these headings” (Cushman, 1924, p. 489). He explained that of the so-called “larger” foraminifera “the genera involved include many small species which are equally valuable for correlation purposes” (Cushman, 1924, p. 489). Finally, Cushman raised the provocative question, “If these larger species are admittedly of excellent character as regards correlation, what is the matter with the smaller ones?” (Cushman, 1924, p. 489).

Charles Schuchert (Fig. 47), acting as a kind of judge, solicited additional opinions from Cushman and others engaged in oil exploration on the value of smaller foraminifera. And, in response to the letters he received, Schuchert whole-heartedly endorsed the utility of foraminifera and pronounced that, “Foraminifera are no longer on trial as guide fossils in underground correlations” (Schuchert, 1924, p. 540).

Schuchert was one of the most eminent paleontologists of the time and his opinions were highly regarded. Following his judgment, and that of Cushman, there was an immediate change in attitudes towards foraminifera. Within a few years foraminifera became

more intensely studied than any other single group of organisms (Henbest, 1952). Indeed, interest became so keen that Cushman (1925), at the request of the Smithsonian Institution, prepared a study guide for the use of beginning workers (Table 15). The issue of the longevity of the foraminiferal species relative to species of other organisms still remains unsettled, but the pursuit of this matter would be an undue digression from the present subject.

For all his recognized authority and assuredness of purpose, Cushman tended to be reserved and cautious. It apparently took some urging on the part of Schuchert for Cushman to finally commit himself to the formal reclassification of foraminifera. In October 1926, Schuchert wrote Cushman, "I have long thought that you are afflicted with too much caution—caution is a very good quality, but too much of it places the owners into the rear guard and that is where you do not belong. Move to the front young man for that is where you should be."⁸ Cushman acknowledged that Schuchert's encouragement was just the stimulus he needed, and early in the following year he published "An Outline of a Re-Classification of the Foraminifera" (Cushman, 1927b).

Cushman's hesitancy to produce a formal classification was largely due to the fact that he felt more knowledge was needed about the "soft parts" and physiology of foraminifera (Cushman, 1927a). When he realized that this kind of knowledge probably would not be acquired for many years, he acceded, at Schuchert's urging, to publish an informal classification which he had put together for the use of his students (Cushman, 1927b). Not long before Schuchert's letter, as the result of a conversation with J. J. Galloway, Cushman had become convinced that he himself was the one best qualified to produce a "natural" classification scheme. Although Cushman was very proud of the positive reactions to his classification, he always retained an appearance of modesty, appreciating that neither his nor any other classification scheme would serve as the final authority. Cushman truly believed that he had accomplished a more natural system of arrangement than any that had been proposed before, but he avoided the pontifical air that seems to characterize the work of Galloway (1933).

While Cushman considered the minute size of foraminifera a difficulty in their study, he did not think that their microscopic nature, in itself, was the real problem. He believed major difficulties in their study had been incurred by previous workers, who had paid inadequate attention to the details, illustration and documentation of foraminiferal species. Cushman was

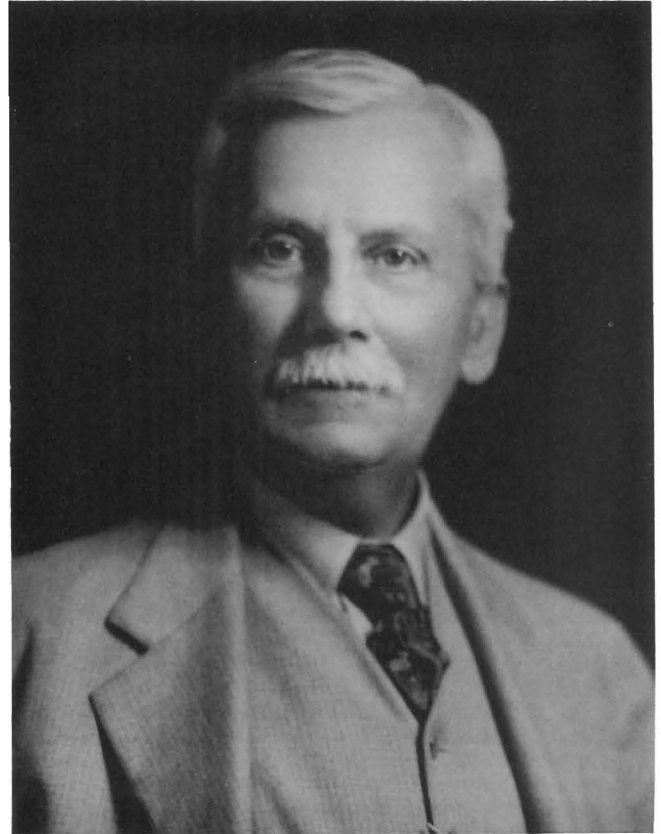


FIGURE 47. Charles Schuchert (1858–1942). (Photo courtesy of the Division of Invertebrate Paleontology, Peabody Museum of Natural History, Yale University.)

convinced that most taxonomic problems could be resolved, and a phylogenetically natural system of classification could be achieved, through the careful observation of generic and specific type specimens, and the examination of type material, rather than by comparison with unreliable plate figures and illustrations (Cushman, 1927b).

Cushman maintained the "principle of recapitulation" as a guiding principle. On many occasions he emphasized the importance of carefully studying the ontogenetic stages of the microspheric form because these provided the links between descendants and their ancestors. The microspheric form, he observed, "is retrospective, going back and repeating in its young many of the stages in its ancestry while the megalospheric form is prophetic and although skipping certain of the early stages, arrives at the stages of adult development earlier and many take on later characters not developed in the microspheric form" (Cushman, 1927b, p. 3).

Cushman believed that a natural classification must

TABLE 15. Cushman's 1925 Classification.

Family 1. GROMIDAE
Family 2. ASTORRHIZIDAE
Subfamily <i>Astrorhizinae</i> — <i>Astrorhiza</i> Sandahl; <i>Rhabdammina</i> Carpenter; <i>Marsipella</i> Norman; <i>Bathysiphon</i> G. O. Sars; <i>Rhizammia</i> H. B. Brady
Subfamily <i>Saccamininae</i> — <i>Psammospaera</i> F. E. Schulze; <i>Sorospaera</i> H. B. Brady; <i>Diffusilina</i> Heron-Allen and Earland; <i>Storospaera</i> F. E. Schultze; <i>Iridia</i> Heron-Allen and Earland; <i>Rhaphidoscene</i> Vaughan Jennings; <i>Saccamina</i> Carpenter; <i>Protonina</i> Williamson; <i>Lagenammia</i> Rhumbler; <i>Pilulina</i> W. B. Carpenter; <i>Pelosina</i> H. B. Brady; <i>Hippocrepina</i> Parker; <i>Technitella</i> Norman; <i>Webbinella</i> Rhumbler; <i>Tholosina</i> Rhumbler; <i>Ammosphaeroides</i> Cushman; <i>Verrucina</i> Goës; <i>Crithionina</i> Goës; <i>Thurammia</i> H. B. Brady
Subfamily <i>Hyperammmininae</i> — <i>Hyperammia</i> H. B. Brady; <i>Psamatodendron</i> Norman; <i>Saccorhiza</i> Eimer and Fickert; <i>Syringammia</i> H. B. Brady; <i>Jaculella</i> H. B. Brady; <i>Dendrophyra</i> Str. Wright; <i>Haliphysema</i> Bowerbank; <i>Sagenina</i> Chapman
Subfamily <i>Ammodiscinae</i> — <i>Ammolagena</i> Eimer and Fickert; <i>Tolypammia</i> Rhumbler; <i>Ammodiscus</i> Reuss; <i>Ammodiscoides</i> Cushman; <i>Glomospira</i> Rzehak; <i>Turritellina</i> Rhumbler
Family 3. LITUOLIDAE
Subfamily <i>Aschemonellinae</i> — <i>Aschemonella</i> H. B. Brady
Subfamily <i>Reophacinae</i> — <i>Reophax</i> Montfort; <i>Hormosina</i> H. B. Brady; <i>Haplostiche</i> Reuss
Subfamily <i>Trochammininae</i> — <i>Trochamminoides</i> Cushman; <i>Haplophragmoides</i> Cushman; <i>Cribrostomoides</i> Cushman; <i>Cyclammia</i> H. B. Brady; <i>Loftusia</i> Carpenter and Brady; <i>Lituotuba</i> Rhumbler; <i>Ammobaculites</i> Cushman; <i>Haplophragmium</i> Reuss; <i>Lituola</i> Lamarck; <i>Placopsilina</i> d'Orbigny; <i>Rotaliammina</i> Cushman; <i>Trochammia</i> Parker and Jones; <i>Globotextularia</i> Eimer and Fickert; <i>Ammochilostoma</i> Eimer and Fickert; <i>Ammosphaeroidina</i> Cushman; <i>Sphaerammina</i> Cushman; <i>Ammosphaerulina</i> Cushman; <i>Nouria</i> Heron-Allen and Earland
Subfamily <i>Neusinae</i> — <i>Neusina</i> Goës; <i>Botellina</i> W. B. Carpenter
Subfamily <i>Orbitolininae</i> — <i>Orbitolina</i> Lamarck; <i>Conulites</i>
Subfamily <i>Endothyriae</i> — <i>Nodosinella</i> Brady; <i>Stacheia</i> Brady; <i>Endothyra</i> Phillips; <i>Bradyina</i> Möller; <i>Involutina</i> Terquem
Family 4. TEXTULARIIDAE
Subfamily <i>Spiroplectinae</i> — <i>Spiroplecta</i> Ehrenberg
Subfamily <i>Textulariinae</i> — <i>Textularia</i> Defrance; <i>Textularioides</i> Cushman; <i>Bigenerina</i> d'Orbigny; <i>Climacammina</i> H. B. Brady; <i>Bolivina</i> d'Orbigny; <i>Pleurostomella</i> Reuss; <i>Pavonina</i> d'Orbigny; <i>Cuneolina</i> d'Orbigny; <i>Bifarina</i> Parker and Jones
Subfamily <i>Verneuilinae</i> — <i>Verneuilina</i> d'Orbigny; <i>Valvulina</i> d'Orbigny; <i>Chrysalidina</i> d'Orbigny; <i>Tritaxia</i> Reuss; <i>Gaudryina</i> d'Orbigny; <i>Tritaxilina</i> Cushman; <i>Clavulina</i> d'Orbigny; <i>Mimosina</i> Millett
Subfamily <i>Bulimininae</i> — <i>Bulimina</i> d'Orbigny; <i>Buliminella</i> Cushman; <i>Virgulina</i> d'Orbigny
Subfamily <i>Cassidulininae</i> — <i>Cassidulina</i> d'Orbigny; <i>Ehrenbergina</i> Reuss
Family 5. LAGENIDAE
Subfamily <i>Lageninae</i> — <i>Lagena</i> Walker and Boys
Subfamily <i>Nodosariinae</i> — <i>Nodosaria</i> Lamarck; <i>Lingulina</i> d'Orbigny; <i>Trifarina</i> Cushman; <i>Cristellaria</i> Lamarck; <i>Marginulina</i> d'Orbigny; <i>Vaginulina</i> d'Orbigny; <i>Fronicularia</i> Defrance
Subfamily <i>Polymorphininae</i> — <i>Polymorphina</i> d'Orbigny; <i>Dimorphina</i> d'Orbigny
Subfamily <i>Uvigerininae</i> — <i>Uvigerina</i> d'Orbigny; <i>Siphogenerina</i> Schlumberger
Subfamily <i>Ramulininae</i> — <i>Ramulina</i> Rupert-Jones; <i>Vitrewebbina</i> Chapman
Family 6. CHILOSTOMELLIDAE— <i>Chilostomella</i> Reuss; <i>Allomorphina</i> Reuss; <i>Seabrookia</i> H. B. Brady; <i>Ellipsoidina</i> Seguenza
Family 7. GLOBIGERINIDAE— <i>Globigerina</i> d'Orbigny; <i>Orbulina</i> d'Or-

TABLE 15. Continued.

bigny; <i>Hastigerina</i> Thomson; <i>Candeina</i> d'Orbigny; <i>Sphaeroidina</i> d'Orbigny; <i>Pullenia</i> Parker and Jones; <i>Hantkenina</i> Cushman
Family 8. ROTALIIDAE
Subfamily <i>Spirillininae</i> — <i>Spirillina</i> Ehrenberg
Subfamily <i>Rotalinae</i> — <i>Patellina</i> Williamson; <i>Discorbis</i> Lamarck; <i>Cymbalopora</i> Hagenow; <i>Tretomphalus</i> Moebius; <i>Planorbulina</i> d'Orbigny; <i>Truncatulina</i> d'Orbigny; <i>Siphonina</i> Reuss; <i>Anomalina</i> d'Orbigny; <i>Carpenteria</i> Gray; <i>Rupertia</i> Wallich; <i>Pulvinulina</i> Parker and Jones; <i>Endothyra</i> Phillips; <i>Rotaliatina</i> Cushman; <i>Rotalia</i> Lamarck; <i>Calcarina</i> d'Orbigny; <i>Siderolites</i> Lamarck; <i>Baculogypsina</i> Sacco; <i>Gypsina</i> Carter; <i>Polytrema</i> Risso; <i>Homotrema</i> Hickson; <i>Sporadotrema</i> Hickson
Family 9. NUMMULITIDAE
Subfamily <i>Fusulininae</i> — <i>Schwagerina</i> Möller; <i>Fusulina</i> Fischer
Subfamily <i>Polystomellinae</i> — <i>Nonionina</i> d'Orbigny; <i>Polystomella</i> Lamarck; <i>Archaediscus</i> H. B. Brady; <i>Amphistegina</i> d'Orbigny; <i>Operculina</i> d'Orbigny; <i>Herostegina</i> d'Orbigny; <i>Nummulites</i> Lamarck; <i>Operculinella</i> Yabe
Subfamily <i>Cyclocypeinae</i> — <i>Orbitoides</i> d'Orbigny; <i>Orthophragmina</i> Munier-Chalmas; <i>Lepidocyclus</i> Gümbel; <i>Miogypsina</i> Sacco; <i>Cyclocypeus</i> Carpenter
Family 10. MILIOLIDAE
Subfamily <i>Cornuspirinae</i> — <i>Cornuspira</i> Schultze; <i>Spiroloculina</i> d'Orbigny; <i>Planispirina</i> Seguenza; <i>Vertebralina</i> d'Orbigny; <i>Nodobacularia</i> Defrance; <i>Nubecularia</i> Defrance
Subfamily <i>Quinqueloculinae</i> — <i>Quinqueloculina</i> d'Orbigny; <i>Massilina</i> Schlumberger; <i>Articulina</i> d'Orbigny; <i>Sigmoilina</i> Schlumberger; <i>Hauerina</i> d'Orbigny; <i>Triloculina</i> d'Orbigny; <i>Adelosina</i> d'Orbigny; <i>Biloculina</i> d'Orbigny; <i>Fabularia</i> Defrance; <i>Nevillina</i> Sidebottom; <i>Idalina</i> Schlumberger and Munier-Chalmas; <i>Peneroplis</i> Montfort; <i>Orbiculina</i> Lamarck; <i>Orbitolites</i> Lamarck; <i>Craterites</i> Heron-Allen and Earland; <i>Alveolina</i> d'Orbigny; <i>Kerammosphaera</i> H. B. Brady

be compatible with the geologic record; however, he was rather cautious when addressing this problem and implied that imperfections in the record were to be expected (Cushman, 1927a–d). Clearly, he did not subscribe to Schubert's acceptance of known stratigraphic ranges at face value. Whenever a discrepancy arose between the stratigraphic range of a genus and his own idea of its development, Cushman disregarded the former. In some cases, there was very good agreement between the two; such was the case with the ancestral stock of the Buliminidae, the genus *Terebralina*, which is structurally primitive and relatively old.⁹ All too often, however, Cushman derived his families from ancestral forms considerably younger than the descendants themselves (Cushman, 1927b, c, 1948).

Cushman proceeded on the assumption that if his ideas on development could be corroborated with evidence from the stratigraphic record, they should hold true generally.¹⁰ In one important case he was vindicated. Cushman, like Neumayr, regarded the arenaceous forms as being more primitive than the calcareous perforate forms. In general, the fossil record supported this view, but there were several reports of

calcareous perforate forms from the lower Paleozoic. For the most part these reports were regarded as dubious, but the discovery of abundant *Spirillina* in the Cambrian of the Malvern Hills (Chapman, 1900) could not be ignored. Cushman disregarded the inconsistencies posed by this report, and was later criticized for doing so (Henbest, 1952). Much later, Alan Wood (1947) found that the *Spirillina* assemblage from the Malvern Hills was of Jurassic, not Cambrian, age. Henbest, always skeptical of the earlier report, said: "From our discussion of that problem I was never quite sure whether Cushman's ignoring of that difficulty was based on hunch or whether fate played favorites with him" (Henbest, 1952, p. 99).

Cushman recognized the importance of, and very early on advocated the adherence to, the rules of zoological nomenclature, although he interpreted the Law of Priority¹¹ loosely, and did not apply it above the generic level. He reinstated older, rarely used names only when he thought it necessary.

The Classification

One obstacle which Cushman encountered, and which caused him delay in proposing a formal classification, was the lack of a publisher for his work. Cushman originally had planned to publish his classification as a series of articles in the *American Journal of Science*. However, a disjointed classification scheme seemed undesirable, and Charles Schuchert as editor of the journal, discouraged the idea. Therefore, Cushman finally decided to publish an outline short enough to fit into his *Contributions* series. It appeared as "An Outline of a Re-Classification of the Foraminifera" and occupied an entire issue of the *Contributions from the Cushman Laboratory of Foraminiferal Research* (Volume 3, Part 1, March 1927). The outline consisted of concise descriptions of families and genera, accompanied by the known stratigraphic ranges of the genera. The introductory section was a bare four pages, and was accompanied by a phylogenetic chart of the genera.

As a result of the very favorable response to the "Outline," Cushman enlarged the scope of its text, and in the following year published a hard-cover, expanded version. This work was published by his own laboratory and appeared as the first in a series of special publications under the title *Foraminifera—Their Classification and Economic Use* (Cushman, 1928).¹² The publication of this work, and several other special publications, was made possible through the financial support of Susan Minns, a cousin of Cushman's.

Cushman rightly regarded his classification (Table

16) as a rather radical departure from anything that had been done in the past. Not only did it mark the first comprehensive, three-dimensional, phylogenetic attempt at foraminiferal classification, but it comprised a much more elaborate treatment of the group than had ever been seen; Carpenter surely would have been astonished. Cushman (1928) recognized 404 genera which he grouped into forty-five families. His generic definitions are tight and nowhere does he express doubts about the stability of genera or species. The recognition of species and genera might sometimes be complicated by factors such as trimorphism, but Cushman felt that these difficulties could be resolved through the proper understanding of the principles of development.¹³

Cushman's phylogenetic approach to foraminiferal classification with its strong emphasis on developmental stages, and also his exacting treatment of genera and species have, of course, had a great effect on the whole modern approach to foraminiferal taxonomy. Yet, it is his little-noticed treatment of wall texture that has turned out to be probably the most important influence of all. While Cushman did not propose any superfamilial categories, he did make a clear, distinct separation between arenaceous, calcareous imperforate and calcareous perforate genera. Brady, it will be recalled, had disallowed the overriding importance of wall texture, or any other single character, in his classification. Cushman's methodology, therefore, constituted a reversion to an older approach to classification. While his method introduced an evolutionary interpretation into foraminiferal classification, it remains largely essentialistic in concept, and not much changed from nineteenth century methods.

Cushman emphasized that the "material of which the test is composed" was "an essential character and must take first rank in classification" (Cushman, 1927a, p. 55). In addition, he pointed out that the "material of the test" is a character which has been "held for very long periods through the fossil sequence" (Cushman, 1927b, p. 3). Cushman's insistence upon using "the material of the test" as the essential character upon which to base the classification of foraminifera, recalls Carpenter's philosophy on the systematic value of test porosity.¹⁴ While it may seemingly provide an evolutionary justification, the persistence of the nature of the foraminiferal test "for very long periods through the fossil sequence" is hardly a persuasive argument for its choice as an "essential character." The fact that wall composition has remained a stable character through geologic time, does not mean that the various wall types observed have not had totally independent,

TABLE 16. Cushman's 1928 Classification.

Family 1. ALLOGROMIIDAE
Family 2. ASTORRHIZIDAE
Family 3. RHIZAMINIDAE
Family 4. SACCAMMINIDAE
Subfamily Psammosphaerinae
Subfamily Saccammininae
Subfamily Pelosininae
Subfamily Webbinellinae
Family 5. HYPERAMMINIDAE
Subfamily Hyperammininae
Subfamily Dendrophryinae
Family 6. REOPHACIDAE
Subfamily Aschemonellinae
Subfamily Reophacinae
Family 7. AMMODISCIDAE
Subfamily Ammodiscinae
Subfamily Tolyammininae
Family 8. LITUOLIDAE
Subfamily Haplophragmiinae
Subfamily Lituolinae
Family 9. TEXTULARIIDAE
Subfamily Spiroplectammininae
Subfamily Textulariinae
Family 10. VERNEULINIDAE
Family 11. VALVULINIDAE
Family 12. FUSULINIDAE
Subfamily Fusulininae
Subfamily Verbeekinae
Family 13. LOFTUSIIDAE
Family 14. NEUSINIDAE
Family 15. SILICINIDAE
Family 16. MILIOLIDAE
Family 17. OPTHALMIDIIDAE
Subfamily Cornuspirinae
Subfamily Nodobaculariinae
Subfamily Opthalmidiinae
Subfamily Nubeculariinae
Family 18. FISCHERINIDAE
Family 19. TROCHAMMINIDAE
Subfamily Trochammininae
Family 20. PLACOPSILINIDAE
Subfamily Placopsilinae
Subfamily Polyphragminae
Family 21. ORBITOLINIDAE
Family 22. LAGENIDAE
Subfamily Nodosariinae
Subfamily Lageninae
Family 23. POLYMORPHINIDAE
Subfamily Polymorphinae
Subfamily Ramulininae
Family 24. NONIONIDAE
Family 25. CAMERINIDAE
Subfamily Archaediscinae
Subfamily Cameriinae
Family 26. PENEROPLIDAE
Subfamily Spirolininae
Subfamily Archaiasinae
Subfamily Orbitolitinae
Family 27. ALVEOLINELLIDAE
Family 28. KERAMOSPHAERIDAE
Family 29. HETEROHELICIDAE
Subfamily Heterohelicinae
Subfamily Pavonininae
Subfamily Gumbelininae
Subfamily Bolivinitinae
Subfamily Spiroplectinatinae
Subfamily Plectofrondicularinae

TABLE 16. Continued.

Family 30. HANTKENINIDAE
Family 31. BULIMINIDAE
Subfamily Terebralininae
Subfamily Turritininae
Subfamily Bulimininae
Subfamily Virgulininae
Subfamily Reussiinae
Subfamily Uvigerininae
Family 32. ELLIPSOIDINIDAE
Family 33. ROTALIIDAE
Subfamily Spirillininae
Subfamily Turrispirillininae
Subfamily Discorbisinae
Subfamily Rotaliinae
Subfamily Siphonininae
Subfamily Bagginae
Family 34. AMPHISTEGINIDAE
Family 35. CALCARINIDAE
Family 36. CYMBALOPORETTIDAE
Family 37. CASSIDULINIDAE
Subfamily Ceretobulimininae
Subfamily Cassidulininae
Subfamily Ehrenbergininae
Family 38. CHILOSTOMELLIDAE
Subfamily Allomorphininae
Subfamily Chilostomellinae
Subfamily Seabrookiinae
Subfamily Allomorphinellinae
Subfamily Sphaeroidininae
Family 39. GLOBIGERINIDAE
Subfamily Globigerininae
Subfamily Orbulininae
Subfamily Pulleniatininae
Family 40. GLOBOROTALIIDAE
Family 41. ANOMALINIDAE
Subfamily Anomalininae
Subfamily Cibicidinae
Family 42. PLANORBULINIDAE
Family 43. RUPERTIIDAE
Family 44. HOMOTREMIDAE
Family 45. ORBITOIDIDAE

self-contained histories. Wall types may have had multiple origins. This explanation was a possibility with which Schubert was prepared to deal, if the stratigraphic record had so indicated. Cushman had no evidence to support the independent developments of the different wall types, other than the apparent earlier origin of the arenaceous forms than the calcareous forms. But even here the issue was in doubt because at the time he wrote, the question of the reported calcareous perforate forms from the Cambrian of the Malvern Hills (Chapman, 1900), had not yet been resolved.

Schuchert, initially, had not been convinced of the systematic value of wall composition, and in November 1926, he wrote, "The grouping noted in your letter sounds old-fashioned and therefore, orthodox, and maybe that is the way it should be. I have long felt, however, that the nature of the test may not be the

best criterion of classification, and especially the arenaceous condition. It is true that I have no evidence of parallel developments but the use of sand for test making is so simple a condition that I often think this condition has little classificatory value.”¹⁵ Schuchert was not a foraminiferal specialist and so it is understandable that he overlooked the heart of the “arenaceous problem.” However, it will be recalled that Jones (1876) had erected a separate suborder for the arenaceous forms, but did not regard this suborder as a natural group because it included both perforate and imperforate forms. Cushman, on the contrary, did regard the arenaceous forms as comprising a natural group.

In answer to Schuchert’s letter, Cushman wrote, “As to the arenaceous group. It has developed such individual chemical products in the cement that it seems unlikely that similar physiological characters could be again and again taken on in parallel lines while form alone could easily be as so in many superficially similar forms with unrelated ancestry. . . . I am more and more strongly convinced that the arenaceous group is a stable one.”¹⁶

Neither here, nor anywhere else, does Cushman ever mention the porosity of arenaceous forms. Banner and Pereira (1981) believe it implicit in his classification that Cushman regarded the arenaceous families as imperforate. It also is very likely that Cushman never gave the matter much thought; he may have followed the lead of Brady who had concluded that the problem of porosity in the arenaceous forms was an irresolvable one and, therefore, attached no importance to it. By ignoring porosity, the “arenaceous problem” which had haunted the nineteenth century was laid to rest, and the door reopened for a fundamentalistic approach to classification. Wall texture again became the cardinal condition in the classification of foraminifera, the arenaceous group standing equivalent in rank to the chitinous, calcareous imperforate and calcareous perforate groups.

Schuchert apparently was satisfied with Cushman’s argument and he gave him his “complete blessings.” When the 1927 classification appeared, it was received with enthusiasm, and Cushman’s treatment of wall texture was never questioned; it still remains unchallenged. What was the reason for this apparently sudden and irrevocable turn about from Brady? It was hardly the result of any new advancement in knowledge; the stratigraphic record remained no less ambiguous than before. In addition, Cushman fully realized the deficiencies in knowledge concerning the life processes by which the various wall types are formed. Therefore,

when he finally committed himself to a formal classification, he must have proceeded largely on intuition. He found the scientific community in a receptive mood. More than anything else, this reversion to a pre-Bradyan outlook seems to illustrate the binding power of essentialistic thinking. Essentialism may be an archaic theory of classification, as Mayr (1969) has so often emphasized, but it does not die easily.

Cushman started with the chitinous family Allogromiidae as the simplest of all forms within the Order Foraminifera, although there is virtually no geologic record of this group, as their lack of hard parts disallows preservation. Cushman found the transition from a “chitinous” to an arenaceous form an easy step since all that seemed to be involved in the process was the incorporation of particles into the outer surface of the wall. The more strongly cemented walls formed a more permanent test capable of preservation. The step to the calcareous wall was a much more difficult one, and it is not clear how the arenaceous wall served as a connecting link between the chitinous and calcareous walls. Originally, Cushman (1927a, b, 1928) proposed the development of the arenaceous and calcareous groups from “entirely different sources”—he depicted both groups as having been independently derived directly from two separate “chitinous” ancestors (Fig. 48). He later adopted a monophyletic scheme (Fig. 49), in which he derived all of the calcareous forms from a single arenaceous ancestor. While this view of the development of wall structure, from a simple “chitinous” form to an advanced calcareous form through an intermediate arenaceous form, has been the view that has prevailed, Cushman’s earlier interpretation of the independent origin of wall structure seems to be just as credible, if not more so.

The simplest and most primitive forms preserved in the fossil record, are the undifferentiated arenaceous forms. Cushman (Fig. 48) depicted three simple arenaceous families as having arisen from a common allogromiid ancestor: the stellate *Astrorhizidae*; the tubular, open-ended *Rhizamminidae*; and the single-chambered *Saccamminidae*. The next stage of development, characterized by forms having an initial proloculus followed by a long, tubular chamber, was represented by two families: the *Hyperamminidae* and the *Ammodiscidae*. In the *Hyperamminidae* the second tubular chamber is straight, while in the *Ammodiscidae* it is coiled. Cushman derived both of these families from the single-chambered *Saccamminidae*. The next stage of development involved the subdivision of the long tubular chamber into several chambers, following which innovation “the various families

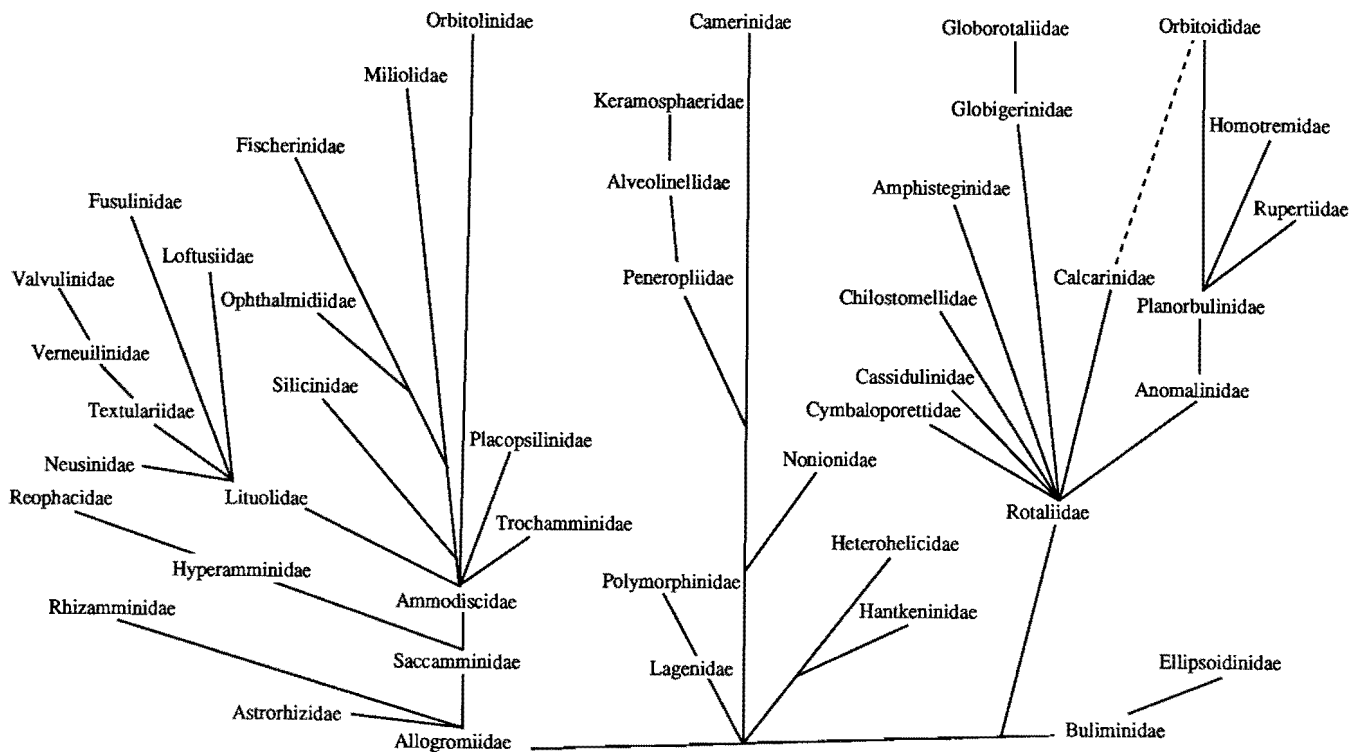


FIGURE 48. Cushman's 1928 phylogeny of the families of Foraminifera.

gradually make their appearance in the fossil series" (Cushman, 1928, p. 48).

The Hyperamminidae gives rise to the rectilinear Reophacidae in Cushman's diagram, but it was the Ammodiscidae that played the major role in Cushman's phylogenetic scheme. From the Ammodiscidae Cushman directly derived, the planispiral Lituolidae, the trochospiral Trochamminidae, the complex Orbitolinidae, and the attached Placopsiliniidae. Cushman also derived the Miliolidae directly from the Ammodiscidae with the genus *Agathammina* as the connecting link (Fig. 50). The genus *Agathammina* is characterized by an undivided tubular test wound about an elongate axis; the test wall is believed to be calcareous imperforate with an arenaceous coating. The Fischerinidae and the Ophthalmitidae are derived from the Miliolidae; both families are characterized by some degree of planispiral coiling, at least in the early stages. Cushman, however, was somewhat inconsistent in his treatment of these two families (Fig. 51). In his 1928 phylogenetic chart of families he shows the Fischerinidae as having arisen from the Miliolidae, and the Ophthalmitidae as having arisen from the Fischerinidae. This was obviously an error because there is no planispiral stage among the Miliolidae to suggest such a connection. While the monotypic family Fis-

cherinidae is trochospiral in its adult form, it appears to have nothing in common with the Ophthalmitidae, except its calcareous imperforate wall. Elsewhere, Cushman (Fig. 52) showed the planispiral, tubular genus *Cornuspira* as the root stock of the Ophthalmitidae, suggesting a direct ancestry of this family from the Ammodiscidae through *Ammodiscus*. On this same plate, *Fischerina* is shown as an offshoot of *Cornuspira*. In later revisions of the textbook, Cushman portrayed the Fischerinidae as having arisen directly from the Ammodiscidae (Fig. 51).

Within the family Trochamminidae, Cushman included arenaceous genera that were either trochoid or irregularly coiled. He considered *Trochammina* to be the most primitive genus in the family, and derived it from the "trochoid spiral forms" of the Ammodiscidae. Cushman included in the family Placopsiliniidae a variable group of attached forms of uncertain relationship.¹⁷ *Placopsilina*, the oldest member of the family, dates back to the Silurian. In the Orbitolinidae he included structurally complex forms having spirally arranged early chambers, annularly added later chambers, and the interior of the chambers subdivided into chamberlets. Cushman (1927b) had originally placed ten genera in this family, but he later (1948) reduced the number to three. He erected the family Siliciniidae

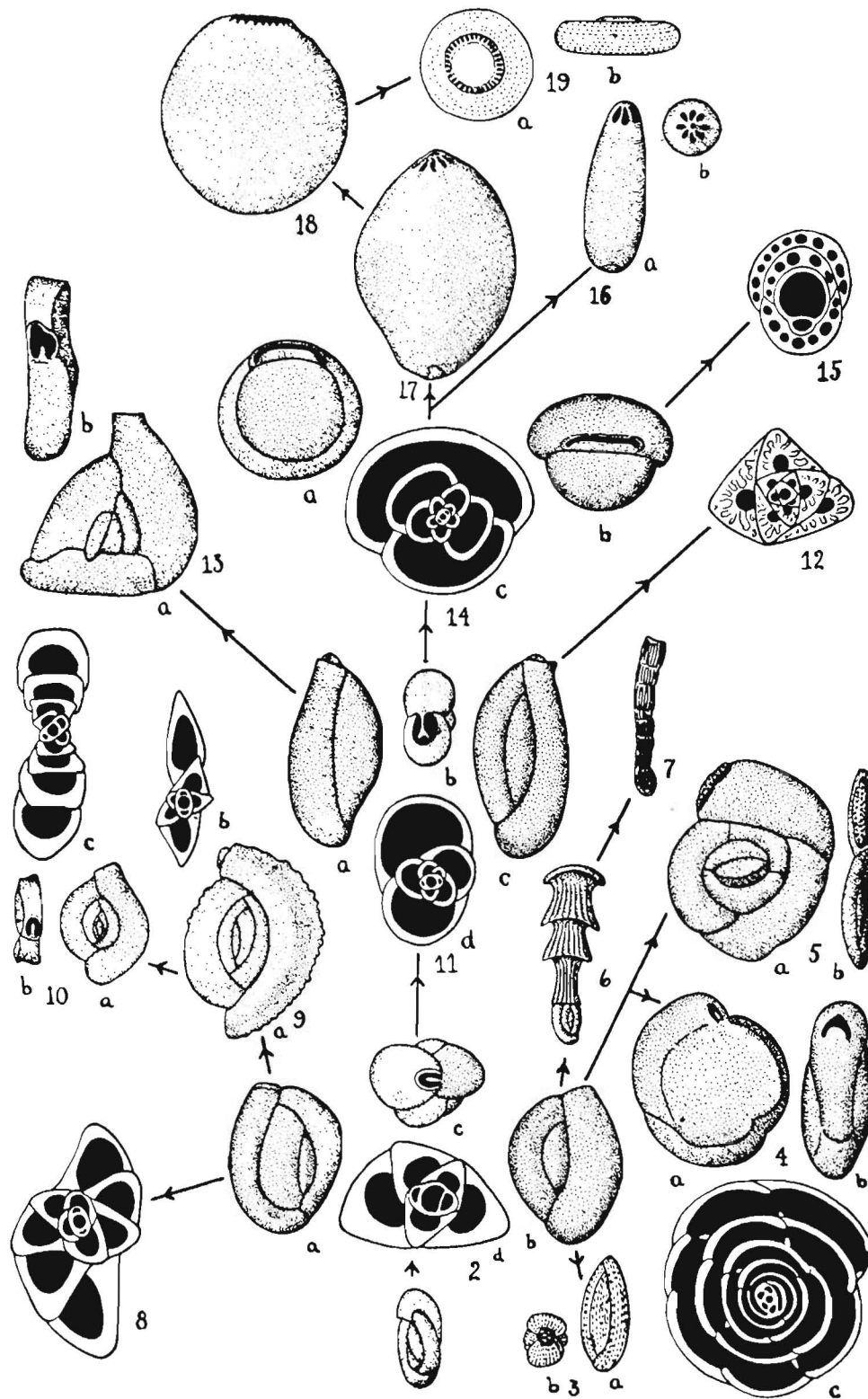


FIGURE 50. Cushman's (1928, 1933, 1940, 1948) scheme of the relationships of the genera of the Miliolidae. 1, *Agathammina pusilla* (Geinitz). 2, *Quinqueloculina vulgaris* d'Orbigny; *a*, *b*, side views; *c*, apertural view; *d*, cross section. 3, *Miliola saxorum*; *a*, side view; *b*, apertural view. 4, *Nummuloculina contraria* (d'Orbigny). 5, *Hauerina bradyi* Cushman. 6, *Articulina sagra* d'Orbigny. 7, *Tubinella funalis* (H. B. Brady). 8, *Sigmoilina herzensteini* Schlumberger. 9, *Massilina secans* (d'Orbigny). 10, *Spiroloculina depressa* d'Orbigny; *a*, side view; *b*,

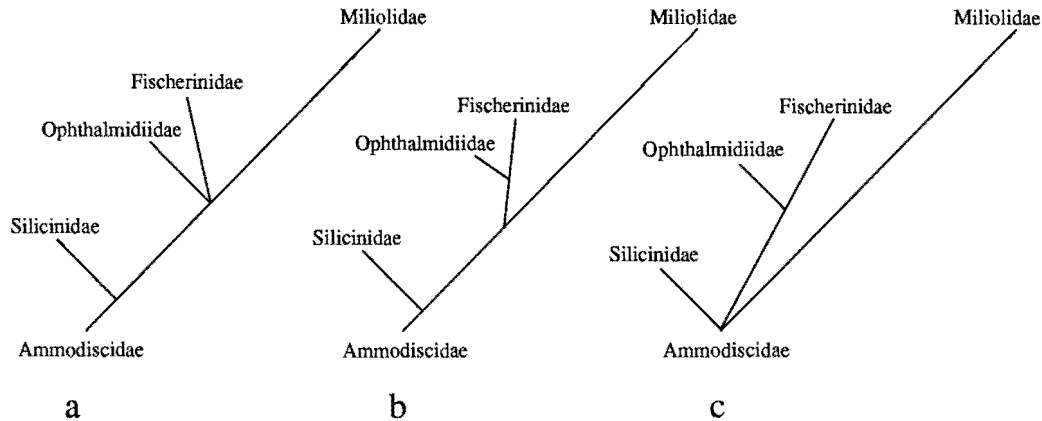


FIGURE 51. Comparison of Cushman's different treatments of the relationships of the families Miliolidae, Fischerinidae and Ophthalmitidae. **a**, From Cushman's 1927b phylogenetic chart. **b**, From Cushman's 1928 phylogeny. **c**, From Cushman's 1933 phylogeny.

Cushman's rationale for having derived the Verneulinidae from the Textulariidae seems puzzling. He described the Verneulinidae as follows: "Test, at least in the early stages, triserial, later biserial in some genera and in most specialized ones becoming uniserial . . ." (Cushman, 1928, p. 121). One would, therefore, expect the Verneulinidae to be ancestral to, rather than descendant from, the Textulariidae. Cushman may have been guided here by two considerations: first, the Verneulinidae are an appreciably younger family than the Textulariidae (Jurassic vs. Carboniferous), and secondly, certain triserial and biserial species seem to be virtually identical except for the difference in chamber arrangement (Fig. 53). Since Cushman was otherwise seldom bothered by anomalies in the fossil record, it seems more likely that he was guided by the second consideration.¹⁹ Nevertheless, he seems to have violated his principle of recapitulation in this instance. On the other hand he derived the Valvulinidae, which included the bulimine arenaceous forms, from the Verneulinidae because they have an early triserial stage.

The arrival of the age of specialization in the field of foraminiferal research was evidenced by the fact that Cushman (1928) had his colleague Yoshiaki Ozawa write the section on the Fusulinidae.²⁰ This large, important group, however, was treated rather summarily. No discussion is given of their complex, specialized morphology, and only eight genera and four subgenera

are included in the family. Cushman recognized that the genus *Endothyra* was ancestral to the Fusulinidae,²¹ nevertheless he retained that genus in the Lituolidae.

As for the calcareous forms, Cushman (1927b, 1928) originally recognized one common, allogromid ancestry for the Lagenidae, the Camerinidae (=Nummulitidae) and Heterohellicidae, a separate one for the Rotaliidae, and another ancestry for the Buliminidae (Fig. 48). He observed that the Lagenidae (=Nodosariidae) was a highly variable group, describing them as "protean."²² He removed *Uvigerina* from the Lagenidae and placed it in the Buliminidae. Generic limits could not always be distinguished as well in the Lagenidae as in other groups, and trimorphism was sometimes problematic.²³ Cushman pointed out, for example, that a microspheric form of *Nodosaria* with a small proloculus might show the generic characters of *Dentalina*, and one with an even smaller proloculus, the generic characters of *Marginulina*. Contrary to his earlier view (Cushman, 1905), he here regarded the unilocular genus *Lagena* as a specialized end form, rather than the most primitive stage of development.

Cushman derived the Polymorphinidae directly from the Lagenidae with the "earliest identifiable genera" appearing in the Jurassic. He later hypothesized that the simplest polymorphinid form, *Eoguttulina*, which is irregularly coiled about the elongate axis, was "undoubtedly derived from some coiled form of the La-

←

apertural view; **c**, cross section. 11, *Triloculina laevigata* d'Orbigny; **a**, **c**, side views; **b**, apertural view; **d**, cross section. 12, *Trillina howchina* Schlumberger. 13, *Flintina triquetra* Cushman; **a**, side view; **b**, apertural view. 14, *Pyrgo bradyi* (Schlumberger); **a**, front view; **b**, apertural view; **c**, cross section. 15, *Fabularia discolithes* DeFrance. 16, *Nevillina coronata* (Millett); **a**, side view; **b**, apertural view. 17, *Idalina antiqua* (d'Orbigny). 18, *Periloculina zitteli* Munier-Chalmas and Schlumberger. 19, *Lacazina compressa* (d'Orbigny); **a**, apertural view; **b**, side view. (Reprinted from *Foraminifera—Their Classification and Economic Use* by Joseph A. Cushman by permission of the Harvard University Press.)

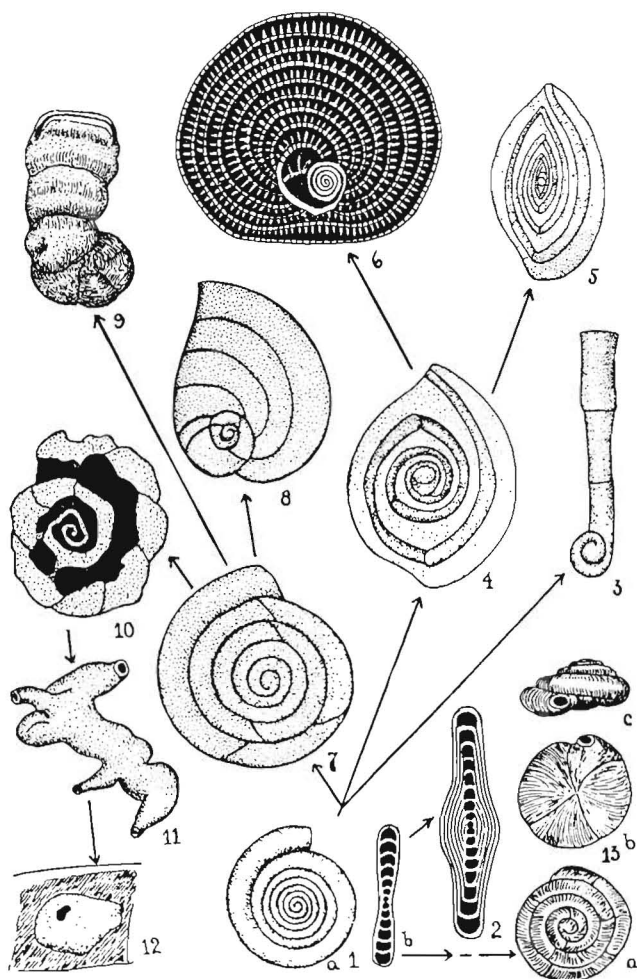


FIGURE 52. Cushman's (1928) scheme of the relationships of the genera of his families Ophthalmitidae and Fischerinidae. 1, *Cornuspira involvens* Reuss; *a*, side view; *b*, cross section. 2, *Vidalina hispanica* Schlumberger. 3, *Nodobaculularia tibia* (Parker and Jones). 4, *Ophthalmitium inconstans* H. B. Brady. 5, *Spirophthalmitium acutimargo* (H. B. Brady). 6, *Discospirina tenuissima* (Carpenter). 7, *Planispirina exigua* H. B. Brady. 8, *Renulina operculina* Lamarck. 9, *Vertebralina striata* d'Orbigny. 10, *Nubecularia lucifuga* Defrance. 11, *Calcituba polymorpha* Roboz. 12, *Squamulina laevis* Schultze. 13, *Fischerina helix* Heron-Allen and Earland; *a*, dorsal view; *b*, ventral view; *c*, side view.

genidae, such as *Marginulina* or *Vaginulina* by introducing a spiral arrangement of chambers" (Cushman, 1933, p. 184). Cushman grouped the planispiral, calcareous forms closely together; the Camerinidae served as the ancestral stock and the Nonionidae and the Peneroplidae appeared as descendant branches. The complex, "larger" Camerinidae were treated in the same manner as the Fusulinidae—rather briefly. In the Nonionidae, Cushman included genera with "septal bridges" across the sutures, such as *Elphidium* and

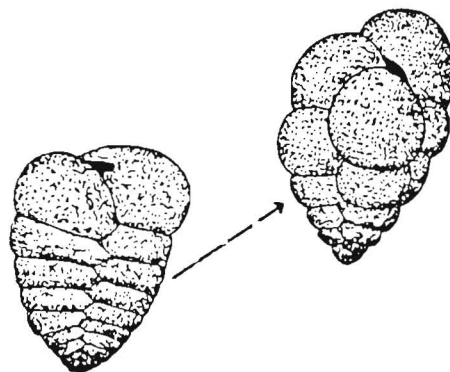


FIGURE 53. Comparison of Cushman's (1927c) figures of the genera *Textularia* (left) and *Verneuilina* (right). Cushman believed that the family Textularidae had given rise to the family Verneulinidae, in apparent contradiction to his general belief that evolutionary progress in Foraminifera involved a reduction in the number of chambers per whorl.

Polystomellina. Later, Cushman (1933, 1940, 1948) changed his mind on the origin of the Nonionidae and derived them from a planispirally coiled ancestor, as he had done with the Lagenidae.

Cushman felt the origin and relationships of the Peneroplidae to be obscure, but connected them with the Camerinidae on the basis of their early planispiral stages, and their similarity in size, development, and habitat preference. Also, he placed great emphasis on the evolutionary significance of the perforate proloculus of the genus *Peneroplis*. He believed the perforate nature of the proloculus and second chamber to indicate a perforate ancestry for the group, and, therefore, concluded that there was no close relationship between the Peneroplidae and the Miliolidae.²⁴ Cushman regarded the elongate, fusiform family Alveolinellidae as directly descendant from the Peneroplidae, and ancestral to the Keramosphaeridae.²⁵ The Heteroheliciidae included a wide variety of forms, both planktonic and benthic, that Cushman nevertheless believed composed a homogeneous group. Cushman conceived of the group as having a primitive planispiral stage, followed by a biserial stage, but believed that both of these stages could be highly reduced or lacking. In those genera in which the early stages were "wanting," relationships could be recognized only by other characters or intermediate forms. Since Cushman's time, the Heteroheliciidae has been almost entirely dismantled and its constituent genera redistributed into other families. Cushman (1928) did not elaborate on the origin or affinities of the family Hantkeninidae, other than to state that the family was related to the Heteroheliciidae. In later editions of his text (1933, 1940,

1948), however, he derived the Hantkeninidae directly from the Globigerinidae.

Cushman described the Buliminidae as a "closely-linked group" in which the development of the family could be traced through the growth stages of the various genera. He observed the ancestral spiral form to be maintained, at least in the early stages of growth, and the loop-shaped aperture retained in most genera. Cushman derived the family Ellipsoidinidae directly from the Buliminidae through the genus *Virgulina*. This family was characterized by a very finely perforate wall and an internal apertural tube "connecting the various chambers." In the early stages of development, the chambers are biserial in arrangement but in later stages of most genera, they adopt a uniserial mode of growth. Cushman thought that the well-developed apertural tube and biserially arranged chambers that characterized the genus *Virgulina* provided a good connecting link to the Buliminidae.

Although he described the genera of the Rotaliidae as "generally trochoid" and septate, Cushman also included tubular planispiral and trochoid genera, such as *Spirillina* and *Turrispirillina*, within this family because he regarded these forms as the ancestral stock of the family. Like Brady, Cushman thought that genera with incompletely formed septa, such as *Patellina*, provided a connecting link between the rotalids and tubular forms. He also included both simple- and double-walled genera in the Rotaliidae. Cushman believed that the genera he placed together in the Rotaliidae formed a "natural grouping closely related to one another," and that the intermediate forms connecting genera were "often well filled by the simpler and more complex species" (Cushman, 1928, p. 280). However, because he did not take into account the numerous stratigraphic anomalies in his inferred ancestor-descendant relationships, the phylogenetic series he proposed for the Rotaliidae, as well as the series shown for his other families, are really no more than morphoserries.

Between the first edition of his textbook, published in 1928, and the fourth and final edition, published in 1948, Cushman added many new genera and a few new families, but very few revisions of the text. Cushman, however, did revise his ideas on the origins of several groups. In the second and subsequent editions, all the calcareous, perforate families were derived directly from the arenaceous Ammodiscidae rather than from the "chitinous" Allogromiidae. In defense of this arenaceous origin for all of the calcareous groups, he stated, "It is known from numerous, well-demonstrated cases that the arenaceous forms develop into calcareous ones. This is seen in the different stages of the

same individual in several species and probably will be found in many others, especially the more primitive genera or species of present calcareous forms" (1933, p. 58; 1940, p. 60; 1948, p. 60). It is not very clear, however, just to which examples Cushman was referring.²⁶

In selecting the Ammodiscidae as the root stock of almost all of his families of foraminifera, Cushman relied heavily on the concept of a coiled and spiral "fundamental form" (Douvillé, 1906).²⁷ A coiled, planispiral ancestor is the hallmark of Cushman phylogenies (Fig. 52); the uniserial condition is usually shown as the end form in evolutionary trends (Fig. 50).

THE CUSHMAN-GALLOWAY AFFAIR

Cushman's main opponent and adversary was Jesse J. Galloway (Fig. 54). Galloway firmly believed that he, himself, had originated the ideas for a modernized classification of foraminifera, and that he had been unfairly denied priority in publication. In the preface to his *Manual of Foraminifera*, Galloway (1933) made this astonishing statement,

"This work was begun in the Fall of 1923 and was presented in an outline before the Paleontological Society of America on December 30, 1925 (abstract in Bull. Geol. Soc. Amer., vol. 37, March, 1926, p. 235). I spent May 8th and May 9th, 1926, at the home and laboratory of Dr. J. A. Cushman, at Sharon, Mass., going over my manuscript and plans for its completion in detail. Dr. Cushman had published in July, 1925, 'An Introduction to the Morphology and Classification of Foraminifera,' embodying the classification and nomenclature used by Brady in 1884. In March, 1927, Dr. Cushman published 'An Outline of a Re-Classification of Foraminifera' which embraced many of the ideas and changes I had advocated in my presentation and manuscript.

"In February, 1928, my completed manuscript was submitted for publication, but was returned with the announcement that Dr. Cushman had a book in press covering the same subject in much the same manner. The publication of his book, 'Foraminifera, Their Classification and Economic Use', in April, 1928, made it advisable to delay the publication of my own Manual" (Galloway, 1933, p. vii).

Letters contained in Cushman's correspondence confirm the accuracy of Galloway's account of the circumstances associated with his and Cushman's classification. Whether Cushman was actually guilty of any piracy of ideas is a question that never has been settled



FIGURE 54. Photograph of Jesse James Galloway (1882–1962). (Photo courtesy of the Department of Geology, Indiana University.)

and perhaps never will be. When there is an exchange of ideas between persons, as had occurred between Cushman and Galloway, it can become a difficult matter to determine what originated from whom. It seems clear that there was a mutual scientific benefit from their association, but an unfortunate lack of cooperation. A manuscript of an early version of Galloway's *Manual*, submitted by Galloway to David White of the U.S. Geological Survey, shows clearly that the essential ideas for a modernized classification of foraminifera originated with Galloway. None of these ideas, however, were of such a nature that one could expect to have a right of patent.

Neither Cushman nor Galloway acted in a manner to their credit. Galloway, throughout his life, remained indignant with Cushman and continually complained of the injustice that had been dealt him. Some of his students perpetuated his bitterness, a feeling which even

today may not be entirely extinct. Galloway, however, aroused very little sympathy within the profession as a whole, partly, no doubt, because of his open, uninhibited manner, which his colleagues often mistook for contentiousness and arrogance. Although at heart a very generous and sincere person, Galloway was almost totally lacking in finesse. Cushman, on his part, was less than straightforward in his dealings with Galloway, and he lacked the good grace to give Galloway even so much as an acknowledgment in his own work.

In 1923, Galloway, then a professor at Columbia University, began a course in micropaleontology. Galloway, like Cushman, was actively engaged as a consultant for the oil industry. At that time, the only available textbook on foraminifera was a book by Chapman (1902), which proved to be inadequate for use by either students or commercial micropaleontologists. Galloway, therefore, prepared a manual which he distributed in 1924–1925, not only among his students, but among the paleontological laboratories of the oil companies as well. The manual contained an outline of a modernized reclassification of the foraminifera which Galloway presented in 1925 at the annual meeting of the Paleontological Society, held in New Haven (Galloway, 1926). By this time, therefore, Galloway's ideas of a new classification had become fairly common knowledge. If he had published at least an outline of his classification at this time, he would have saved himself considerable grief.

Galloway (1933) claimed that his treatment of the families and genera of foraminifera differed from earlier classifications as follows,

“mainly, (1) in the application of the rules of biologic nomenclature to families and subfamilies as well as to genera and species; (2) in the application of the natural laws of evolution [such as recapitulation, pangenesis, acceleration or tachygenesis, retardation or bradygenesis, atavism or reversion, orthogenesis, and convergence and isomorphism] to determine the classification rather than general structural resemblance; (3) in the greater precision and completeness of definitions, synonymy and references; (4) the recognition of the importance of the geologic record in interpreting phylogeny; and (5) particularly in the interpretation of the phylogeny resulting in a considerably different classification from that in any published work” (Galloway, 1933, p. 2).

Galloway, however, had not introduced any new concepts in his classification. Cushman, and other earlier workers, had also designated type species and had

applied the Rules of Nomenclature to generic names. Both Cushman and Schubert had used developmental stages to interpret phyletic relationships. Galloway, however, had the originality and daring to apply these principles and methods, for the first time, to a general classification of foraminifera. Moreover, Galloway could take credit for the reintroduction of wall structure as an invariant familial character; this fact, as much as anything else, set the course of modern classification.

The classification that Cushman had presented in his 1925 paper (Table 15) was essentially identical to Brady's 1884 scheme of classification.²⁸

Early in 1926, Cushman was shown a manuscript copy of Galloway's *Manual* by David White of the U.S. Geological Survey; Cushman's comments and criticisms were transmitted to Galloway and made use of by him in later revisions. Cushman invited Galloway to visit him in Sharon for a weekend in May 1926, during which they reviewed his manuscript and discussed it in detail.²⁹

Galloway claimed that he had had no prior knowledge of Cushman's intention to publish a classification until the *Outline* appeared in March 1927. Yet, Cushman had mentioned, in a letter to Galloway dated December 1926, that he was working on a classification.³⁰

When the *Outline* appeared in print, Galloway responded (9 March 1927) with mild indignation.³¹ The real trouble began when Cushman informed Galloway, in a letter dated April 26, 1927, that he planned an expanded revision of the *Outline*.³² Galloway perceived a definite encroachment upon his own work³³ and, in a letter dated April 29, 1927, he expressed his concern about the question of priority, "It seems to me, therefore, and to many others with whom I have discussed the matter, that I have priority as regards a complete study and reclassification of the Foraminifera. We are also convinced that you got the idea from me; the similarity of your treatment to mine is obvious. Now, therefore, we are also convinced that you should abide by the rules of courtesy extended from one scientific man to another when one learns that the other is working on a definite problem, and should refrain from publishing a similar thing until after the work of the first one is published. . . ." In the same letter, Galloway told Cushman that the *Manual* was practically completed and closed by asking, "In view of the above facts, and in order to maintain the cordial relations which have existed between us, I ask you to give me your assurance that you will not publish your revision until mine has been published."³⁴

Cushman replied to Galloway's accusations, in a letter dated May 2, 1927,

"As to the classification, we are evidently working along such different lines and viewpoints, as far as derivations are concerned, that there may be room for both. My complete work will mean as complete a study of types as possible, and will be an elaboration of the present outline. As you say that your work is practically ready for press, it will probably be published before my complete work is ready, as it may be a year or more before that can be completed to my satisfaction. If your paper appears first, as seems likely, from your letter, I shall gladly accept such of it as meets with the results of my own work. My final conclusions in many groups will be reached only after consultation with a number of others of the older workers on the forams, and I expect that some of the chapters will be written by them. You may be sure that I shall consider any conclusions you may reach in your work, if they meet the tests of my experience and study."³⁵

It is interesting to note that, in his reply, Cushman never denied Galloway's right of priority, but neither did he give Galloway assurance, whatsoever, about holding back his own work. Cushman was noncommittal but firm, and his tone expressed the newly gained confidence of a superior authority. It will be recalled that just two months earlier Cushman had expressed the hope that Galloway could incorporate parts of his own classification into the *Manual*. Nevertheless, relations seemingly remained unstrained until early the following year. As late as January 16, 1928, Galloway had showed no ill will towards Cushman, when, in a letter to M. A. Hanna, Secretary-Treasurer of the Society of Economic Paleontologists and Mineralogists, he strongly supported the re-election of Cushman to the editorship of the *Journal of Paleontology*. However, events soon changed rapidly.

On February 23, 1928, Galloway sent Cushman a sharp letter, in which he enclosed a copy of an article he had prepared for *Science* entitled, "A Question of Priority." Galloway explained to Cushman that he felt "it necessary to make this a public statement" because Cushman's unfairness had caused him "great inconvenience and damage." Galloway also informed Cushman that he would no longer support his re-election to the editorship of the *Journal of Paleontology*.

In the enclosed article, Galloway elucidated how Cushman had suddenly adopted his own principles of classification without giving him any acknowledgment, and that, "A comparison of Dr. Cushman's classifi-

cation, definitions and nomenclature of his 1925 and 1927 papers . . . will show how suddenly and completely he abandoned the classification and method he had used for over twenty years, and how fully he adopted the ideas which I had developed and presented publicly and to him personally.”³⁶

The article was never published. In March 1928, Galloway sent Cushman a letter explaining the difficulties that had led him to attempt such a drastic public proclamation,

“As you know, I have been working for five years on a revision of Foraminifera. That fact is well known here to the University authorities, and my promotion is awaiting publication of my book. The University and I have put into the book directly for figures and assistance over \$2000.00. John Wiley and Sons, who intended to publish my *Manual*, have learned about your proposed book on the same subject and are delaying the publishing of mine until they learn more about the character of your book and its possible influence on the sale of mine.

“This interference by you, intentional or unintentional, is working on me a grave injustice, and explains by present attitude toward you. Since neither you or anybody else ever showed any indication prior to 1927 of making the much needed revision of the Foraminifera, and since I did announce publicly in 1925 that I was at work on such a thing, and since you told me in May, 1926, that you were engaged in no such thing, I believe I should not be denied the credit that is due me, and particularly the material advantages which promotion here at the University brings.”³⁷

Galloway closed the letter by once more asking Cushman to delay publication of his book.

Cushman made reply in a long, ostensibly sympathetic letter. Again, Cushman did not deny that Galloway had the right of priority, but he did point out the circumstances of the previous year when Galloway had said that the *Manual* was practically ready for publication and Cushman had informed Galloway that his own work would not be completed until the following year. In any case, Cushman could not, or at least would not, delay his book because it was already being set in type.³⁸

In this same letter, Cushman responded to Galloway’s “various contentions” by showing that the methods and principles Galloway had employed were by no means original. He went on to express surprise and sympathy that a promotion was being denied Galloway and then offered some dubious advice; he suggested

that Galloway expand his *Manual* into a larger work that could serve as a general textbook on micropaleontology.³⁹ There was the overwhelming implication in Cushman’s advice, however, that Galloway should abandon his classification. Cushman wrote, “You will of course have the free use of my work on the forams and I am sure the workers on the other groups will give equally of their works. Wouldn’t it be a far more constructive thing all around to do something really big like this than to bother about our having two distinct classifications of the forams. Please think this possibility over and I believe if you will take it up with Columbia and several publishers you will find a solution of the problem which will add greatly to your prestige in many ways.”⁴⁰

Galloway interpreted this advice as a move by Cushman to have the classification of the *Manual* suppressed. Therefore, he took his grievance to Henry Howe, President of the Society of Economic Paleontologists and Mineralogists. In a letter to Howe, Galloway reviewed the history of the affair and then wrote: “Dr. Cushman has hurried through his elaboration of his ‘Outline,’ has it now in type, and wants me to suppress my work, and has interferred [sic], intentionally or otherwise, with the publishers with whom I had arranged to publish my *Manual* so that they will not now publish my book until they see what Dr. Cushman’s is like and what its effect in the field will be.” In this letter, Galloway not only suggested that Cushman had deliberately tried to beat him to publication, but he also virtually accused Cushman of leaking information on his own forthcoming work to John Wiley and Sons, Galloway’s publisher.⁴¹

In many ways it does appear that Cushman was pressed for time. The first edition of Cushman’s textbook (1928) contained a large number of typographical errors, suggesting that he had done a hasty job of proof-reading. The real mystery, however, was how Galloway’s publisher had learned about Cushman’s book, as well as the similarities between Cushman’s text and Galloway’s *Manual*.

Howe replied to Galloway,⁴² and came to Cushman’s defense, even before hearing Cushman’s side of the case. Howe asserted that, unless Galloway could produce “documentary evidence” that Cushman had either definitely accorded him precedence in publication or had deliberately interfered with the publishers to prevent the *Manual* from going to press, no good purpose would be served by the continued expression of the grievance.⁴³

Cushman answered Galloway’s charges in a letter to Howe in which he cited parts of the March 8, 1928

letter sent to Galloway. Cushman stated that neither had he knowledge of Galloway's publisher, prior to Galloway's letter of March 2, nor had he been concerned about it. He stated that he would, in fact, welcome the publication of Galloway's work "as it alone would prove the absurdity of many of the statements made about the similar basis of the two."⁴⁴ Indeed, there is nothing contained in Cushman's correspondence files to indicate that Cushman had had any knowledge of Galloway's publisher prior to his being informed by Galloway.

The Galloway affair was now closed as far as Cushman and the Society of Economic Paleontologists and Mineralogists were concerned; Cushman continued as editor of the *Journal of Paleontology*. Galloway left Columbia University a few years later to accept a position at the University of Indiana and abandoned research in foraminifera. Galloway's *A Manual of Foraminifera* was finally published in 1933, but it did not nearly achieve the following of Cushman's book. Actually, even if Galloway had been granted the priority to which he thought he was entitled, it is doubtful that his *Manual* could have seriously competed with Cushman's text.

Practically all of the leading members of the profession thought that Cushman, as the foremost authority on foraminifera, was entitled to a textbook, and it was his lead that they were bound to follow. Important too, was the fact that Cushman as a conservative was an embodiment of conventional thinking. Although Cushman was at first apprehensive that his classification might be considered radical, it actually contained nothing to disturb the common sense of the time. Galloway, on the other hand, was unorthodox and most workers found his interpretations difficult to accept, even though in many cases, he upheld his ideas with convincing arguments.

THE GALLOWAY CLASSIFICATION

Galloway (1933) recognized 542 genera in his classification of foraminifera, as compared to Cushman's 404, but only 35 families, compared to Cushman's 45. Galloway's classification (Table 17) had the same structural basis as Cushman's and followed the same phylogenetic principles. He considered wall structure the primary criterion for grouping genera into families and he interpreted phylogenetic relationships using the law of recapitulation. Like Cushman, Galloway avoided the use of superfamilial groupings. There were, however, marked differences between the two authors in their arrangement of genera and their conception of

families. These differences reflect not only their opposing interpretations of structures and of the fossil record, but also their distinct philosophical points of view. Indeed, the classifications almost defy side by side comparison. In Galloway's classification there was the strong implication that the three generally recognized types of wall structure were a relatively modern development and of multiple origin. And, Galloway's classification suffered from the fact that he had relied solely on the original figures for the definition of the type species of his genera, illustrations which in a number of cases are obscure and dubious.

The principle difference between the two classifications lay in their respective interpretations of the wall structure of Paleozoic forms. In his classification, Cushman used the conventional three-fold, arenaceous/calcareous imperforate/calcareous perforate divisions of wall structure, which he thought adequate to accommodate all foraminifera except for the "chitinous" forms. Following the examples set by Brady, Neumayr, and previous workers, Cushman maintained that the Paleozoic foraminifera were "predominantly or exclusively arenaceous" (Cushman, 1928, p. 44).⁴⁵ Galloway opposed this interpretation and maintained that, "The walls of nearly all Paleozoic Foraminifera, instead of being constructed of agglutinated foreign particles, as has been held for many years, are calcareous and were secreted by the animal" (Galloway and Harlton, 1928, p. 338).⁴⁶

Galloway totally rejected the idea that the arenaceous wall structure was a primitive character, and believed that, "Arenaceous forms were derived from calcareous forms, instead of the reverse" (Galloway and Harlton, 1928, p. 338). He believed the arenaceous wall to be a specialized or degenerate end form of multiple origin (Fig. 55). Galloway envisioned the arenaceous wall as having developed by an increase in concentration of agglutinated particles in a gelatinous, "chitinous," or calcareous matrix. One of Galloway's principal arguments against the arenaceous wall as being the primitive condition, involved emphasizing that although there were examples of "many calcareous forms" in which foreign or arenaceous particles had been incorporated into the wall during later stages of ontogeny, there were no known foraminifera which exhibited an "arenaceous nepionic or neanic stage followed by a calcareous ephebic stage" (Galloway, 1933, p. 18). Therefore, in accordance with the law of recapitulation, the arenaceous wall could not represent the primitive condition.

The fossil record also seemed to contest the primitive nature of the arenaceous wall. At the time that

TABLE 17. Galloway's 1933 Classification.

Family 1. LAGYNIDAE
Subfamily Lagyninae
Subfamily Amphitreminae
Subfamily Myothecinae
Subfamily Allogromiinae
Subfamily Rhynchogromiinae
Family 2. ASTORRHIZIDAE
Subfamily Saccammininae
Subfamily Proteonininae
Subfamily Astrorrhizinae
Subfamily Hyperammininae
Family 3. SPIRILLINIDAE
Subfamily Spirillininae
Subfamily Problematininae
Subfamily Patellininae
Family 4. AMMODISCIDAE
Family 5. MILIOLIDAE
Subfamily Cornuspirinae
Subfamily Nubeculariinae
Subfamily Miliolinae
Subfamily Hauerininae
Family 6. SORITIDAE
Subfamily Peneroplinae
Subfamily Orbitolitinae
Family 7. ALVEOLINELLIDAE
Subfamily Alveolinellinae
Subfamily Keramosphaerinae
Family 8. ENDOTHYRIDAE
Subfamily Endothyrinae
Subfamily Tetrataxininae
Family 9. NODOSINELLIDAE
Family 10. REOPHACIDAE
Family 11. TROCHAMMINIDAE
Subfamily Trochammininae
Subfamily Placopsilininae
Family 12. LITUOLIDAE
Subfamily Lituolinae
Subfamily Neusininae
Family 13. ORBITOLINIDAE
Family 14. ATAXOPHRAGMIIDAE
Subfamily Ataxophragmiinae
Subfamily Verneulininae
Family 15. TEXTULARIIDAE
Subfamily Palaeotextulariinae
Subfamily Textulariinae
Family 16. NODOSARIIDAE
Subfamily Frondiculariinae
Subfamily Nodosariinae
Subfamily Robulinae
Family 17. POLYMORPHINIDAE
Subfamily Polymorphininae
Subfamily Ramulininae
Family 18. NONIONIDAE
Subfamily Nonioninae
Subfamily Elphidiinae
Family 19. ROTALIIDAE
Subfamily Rotaliinae
Subfamily Discorbinae
Subfamily Cibicidinae
Subfamily Planorbulininae
Family 20. ACERVULINIDAE
Subfamily Rupertiinae
Subfamily Acervulininae
Family 21. TINOPORIDAE
Family 22. ASTERIGERINIDAE
Family 23. CHAPMANIIDAE

TABLE 17. Continued.

Family 24. CHILOSTOMELLIDAE
Family 25. ORBULINIDAE
Family 26. PEGIDIIDAE
Family 27. HETEROHELICIDAE
Subfamily Heterohelicinae
Subfamily Gumbelininae
Subfamily Bovinitinae
Family 28. BULIMINIDAE
Subfamily Turritininae
Subfamily Bulimininae
Family 29. CASSIDULINIDAE
Family 30. UVIGERINIDAE
Subfamily Uvigerininae
Subfamily Angulogerininae
Family 31. PLEUROSOMELLIDAE
Family 32. FUSULINIDAE
Subfamily Fusulininae
Subfamily Schwagerininae
Subfamily Verbeekinae
Family 33. CAMERINIDAE
Subfamily Camerininae
Subfamily Heterostegininae
Family 34. ORBITOIDIDAE
Subfamily Orbitoidinae
Subfamily Miogypsiniinae
Subfamily Omphalocyclusinae
Family 35. CYCLOCYPEIDAE
Subfamily Cyclocypeinae
Subfamily Discocyclininae

Galloway wrote, the oldest recorded occurrences of arenaceous forms were from the Silurian, while the range of calcareous, non-arenaceous forms supposedly extended back to the Precambrian. However, these early records of calcareous forms have since been discredited.⁴⁷

Nevertheless, Galloway, by calling attention to the fact that many Paleozoic forms had a wall structure that did not conform to the three generally recognized types, made an important contribution. He also showed that the generally accepted model of the evolutionary development of a calcareous-walled form from an arenaceous-walled ancestor could not be taken for granted, and, actually, that the reverse type of transformation was at least as plausible.

Galloway also opposed the conventional views concerning the development of form. Galloway maintained that symmetrical forms were more primitive than irregular forms. Irregular forms he regarded as "specialized or degenerate," on the grounds that "the most primitive forms of life have the smallest surface area in proportion to volume," while the higher types of life have a larger surface area-to-volume ratio (Galloway, 1933, p. 17). Importantly, Galloway also challenged the belief that multilocular forms had developed by the gradual septation of a primitive tubular form

of test, with the chambers later assuming a globular or irregular shape—Galloway believed the globular form to be the most primitive form of test. His principal argument was that the proloculus, of all forms which have a proloculus, was always globular in shape, but never tubular. Additional chambers, either globular or tubular in form, were added as discrete entities. In addition, he made the observation that none of the members of the Rotaliidae, Buliminidae or Camerinidae, have a tubular-shaped nucleconch.⁴⁸

In Galloway's phylogeny of foraminiferal families (Fig. 56), two foraminiferal stocks are shown, both of which are derived from a mastigophoran ancestor. One stock, the "chitinous," single-chambered, Lagynidae, is shown as ancestral to both the simpler arenaceous families and the calcareous imperforate, porcellaneous families. The other stock, the fibrous of granular calcareous Endothyridae, is shown as the root of all other foraminiferal families. Galloway's contention that the arenaceous forms were of multiple origin and had never given rise to calcareous forms, is well illustrated in this phylogeny.

The Lagynidae directly gave rise to the Astrorhizidae by the incorporation of agglutinated particles into the "chitinous" wall, and to the Spirillinidae by the secretion of a calcareous wall. For Galloway, the Astrorhizidae comprised a much broader family than it had for Cushman. In it he included tubular forms with a proloculus, as well as the typical branching forms. Evolution within the family was seen to occur through apertural loss and, either through an elongation of the single chamber, or through the addition of a tube to the original, prolocular chamber. Galloway considered the Astrorhizidae to be a specialized or degenerate end group that was ancestral to no known families or genera of either calcareous or higher arenaceous forms. One of the main reasons that Galloway considered this family to be a derived group involved their restricted occurrence to mostly cold, deep waters, a habitat he viewed as "a special habitat, not a primitive one" (Galloway, 1933, p. 58).

The arenaceous Ammodiscidae and the porcellaneous Miliolidae are shown as having descended from the Spirillinidae, a family characterized by a single, coiled, tubular chamber, sometimes weakly septate, with a secreted calcareous or siliceous wall. Galloway was ambiguous about the wall structure of the Spirillinidae; the wall might be perforate or imperforate, hyaline or granular but never "typically" porcellaneous. He also included within this family the supposedly siliceous forms *Silicina* and *Involutina*; their siliceous wall, he hypothesized to have resulted from

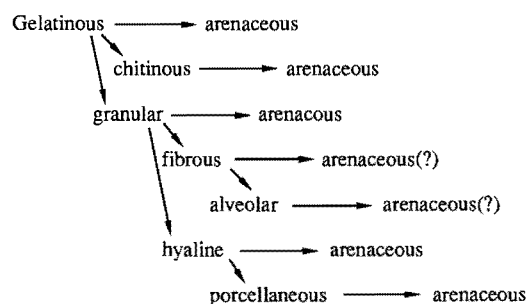


FIGURE 55. Galloway's (1933) diagram illustrating the evolution of wall structure was accompanied by the following passage, "The primitive wall material was gelatinous, from which developed the chitinous and calcareous, cryptocrystalline or granular wall; from the granular, the hyaline and fibrous walls developed; hyaline walls developed into porcellaneous walls, and fibrous walls developed into alveolar structure. All of these were secreted by the animal. Arenaceous walls developed from gelatinous, chitinous, granular, hyaline, porcellaneous, and fibrous ones. In no case did arenaceous walls develop into any other kind" (Galloway, 1933, p. 19).

the silicification of originally calcareous walls, secreted by the organism.

Galloway denied not only that the genus *Spirillina* was the most primitive member of the Rotaliidae, as had been proposed by Brady,⁴⁹ but also that the genus *Patellina* represented the connecting link between *Spirillina* and the Rotaliidae. Galloway had found the walls of these genera, and other Spirillinidae, not perforate in the same way as the Rotaliidae.⁵⁰ On the other hand, he saw a close connection between the Spirillinidae and the Ammodiscidae because of the almost indistinguishable wall structures observed in Paleozoic forms of both families. *Ammodiscus* is very finely arenaceous with abundant cement and therefore has a granular appearance like *Spirillina*.

Galloway also derived the Miliolidae from a *Spirillina* ancestor because he found the wall structure of Paleozoic species of *Cornuspira*, the simplest genus of this family, difficult to distinguish from *Spirillina* as Paleozoic forms of *Cornuspira* do not always have a distinctive porcellaneous texture. The porcellaneous families Soritidae and Alveolinellidae were both derived from the Miliolidae; evolutionary development within these families involved the loss of primitive ontogenetic stages through acceleration and changes in mode of growth.⁵¹

The Endothyridae encompassed the planispiral and trochoid Precambrian and Paleozoic forms, characterized by a "calcareous and granular or fibrous" wall (Galloway, 1933, p. 153).⁵² Galloway perceived evolutionary development within the family as having proceeded "in two directions," from a primitive form

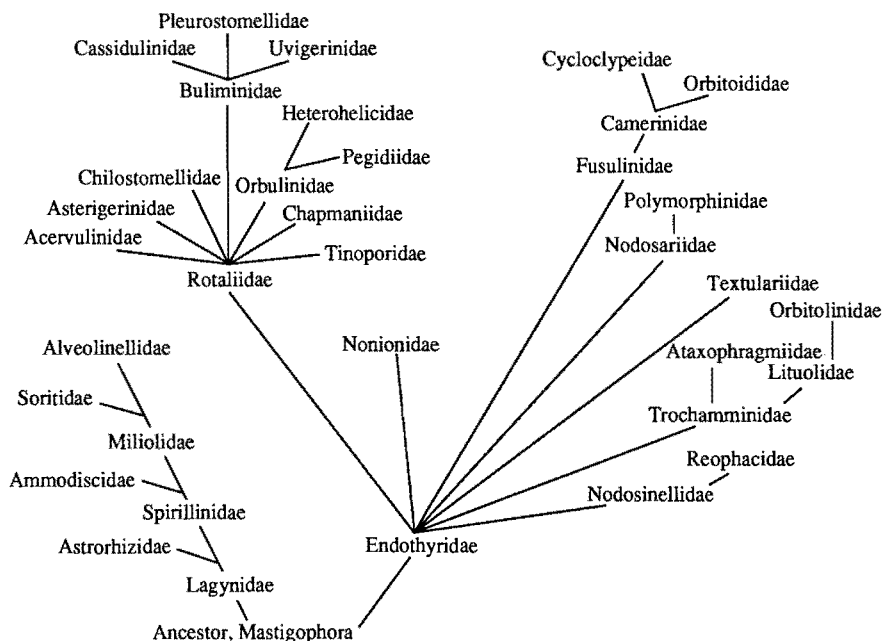


FIGURE 56. Galloway's (1933) phylogeny of the families of Foraminifera.

with globular, irregularly arranged chambers, to both a planispirally coiled form (Endothyridae) and a conical, trochoid form (Tetraxinae). The family was conceived broadly enough for Galloway to have derived from it all of the principal late Paleozoic and post-Paleozoic stocks. The principal evolutionary development involved a change in, and in most cases, a modernization of, wall structure. From the Endothyridae he derived: the uniserial or single-chambered Nodosinellidae, which retained the endothyrid type of wall; the arenaceous, biserial Textulariidae and trochoid Trochamminidae; the complex-walled Fusulinidae; and the hyaline Nodosariidae, Nonionidae and Rotaliidae.⁵³ Galloway also placed the dubious Precambrian and Cambrian genera *Cayeuxina* (Precambrian), *Matthewina* (Cambrian) and *Terquemina* (Devonian) in the Endothyridae, believing that they represented the early stages of development of the family. Cushman, and others, had previously interpreted the endothyrid wall structure as arenaceous and Galloway pointed out their error. Galloway's own error was to accept these genera as "real foraminifers" (Galloway, 1933, p. 154).⁵⁴

The Nodosinellidae is a late Paleozoic family, and in its original description Rhumbler included both calcareous and arenaceous forms. Cushman never recognized the family and placed its genera either in calcareous or arenaceous families. Galloway considered

the group to constitute a "natural family which appears well-characterized in the Paleozoic" (Galloway, 1933, p. 163), and restricted the group to include uniserial or single-chambered forms displaying a rectilinear or curvilinear serial chamber arrangement and the "distinct" Paleozoic type of wall structure.⁵⁵

Galloway placed the arenaceous forms in the family Reophacidae which he derived from the Nodosinellidae by the addition of sand grains to the calcareous wall. The Trochamminidae included both trochoid and planispiral arenaceous forms which Galloway derived directly from the genus "*Endothyra*, or a similar, calcareous form" (Galloway, 1933, p. 180). He derived the families Ataxophragmiidae and Lituolidae, which subsequently gave rise to the Orbitolinidae, from the family Trochamminidae. In the Lituolidae, he included both trochoid and planispiral arenaceous forms, and in contrast to Cushman, he defined the family as having a labyrinthic interior.⁵⁶ Galloway, like Cushman, restricted the family Textulariidae to include only the arenaceous biserial forms.⁵⁷

The Fusulinidae demonstrated obvious affinities with the Endothyridae.⁵⁸ Galloway derived the post-Paleozoic Camerinidae (=Nummulitidae), directly from the Fusulinidae, thus inferring an origin of this hyaline family and its successors (the families Cycloclypeidae and Orbitoididae), distinct from the other hyaline families.⁵⁹

Galloway grouped thirteen of the hyaline families closely together, with the Rotaliidae appearing as the most primitive group. Surprisingly, he derived the Rotaliidae from the planispiral genus *Endothyra*, rather than from a trochoid form such as *Tetrataxis*. Galloway regarded *Globorotalia* as the most primitive genus of the Rotaliidae and reported its earliest occurrence to be the Triassic. The structure and architectural design of *Globorotalia*, however, seemed to have eluded Galloway, as he confused this genus with *Eponides*, *Discorbis* and other genera. Forms misidentified as *Globorotalia* are very apparent in the paper by Galloway and Wissler (1927) on the Pleistocene foraminifera from the Lomita Quarry, Palos Verdes Hills, California. Although Galloway considered all of the rotaliform, hyaline genera to be structurally very similar, he recognized several families based on inferred trends in specialization and development. However, he saw no connection between the Rotaliidae and the Camerinidae and disregarded the double septum of *Rotalia* which Carpenter and Brady thought might demonstrate a connection between these two families (see Fig. 22).

Galloway believed that small pores represented a primitive condition because the pores of early rotalids appeared small.⁶⁰ Only one family, the Acervulinidae, had developed distinctly large pores and Galloway regarded this family as degenerate.⁶¹ On the other hand, the family Orbulinidae (=Globigerinidae) seemed to represent a primitive group because of their simple inflated chambers and "unspecialized" apertures, and Galloway thought that it might be possible that they were ancestral to the Rotaliidae, with the line of descent proceeding from *Endothyra* to *Globigerina* to *Globorotalia* to *Rotalia*.⁶²

Galloway derived the Heterohelicoidea which contained such diverse genera as *Heterohelix*, *Bolivina*, and *Plectofrondicularia*, from the Orbulinidae on the basis of the planispirally coiled nucleocoenoch of the genus *Heterohelix*, which he thought closely resembled "most *Globigerina* or simple forms of *Globotruncana* of the Jurassic and Cretaceous" (Galloway, 1933, p. 342).⁶³

In the Buliminidae, Galloway included high-spined forms with an aperture at the base of the septal face. He also included those forms in which the number of chambers per whorl had been reduced to two, such as *Virgulina*. However, he excluded the genus *Bolivina* from the Buliminidae, because he believed *Bolivina* to be so purely biserial, that a high-spined origin for this genus was unlikely.⁶⁴ He derived the Buliminidae from the high-spined rotalid ancestor, the genus *Rotaliatina*,

and denied any "close connection between the family Buliminidae and the families usually associated with them, the Heterohelicoidea, the Textulariidae, the Verneulinidae and the Cassidulinidae" (Galloway, 1933, p. 357). Galloway recognized the Uvigerinidae as a separate family which Cushman never did—Cushman considered the group to be a subfamily of the Buliminidae. Although he did not deny the close affinities of this group with the Buliminidae, Galloway thought that the terminal aperture of the uvigerinids characterized enough genera to warrant the erection of a new family.⁶⁵

Dick Cifelli died on May 21, 1984, before he could complete his manuscript on the history of the classification of foraminifera.

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**A HISTORY OF THE CLASSIFICATION OF
FORAMINIFERA (1826-1933)**

**PART II
NOTES ON CIFELLI'S "FORAMINIFERAL CLASSIFICATION
FROM D'ORBIGNY TO GALLOWAY"**

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NOTES ON CIFELLI'S "FORAMINIFERAL CLASSIFICATION FROM D'ORBIGNY TO GALLOWAY"

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I. EARLY VIEWS OF FORAMINIFERA

(Numbered notes refer to superscripts in Part I)

¹ Sherborn's remarkable *Index to the genera and species of the Foraminifera* included all species and genera of foraminifera published up to December 1889. Originally published by the Smithsonian Institution in two parts (1893, 1896), the Index was later reissued as a single volume (1955).

² According to the bibliographical references of Williamson (1858). By the year 1800, the number of publications had increased to 41.

³ Many of these early works are briefly mentioned in the historical summaries of Williamson (1858), Carpenter (Carpenter and others, 1862), and Brady (1884).

⁴ Janus Plancus was the pseudonym of Simon Giovanni Bianchi.

⁵ Fichtel and Moll (1798, 1803) described and illustrated twelve varieties of *Nautilus calcar* (α through μ). In Rögl and Hansen's 1984 revision of *Testacea microscopica*, these twelve varieties of *N. calcar* were referred to seven different species of *Lenticulina*.

⁶ Brown (1827) referred ten species to the genus *Nautilus* in his *Illustrations of the Conchology of Great Britain and Ireland*.

⁷ The genus *Ammonia* was introduced by Brönnich (1772) in his *Zoologiae Fundamenta* and the genus *Lagena* was introduced by Walker and Boys (1784) in their work *A collection of the minute and rare shells, lately discovered in the sand of the sea shore near Sandwich*.

⁸ According to a tabulation made from the Sherborn Index (1893, 1896, 1955).

⁹ Carpenter's lively and colorful comments on the genera figured and described by Lamarck and de Montfort illustrate well the difficulties involved with many of the taxa established by the early workers, "Although [Lamarck's] genera were created under a total misapprehension of the true nature of the group, and were by no means satisfactorily defined, yet many of them

(such as *Nodosaria*, *Cristellaria*, *Rotalia*, *Nummulites*, *Polystomella*, *Orbitolites*, and *Orbiculina*) were truly natural, and have been retained in all subsequent classifications. . . . A very different appreciation of the value of the characters was shown by Denys de Montfort, who introduced into his systematic and illustrated treatise on Conchology . . . descriptions and figures of several of the minute shells now ranked as Foraminifera. . . . His delineations of them, however, are of the rudest and most inaccurate character, and his descriptions are no less erroneous, whilst his systematic arrangement displays the worst form of the worst school of naturalists,—varieties being erected, not only into species, but even into genera, upon the slenderest possible basis of difference, and without the least regard to the constancy of the characters assumed for their definition" (Carpenter, 1862, p. 4).

II. THE BEGINNING OF CLASSIFICATION

¹ D'Orbigny maintained that the *Prodrome de Paléontologie* (1850–1852) contained the evidence upon which the generalizations he proposed in the *Cours Élémentaire de Paléontologie* (1852) were based. Together these two works "set forth the scientific doctrine of d'Orbigny, and he says himself, in the Introduction to the 'Prodrome,' that it is his 'profession of faith'" (Heron-Allen, 1917, p. 61).

² "No doubt some of d'Orbigny's critics regarded him as a lunatic, doubtless he was a lover, and most certainly he was a poet," Heron-Allen maintained, "and one is tempted to quote Theseus in the 'Midsummer's Night's Dream,' and to think that sometimes 'his eye in a fine frenzy rolling' gave to airy nothings 'a local habitation and a name'" (Heron-Allen, 1917, p. 74).

³ "Although d'Orbigny had originally been taught the doctrines of Cuvier," Blow explained, "he realised that complete destruction of fossil faunas at the end of each of his stages had not, in fact, occurred. As early

as 1839, d'Orbigny had recognised that, among the two-hundred and twenty-eight species of fossil foraminifera found by him in the Tertiary of the Vienna Basin, some twenty-seven species were still living in present-day seas. The idea of overwhelming, total catastrophe, with complete extinction and subsequent total re-creation (of the school of Cuvier) was replaced by the concept of sudden world-wide marine regressions, subsequent re-population of the areas involved (with the appearance of many new genera and species) occurring during violent transgressions. Although it is not explicit in d'Orbigny's later writings, it is implicit that he recognised the successive development of new species and genera, which could co-exist with other species and genera which had survived from former times" (Blow, 1979, p. 237).

⁴ His father, Charles d'Orbigny, by profession a doctor, pursued the scientific study of foraminifera, collecting and examining sands from various localities. As the senior d'Orbigny's eyesight failed, he increasingly relied on his son Alcide for the examination and observation of these microscopic curiosities. In a letter to Fleurian de Bellevue dated 1819, Charles d'Orbigny related the following observations, "I have just made a discovery of considerable zoological importance, and I hasten to apprise you of it. I think I have already told you the species of microscopic Cephalopods related to those observed in the sands of Rimini were to be found in great numbers in our sands of the Golfe de l'Aguillon, and of Angoulins; I have already described more than a hundred species or varieties from these two localities, and my son is occupied drawing them, for I have observed so much in my life that I can hardly see at all, and I am often obliged to borrow his eyes. The great number of shells of these mollusca which are found in our sands, led me to presume that the animal lived on our shores, and set me to look for them; the difficulty was to discover such small creatures; their exceeding smallness was a great obstacle; even my son, in spite of his piercing and trained sight, had not yet discovered anything when one day he brought me some Polyzoa (*Polypiers*) which he had gathered on the rocks at Marsilly at very low tide; we placed them in sea-water with the idea of seeing one of the Polyps develop; my son thought he saw some grains of fine sand which had fallen to the bottom of the bowl, move, we put some of this supposed sand in a watch-glass on a mirror, we watched it and we had the extreme satisfaction of seeing swim in it 'Lenticulines, Rotalies, Discorbes, Spirolines,' etc., whose shell one could perfectly well make out through the animal, which is ornamented with the most lively colours; we

saw them moving little arms or tentacles, the number of which we could not count, our magnifier not enlarging sufficiently." D'Orbigny closed the letter by asking for the loan of the microscope of the "Cabinet d'Histoire Naturelle" (cited in Heron-Allen, 1917, p. 6).

⁵ Colored prints of two of the completed plates are reproduced in Heron-Allen (1917).

⁶ Heron-Allen commented that, "Sometimes, it must be confessed, Berthelin's tracings were too faithful, and remind one of the . . . tailor who conscientiously reproduced the patches in the worn trousers he was given to copy. D'Orbigny made corrections on these sketches *currente calamo*, and these are faithfully reproduced in Berthelin's tracings. Cf. the figure of *Bulimina arcuata*, where d'Orbigny mistook a foreign speck for an aperture and put it in. He subsequently put his pencil through it, and this is apparent in Dr. Fornasini's figure" (Heron-Allen, 1917, p. 36, footnote) (see Fig. 1).

⁷ "The original Models cut by the hand of d'Orbigny, from which the matrices were made for multiplying them, are in the cabinet of the Director of the Musée de Paléontologie in Paris. They are apparently cut in a brown gypsum, and are still covered with traces of the white plaster used for making the moulds. They were presented to the Museum about the year 1894 by his son Henri d'Orbigny, who was an entomologist, and who died in Paris in 1915" (Heron-Allen, 1917, p. 15).

⁸ Parker, Jones and Brady (1865) published a complete translation of the label, the text of which reads, "Models of microscopic Cephalopods, recent and fossil, representing one individual of each of the principal divisions of a new method based on the mode of growth of the shells. The Models are from forty to two hundred times the size of the originals, so as to show their characters distinctly. By M. Alcide Dessalines D'Orbigny, junior. There are Four Fasciculi, each comprising twenty-five Models; besides, for the first sixty subscribers, three or four shells. The great rarity of the originals does not allow any more to be promised. (The specimens are in glass boxes, which must be opened with great care.) The Four Fasciculi will be issued in the course of the first six months of 1823: the price of each is twenty francs, payable either at Rochelle to the author (Jardin des Capucins), or at Paris to M.—. Letters and money to be post-free. The First Fasciculus of the Models may be seen at Paris, at the Museum of Natural History of the Jardin du Roi, and at M.—'s. The subscribers will receive with the Fourth Fasciculus the Systematic Table of the Distribution of these Cephalopods, indicating, by numbers corre-

sponding to those of the Models, the names of the specimens sent, and the order of their classification" (Parker and others, 1865, p. 16). The following note accompanied the issue of the fourth "Fasciculus," "The coloured Models represent the fossil shells; the white Models, the recent shells. The place and shape of the siphuncles are indicated by the marks or black spots" (Parker and others, 1865, p. 17).

⁹ D'Orbigny wrote that, "The Cephalopoda of this Order have a bursiform body, in the posterior portion of which the shell is enclosed; this body is sometimes of great volume compared with that of the head, to which it serves as a refuge in moments of danger, enclosing it almost entirely in the anterior folds of the skin. This head is very small, slightly, or not at all, distinct from the body, and terminated by numerous tentacles, which are disposed in several rows around the mouth, which is central" (d'Orbigny, 1826, p. 245).

¹⁰ D'Orbigny had described four species of *Oolina* from South American sands, and commented that, "We have, for a long time known of these little bodies, but having continually found them in localities where there were many *Nodosarias* and *Dentalinas*, we took them for the young of these genera, and we would without a doubt still maintain this notion, if we had not found them in great numbers at Malouines [Falkland Islands], without encountering there either *Nodosarias* or *Dentalinas*; . . . that which compels us to consider them as whole bodies and not as juvenile individuals. Once this opinion stopped, we then found *Oolinas* in almost all sands, and we must consider them as a distinct genus" (d'Orbigny, 1839, p. 18).

¹¹ Dujardin proposed, "To name *sarcode* that which other observers have called living jelly [*gelée vivante*], this diaphanous, glutinous substance, insoluble in water, contracting into globular masses, attaching itself to dissecting-needles and allowing itself to be drawn out like mucus; lastly, occurring in all the lower animals interposed between the other elements of structure" (Dujardin, 1835b, p. 367, translated in Geison, 1971, p. 235).

Although Dujardin extended his definition of the term "sarcode" to the living substance of lower animals, he never connected sarcode with the "protoplasm" of plants, nor did he integrate his concept with cell theory (Geison, 1971). It was not until 1861 that the common identity of plant protoplasm and animal sarcode was recognized by Max Schultze (1861) who demonstrated that "a single substance, called protoplasm, was the substratum of vital activity in the tissues of all living organisms, however simple or complex" (Geison, 1969, p. 276).

¹² These conclusions on the apparently homogenous and structureless nature of the living substance of the rhizopods, caused Dujardin to reject the popular "polygastric hypothesis" of Ehrenberg ("the foremost protozoologist of the era"), who had maintained that protozoa possessed miniature organ systems comparable to those observed in higher organisms. Dujardin's observations and experiments led him to conclude that the "multiple tiny stomachs" which Ehrenberg had described were actually spontaneously produced vacuoles. "The strangest property of *sarcode*," Dujardin remarked, "is the spontaneous production in its mass, of vacuoles or little spherical cavities, filled with the surrounding fluid" (Dujardin, 1835d, p. 368, translated in Geison, 1971, p. 235).

¹³ Dujardin (1835a) presented the results of his observations on these supposed microscopic cephalopods at a January meeting of the Société des Sciences Naturelles de France. He offered the conclusions that not only were these tiny organisms not molluscs, but neither were they members of any of the established classes of the animal kingdom. Dujardin originally proposed the name *Symplectomeres* for these simple animals, but further observations of *Gromia* led him to designate them as the *Rhizopodes* (Dujardin, 1835b). "These animals emit filaments of a glutinous consistency having the appearance of molten glass, with nodes which advance in one direction or the other"; Dujardin observed, "They are retractile, susceptible to separating into branches, and to anastomosing, and to melting together, serving as the foot of the animal for movement by crawling, and their aspect of rootlike fibers justifies entirely the name of *rhizopodes*" (Dujardin, 1835c, p. 338).

III. THE ENGLISH SCHOOL AND THE QUESTION OF VARIATION

¹ "Not only . . . did there prove to be this complete harmony in our general results, but there was also a singular unity in the aggregate of the work we had respectively accomplished . . ." (Carpenter, 1862, Preface, p. vi).

² For many years Brady's collection of figured *Challenger* material was split between the British Museum (Natural History) and the Zoological Museum, Cambridge. During the late 1930's Heron-Allen arranged for the Cambridge specimens to be transferred to the British Museum (Natural History), the last of the specimens arriving in 1957 (C. G. Adams, written communication, 1983).

³ Brady was an active member of the Tyneside Nat-

uralists' Field Club and the Northumberland, Durham and Newcastle-upon-Tyne Natural History Society (Adams, 1978).

⁴ Carpenter, 1862, p. vi.

⁵ Williamson stated, "When I first contemplated the preparation of a Monograph . . . , I proposed appending to it a general history of this class of objects; reviewing the various modification of their structure, their zoological affinities, and their geological history. The Council of the Ray Society have thought it desirable that these subjects should be more elaborated than could be done in the introduction to a monograph, and they have consequently intrusted my friend Dr. Carpenter with the preparation of a separate volume, embracing the entire history of Foraminifera. . . . When it appears, though following the present volume in order of publication, Dr. Carpenter's publication will be the true introduction to mine" (Williamson, 1858, p. v).

"Some disappointment may be sensed in these words of Williamson, but he accepted the decision of the Council with grace" (Cifelli, manuscript comment).

⁶ "Much as many people today satisfy similar curiosities by watching the various natural history series on television" (Cifelli, manuscript comment).

⁷ Williamson commented, "It follows from the preceding remarks that though in the descriptive portions of this volume I have employed the machinery of binomial classification, I have only done so provisionally as a useful mode of indicating special types of form" (Williamson, 1858, p. xi).

⁸ In his Preface, Carpenter rather emphatically stated, "Those who look for precise definitions will not find them here, for the simple reason that the conclusion has been forced upon us that *sharply defined divisions*—whether between species, genera, families or orders—*do not exist among Foraminifera*" (Carpenter, 1862, p. vii).

⁹ Jones and Parker explained this idea, "Our own experience of the wide limits within which any specific group of the *Foraminifera* multiply their varietal forms, related by some peculiar conditions of growth and ornamentation, has led us to concur fully with those who regard nearly every species of *Foraminifera* as capable of adapting itself, with endless modifications of form and structure, to very different habitats in brackish and salt water,—in the several zones of shallow, deep, and abyssal seas,—and under every climate, from the poles to the Equator" (Jones and Parker, 1860, p. 294).

¹⁰ "This view has recently been revived in a somewhat modified form by modern planktonic workers who, more and more, are inclined to believe that mor-

phology may be ecologically regulated" (Cifelli, manuscript comment).

¹¹ Brady commented that, "In some families not merely species but reputed genera are connected by a close array of intermediate modifications, with characters differing only in degree of development, as well as by dimorphous forms in which the typical features of allied genera are combined; and in such cases it is not too much to say that 'all sharp demarcations' have ceased to exist. There are other groups, however, in which, possibly owing to our defective knowledge, the successive modifications appear to be less closely connected and to possess distinctive characters of greater persistence" (Brady, 1884, p. vi).

¹² "This attitude was by no means unique to the English school and it can still be clearly recognized today. Many paleontologists and biologists continue to question the concept of the foraminiferal species. Many years passed before it became accepted that foraminifera could have stratigraphic value or that their fossil record showed evolutionary trends. Vaughan (1923) denied the stratigraphic value of "smaller" foraminifera, even though at the time they were being used extensively for correlations in oil exploration. Until recently, a foraminiferal example demonstrating an evolutionary principle in a textbook was a rarity" (R. Cifelli, manuscript comment). [Futuyama (1986) used a planktonic foraminiferal example from Cifelli (1969) to illustrate iterative evolution in the second edition of his text, *Evolutionary Biology*.]

¹³ Carpenter, 1862, p. vi.

¹⁴ "To illustrate the difference between these two approaches to taxonomy with a foraminiferal example, compare the narrowly defined nodosarid species of the German Jurassic (Bartenstein and Brand, 1937), with the wide-set species of the English Jurassic (Barnard, 1950; Adams, 1957; Cifelli, 1959)" (Cifelli, manuscript comment).

IV. LATE NINETEENTH CENTURY ADVANCES

¹ "With his heavy professional commitments, it was questionable whether he would have been able to find the time to complete the more elaborate introduction to his monograph that he had originally planned, which the Ray Society decided to entrust to Carpenter" (Cifelli, manuscript comment).

² Williamson had observed that, ". . . the same individual Foraminifer often undergoes important changes in its progress to maturity, the newer segments differing from the older ones; we must here carefully distinguish between true primary variations and those

merely dependent on age and unequal development. The tendency to such ultimate differentiation in each individual . . . must be distinguished from the variations between different individuals, *the sum of which variables, whether potential or actual, constitute the characteristics of the species distinguishing it from all other species*" (Williamson, 1858, p. xi). [Italics are Williamson's.]

³ Williamson remarked that, "The more extensive our experience, the weaker become our convictions respecting the limits of variation in any species. Examples abound which we are unable to locate with confidence; and we are at length tempted to believe that amongst the Foraminifera specific distinctions have no existence. This is not, however, the conclusion at which I have arrived. I should rather infer that the hard shells of the Foraminifera do not constitute a sufficiently constant and important element in their organization to justify our trusting them as guides in the discrimination of species. They appear to be a variable feature, like the hair amongst human beings, or the changing contours of a protean Amoeba. That species exist amongst the Foraminifera as elsewhere, analogy would, of course, lead us to infer; but I believe there are several indications of the fact, more substantial than what can be supplied by mere analogy. But we have hitherto failed to detect the real specific peculiarities, or even to ascertain in what part of the living organism they are likely to be found. As yet they are but unseen potentialities, of which the eye has hitherto been unable to detect any concrete or objective manifestation; and I strongly suspect that the remark is equally applicable to the entire group of the Rhizopoda as to the Foraminifera" (Williamson, 1858, p. x).

⁴ Wall texture "has not proven to be a panacea of classification, a problem surfaced at the outset which has not been so much resolved as ignored" (Cifelli, manuscript comment).

⁵ Schultze's 1854 classification of the Rhizopoda is as follows:

- A. Nuda
- B. Testacea
 - I. MONOTHALAMIA
 - Family LAGYNIDA
 - Family ORBULINIDA
 - Family CORNUSPIRIDA
 - II. POLYTHALAMIA
 - Family MILIOLIDA
 - Family TURBINOIDA
 - Subfamily Rotalida
 - Subfamily Uvellido

- Subfamily Textularida
- Subfamily Cassidulinida
- Family NAUTILOIDA
- Subfamily Cristellarida
- Subfamily Nonionida
- Subfamily Peneroplida
- Subfamily Polystomellida
- Family ALVEOLINIDA
- Family SORITIDA
- Family NODOSARIDA
- Family ACERVULINIDA

⁶ Loeblich and Tappan (1964), however, described the genus *Nubecularia* as having a calcareous, imperforate wall which "commonly incorporates small grains of sand," and in their remarks they comment on Recent specimens which are "coarsely agglutinated" (Loeblich and Tappan, 1964, p. C445). Thus it seems plausible that Reuss could have easily mistaken the nature of the wall material in this genus, depending on which species or specimens he had examined.

⁷ "The question of the arenaceous miliolids was not addressed by Reuss, but the textularids clearly formed a 'knot'" (Cifelli, manuscript comment).

⁸ Brady grouped the genera *Bolivina* and *Textularia* together in the same family, the Textularidae, and criticized Reuss for having divided "certain genera and plac[ed] the two halves in different suborders; thus *Textularia* appears as *Textularia* amongst the hyaline forms and as *Plecanium* amongst the arenaceous" forms (Brady, 1884, p. 56).

⁹ Carpenter remarked that, "The size of the greater part of these organisms is so small, that many hundreds, thousands, or even tens of thousands of them, may be contained in a pill-box; and yet it is usually not too minute to prevent the practised observer from distinguishing the most important peculiarities of each individual by a hand-magnifier alone, or from dealing with it separately by a very simple kind of manipulation. Hence the Systematist can easily select and arrange in a series such of his specimens as display sufficient mutual conformity, whilst he sets apart such as are transitional or osculant; and an extensive range of varieties may thus be displayed within so small a compass, that the most divergent and the connecting forms are all recognisable nearly in the same glance. I am not acquainted with any other group of natural objects, in which such ready comparison of great numbers of individuals can be made" (Carpenter, 1862, p. viii).

¹⁰ At the end of his Preface to the *Introduction to the Study of the Foraminifera*, Carpenter (1862) elaborated the following "general propositions":

"I. The range of variation is so great among *Foraminifera*, as to include not merely the differential characters which systematists proceeding upon the ordinary methods have accounted *specific*, but also those upon which the greater part of the *genera* of this group have been founded, and even in some instances of its *orders*.

"II. The ordinary notion of *species*, as assemblages of individuals marked out from each other by definite characters that have been genetically transmitted from original prototypes similarly distinguished, is quite inapplicable to this group; since even if the limits of such assemblages were extended so as to include what would elsewhere be accounted *genera*, they would still be found so intimately connected by gradational links, that definite lines of demarcation could not be drawn between them.

"III. The only natural classification of the vast aggregate of diversified forms which this group contains, will be one which ranges them according to their direction and degree of divergence from a small number of principal family-types; and any subordinate groupings of *genera* and *species* which may be adopted for the convenience of description and nomenclature, must be regarded merely as assemblages of forms characterised by the nature and degree of the modifications of the original type, which they may have respectively acquired in the course of genetic descent from a common ancestry.

"IV. Even in regard to these family-types, it may fairly be questioned whether analogical evidence does not rather favour the idea of their derivation from a common original, than that of their primitive distinctiveness.

"V. The evidence in regard to the genetic continuity between the *Foraminifera* of successive geological periods, and between those of the later of these periods and the existing inhabitants of our seas, is as complete as the nature of the case admits.

"VI. There is no evidence of the fundamental modification or advance in the Foraminiferous type from the Palaeozoic period to the present time. The most marked transition appears to have taken place between the Cretaceous period, whose Foraminiferous fauna seems to have been chiefly composed of the smaller and simpler types, and the commencement of the Tertiary series, of which one of the earliest members was the Nummulitic limestone, which forms a stratum of enormous thickness that ranges over wide areas in Europe, Asia, and America, and is chiefly composed of the largest and most specialized forms of the entire group. But these were not unrepresented in previous

epochs; and their extraordinary development may have been simply due to the prevalence of conditions that specially favoured it. The Foraminiferous fauna of our own seas probably presents a greater range of variety than existed at any preceding period; but there is no indication of any tendency to elevation towards a higher type.

"VII. The general principles thus educed from the study of the Foraminifera should be followed in the investigation of the systematic affinities of each of those great types of Animal and Vegetable form, which is marked out by its physiological distinctness from the rest. In every one of these there is ample evidence of variability; and the limits of that variability have to be determined by a far more extended comparison than has been usually thought necessary, before the real relations of their different forms can be even approximately determined.

"VIII. As it is the aim of the Physical Philosopher to determine "what are the fewest and simplest assumptions, which being granted, the whole existing order of nature would result," so the aim of the Philosophic Naturalist should be to determine how small a number of primitive types may be reasonably supposed to have given origin by the ordinary course of "descent with modification" to the vast multitude of diversified forms that have peopled the globe during the long succession of geological ages, and constitute its present Fauna and Flora" (Carpenter, 1862, p. x-xii).

¹¹ Carpenter emphatically reiterated this belief in his response to a review of the *Introduction to the Study of Foraminifera* that had been published by *The Athenaeum* (28 March 1863, p. 417-419), "Under the influence of [the reviewer's] foregone conclusion that I have accepted Mr. Darwin as my master and his hypothesis as my guide, your reviewer represents me as blind to the significance of the general fact stated by me, that 'there has been no advance in the foraminiferous type from the palaeozoic period to the present time. But for such a foregone conclusion, he would have recognized in this statement the expressions of my conviction that the present state of scientific evidence, instead of sanctioning the idea that the descendants of the primitive type or types of Foraminifera can ever rise to any higher grade, justifies the *anti-Darwinian* inference, that however widely they diverge from each other and from their originals, *they still remain Foraminifera*'" (Carpenter, 1863, p. 461).

¹² Darwin, 1866, p. 402.

¹³ "As all these earlier forms still flourish under conditions which (so far as can be ascertained) are precisely

the same, there is no ground to believe that any one of them is better fitted to survive than another. They all imbibe their nourishment in the same mode; and no one type has more power of going in search of it than another. That they are all dependent on essentially the same conditions of temperature and depth of water, is shown by their occurrence in the same marine areas. That they all equally serve as food to larger Marine Animals, can scarcely be doubted; and it is hardly conceivable that any of their devourers would discriminate (for example) between the disks of a large *O. marginalis*, a middle-sized *O. duplex*, and a small *O. complanata*, which even the trained eye of the Naturalist cannot distinguish without the assistance of a magnifying glass" (Carpenter, 1883, p. 570).

¹⁴ The concept of "undifferentiated protoplasm" held by Carpenter and his collaborators, may also have contributed to their philosophy of the extreme "variability of form" observed in the Foraminifera. Carpenter wrote, "As less differentiation of parts exists among Rhizopoda than in either of the other classes, and as the beings of which that class is composed may be considered as exhibiting the distinctive attributes of Animal life in their least specialised condition, its place is obviously at the bottom of the series" (Carpenter, 1862, p. 12). Not only did they perceive the rhizopods to lack protoplasmic differentiation, they also believed that foraminiferans lacked a nucleus. Carpenter (1862) remarked that in some rhizopods, "The original protoplasmic condition is most completely retained (as seems to be the case with *Gromia*, and with the *Foraminifera* generally)," and "no nucleus can be distinguished" (Carpenter, 1862, p. 14). Jones commented on the difficulties that such a lack of differentiation caused in the classification of Foraminifera, "It is difficult to define the relative value of pseudopodial characters, which do not coincide with the absence or the development of those more important organs, the 'Nucleus' and 'Contracting Vesicle,' . . . No evidence of either organ having been found in *Foraminifera* and *Polycystina*, they stand . . . low in the scale of Rhizopods" (Jones, 1876, p. 65).

Ironically, this emphasis on the low organizational level of the foraminiferan was interpreted by an unknown reviewer (Anonymous, 1863) of their *Introduction to the Study of the Foraminifera*, as evidence in support of the theory of spontaneous generation. The reviewer found in the foraminifera (which he viewed as "aggregates of slime, snot, or protoplasm"), a perfect example of the "primordial form into which life was first breathed" (Darwin, 1859, p. 484). This process he described as follows, "Under what modi-

fications or combination of the general polarizing force, the slime of mud or ooze is first condensed into a protoplasmic centre of such low vital force is still undetermined; but once begun, and growing as such, it successively puts forth other portions or centres. . . . The primitive protoplasmic centre of a potential foraminifer, however, contains lime-water in much greater proportion than either of the substances defined by the author as composing it; it combines the calcium of such water with carbonic acid, and precipitates it on its exterior as a thin porous crust. The sarcode or protoplasmic matter can extend itself, like threads, from the pores of the crust or shell, and hence the name 'foraminifer.' It is an 'organism' without organs; and manifests life at its lowest grades" (Anonymous, 1863, p. 417).

Carpenter countered these interpretations in the following excerpt from his letter to *The Athenaeum*, "If your reviewer prefers to suppose that new types of Foraminifera originate from time to time out of the 'ooze,' under the influence of 'polar forces,' he has, of course, a right to his opinion; though by most naturalists such 'spontaneous generation' of rotalines and nummulites will be regarded as a far more 'astounding hypothesis' than the one for which it is offered as a substitute. But I hold that mine is the more scientific, as being conformable to the fact that Foraminifera do propagate their kind with more or less modification; whilst his is not supported by any evidence that rotalines or nummulites ever originate spontaneously, either in 'ooze' or anywhere else" (Carpenter, 1863, p. 461).

¹⁵ Carpenter wrote, "Those who find in 'natural selection' or 'survival of the fittest' an all-sufficient explanation of the 'origin of species,' seem to have entirely forgotten that before 'natural selection' can operate, there must be a range of varietal forms to select from; and that the fundamental question is (as Mr. Darwin himself clearly saw, at any rate in his later years), *what gives rise to variations?* No exercise of 'natural selection' could *produce* the successive changes presented in the evolutionary history of the typical *Orbitolites*" (Carpenter, 1883, p. 569).

¹⁶ Earlier workers had separated the foraminiferans and the gromids into different orders. Claparède and Lachmann (1859) divided the Rhizopoda into four orders: the Proteina, the Echinocystida, the Gromida and the Foraminifera. Carpenter (1862) brought together the Foraminifera and the Gromida to form his order Reticularia of the class Rhizopoda. Although Carpenter (1862) initially proposed the name "Reticulosa" for this order (p. 17), in subsequent passages of

his monograph he refers to this group as the order Reticularia (p. 40).

¹⁷ Carpenter's rationale for retaining the family Gromida within his classification, clearly reflects his training as a physiologist. "If we attach a greater value to the characters furnished by the animal than to those afforded by the material of its envelope (and this appears to me to be a more natural method), we find that the affinity of the Gromida to those Foraminifera whose shells, being imperforate, do not give passage to pseudopodia, is even closer than is that of the Foraminifera having imperforate shells to those of which the shells are perforated" (Carpenter, 1862, p. 61). He also emphasized that "there seems the more reason for including *Gromida* . . . when it is borne in mind that the limitation of the origin of the pseudopodia to one part of the body these forms bear a closer relationship to the Foraminifera of the *Milioline* series, than the latter do to those of the *Rotaline*, in which the pseudopodia seem to extend themselves equally from any part of the sarcode-body" (Carpenter, 1862, p. 41).

¹⁸ "As we proceed in our study," Carpenter wrote, "We shall find that from the lowest to the highest of these forms each is most remarkably connected with the other parts of the series by links of affinity so strong as to forbid their dissociation; so that, starting from the humblest or simplest types, we are gradually conducted, with scarcely any decided interruption, to the highest or most specialized" (Carpenter, 1862, p. 68).

¹⁹ Carpenter did not present a scheme of relationships of the genera he included in the family Lituolida, as he had with many of his other families, but in his introductory remarks on this family he described how he envisioned the development of the genera in the family may have occurred. "The first, *Trochammina*, starts from a rank parallel to that of *Cornuspira* in the porcellaneous, and of *Spirillina* in the vitreous series, but has a much wider range of variation in form, and the cavity of which, though originally unilocular, not infrequently becomes multilocular by the formation of imperfect septa; the second, *Lituola*, closely corresponds with *Nubecularia* in its lower adherent forms, but ranges in its higher free forms with the "spirilline" variety of *Peneroplis*, and, in the subdivision of its principal chambers presents a rude sketch of *Orbiculina*; whilst the third, *Valvulina*, presents features of approximation to certain occasionally arenaceous types of the vitreous series, not merely in a very close similarity of external configuration, but also in the primary investment of its body by a thin lamina of shell formed upon the perforated vitreous type, which is subsequently covered-in by a layer of arenaceous cement-

substance, so as to be rendered actually imperforate" (Carpenter, 1862, p. 140).

²⁰ Carpenter commented that, "So perfect a transition exists between the Monothalam [*Lagena*] and the polythalamous *Nodosaria*, as renders it impossible to doubt the close affinity of these two forms. From the rectilinear *Nodosaria*, through the gently curved *Dentalina* and the more strongly curved *Marginulina*, we are led, in a series so perfectly gradational as to forbid lines of demarcation from being anywhere drawn across it to the spiral *Cristellaria*, which may be regarded as the highest manifestation of the lagenoid type" (Carpenter, 1862, p. 154).

²¹ Carpenter explained that, "The continuous tube of a *Spirillina* may contract itself at intervals so as to form a succession of chambers, just as we have seen a *Cornuspira* convert itself into a spiroloculine *Miliola*" (Carpenter, 1862, p. 173).

²² Carpenter reasoned that, "The very marked participation in certain characters of the Nummuline series which is exhibited by this genus, would suffice, if taken by itself, to justify its claim to a place among them; the relationship of its most developed forms to those of *Polystomella* in particular being so intimate, that the two cannot be justly considered as far removed from each other. But, on the other hand, the general affinity of *Rotalia* to the other genera of the Rotaline series is so close, that it is quite impossible to detach it from them, and it must be regarded, therefore, as the link which establishes the transition between the ordinary Rotaline and the Nummuline series" (Carpenter, 1862, p. 214).

²³ In the following passage, Carpenter gave his justification as to why he believed *Carpenteria* showed affinities with the "Globigerine type." Notwithstanding these marked peculiarities in the general plan of conformation of *Carpenteria*, a comparison of specimens in different stages of evolution, and the removal from the older specimens of one whorl after another until the original nucleus is arrived at, make it evident that the early condition of this organism essentially accords with that of the Globigerine type of Foraminifera" (Carpenter, 1862, p. 188).

²⁴ Actually, although Carpenter made no mention of this in his introductory remarks on the Family Globigerinida, in his remarks on "The Sub-Order Perforata" Carpenter (1862) discussed how he imagined the development of the textularids had occurred: "If . . . we take *Orbulina* as our starting point, and look for its nearest alliances in the perforated series, we shall have no difficulty in fixing upon *Globigerina* as its connecting link with higher types; the polythalamous

shell of that genus being formed by an aggregation of globular segments that are united to each other by external adhesion only, each segment possessing its own separate aperture. . . . Now such a series of globigerine chambers, budded forth alternately on the two sides of a linear axis, becomes a *Textularia*; whilst if the succession follows the course of a spire resembling that of a *Buliminus*, a *Bulimina* is formed" (Carpenter, 1862, p. 150).

²⁵ Brady commented that there was in the systematic arrangement of "Dr. Carpenter and his colleagues . . . but little infringement of natural relationship[s] . . . except, perhaps, the association of *Textularia* and its immediate allies with *Globigerina* and the Rotaline genera" (Brady, 1884, p. 56).

²⁶ "That some of our generic distinctions may be invalidated by more extended research, is just as likely as that new generic types may present themselves among the collections from ocean beds yet unexplored, or from geological formations as yet unscrutinised. The whole study of this group must still be regarded as in its infancy; and the utmost that we can hope for this Introduction is, that it may help to give a *right direction* to that study. We have the fullest confidence in the correctness of our general principles; and shall not shrink from the consequences of their application to our own work, however large a part of it may thereby be superseded by something better. I have endeavored throughout my own scientific career to keep in view the noble character given by Schiller of the true philosopher, as distinguished from the trader in science, that 'he has always loved truth better than his system; and will gladly exchange her old and defective form for a new and fairer one'" (Carpenter, 1862, p. vii).

²⁷ The "systematic grouping of Foraminifera" which accompanied Jones' 1876 paper "Remarks on the Foraminifera," had been reproduced with minor modifications from the third edition of Griffith and Henfrey's *Micrographic Dictionary*. (Jones is credited on the title page of the *Dictionary* as having assisted the editors.) His 1876 classification represented an increase in four genera and twelve subgenera, and encompasses only a few minor changes to its structure. Below is given the "Synoptical list of the genera and subgenera of Foraminifera" which accompanied Jones' (1875) article on "Foraminifera" in *The Micrographic Dictionary*.

I. IMPERFORATE OR PORCELLANEUS FORAMINIFERA

1. NUBECULARIDA—*Squamulina* Schultze; *Nubecularia* Defrance
2. MILIOLIDA—*Vertabralina* d'Orbigny (*Articu-*

lina d'Orbigny); *Cornuspira* Schultze; *Miliola* Lamarck (*Uniloculina* d'Orbigny; *Biloculina* d'Orbigny; *Triloculina* d'Orbigny; *Quinqueloculina* d'Orbigny; *Cruciloculoculina* d'Orbigny; *Spiroloculina* d'Orbigny); *Hauerina* d'Orbigny; *Fabularia* Defrance

3. PENEROPLIDA—*Peneroplis* Montfort (*Spirolina* Lamarck (restricted); *Dendritina* d'Orbigny)
4. ORBICULINIDA—*Orbiculina* Lamarck; *Orbitolites* Lamarck (*Pavonina* d'Orbigny); *Alveolina* d'Orbigny
5. DACTYLOPORIDA—*Haploporella* Gümbel; *Dactyloporella* Gümbel; *Thyrsoporella* Gümbel; *Gyroporella* Gümbel; *Cylindrella* Gümbel; *Uteria* Michelin; *Acicularia* D'Archiac

II. ARENACEOUS FORAMINIFERA

1. PARKERIADA—*Parkeria* Carpenter; *Loftusia* Brady
2. LITUOLIDA—*Involutina* Terquem; *Endothyra* Phillips; *Trochammina* Parker and Jones; *Webbina* d'Orbigny; *Valvulina* d'Orbigny; *Tetraxis* Ehrenberg; *Saccamina* Sars; *Astrorhiza* Sars; *Botellina* Carpenter; *Lituola* Lamarck; *Placopsilina* d'Orbigny; *Haplophragmium* Reuss; *Polyphragma* Reuss; [*Ataxophragmium* Reuss (sandy *Bulimina*); *Plecanium* Reuss (sandy *Textilaria*)]

III. PERFORATE OR HYALINE FORAMINIFERA

1. LAGENIDA—*Ellipsoidina* Seguenza; *Lagena* Walker and Jacob in Kanmacher (*Entosolenia* Ehrenberg; *Fissurina* Reuss); *Nodosarina* Parker and Jones (*Glandulina* d'Orbigny; *Nodosaria* Lamarck; *Dentalina* d'Orbigny; *Dentalinopsis* Reuss; *Lingulina* d'Orbigny; *Lingulinopsis* Reuss; *Rimulina* d'Orbigny; *Vaginulina* d'Orbigny; *Marginulina* d'Orbigny; *Cristellaria* Lamarck; *Planularia* Defrance; *Flabellina* d'Orbigny; *Fronicularia* d'Orbigny; *Amphimorphina* Neugeboren); *Orthocerina* d'Orbigny
2. POLYMORPHINIDA—*Polymorphina* d'Orbigny (*Dimorphina* d'Orbigny); *Uvigerina* d'Orbigny (*Sagrina* d'Orbigny)
3. BULIMINIDA—*Bulimina* d'Orbigny (*Bolivina* d'Orbigny; *Virgulina* d'Orbigny; *Bifarina* Parker and Jones; *Robertina* d'Orbigny; *Ataxophragmium* Reuss (sandy)); *Cassidulina* (Ehrenbergina Reuss)
4. TEXTILARIDA—*Textilaria* Defrance (*Vulvulina* d'Orbigny; *Cuneolina* d'Orbigny; *Spiroplecta* Ehrenberg; *Bigenerina* d'Orbigny;

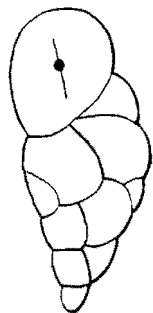


FIGURE 1. Tracing of *Bulimina arcuata* made by Berthelin from d'Orbigny's "Planches inédites," which was faithfully reproduced by Fornasini (1908, pl. 1, fig. 12).

Venilina Gümbel; *Clavulina* d'Orbigny; *Verneuilina* d'Orbigny; *Tritaxia* Reuss; *Candeina* d'Orbigny; *Gaudryina* d'Orbigny; *Heterostomella* Reuss; *Plecanium* Reuss (sandy)

5. GLOBIGERINIDA

1. Globigerinina—*Ovulites* Lamarck; *Orbulina* d'Orbigny; *Globigerina* d'Orbigny; *Pullenia* Parker and Jones; *Sphaeroidina* d'Orbigny; *Allomorphina* Reuss; *Chilostomella* Reuss; *Carpenteria* Gray
2. Rotalina—*Spirillina* Ehrenberg; *Discorbinia* Parker and Jones; *Planorbulina* d'Orbigny (*Planulina* d'Orbigny; *Truncatulina* d'Orbigny); *Pulvinulina* Parker and Jones; *Rotalia* Lamarck; *Cymbalopora* Von Hagenow; *Thalamopora* Reuss; *Calcarina* d'Orbigny; *Tinoporus* Montfort; *Patellina* Williamson; *Polytrema* Risso
3. Polystomellina—*Polystomella* Lamarck (*Nonionina* d'Orbigny)
4. Nummulinina—*Nummulina* d'Orbigny (*Operculina* d'Orbigny; *Assilina* d'Orbigny); *Amphistegina* d'Orbigny; *Heterostegina* d'Orbigny; *Cycloclypeus* Carpenter; *Orbitoides* d'Orbigny; *Fusulina* Fischer; *Orobias* d'Eichwald; *Eozoon* Dawson

²⁸ Jones commented that, "The [arenaceous kind of 'shell-structure'] appears to be, in some instances at least, a modification of the porcellaneous kind, by the addition of grains of sand, comminuted shels [*sic*], minute Foraminifera, &c., in variable proportion to the calcareous matrix, and with differences of arrangement, the particles sometimes projecting beyond the surface, and sometimes neatly imbedded, as sand in smooth cement. So also some of the 'hyaline' forms

(such as *Textilaria* and *Bulimina*) become rough and thickened in the aged state, with the imbedding of foreign particles. The 'arenaceous' shells, therefore, do not constitute a really distinct zoological group, though convenient as comprising the common *Lituolae*, *Valvulinae*, *Trochamminae*, &c." (Jones, 1872, p. 175).

²⁹ Jones had remarked that, "In a strict zoological sense, a Foraminiferal *Genus* has but the value of common *Species*, . . ." (Jones, 1872, p. 178).

³⁰ Although Jones mentioned, however, in a footnote to the classification that, "The *Polymorphinida* are separated from the *Lagenida* only on account of their alternate arrangement of chambers" (Jones, 1876, p. 90).

³¹ Carpenter had presented the following argument, "It would probably be correct to say that the true 'shell' of *Foraminifera* is uniformly *calcareous*, and that when this is replaced by a siliceous 'test' the materials of such test have been drawn together from external sources. There are certain cases, on the other hand, in which the sandy particles are . . . embedded in a calcareous cement which forms the essential constituent of the shell; in these the arenaceous texture, being superficial only, and to a certain extent accidental, has not that importance as a differential character which it bears when extending throughout the thickness of the shell" (Carpenter, 1862, p. 47).

³² "Possibly because of his pharmaceutical experience in commerce" (Cifelli, manuscript comment).

³³ Brady remarked that, "The various modifications which have been referred to differ not merely in details of form and structure but in habit; they are met with under diverse conditions as to latitude, depth of water, nature of sea-bottom, and the like, and their modes of life are often totally distinct" (Brady, 1884, p. vi).

³⁴ Brady commented that, "The study of Foraminifera as assemblages of forms grouped round a comparatively small number of central or typical species, as advocated by Carpenter and his colleagues, is, I am convinced, the only means of arriving at a correct understanding of the biological relations of the group; but this mode of treatment, whilst determining the general lines of classification furnishes no direct basis for the construction of a synopsis suited to the requirements of the systematic zoologist. The scheme which I now venture to propose differs in many respects somewhat widely from that foreshadowed by the authors referred to, but in its essential elements there is little or nothing that is incompatible with the conclusions they have so ably expounded; and I have the satisfaction of knowing that it has their general approval" (Brady, 1884, p. 58).

³⁵ Brady's own words describe his perception of the

continuous variation which characterized these families, the terms of which formed an "unbroken morphological series, with no lines of demarcation indicating the limits of the successive groups into which, for convenience, it has been divided; and the relationship between the various types of structure is strengthened and further complicated by the existence of intermediate forms, which present in the same individual, the characters of two or more types" (Brady, 1884, p. 440).

³⁶ And Brady "felt fully confident that the discontinuities were real and not artifacts of inadequate sampling" (Cifelli, manuscript comment).

³⁷ Brady (1881) published a preliminary version of his classification in the *Quarterly Journal of Microscopical Science*. Comparing this early classification to his 1884 scheme, it is apparent that he made only a few modifications to its structure before arriving at a final arrangement. His 1881 classification is comprised of eleven families and only ten subfamilies; he subdivided several of these families further, elevated many of his subspecies to species and subsumed one of his original families (the Parkeridae) into the Lituolidae, to produce the 1884 classification. Below is given the scheme of classification which Brady (1881) presented in his paper, "Notes on some of the Reticularian Rhizopoda of the 'Challenger' Expedition":

Class RHIZOPODA Dujardin

Order FORAMINIFERA d'Orbigny (RETICULARIA Carpenter)

Family I. GROMIDAE—*Gromia* Dujardin; *Lagynis* Schultze; *Lieberkühnia* Claparède; *Shepherdella* Siddall

Family II. MILIOLIDAE

A. Miliolininae—*Bathysiphon* G. O. Sars; *Squamulina* Schultze; *Nubecularia* Defrance; *Uni-*, *Bi-*, *Spiroloculina* d'Orbigny; *Miliolina* Williamson; *Cornuspira* Schultze (*Ophthalmidium* Kubler); *Hauerina* d'Orbigny; *Vertebralina* d'Orbigny (*Articulina* d'Orbigny); *Fabularia* Defrance

B. Orbitolitinae—*Peneroplis* de Montfort; *Orbiculina* Lamarck; *Orbitolites* Lamarck; *Alveolina* d'Orbigny

C. ?Dactyloporinae—*Ovulites* Lamarck; *Dactylopora* Lamarck and subgenera

Family III. ASTRORHIZIDAE—*Psammosphaera* Schultze; *Sorosphaera* Brady; *Saccamina* M. Sars; *Pilulina* Carpenter; *Storthisphaera* Schultze; *Technitella* Norman; *Pelosina* Brady; *Aschemonella* Brady; *Astrorhiza* Sandahl; *Dendrophrya* Str. Wright; *Rhabdammina* M. Sars; *Jaculella* Brady; *Hyperammina* Brady; *Psammatodendron* Norman (Ms); *Sagenella* Brady; *Bottelina* Carpenter; *Marsipella* Norman; *Haliphysema* Bow-erbank; *Polyphragma* Reuss

Family IV. LITUOLIDAE—*Lituola* Lamarck (*Reophax* de Montfort; *Haplophragmium* Reuss; *Haplostiche* Reuss; *Placopsilina* d'Orbigny; *Bdelloidina* Carter); *Trochammina* Parker and Jones (*Hormosina* Brady; *Ammodiscus* Reuss; *Webbina* d'Orbigny); *Nodosinella* Brady; *Involuntina* Terquem; *Endothyra* Phillips; *Stacheia* Brady; *Thurammina* Brady; *Hippocrepina* Parker; *Cyclammina* Brady

Family V. PARKERIDAE—*Parkeria* Carpenter; *Lof-tusia* Brady

Family VI. TEXTULARIDAE

A. Textularinae—*Textularia* Defrance (*Bigenerina* d'Orbigny; *Pavonina* d'Orbigny; *Spiroplecta* Ehrenberg; *Cuneolina* d'Orbigny); *Verneuilina* d'Orbigny (*Gaudryina* d'Orbigny; *Chrysalidina* d'Orbigny; *Tritaxia* (Reuss); *Valvulina* d'Orbigny (*Clavulina* d'Orbigny)

B. Bulimininae—*Bulimina* d'Orbigny (*Virgulina* d'Orbigny; *Bolivina* d'Orbigny; *Pleurostomella* Reuss)

C. Cassidulininae—*Cassidulina* d'Orbigny; *Ehrenbergina* Reuss

Family VII. CHILOSTOMELLIDAE—*Chilostomella* Reuss; *Allomorphina* Reuss; *Ellipsoidina* Seguenza

Family VIII. LAGENIDAE

A. Lageninae—*Lagena* Walker and Jacob; *Ramulina* Jones; *Nodosaria* Lamarck (*Lingulina* d'Orbigny); *Fron-dicularia* Defrance (*Flabellina* d'Orbigny); *Vaginulina* d'Orbigny (*Rimulina* d'Orbigny; *Rhabdogonium* Reuss); *Marginulina* d'Orbigny; *Cristellaria* Lamarck

B. Polymorphininae—*Polymorphina*

d'Orbigny (*Dimorphina* d'Orbigny);
Uvigerina d'Orbigny (*Sagrina* d'Orbigny)

Family IX. GLOBIGERINIDAE—*Globigerina* d'Orbigny (*Orbulina* d'Orbigny); *Hastigerina* Wy. Thomson; *Pullenia* Parker and Jones; *Sphaeroidina* d'Orbigny; *Candeina* d'Orbigny

Family X. ROTALIDAE—*Spirillina* Ehrenberg; *Patellina* Williamson; *Discorbina* Parker and Jones; *Planorbulina* d'Orbigny (*Truncatulina* d'Orbigny); *Anomalina* d'Orbigny; *Rupertia* Wallich; *Carpenteria* Gray; *Polytrema* Risso; *Tinoporus* de Montfort (*Gypsina* Carter); *Cymbalopora* Hagenow; *Pulvinulina* Parker and Jones; *Rotalia* Lamarck; *Calcarina* d'Orbigny

Family XI. NUMMULINIDAE

A. Polystomellinae—*Nonionina* d'Orbigny; *Polystomella* Lamarck

B. Nummulitinae—*Archaeodiscus* Brady; *Amphistegina* d'Orbigny; *Fusulina* Fischer; *Eozoon* (?) Dawson; *Orbitoides* d'Orbigny; *Cycloclypeus* Carpenter; *Heterostegina* d'Orbigny; *Operculina* d'Orbigny; *Nummulites* Lamarck

³⁸ Although Brady may have appeared to generally ignore the "question of porosity" in the arenaceous forms, he summarized his views on the subject in his discussion of the genus *Psammospaera*. "It has been the custom to consider that the tests of the arenaceous Rhizopoda are of necessity imperforate; in other words, that except the general pseudopodial orifice the investment is non-porous, and the fact of these specimens having no general aperture created a doubt as to their Foraminiferal character. But it is now well understood that the term 'imperforate' is only applicable to a limited number of genera, and that some at least of the sandy forms have more or less porous tests, though, owing to their composite texture and the irregularities of the surface, the orifices are but little apparent on the exterior" (Brady, 1884, p. 250).

³⁹ Brady also included two other subfamilies, the Trochammininae and the Loftusinae, in the Lituolidae. He characterized the Trochammininae as having a thin test, "composed of minute sand-grains incorporated with calcareous or other inorganic cement, or embedded in a chitinous membrane; exterior smooth, often polished; interior smooth or (rarely) reticulated; [and] never labyrinthic" (Brady, 1884, p. 66). The Loft-

tusinae he described as having a "test of relatively large size; lenticular, spherical, or fusiform; constructed either on a spiral plan or in concentric layers, the chamber-cavities occupied to a large extent by the excessive development of the finely arenaceous cancellated walls" (Brady, 1884, p. 67).

⁴⁰ In his description of this genus, Cushman remarked on the genus *Bolivina*. "Although resembling *Bulimina* in some ways, its affinities seem closer to *Textularia* and related genera. The aperture is not usually asymmetrical to any extent, as claimed by Brady" (Cushman, 1911, p. 32).

⁴¹ Loeblich and Tappan (1964) included 87 genera in the Nodosariacea.

⁴² "The Family GLOBIGERINIDAE, as now proposed," Brady noted, "corresponds in the main with the Sub-family GLOBIGERINAE of Carpenter, Parker and Jones; but for reasons which will be stated on a subsequent page, the genus *Carpenteria*, which has hitherto been included in the group, is omitted, and the genera *Hastigerina* and *Candeina*, the characters of which were imperfectly understood when the 'Introduction' was written, occupy its place in the series" (Brady, 1884, p. 588).

⁴³ "Although the Family, as a whole, does not present that unbroken succession of minute modifications which has been remarked in some other groups of similar extent," Brady observed, "the salient features of the more important types are sufficiently alike to indicate close natural affinity, and their relationship is further attested by the similarity of the conditions under which they live" (Brady, 1884, p. 588).

⁴⁴ "The question of a supplementary skeleton has turned out to be far more complicated than Brady could possibly have imagined. The lamellar construction of globigerine walls is still disputed (see Reiss, 1963; Blow, 1969; Bé and Hemleben, 1970; Towe, 1971)" (Cifelli, manuscript comment).

⁴⁵ Brady remarked that, "The most noteworthy characteristic of the GLOBIGERINIDAE as a Family is the pelagic habit of most of the species. Certain genera, like *Hastigerina*, are exclusively pelagic; and of these a great majority of the known varieties have been found in the free-swimming condition. Even *Pullenia* and *Sphaeroidina*, of which the reputed typical species have only hitherto been met with in bottom-dredgings, have well-marked pelagic representatives" (Brady, 1884, p. 589).

⁴⁶ D'Orbigny, in his *Voyage dans l'Amérique Méridionale*, described the species *Nonionina pelagica* as: "... an extraordinary exception among the essentially coastal-dwelling Foraminifera, seeing that we have taken it in the open ocean, at a great distance off the coast

of Peru, in the Pacific Ocean, about 20° latitude South and 89° longitude West of Paris, where it appeared to be very rare" (d'Orbigny, 1839, p. 28).

⁴⁷ Not only were specimens of *Pulvinulina* captured in net-tows, the fact that living individuals were captured is evidenced by the following excerpt from a log entry dated September 6, 1875, corresponding to Station 271 in the South Pacific. "Tow-net on a dredge-line at 2425 fathoms," contained "spinous specimens of *Globigerina bulloides*, together with *Globigerina aequilateralis* and *Pulvinulina menardii*, the chambers filled with sarcode" (Brady, 1884, p. 114).

⁴⁸ Brady believed that, "The Foraminifera of the Family ROTALIDAE form a complicated and difficult group, assuming characters so diverse in their extreme modifications, that there is scarcely a single feature, beyond the calcareous shell and its hyaline and perforate texture, that is common to the whole of the members" (Brady, 1884, p. 624).

⁴⁹ Brady commented that, "The much debated question of the origin and structure of Eozoon lies outside the scope of the present Report. It may however be stated that according to the views of Dawson, Carpenter, Rupert Jones, and others, *Eozoon canadense*, the type of the genus instituted by the first-named author, is a fossil Foraminifera. . . . On the other hand it is maintained by King and Rowney, Carter, Moebius, and those who follow them that the structures referred to are of purely mineral origin, and require no organic hypothesis for their explanation" (Brady, 1884, p. 752).

⁵⁰ Brady first described the genus *Archaediscus* as a "new type of Carboniferous Foraminifera" in a paper published in *The Annals and Magazine of Natural History*. In this paper Brady described the details of its morphology as observed in thin section and concluded that "the new organism has many affinities to the Nummulitic type, though less complex in structure" (Brady, 1873, p. 289). Brady elaborated further on the perceived affinities of this genus in his 1884 *Challenger Report* in which he explained that, "The little Carboniferous fossil *Archaediscus*, exemplifies the lowest type of Nummuline structure, and stands in very much the same relation to the genus *Nummulites* that *Spirillina* bears to the higher Rotalines" (Brady, 1884, p. 723).

Loeblich and Tappan (1964, 1987) have placed the genus *Archaediscus* in the Suborder Fusulinina.

V. NATURAL CLASSIFICATION AND EVOLUTION

¹ Blow (1979), in a discussion of the "fundamental philosophy which governs . . . the whole of his taxo-

nomic thinking," commented on the evolutionary approach to classification, "In the view presented here, the recognition of an evolutionary sequence in fossil taxa is considered as doubly subjective since evolution, in itself, can be never recognized purely from an observation of a succession of fossil forms no matter how completely associated into taxa called 'chronospecies.' This so-called 'evolution' is purely an inference from what a sequence of fossil forms appears to do. The observer does not see an evolutionary sequence, he does not even arrange specimens, or differentiated specimen groups (taxa), into evolutionary sequences and all that can be done by the most experienced and most supremely competent worker is to recognise a morphogenesis. . . . It is an inference to recognise a morphogenetic sequence of morphotypes in time as being an evolutionary sequence and thus a lineage composed of 'chronospecies' with each member of the lineage naturally determinative of some true biological process or entity" (Blow, 1979, p. 703).

² The "allegoric parable" of the cave is illustrated more clearly by the following excerpt from Book VII of Plato's *Republic*. De Santillana (1961, p. 204) tells us that it is Socrates speaking in the first person.

"Next, then," I said, "take the following parable of education and ignorance as a picture of the condition of our nature. Imagine mankind as dwelling in an underground cave with a long entrance open to the light across the whole width of the cave; in this they have been from childhood, with necks and legs fettered, so they have to stay where they are. They cannot move their heads round because of the fetters, and they can only look forward, but light comes to them from fire burning behind them up at a distance. Between the fire and the prisoners is a road above their level, and along it imagine a low wall has been built, as puppet showmen have screens in front of their people over which they work their puppets."

"I see," he said.

"See, then, bearers carrying along this wall all sorts of articles which they hold projecting above the wall, statues of men and other living things, made of stone or wood and all kinds of stuff, some of the bearers speaking and some silent as you might expect."

"What a remarkable image," he said, "and what remarkable prisoners!"

"Just like ourselves," I said. "For, first of all, tell me this: What do you think such people would have seen of themselves and each other except their shadows, which the fire cast on the opposite wall of the cave?"

"I don't see how they could see anything else," said he, "if they were compelled to keep their heads unmoving all their lives!"

"Very well, what of the things being carried along? Would not this be the same?"

"Of course it would."

"Suppose the prisoners were able to talk together, don't you think that when they named the shadows which they saw passing they would believe they were naming things!"

"Necessarily."

"Then if their prison had an echo from the opposite wall, whenever one of the passing bearers uttered a sound, would they not suppose that the passing shadow must be making the sound? Don't you think so?"

"Indeed I do," he said.

"If so," said I, "such persons would certainly believe that there were no realities except those shadows of handmade things."

"So it must be," said he.

³ See Hull's 1965 article, "The effect of essentialism on taxonomy—Two thousand years of stasis," *British Journal for the Philosophy of Science*, for an analysis and discussion of the remnants of Aristotelian definition apparent in contemporary concepts of species.

⁴ Russell commented that, "Aristotle's metaphysics . . . may be described as Plato diluted by common sense. He is difficult because Plato and common sense do not mix easily" (Russell, 1945, p. 162).

⁵ "In describing matter, Aristotle made a distinction between potentiality and actuality. For example, a biological individual such as a kitten has the potential to become a cat but does not do so until it is fully grown. The essence of the species is not totally realized until maturity is achieved. Russell thought that Aristotle's usage of potentiality was confused, and probably it was. [Russell commented, 'When potentiality is used as a fundamental and irreducible concept, it always conceals confusion of thought' (Russell, 1945, p. 167).] The notion of potentiality, however, may have been ingrained in the minds of the early naturalists, for example, it could account for both the great emphasis that nineteenth century taxonomists placed on the adult form of the foraminiferal test, and their almost total disregard for the early stages of growth" (Cifelli, manuscript comment).

⁶ As Brumbaugh described it, "The efficient cause first gives an appropriate matter its start toward achieving a complete form. It releases a process of growth,

at each stage of which there is a power to take on new form, and a desire to reach it" (Brumbaugh, 1964, p. 194).

⁷ Brumbaugh elaborated, "The form of a complete adult of the species acts as a *goal* and *ideal* to guide the growth of the individual through a predictable life cycle, as its inner drive for self-realization and inner 'powers' act together to direct its physical growth and behavior" (Brumbaugh, 1964, p. 190).

⁸ Cain stated that, "According to Aristotelian logic, the genus should not be regarded as merely a collection of species. The genus and the differentia taken together are the definition of the species, the statement of its essence" (Cain, 1958, p. 145).

⁹ Logical division involves the taking of a particular genus and distinguishing the species within it. Or, in the words of Linnaeus himself, "Whatever makes the first division should be given first, consequently the generic is stated before the specific name: before I distinguish something I need to know what is to be distinguished, and so I shall give the genus which is divided into parts by the differentia, before I touch the species" (Linnaeus, 1737, cited in Cain, 1958, p. 146).

¹⁰ Cain explained, "Where logical division is possible, we can have a *taxonomy of analysed entities*; where not, only a *taxonomy of unanalysed entities* is possible, and the best example of it is indeed biological taxonomy" (Cain, 1958, p. 146).

¹¹ "By common sense is meant an assessment of relationships based on an evaluation of a combination of characters" (Cifelli, manuscript comment).

¹² Cuvier, in the introduction to his *Règne Animal*, outlined the methods he believed should be followed in establishing natural groups. When it is not possible to determine which are the most "important characters" in a group, he recommended that, "Simple observation must be used, and a sure means of recognizing the important characters which derives from their very nature is that they are the most constant, and that in a long series of diverse entities, grouped together according to their degrees of likeness, these characters are the last to vary. From their influence and their constancy equally results the rule, that they should be preferred for distinguishing the great divisions, and that in proportion as one descends to lower subdivisions, one may descend also to subordinate and variable characters" (Cuvier, 1829, cited in Cain, 1959, p. 188).

¹³ "Ockham battled against the universals that had been introduced by Plato, the notion that the only true realities were the ideal objects of which the earthly objects sensible to perception were only imperfect cop-

ies. These ideals Ockham considered abstractions, mere names (hence the expression 'nominalism' for this philosophy), and held that only the objects perceived were real" (Asimov, 1982).

¹⁴ In his *Zoological Philosophy*, Lamarck commented on the artificiality of taxa. "These groupings," he wrote, "of which several have been so happily drawn up by naturalists, are altogether artificial, as also are the divisions and sub-divisions which they present. Let me repeat that nothing of the kind is to be found in nature, notwithstanding the justification which they appear to derive from certain apparently isolated portions of the natural series with which we are acquainted. We may, therefore, rest assured that among her productions nature has not really formed either classes, orders, families, genera or constant species, but only individuals who succeed one another and resemble those from which they sprung" (Lamarck, 1816, p. 20).

The same sentiment was later expressed unequivocally by Bessey. "Nature produces individuals, and nothing more. She produces them in such countless numbers that we are compelled to sort them into kinds in order that we may be able to carry them in our minds. . . . [S]pecies have no actual existence in nature. They are mental concepts and nothing more. . . . species have been invented in order that we may refer to great numbers of individuals collectively" (Bessey, 1908, p. 218).

¹⁵ Darwin would later emphasize the difference between classifications of animate and inanimate objects by recognizing that, "From the first dawn of life, all organic beings are found to resemble each other in descending degrees, so that they can be classed in groups under groups. This classification is evidently not arbitrary like the grouping of the stars in constellations" (Darwin, 1859, p. 411).

¹⁶ Darwin (1859) explained how "descent with modification" would account for the observed order. "Naturalists try to arrange the species, genera, and families in each class, on what is called the Natural System. But what is meant by this system? Some authors look at it merely as a scheme for arranging together those living objects which are most alike, and for separating those which are most unlike; or as an artificial means for enunciating, as briefly as possible, general propositions,—that is, by one sentence to give the characters common, for instance, to all mammals, by another those common to all carnivora, by another those common to the dog-genus, and then by adding a single sentence, a full description is given of each kind of dog. The ingenuity and utility of this system are indisputable. But many naturalists think that something more

is meant by the Natural System; they believe that it reveals the plan of the Creator, but unless it be specified whether order in time or space, or what else is meant by the plan of the Creator, it seems to me that nothing is thus added to our knowledge. Such expressions as that famous one of Linnaeus, and which we often meet with in a more or less concealed form, that the characters do not make the genus, but that the genus gives the characters, seem to imply that something more is included in our classification, than mere resemblance. I believe that something more is included; and that propinquity of descent,—the only known cause of the similarity of organic beings,—is the bond, hidden as it is by various degrees of modification, which is partially revealed to us by our classifications" (Darwin, 1859, p. 413).

Cain succinctly summarized this idea. "The natural classification was built up by non-evolutionists on natural affinity; the explanation is to be found in the theory of evolution" (Cain, 1959, p. 208).

¹⁷ Brady explained, "Thus, whilst recognising fully the value of the plan . . . of grouping the almost endless varieties of Foraminifera round a small number of typical and subtypical species, as a method of study, and indeed as almost the only means of obtaining a serviceable knowledge of the entire Order, I have been unable to follow them so far as to make it a basis of nomenclature" (Brady, 1884, p. vii).

¹⁸ "Linnaeus' statement, in fact, is contradictory to his own principles" (Cifelli, manuscript comment).

¹⁹ Darwin observed that, "With species in a state of nature, every naturalist has in fact brought descent into his classification; for he includes in his lowest grade, or that of a species, the two sexes; and how enormously these sometimes differ in the most important characters, is known to every naturalist. . . . The naturalist includes as one species the several larval stages of the same individual, however much they may differ from each other and from the adult; as he likewise includes the so-called alternate generations of Steenstrup, which can only in a technical sense be considered as the same individual. He includes monsters; he includes varieties, not solely because they resemble the parent-form, but because they are descended from it" (Darwin, 1859, p. 424).

²⁰ Darwin commented, "It may even be given as a general rule, that the less any part of the organisation is concerned with special habits, the more important it becomes for classification" (Darwin, 1859, p. 414).

²¹ Darwin stated that, "Their importance for classification . . . depends on their greater constancy throughout large groups of species; and this constancy

depends on such organs having generally been subjected to less change in the adaptation of the species to their conditions of life" (Darwin, 1859, p. 415).

²² Darwin made the observation, "That the mere physiological importance of an organ does not determine its classificatory value, is almost shown by the one fact, that in allied groups, in which the same organ, as we have every reason to suppose, has nearly the same physiological value, its classificatory value is widely different" (Darwin, 1859, p. 415).

VI. ESSENTIALISM AND EMPIRICISM IN NINETEENTH CENTURY FORAMINIFERAL CLASSIFICATION

¹ "There is no reason not to take d'Orbigny at his word when he said that he deliberated a long time before reaching a decision on how to define his families. Actually, there are just two aspects of a foraminiferal test that might be considered of fundamental importance. One concerns its mode of growth and is reflected in the arrangement of chambers, the other concerns secretion of the test which is reflected in the texture of the wall. The reason d'Orbigny may have chosen chamber arrangement, a reflection of growth, is that most foraminifera were still grouped with cephalopods at the time. To combine such disparate organisms, the chambered condition of growth had to be considered an essence of first importance. Single-chambered forms were problematic because, unlike other foraminifera, they do not grow by the addition of chambers. In his original classification, d'Orbigny made no provision for single-chambered forms" (Cifelli, manuscript comment).

² Dujardin's discovery that foraminiferans were not "microscopic cephalopods" had, in the words of Brady, "Made it known the true nature of the organisation of the Rhizopoda, and had necessitated the removal of the group to a lower position in the zoological scale" (Brady, 1884, p. 48).

³ "Schwager (1876) showed his consistency, however, by separating the lagenid genera into several families, and in a formalistic sense was therefore justified in regarding his classification as natural" (Cifelli, manuscript comment).

⁴ Williamson, in the Preface to his *Recent Foraminifera of Great Britain*, commented that, "Though of late years many inquiries have paid special attention to these minute creatures, it is surprising how much ignorance still exists respecting their philosophy and

general affinities; an ignorance that reflects itself in most of the works that have been devoted to their classification and description" (Williamson, 1858, p. v). Later on in the preface, he rather dramatically concluded that: "In the absence of direct knowledge, we can only concentrate such faint rays as gleam through the darkness, and thus try to obtain some glimpses into this obscure recess of nature's domain" (Williamson, 1858, p. x).

⁵ Williamson noted that, "Such differences in the chemical and histological composition of these shells probably indicate correlate physiological differences in the living sarcode, or secreting animal substance, that have at least specific value" (Williamson, 1858, p. xi).

⁶ "Hence, . . . it has been found," Darwin emphasized, "that a classification founded on any single character, however important that may be, has always failed; for no part of the organisation is universally constant" (Darwin, 1859, p. 417).

⁷ Carpenter had pronounced that there was "no evidence of any fundamental modification or advance in the Foraminiferous type from the Palaeozoic period to the present time" (Carpenter, 1862, p. xi).

⁸ Darwin concluded that, "It is not an insuperable difficulty that Foraminifera have not progressed in organisation, as insisted on by Dr. Carpenter, since that most ancient of all epochs the Laurentian formation of Canada; for some organisms would have to remain fitted for simple conditions of life and what better for this end than these lowly organised Protozoa?" (Darwin, 1866, p. 402).

⁹ "Natural selection acts," Darwin believed, "exclusively by the preservation and accumulation of variations, which have been beneficial under the organic and inorganic conditions of life to which each creature has been exposed at each successive period of time. The ultimate result is that each creature tends to become more and more improved in relation to its conditions of life. This improvement inevitably leads to the gradual advancement of the organisation of the greater number of living beings throughout the world" (Darwin, 1866, p. 140).

¹⁰ Darwin's rationale was as follows. "But it may be objected that if all organic beings thus tend to rise in scale, how is it that throughout the world a multitude of the lowest forms still exist; and how is it that in each great class some forms are far more highly developed than others? Why have not the more highly developed forms everywhere supplanted and exterminated the lower? . . . On my theory the present existence of lowly organised productions offers no difficulty; for natural selection includes no necessary and universal law of

advancement or development—it only takes advantage of such variations as arise and are beneficial to each creature under its complex relations of life. And it may be asked what advantage, as far as we can see, would it be to an infusorian animalcule to be highly organized? If it were no advantage, these forms would be left by natural selection unimproved or but little improved; and might remain for indefinite ages in their present little advanced condition. And geology tells us that some of the lowest forms, as the infusoria and rhizopods, have remained for an enormous period in nearly their present state” (Darwin, 1866, p. 143).

Cifelli in his manuscript commented that, “This argument sounds not at all convincing and one wonders whether Darwin truly believed it. Even if correct it could not have resolved the erroneous dilemma posed by Carpenter.”

¹¹ Carpenter (1862) and Williamson (1858), however, both seemed to harbor a sense of the “potentialities” of the simple foraminiferan. Carpenter had believed that the complex structure of the foraminiferal shell indicated the “*potentialities* of the apparently homogenous jelly-like mass which it encloses” (Carpenter, 1862, p. 44). While Williamson lamented the fact that, “We have hitherto failed to detect the real specific peculiarities, or even to ascertain in what part of the living organism they are likely to be found. As yet they are but unseen *potentialities* of which the eye has hitherto been unable to detect any concrete or objective manifestation” (Williamson, 1858, p. x).

¹² Nonetheless, Darwin maintained that, “To suppose that most of the many now existing low forms have not in the least advanced since the first dawn of life would be extremely rash; for every naturalist who has dissected some of the beings now ranked as very low in the scale must have been struck with their really wondrous and beautiful organization” (Darwin, 1866, p. 143).

¹³ “Actually, foraminifera have been even more innovative in shell design, displaying a greater variety in chamber arrangement, coiling, wall structure and internal structure. By comparison, the cephalopods have displayed a more ‘locked in’ architecture and their only real advancement has been to completely discard the shell, as in the octopus and the squid” (Cifelli, manuscript comment).

¹⁴ “This oversight seems all the more odd since the ammonites, which display a similar but much more limited shell design and a less continuous fossil record, have always been considered prime examples in support of evolutionary theory” (Cifelli, manuscript comment).

¹⁵ In his original manuscript, Cifelli commented, “If a finger has to be pointed at a single ‘culprit,’ my choice would be Dujardin, who relegated the foraminifera to the ‘lowest forms of life.’ Dujardin’s very expression in dropping the foraminifera in hierarchical rank suggests a certain amount of scorn. Darwin stated that ‘some organisms would have to remain fitted for the simple conditions of life and what could be better fitted than these lowly organized Protozoa?’ (Darwin, 1866, p. 402). This statement reads like a social attitude about class translated into scientific jargon. It may sound far-fetched to suggest that the foraminifera have been ‘discriminated against,’ but probably about anybody who has pursued a career in this field has heard a remark from a paleontological colleague at one time or another implying that foraminifera, while being of commercial value, really do not have the scientific importance of organisms higher up the evolutionary scale.”

¹⁶ Von Baer’s Law states that development proceeds from the generalized condition to the specialized condition; therefore, the embryonic stages of closely related organisms may be identical. Distinguishing traits develop later in ontogeny.

¹⁷ Palingenesis involves the repetition (or recapitulation) in the ontogeny of an individual, of earlier phylogenetic stages.

¹⁸ Cenogenesis involves the development of new adaptive characters in the embryonic or larval stages of an organism that were not present in the ontogeny of the ancestor.

¹⁹ “Scarcely a decade after the publication of the *Origin of Species*, Waagen (1869) proposed [evolutionary] lineages for ammonite families in the Jurassic” (Cifelli, manuscript comment).

²⁰ “With this kind of shell to work with, it is not surprising that ammonite specialists became enthusiastic about Haeckel’s law of recapitulation. According to this law (actually a corruption of the original biogenetic law), evolution proceeds through a succession of adult stages, so that the early stages of an individual represent the adult stages of its ancestors. Alpheus Hyatt was the leading protagonist of recapitulation and he convinced not only other ammonite specialists but paleontologists in general that this simple morphogenic principle provided the key to natural classification. Hyatt, an eminent teacher at Harvard, was influential between 1880–1930 (Arkell, 1957). At times, of course, it was difficult to reconcile recapitulation with the realities of nature. Missing or improper developmental stages, therefore, were considered ‘teloscoped,’ ‘retarded,’ or ‘accelerated,’ which resulted in some family groupings of genera with little morpho-

logic similarity (Arkell, 1957)" (Cifelli, comment from an earlier version of the manuscript).

²¹ The *dimorphism* of Munier-Chalmas should not be confused with the same term which was used by Brady (1884) and others to refer to a change in growth plan of a particular individual species.

²² "He unfortunately wrote in a heavy, nineteenth century style of German that is difficult for a foreigner to fathom. Discouraging difficulties are encountered from the very beginning of his papers. (How does one translate the title of his 1897 paper 'Über die phylogenetisch abfallende Schalen-Ontogenie deren Foraminiferen und der Erklärung?') (Cifelli, manuscript comment).

²³ From the following excerpts of Rhumbler's (1897) paper, it seems clear that Rhumbler was comparing the development of foraminifera and metazoans at the cellular level and not at the organismal level, as Cifelli implies. "Perhaps there can be gained from this some information or at least illuminating sidelights for the phylogenetic behavior of cells in general, I mean the cellular tissue in the metazoan body also, for the evolution and transformation of an animal species will always be bound up with qualitative or quantitative alterations in the tissues, and these alterations probably scarcely progress without a corresponding alteration of the cells themselves. The question that appears to me to claim further interest and that I therefore would like to discuss here reads: is there in the development of the foraminifera a single law to be recognized and is this law perhaps not also meaningful for the phylogenetic development of the cells of metazoans in some way or another?" (Rhumbler, 1897, p. 162).

"Foraminifera are single *cells*," Rhumbler (1897, p. 188) emphasized. He argued that selection could also operate on cellular variations—such a process acting in metazoan development could lead to larval adaptations which might then result in radically different adult forms. And this phenomenon, he concluded, could not "have arisen without the independence of the variations of the single cell stage that is in question, being present also among the cells of metazoan development just as it surely is present among the foraminiferal cells" (Rhumbler, 1897, p. 188). [English translation of sections of Rhumbler's paper provided by R. Röttger, May 1982.]

²⁴ Heterochrony can be defined as an evolutionary change in the timing or onset of development; consequently, the appearance of a feature during development may occur at an earlier or later stage in the ontogeny of the descendant, than it had in the ancestor's ontogeny.

VII. EARLY TWENTIETH CENTURY STATUS OF FORAMINIFERAL CLASSIFICATION

¹ Schlumberger commented that, "These anomalies in the work of an author as conscientious and as experienced as Brady, is explained by the great and justifiable influence that Carpenter exerted, chiefly in England, on the manner of viewing and understanding of the zoologists that concerned themselves with the Foraminifera" (Schlumberger, 1891, p. 155).

² Neumayr made the following remark "We owe to Brady the newest classification of the Foraminifera, which brings together the total number of forms into ten families and within these he discerns more subfamilies; the majority of the divisions, which this learned scientist erects, correspond to good or roughly accurate natural groups, even if some points of divergence are necessary; it is however an unsatisfactory attempt that he made, to resolve the relationships to each other of the principal families. . . . In any case however we put Brady's classification to practical use and in details it is the most correct attempt at classification that we have so far" (Neumayr, 1887, p. 158).

³ Lister's (1903) rationale for the existence of species in foraminifera echoed the arguments proposed around the turn of the century, in support of discontinuous variation or inheritance. Proponents of "continuous variation," the majority of whom were biometricians and "strict Darwinians," believed in a blending theory of inheritance (Allen, 1978). That is, they believed that certain traits observed in the offspring were a blend (or an average) of those seen in the parents. Inherited characteristics transmitted in this way would not be seen to segregate in later generations.

The biometricians used statistical studies of variation within populations to support their ideas. Their opponents, however, maintained that while variation within a population may be of a continuous nature, variation between populations was observed to be discontinuous. Proponents of the view that hereditary variations were discontinuous soon found justification for their viewpoint when, sometime after 1900, the Mendelian "laws" of heredity were rediscovered (Allen, 1978).

Lister (1903) argued that, "It has long been recognised by systematists that in many cases the limits of the characters of the species of Foraminifera do not admit of being drawn with any exactness. This view was insisted on by Carpenter, who, in the '*Challenger*' Report on *Orbitolites* (p. 9), quotes with approval the doctrine that among the porcellaneous and vitreous Fo-

raminifera 'everything passes into everything else.'"

"... The question, however, appears to be not whether all intermediate terms do or do not exist between dissimilar forms, but whether the whole body of forms, as they occur in nature, tend to group themselves, or are aggregated about certain centres. If this is the fact, and the forms, as they occur in nature, are disposed not in a continuous series, but in a discontinuous one, the large number of individuals being grouped about distinct centres, we have the phenomenon which is comparable with that of species in other animals and in plants, whether the centres are or are not connected by intermediate terms. To refuse to recognise the existence of these centres, because transitional forms exist between them, is to ignore an essential fact. ... In a very large number of cases, at any rate, such centres do exist among the Foraminifera, as among other organised beings, and the characters of the middle individuals of them are those of the species" (Lister, 1903, p. 134).

⁴ Lister made the observation that: "The more complex members (*Orbitolites* ...) of the *Peneroplis-Orbitolites* ... series present excellent examples of the multiform condition. The facts that each of these is a series of closely related genera, and that the simpler members of each present in a permanent form the arrangement which is transitory in the growth of the more complex, appear to give substantial support to the view urged by Carpenter that the stages which we have called peneropline and orbiculine, ... in the growth of *Orbitolites* ... are, in fact, repetitions in ontogeny of a phylogenetic history" (Lister, 1903, p. 135).

⁵ Lister commented that, "Rhumbler, like Carpenter, regards the multiform tests of Foraminifera as of great value in tracing out phylogeny, but for precisely opposite reasons, for while Carpenter considers the early phases as representing a stage through which the stock has passed, Rhumbler sees in them the higher stage towards which it is advancing.

"As will be gathered from what has gone before, it does not appear to me that sufficient reason has been shown for discarding the view of Carpenter" (Lister, 1903, p. 137).

⁶ Douvillé had observed that, "The character of the test appears to depend, above all, on the habitat, it is arenaceous, compact or alveolar in forms of the deep, — calcareous imperforate in animals of the zone of calcareous algae, — calcareous perforate in pelagic forms. One realizes then that a simple change in habitat is sufficient to bring about profound modifications in the nature of the test" (Douvillé, 1906, p. 591).

⁷ Cushman stated that, "The Foraminifera as unicellular animals seem to present the simplest conditions and examples for the expression of the various laws of development that can be found anywhere in the animal kingdom" (Cushman, 1905, p. 547).

It was also in this paper that Cushman first defined the term *proloculum* which he believed to "correspond with the term applied to the embryonic shell of other groups already worked out in the Metazoa" (Cushman, 1905, p. 538). In his dissertation, Cushman expanded this idea and commented that, "The proloculum may be considered as the phylembryonic stage, and the equivalent in the Foraminifera of the protodissoconch stage as shown by Jackson in the Pelecypoda, or to the protegulum in Brachiopoda and the protapsis in Trilobita as shown by Beecher" (Cushman, 1909, p. 89).

⁸ Hyatt's Law of Morphogenesis states that, "A natural classification can be made by means of a system of analysis in which the individual is the unit of comparison, because its life in all its phases, morphological and physiological, healthy or pathological, embryo, larva, adolescent, adult, and old (ontogeny), correlates with the morphological and physiological history of the group to which it belongs (phylogeny)" (Hyatt, 1889, p. viii).

⁹ Hyatt maintained that, "All modifications and variations in progressive series tend to appear first in the adolescent or adult stages of growth, and then to be inherited in successive descendants at earlier and earlier stages according to the law of acceleration, until they either become embryonic, or are crowded out of the organisation, and replaced in the development by characteristics of later origin" (Hyatt, 1889, p. ix).

¹⁰ Hyatt maintained that, "The degraded uncoiled forms of the Nautiloidea and Ammonoidea, ... invariably have coiled young, showing that they were the offspring of coiled or nautilian shells, that is, of progressive forms which have themselves been evolved from a series of straight arcuate and gyroceran predecessors. Their uncoiling is a truly retrogressive character and this tendency is inherited in successive forms in several series, and thus the whole structure is finally affected, the whorl reduced in size, and the complication of the sutures and shells at all stages of growth is degraded until, in the development of the individual, only the close-coiled young remain to testify to their exalted ancestry. In other words, the forms really inherit degraded characteristics at such an early stage that it affects their whole life except the earlier stages" (Hyatt, 1894, p. 371).

¹¹ Atavism is defined as the appearance in an organism of an ancestral trait that had not been expressed

in recent generations. The aberrant individual is sometimes called a "throwback."

¹² "Moreover, he ignored the possibility of a ceno-genetic interpretation, and made no reference to Rhumbler's work. As it happened, Cushman's effort to model developmental stages received even less notice than Rhumbler's had, and it quickly passed into obscurity. Cushman never again tried to view the foraminifera in a broader biologic context and thereafter confined himself to the role of specialist" (Cifelli, manuscript comment).

¹³ Lister had emphasized that, "There seems good reason to hope that the study of the plan of growth of both forms [microspheric and megalospheric] of the species during the early stages of their life-histories may throw light on the complicated problems of phylogeny. Until these early stages have received fuller attention, and we have arrived at a conclusion as to the relation of the early to the later stages of the multiform test, efforts at forming a 'natural classification' appear to be premature" (Lister, 1903, p. 140).

¹⁴ Cushman explained his method as follows, "In general those species which have similar stages in development should be grouped together as species within a genus, or in associated genera. Such species may differ much in the adult. The development, as is proved in other groups of animals should be taken as a basis for genetic relationships. On this basis a classification may be built up which is in accordance with the facts of development, and therefore with true relationships and the various differential lines of development definitely connected with the more primitive types" (Cushman, 1909, p. 15).

¹⁵ Cushman stated that, "As shown by Hyatt the ideal classification should be built up by comparative study of the young and adult and a correlation of these with successive genera in geological time. Such classifications have been worked out by Hyatt for the Cephalopoda, by Jackson for the Pelecypoda and Echini, and by Beecher for the Brachiopoda and Trilobita" (Cushman, 1909, p. 15).

¹⁶ "One of the thornier problems in Cushman's scheme of relationships based on similarity of early developmental stages was posed by the perforate proloculus of *Peneroplis* discovered by Rhumbler (1897) and confirmed by Lister (1903). Cushman had no solution to the problem and merely suggested that *Peneroplis* may have been derived from a perforate ancestor" (Cifelli, manuscript comment).

¹⁷ "Of course, Cushman was not totally responsible for this reversal of attitude, because his thesis was never published. Cushman's methods did not become fully

known until his classification appeared in 1927" (Cifelli, manuscript comment).

VIII. THE AGE OF CUSHMAN

¹ The fourth edition of *Foraminifera—Their Classification and Economic Use* underwent its sixth printing in 1980 and copies of the text are still available today from the Harvard University Press.

² "From his boyhood, Cushman showed a keen interest in natural history and collected all kinds of objects. He also retained a lifelong interest in sports and was a good enough athlete to have been elected captain of his high school baseball team (Todd, 1950). In addition, he was a rather gifted artist, showing a talent for watercolor and pen and ink work. A number of his watercolors of New England landscapes and other scenes, now hang in the Cushman Room that houses the foraminiferal collections in the National Museum of Natural History. A curious hobby of Cushman's was his pen and ink drawings of animated penguins. [See Fig. 2.] Through these drawings he caricatured himself and his family, and showed his affectionate regard for New England history. During the years of the Depression he used these penguins to voice his conservative, anti-New Deal political views" (Cifelli, manuscript comment).

³ Cushman published several papers on the desmids (microscopic, unicellular freshwater plants) of New England, Ohio, Colorado, Newfoundland, and other areas. See the "Bibliography of Joseph A. Cushman" in the Memorial Volume of the Cushman Laboratory for Foraminiferal Research published in 1950 for a complete listing of his early papers.

⁴ The Museum agreed not to send Cushman "the entire collection at once," but to forward it "in lots from time to time" as "the number of samples of ocean bottom containing foraminifera is very large, and the labor of working out these minute objects will necessarily take much time." It was also agreed that Cushman's complete investigations "would be published by the National Museum, but interesting finds or the description of new species should they be discovered, could be printed in advance in separate preliminary papers, in the Proceedings of the Museum." (Rathbun to Cushman, 16 March 1906, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.)

⁵ Cushman's early work with the Survey involved the study of the foraminiferal faunas identified in Panamanian material that had been collected in 1911 by

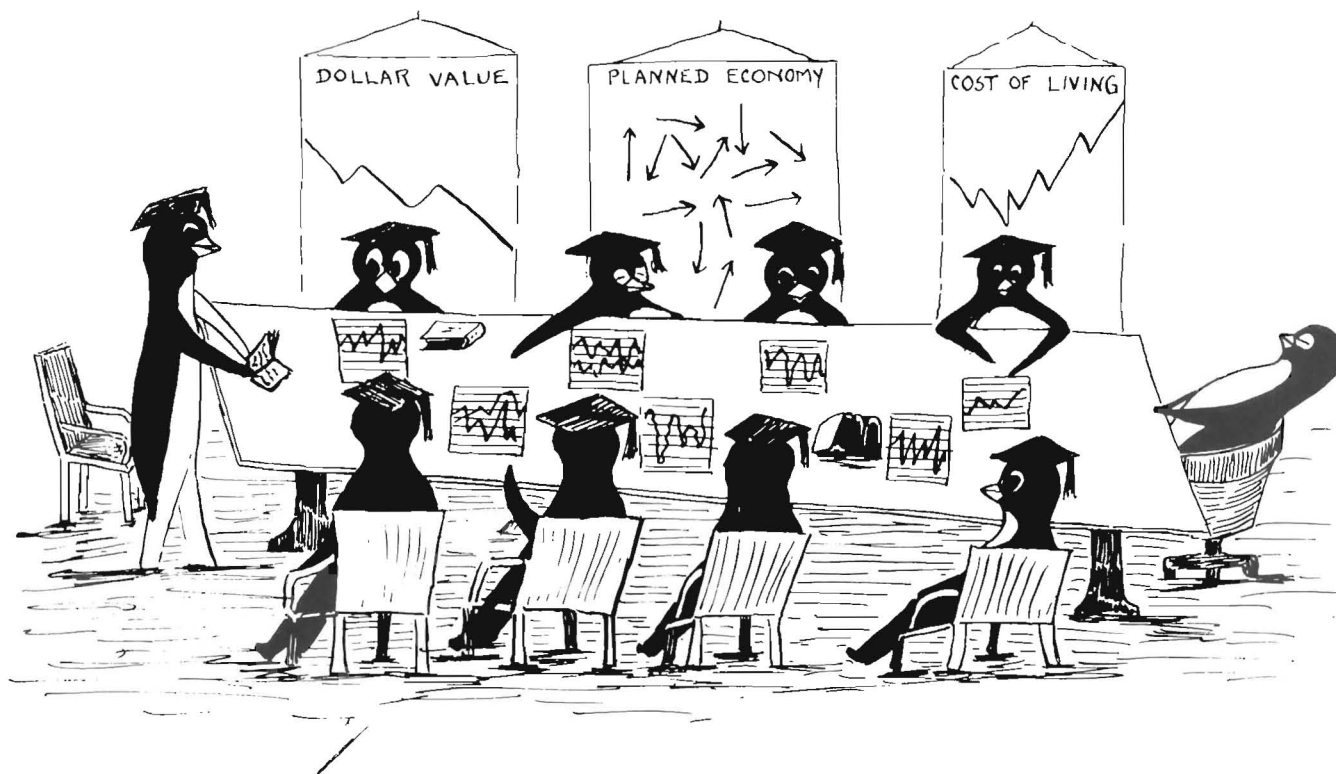


FIGURE 2. Political cartoon sketched by Joseph Cushman. (Photo courtesy of the Todd Library for Foraminiferal Research, Smithsonian Institution, Washington, DC.)

T. Wayland Vaughan and Donald F. MacDonald, and the analysis of Cretaceous and Tertiary "foraminiferal material" collected from "various North American localities" in the Coastal Plain. Information obtained from the Panamanian study was incorporated into the reports sent by Vaughan to the Isthmian Canal Commission, and was eventually published in the *Bulletin of the U.S. National Museum* (Cushman, 1918a, b). Material for the Coastal Plain study, which included both surface and subsurface samples, was sent to Cushman in Boston from various sources including the U.S. National Museum, the Philadelphia Academy of Sciences, Johns Hopkins University, and the State Museum of Alabama. Some of the results from the Coastal Plain study were incorporated into a U.S. Geological Survey Professional Paper on "A Deep Well at Charleston, South Carolina" (Stephenson, 1915) in which Cushman reported on the distribution of foraminiferal species within the well and recognized not only stratigraphic zonations, but also some paleoecological implications of the faunas. Another paper on "Some Pliocene and Miocene Foraminifera of the Coastal Plain of the United States" was later published by the Survey (Cushman, 1918c).

In 1917, due to the increasing demands on the Survey for "work in connection with military affairs," all paleontological work was temporarily suspended. No provisions were made for "any Coastal Plain paleontology" and consequently no allotment was made to Cushman for his work. Cushman, however, continued his work without remuneration from the Survey.

Cushman was concerned about his personal contribution to the war effort and in May 1917 he received permission from the Survey to enlist in a State Guard company which was then forming in Sharon. Cushman must also have been seriously considering going abroad to help, in other more direct ways, win the war. In an attempt to dissuade him from such action, T. Wayland Vaughan wrote, "Your work on fossil forams may not seem of much importance to you: but it is! and through it you will almost certainly contribute more to winning the war than you can be serving as a member of a Red Cross unit. You know I am trying to bring together the results of a number of investigators, in order that geologic formations may be finely discriminated and defined. And just as rapidly as possible I am trying to make the results available for use by those who are conducting field operations, probably but little per-

sonal reward, either financial or in credit, will come to any of us, but if the work is done properly, we shall have accomplished much in making possible the intelligent development of the natural resources of the earth, and thereby we shall have rendered a public service of no small value.

"For you to continue your work without the support it should have may be a greater sacrifice than you can stand; but, if it is practicable, I hope you will continue the researches in which you have now become our preeminent authority. Others may render Red Cross service, but you are the only one we have who can do trustworthy work on forams." (Vaughan to Cushman, 29 November 1917, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.)

Cushman replied, "You know much more than I of the worth of my present work and its bearing on the bigger problems ahead of us. I feel that what you write is both from professional interest and personal interest as well. I know too that I can rely on your judgement. For some time I have wondered if I could not do something more definitely in the line of helping in the direct war work and of putting my energies where they would seem to throw weight directly to that end. The work of State Guard drill seems sometimes rather a poor outlet for my energies but they seem more likely to perhaps be of some use. But . . . that has not seemed to me to be my real job. There are plenty of others who have no special training for any particular line of work who can do that just as well. I realize that no one has worked very much in this country with the forams and they are getting nearer every month to definite positions and correlations. There is so much that I wish to do with them. Your letter seems to definitely remove the objection I would have made that they can wait. Perhaps all the other work can wait or be done better by someone else. It had been hard for people to understand how my work here at the Museum in working on fossils for the U.S.G.S. could really be doing any public good. It will be easier to deal with hereafter." (Cushman to Vaughan, 1 December 1917, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.)

In May 1918 Cushman left Boston for North Carolina to do field work on the marls and limestones of the eastern part of the state, and in addition to make a detailed study of the Newbern quadrangle for the purpose of preparing a report embodying information of military value. He was unable, however, to complete the project, having undergone a recurrence of a pul-

monary condition, and was forced to return home to Sharon to recuperate.

⁶ Cushman was later taken back on briefly with the Survey, but then resigned again just before setting out for Mexico in January 1923 (Todd to Cifelli, 26 February 1983, Cifelli Correspondence, Department of Paleobiology, National Museum of Natural History, Washington, DC).

⁷ "While Cushman was at the top grade level in the Survey, his salary was hardly enough to meet the expenses of the Laboratory. However, among Cushman's numerous talents was one for investing. With no interruption to his research schedule, he not only managed to survive the depth of the Depression, but he eventually amassed a small fortune in the stock market by following the financial reports in the newspaper and on the radio (Henbest, 1952)" (Cifelli, manuscript comment).

⁸ Schuchert to Cushman, 17 October 1926, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.

⁹ Cushman described this evolutionary scenario in the "phylogeny of the Buliminidae" as follows "In the Lias there is developed an elongate spiral form which has an elongate simple tubular chamber of several volutions, ending in a simple aperture, somewhat constricted. This is the genus *Terebralina* Terquem . . . From this simple structure may be derived by successive stages all the other genera of the family" (Cushman, 1927b, p. 319).

¹⁰ "An ideal classification should be based upon the known phylogeny of a group as shown by the fossil record, and coupled with the ontogeny of the individual as shown in its complete development together with what may be learned of the morphology and physiology of the group" (Cushman, 1928, p. 47).

¹¹ The Law of Priority states that, "The valid name of a taxon is the oldest available name applied to it" (Stoll and others, 1961, p. 23).

¹² Cushman's textbook underwent subsequent revision; the second edition appeared as Special Publication No. 4 of the Cushman Laboratory (Cushman, 1933), while the third and fourth editions were published by the Harvard University Press (Cushman, 1940, 1948).

¹³ Cushman (1928) devoted an entire chapter to "Trimorphism," in which he discussed the problems associated with the phenomenon and suggested methods of dealing with it in taxonomic analyses. He concluded his discussion with the following commentary. "A closer understanding of the results of the trimorph-

ism must lead to a simplification of our treatment of species entirely from the megalospheric form even though that may be the more common one. Sections should be obtained, if necessary to know whether the worker is dealing with a microspheric or a megalospheric form that he may search his material for the microspheric form if he does not have it. It will undoubtedly be possible to unite species under a single name where they now may be placed as different species and under different genera. This task of simplification and grouping together of forms does not mean that there are not very many species and genera of the foraminifera, but that the known facts of development have not been taken into account in naming forms or in grouping them" (Cushman, 1928, p. 360).

¹⁴ Carpenter, it will be recalled, believed that, "A very decided differentiation may be established between the two series of *imperforate* and *perforated* FORAMINIFERA; and this primary differentiation will be found so constantly to harmonize with the grouping which would be based on the principle of continuity of gradation, that I cannot entertain a doubt of its being the one on which . . . our classification may be most securely based" (Carpenter, 1862, p. 52).

¹⁵ Schuchert to Cushman, 22 November 1926, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.

¹⁶ Cushman to Schuchert, 26 November 1926, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.

¹⁷ In later versions of the text, Cushman commented that although these forms "all have certain characters in common, . . . it may be that some of these are more or less degenerate forms, and do not have the same ancestral source" (Cushman, 1940, p. 190; 1948, p. 207).

¹⁸ "The principle of acceleration is risky where morphologic evidence is totally lacking and it becomes difficult to maintain consistency. It is not at all clear how a form like *Nodosaria* can be distinguished from the uniserial *Reophacidae*" (Cifelli, manuscript comment).

¹⁹ In fact, in later editions of the text, Cushman remarked that, "The earliest known species of *Verneuilina* are . . . very elongate, and resemble *Textularia* in all respects except that they are triserial. The only difference between these Jurassic forms and the type is the sharp angles in the later forms of the Cretaceous. Some specimens of *Gaudryina* from the Triassic also have an intermediate form in the rounded angles of

the chambers. Typical biserial *Textularias* occur with these triserial *Verneuilinas*, and the resemblance is very close" (Cushman, 1933, p. 112).

²⁰ In the second and third editions (1933, 1940) of Cushman's textbook, the section on the family Fusulinidae was written by Carl O. Dunbar. In the fourth edition (Cushman, 1948), Dunbar authored a section on "Fusuline Foraminifera," in which he revised the family Fusulinidae, and described the family Neoschwagerinidae for the first time.

²¹ In his chapter on "Classification," Cushman mentioned that "In the Fusulinidae, derived from *Endothyra*, are some of the largest Paleozoic foraminifera, which become complex in their internal structure" (Cushman, 1933, p. 56).

²² In the same manner that many earlier workers had used the term "protean" to describe the variable nature of the Foraminifera as a whole, Cushman thus characterized his family Lagenidae. "In many ways the entire group appears protean. The genera are not clearly defined as are those of most other families. It is possible in the same species from a single fossil sample or recent dredge haul to find megalospheric forms referable to *Nodosaria*, specimens with a small proloculum and curved test referable to *Dentalina*, and one with a still smaller proloculum coiling at the base and referable to *Marginulina*" (Cushman, 1927a, p. 47; 1928, p. 194).

²³ "As it is well known that the Lagenidae form one of the most plastic groups of the foraminifera and that polymorphism or trimorphism is present to a large extent, generic characters are much harder to define than in some of the more stable families" (Cushman, 1928, p. 194).

²⁴ "The early perforate chambers form a very puzzling problem in the classification of the group showing that they were derived from a perforate ancestry. Just what that ancestry may be is not easily seen at present but must be solved by a study of Cretaceous material where there are forms referred to *Peneroplis* that seem to hold the clue to this problem. They have kept to the planispiral form and in many ways show a close resemblance to the Camerinidae" (Cushman, 1928, p. 223).

²⁵ Their form was "easily derived from such a genus as *Peneroplis* by the division of the close coiled forms into chamberlets and an elongation of the axis" (Cushman, 1928, p. 227). However, in later editions of the text Cushman dropped this statement and made no other reference to the possible origin of this family, other than commenting that, "From the Ammodiscidae have probably developed the planispiral forms,

one group of which, the Peneroplidae, Alveolinellidae, and Keramosphaeridae, have an imperforate calcareous test in the adult, but the earliest stages in some forms are apparently perforate" (Cushman, 1948, p. 58).

²⁶ Galloway (1933) denied that there were any known instances of an arenaceous form becoming calcareous in the later stages of its ontogeny.

²⁷ On this idea, Cushman further elaborated. "H. Douvillé . . . has given some statements along the line of classification that can hardly be improved upon. 'The foraminifera are all derived from a fundamental form which is spirally coiled and symmetric.' This is true for most groups and the spiral forms of *Ammodiscus*, *Spirillina* and *Cornuspira* with their modifications into spirals of various types from early simple genera in most of the more primitive families in this outline" (Cushman, 1927a, p. 3).

²⁸ About this classification, Cushman explained in a June 1925 letter to Galloway, "The paper that the Smithsonian is publishing of mine is simply a paper to place in the hands of workers, giving figures of the various genera as at present used with short descriptions, and something as to general development, etc., with a bibliography. It is in no way a revision of the genera, such as you are undertaking, but simply a sort of primer of the forams." (Cushman to Galloway, 1 June 1925, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.)

A comparison of Cushman's 1925 classification with Brady's 1884 scheme will show that Cushman adopted Brady's family groupings and subfamilial divisions with very few modifications.

²⁹ Earlier that spring, Galloway had remarked that it would be another year before he could get the *Manual* out, and that, "The manual is coming along slowly. I have rewritten it and have 325 good genera and 150 synonyms placed, with about 200 generic names to study and place." (Galloway to Cushman, 19 April 1926, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.) Cushman replied immediately, in a letter dated the next day, and invited Galloway to Sharon for a weekend. "I am very much interested in your coming manual, and I want to do everything possible to help make it in such a form that it will meet all criticism, so that we may go ahead on the basis of the genera given and have a uniform terminology, even though it may not be followed outside of America at once. If you could find some week end next month, I should be very glad indeed to have you

come up and spend it with me here, when we could have an opportunity to go over many of the questions that may have arisen, and find means for their complete solution if possible." (Cushman to Galloway, 20 April 1926, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.)

Galloway then made arrangements to take the train from New York to Sharon over the weekend of May 8, 1926. The weekend conference was apparently mutually beneficial, and on May 10, Cushman wrote Galloway, "The present scheme as you have it is in my mind so very much nearer the truth than was that which you had at New Haven that it has pleased me immensely. I think that there are various other changes that might possibly be made after the study of more material and going over some of the other possibilities. There is plenty of time, however, to do this, and I think you were very wise in not letting it get into permanent form until it met with your entire satisfaction along every line. There are a number of things that even in my present state of lack of concentration [Cushman had just had an abscessed tooth extracted that afternoon] I can see might have different solutions, and I would like very much to think these over and then perhaps suggest them for your consideration. I hope you may be able to get to Europe this summer, and possibly get hold of some of the earlier types, which would once and for all settle not only some of the difficulties of the genera but also what must come later what are certain of the older species." (Cushman to Galloway, 10 May 1926, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.) Cushman concluded the letter by inviting Galloway's students to visit the Laboratory "at any time," as well as to make use of "anything in the way of books or specimens," and he expressed the hope that it would not be long before Galloway, himself, returned to Sharon.

³⁰ In this letter he had casually remarked that, "It is fascinating work to study the actual young of many of these forms, and I am putting much of it together into a classification that will meet many of the tests of study of development." (Cushman to Galloway, 10 December 1926, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.)

It was not until February 1927 that Cushman informed Galloway of his forthcoming paper. "Very soon I shall have ready a paper on which I shall be glad of your comments. In getting ready for my students, this

last year, it became necessary for me to go over my notes during the twenty-five years I have worked on the forams, and to fit in many of them with the work that had been done by the many other writers on the group. As a result, many things that had been held back for years came to the fore, and out of it came what I am calling 'An Outline of a Re-Classification of the Foraminifera.' It was necessary to get it into such form that my students could have it, and it will help answer the flood of letters that pour into the Laboratory from this country and outside asking my opinion of this and that genus, often accompanied by specimens. There is so much of this that I have often become swamped, and it has been difficult to answer fully without sending figures or specimens. This simple outline will give my own ideas based really on the published work that has accumulated during the last twenty-five years from other writers. I hope you can take over a lot of it into your Manual when it is published, although it is very different in structure from your groupings as expressed in the table, you left me last spring. I have studied many specimens in section as well as large fossil and recent series, and feel that I have come much nearer to the truth than as it was expressed in the earlier classifications. I am enlarging . . . the phylogenetic side in a series of papers in the American Journal as Professor Schuchert has been after me to do for about five years. The paper will make the next number of our Contributions, and should be mailed this coming week. I shall value your comments on it." (Cushman to Galloway, 21 February 1927, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.)

³¹ Galloway claimed, "Your Outline of a Re-Classification came to me as a distinct surprise, as I had no idea that you were working on such a thing, since you made no mention of it at New Haven, or when I visited you last year, nor in your letters, and since you had just published a classification two years ago. The new classification, I believe, contains a great deal of truth, for it embraces many of the ideas which I have expressed publicly and to you in our conferences and correspondence. Schubert was the first, so far as I know, to make a classification based on phylogeny and basing the phylogeny on ontogeny, about 30 years ago. The final classification of Foraminifera will undoubtedly be based on structure, ontogeny, geologic range and the resulting interpreted phylogeny. While your classification is on the right track, I entertain no idea that it is the final one. Your method of showing relationships by illustrated phylogenetic trees in very effective. It is

the same kind that I am using in my Manual and that I showed in slides in New Haven." Galloway concluded his letter with the following statement, "I do not care for priority or I should have published my preliminary outline long ago, but I do care for the truth and stability." (Galloway to Cushman, 9 March 1927, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.)

Cushman responded to Galloway's criticisms, rather cheerfully and commented that, "This grouping is not Utopia but I feel it is a forward step." (Cushman to Galloway, 16 March 1927, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.)

³² Cushman wrote, "Now that you and I are so close on so many generic names, there seems to be great hope of a rather uniform terminology which will be very useful. I hope before my larger work is completed that we shall be still nearer on the classification based on developmental stages." (Cushman to Galloway, 26 April 1927, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.)

³³ "I am at a loss to know why you think it necessary or advisable to publish a revision of the classification which will be necessarily very much like my own." (Galloway to Cushman, 29 April 1927, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.)

³⁴ Galloway to Cushman, 29 April 1927, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.

³⁵ Cushman to Galloway, 2 May 1927, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.

³⁶ Galloway to Cushman, 23 February 1928, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.

³⁷ Galloway to Cushman, 2 March 1928, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.

³⁸ "Please be very sure that I have no personal feeling in the matter of the forams at all. I am sorry if the fact of my own work on the forams has caused difficulties. From your letter of nearly a year ago in which you

stated that your final work was practically ready for the press, I told you that it would not be until this spring before my final work was published. I had therefore expected to hear that your book would be out this fall, and have been looking for it. Mine had to await the actual examination of genotype specimens in Europe, and the going over of various points personally with some of the European workers. Others have written some of the chapters in my work, and in fairness to them and to the publishers as the work is now in type, I am sorry it cannot be held up.” (Cushman to Galloway, 8 March 1928, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.)

³⁹ “I have been asked as to the possibility of my getting out a general work on Micro-paleontology covering forams, ostracods and the other groups. I should like very much to do this and have the matter in mind. Some of the groups I have never done any personal work with and the necessary studies would take time from what I consider my special field.”

“Why do you not go one step further and take up this side also? You are conversant from your teaching and experience with the various micro-paleontologic groups. Can you not enlarge your book to take in the other groups and make what would be a real text book of micro-paleontology which publishers would compete with one another to get with the growing interest in the subject.” (Cushman to Galloway, 8 March 1928, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.)

⁴⁰ Cushman to Galloway, 8 March 1928, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.

⁴¹ “I am sure that Dr. Cushman got the idea of making a revision of the genera of Foraminifera from me, that he saw it was too good a thing to let anyone else do, and that he deliberately decided, after May, 1926, to forestall me with a similar work of his own.” (Galloway to Howe, 9 March 1928, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.)

⁴² “I do not consider that any man has a monopoly upon revisions or classifications of any group of the animal kingdom, and even if you both had published or were about to publish such a revision and I felt that I were in a position to publish such a revision myself, which in all probability would not agree with either of

yours, I should feel myself perfectly free to do so. In other words text books are not in the same category with original material. I cannot feel that you have any monopoly upon expressing opinions as to other persons genera, tho [*sic*] I would of course at once consider that you had a monopoly upon any *new* genus or *new* species that you might have found, or upon any unmonographed group or fauna upon which you might be working, tho [*sic*] in the latter case there is unquestionably a time factor of some importance.” (Howe to Galloway, 13 March 1928, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.)

⁴³ “I do not think you will help yourself, and certainly you will do great damage to the society by raising a clamor over it, for it then resolves itself into a question of one man’s word against another with the odds all in Cushman’s favor, for it hardly seems likely that he would have pledged away his right to publish a text book upon the group to which he has devoted his life work.” (Howe to Galloway, 13 March 1928, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.)

⁴⁴ Cushman to Howe, 15 March 1928, Cushman Papers, Todd Library for Foraminiferal Research, Department of Paleobiology, Smithsonian Institution, Washington, DC.

⁴⁵ This statement on the arenaceous nature of Paleozoic foraminifera was made by Cushman in his chapter on “Geologic Distribution,” and can be found in all editions of his textbook. As previously mentioned, the sections on fusulinids and fusuline foraminifera had been written, not by Cushman, but by other authors; Ozawa, in the first edition, and Dunbar, in the second, third, and fourth editions. Ironically, while Dunbar (in Cushman, 1933, p. 126) described the fusulinid wall as being calcareous, and imperforate (1933) or perforate (1940, 1948), Cushman reiterated his views on the arenaceous wall-types of Paleozoic forms, through all four editions of his text (1928, p. 44; 1933, p. 47; 1940, p. 49; 1948, p. 49).

⁴⁶ Galloway described his interpretations of the wall structure of Paleozoic forms in detail. “Calcareous walls, composed of minute, granular crystals of calcite, occur in many Paleozoic genera, such as *Matthewina*, *Endothyra*, *Globovalvulina* and *Monogenerina*. Such walls have been interpreted as finely arenaceous because the crystals appear as granules under high magnification. The crystals are not abraded nor are they

cemented together, and it is therefore probable that they were secreted by the animal. . . . Calcareous, transversely fibrous, crystalline walls are seen in many Paleozoic genera, such as *Endothyranella*, *Spandelina*, *Archaediscus* and in the Fusulinidae. The fibrous walls are interpreted by some students as due to recrystallization and are regarded as arenaceous by others. It is more likely that they are in their original condition and were secreted by the animal, for the walls and test are not distorted but show all the other structural characters as they were originally. The walls of the Orbitoididae are also transversely fibrous and apparently in their original condition. . . . Some genera have walls made up of an inner fibrous, calcareous layer and an outer, granular layer in which may be included large, calcareous grains, as in *Tetraxis*, *Palaeotextularia*, *Deckerella* and *Bradyina*. Such walls have been regarded by many authors as entirely arenaceous instead of what they are, viz., calcareous walls, secreted by the animal, with attached foreign grains. . . . Alveolar, calcareous walls, with thin, outer, minutely granular layer, are typical of the Schwagerininae, Verbeekinae and some of the Endothyridae and Nodosinellidae. Some authors have interpreted such walls as being arenaceous, for which interpretation there is little or no evidence. The walls are more likely in their original condition, excepting for the infiltration of calcite in the alveoli, and were secreted by the animal" (Galloway, 1933, p. 30).

⁴⁷ Galloway interpreted the wall structure of the Precambrian genus *Cayeuxina* and the Cambrian genus *Matthewina* as calcareous. *Cayeuxina* and *Matthewina* are now thought to be of inorganic origin (Loeblich and Tappan, 1964).

⁴⁸ "The origin of the development of septation remains an unsolved problem although various growth models have been proposed, most recently by Brasier (1982)" (Cifelli, manuscript comment).

⁴⁹ Brady had said that, "The simplest of all spiral and perforate Foraminifera are comprised in the genus *Spirillina*, the test of which consists typically of an undivided tube coiled regularly upon itself" (Brady, 1884, p. 624).

⁵⁰ Galloway explained, "*Spirillina* was considered by Brady and others to be the simplest member of the Rotaliidae, on the basis of the hyaline wall and supposed perforations in the wall. But the wall of *Spirillina* is not perforate in the same way that the walls of the Rotaliidae are, and none of the Rotaliidae has a tubular nucleoconch, so that *Spirillina* cannot be the ancestor of the Rotaliidae. *Patellina*, the supposed connecting

link between *Spirillina* and the Rotaliidae, does seem to have a coiled, tubular nucleoconch, but the walls are not perforate in the same way as are the walls of the Rotaliidae" (Galloway, 1933, p. 83).

⁵¹ Galloway remarked that, although the "ancestry and evolution of the family are difficult to determine" (1933, p. 133), the ancestral form of the Soritidae was most likely represented by the genus *Planispirina*. He found the most primitive form of the Alveolinellidae, the genus *Borelis*, to be characterized by a milioline nucleoconch and have evolved from the miliolid genus *Pyrgo*.

⁵² Galloway elaborated on this idea, "All students of upper Paleozoic Foraminifera, except Möller, have considered that the walls of the Endothyridae are composed of foreign grains cemented together. This is a mistake. The calcite of the walls has usually been crystallized in fossilization, and corroded by ground water or by weathering, so that the surface may be roughened and the granules enlarged. There may be a few attached foreign grains, or even some included foreign grains, as in some species of *Bradyina*, but the wall was fundamentally secreted by the animal, and not fundamentally composed of foreign grains with only the cement secreted by the animal" (Galloway, 1933, p. 153).

⁵³ Galloway explained how he envisioned these transformations were accomplished: "*Endothyra* evolved into the Trochamminidae by the walls becoming arenaceous; into the Nodosariidae by the walls becoming perforate and the aperture migrating to the outer edge of the chamber; into the Nonionidae by the walls becoming finely perforate and the coiling symmetrical; into the Rotaliidae by becoming perforate and more asymmetrically coiled; and into the Fusulinidae by the chambers embracing at both ends of the axis of coiling" (Galloway, 1933, p. 154).

⁵⁴ *Cayeuxina* and *Matthewina* are now thought to probably represent inorganic forms, while *Terquemina* is not considered to be a foraminiferan at all (Loeblich and Tappan, 1964).

⁵⁵ Galloway considered the wall structure of the Nodosinellidae to be "neither typically arenaceous nor hyaline nor porcellaneous," but of "distinct kinds found only in Paleozoic Foraminifera, and to which nearly all Paleozoic genera belong" (Galloway, 1933, p. 164).

⁵⁶ Cushman characterized the Lituolidae as having a test which was "either simple or labyrinthic" (Cushman, 1928, p. 105).

⁵⁷ Galloway (1933) also portrayed the family Nodosariidae as having been directly derived from the Endothyridae, in his chart of the "Phylogeny of the

Families of Foraminifera.” In the text, however, he described the most primitive member of the family, the genus *Lenticulina*, as having evolved from the Upper Paleozoic *Orobias*, a form Galloway placed in the Fusulinidae. Loeblich and Tappan included the genus *Orobias* Eichwald, 1860, in their listing of “Unrecognizable Generic Names Applied to Foraminiferida” (Loeblich and Tappan, 1964, p. C785).

In spite of his contradictory presentation of the ancestry of this family, Galloway believed the Nodosariidae to be, “The best family among the Foraminifera to illustrate the principles of paleontology, and probably the best and most convenient group for such purposes among fossil organisms. Evolution is shown by innumerable gradational stages and the appearance of new characteristics in later geologic periods after the appearance of the generalized forms” (Galloway, 1933, p. 233).

Galloway perceived the general evolutionary trends within this family as involving the tendency to become “evolute and rectilinear, and finally . . . unilocular” (Galloway, 1933, p. 233), consequently he viewed the genera *Lagena* and *Oolina* as representing highly evolved and specialized forms.

Although Galloway excluded the Polymorphinidae from his family Nodosariidae, he derived the aforementioned family directly from a nodosariid ancestor, which he hypothesized to be either the genus *Astacolus* or the genus *Marginulina*.

⁵⁸ Galloway explained, “The Fusulinidae were derived from *Endothyra*, as has been noted by many authors, since the nucleocoenochs in the more primitive genera have the structure of *Endothyra*, in form, method of coiling, arrangement of chambers and wall structure” (Galloway, 1933, p. 393).

⁵⁹ Galloway commented that, “It is generally agreed that the Cycloclypeidae were derived from *Heterostegina* of the Camerinidae, but the ancestry of the Orbitoididae is in dispute” (Galloway, 1933, p. 423). He concluded that the “typical orbitoids” comprised a distinct family and he appeared to accept Douville’s proposal that the camerinid genus *Arnaudiella* represented the most likely ancestor of the orbitoids.

Galloway also separated the Nonionidae from the Camerinidae, restricting the Camerinidae to include those forms with more complex wall structure and more specialized tests. He considered the genus *Nonion* to be the most primitive member of this family and hypothesized that it had evolved from the genus *Endothyra* “by becoming symmetrically planispiral and by the wall becoming distinctly perforate” (Galloway, 1933, p. 264).

⁶⁰ “The forms with the smaller pores are here considered to be the more primitive and are put ahead of the forms with coarse pores, in the classification, the reverse of the classification made by Brady. The finely-pored genera are considered to be the more primitive because the genera which appear first in time are fine-pored; because fine pores are characteristic of Foraminifera in general; and because the coarsely-pored line gave rise to only one new family, the Acervulinidae, which is degenerate, whereas the fine-pored line gave rise to many new and progressive families, all of which have fine pores” (Galloway, 1933, p. 274).

⁶¹ Galloway grouped together in the Acervulinidae a group of attached forms that he believed all represented “degenerate forms derived from the Rotaliidae” (Galloway, 1933, p. 300).

On the other hand, he interpreted the families Tinozoidae and Chapmaniidae to have been derived from rotaliid ancestors through increased specialization. Galloway derived two other families directly from the Rotaliidae; the Asterigerinidae which was comprised of only two genera, *Asterigerina* and *Amphistegina*, and the Chilostomellidae, which he thought to represent “a good example of the law of recapitulation” (Galloway, 1933, p. 322).

⁶² Galloway explained, “The similarity of some of the Rotaliidae . . . to the Orbulinidae shows that there must be some close relationship between the two families, and it is a difficult matter to decide whether the Rotaliidae gave rise to the Orbulinidae, or *vice versa* . . . the Orbulinidae are more simple in the inflated shape of the chambers, and in the unspecialized aperture, but appear slightly later in time (Jurassic) and are specialized for a pelagic life, so that it may be best to consider the Orbulinidae as having been derived from the Rotaliidae. But the phylogenetic line *Endothyra*–*Globigerina*–*Globorotalia*–*Rotalia* seems as reasonable and may be the correct one” (Galloway, 1933, p. 273).

⁶³ Galloway also derived the Pegidiidae, a family which he commented “bears no very close resemblance to any other family” (Galloway, 1933, p. 335), directly from the Orbulinidae. The simplest member of the Pegidiidae, the genus *Sphaeroidinella*, he hypothesized to have evolved from the genus *Globigerina* “by the tendency of chambers to overgrow the aperture, making necessary the leaving of a sutural fissure down to the aperture” (Galloway, 1933, p. 336).

⁶⁴ “The resemblance of *Bolivina* to some rare species of *Virgulina*, together with the elongate aperture, has suggested to Brady and to Schubert that *Bolivina* was derived from *Virgulina*, which in turn evolved from

Bulimina. That interpretation has been followed by Cushman. While it is admitted that some species of *Bolivina* may have evolved from *Virgulina*, the obvious similarity of *Bolivina* to *Bolivina*, *Bolivina* and *Bolivina*, which genera are probably no more than species of *Bolivina*, and which belong to the family Heterohelcidae, gives prepondering evidence that the type species of *Bolivina* has a coiled beginning, either planispiral or high spired, so the relationship cannot be told in that way. The symmetry of the aperture indicates that it belongs in this family, as well as the wall structure, compression of the test and closely appressed condition of the chambers" (Galloway, 1933, p. 343).

⁶⁵ Galloway considered the genus *Uvigerinella* to be the most primitive member of his family Uvigerinidae and hypothesized that this genus had evolved from a *Bulimina* ancestor by "developing a terminal aperture with a raised rim" (Galloway, 1933, p. 371).

Galloway also derived his families Cassidulinidae and Pleurostomellidae from bulimine ancestors. *Cassidulinoides*, the most primitive genus in his family Cassidulinidae, he derived from a *Virgulina* ancestor. Galloway believed the similarities in wall structure, chamber arrangement and apertural characteristics between members of the Buliminidae and the Cassidulinidae clearly demonstrated the close affinity of these two families. Cushman, in contrast, saw "a very definite development of this family from the Rotaliidae" (Cushman, 1933, p. 253), based on the form of the aperture.

Galloway also hypothesized that the most primitive member of his family Pleurostomellidae, the genus *Pleurostomella*, had evolved from a *Virgulina* ancestor through modification and relocation of the aperture. He believed that this family contained "many of the best examples of convergence to be found in the Foraminifera," as illustrated by the isomorphism of many of its genera with genera in the families Nodosariidae, Polymorphinidae, Chilostomellidae and Buliminidae (Galloway, 1933, p. 380).

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