

# BIOZONATION

MONIQUE FEIST,<sup>1</sup> with contributions from LU HUINAN,<sup>2</sup> WANG QIFEI,<sup>2</sup> and ZHANG SHENZHEN<sup>2</sup>

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## INTRODUCTION

MONIQUE FEIST

Interest in the stratigraphy of the charophytes was revealed during the development of research on the group during the 1950s. MÄDLER (1952) established the sequence of some species for the upper Oligocene and Miocene in Germany and Switzerland, but for many of them the range appears too long. PECK (1957), in his studies of the Mesozoic charophytes of North America, insisted on their stratigraphic significance. Likewise, for the Eocene and Oligocene formations of the Paris basin studied by GRAMBAST (1958, 1962a), charophytes have been revealed as very accurate biostratigraphic indicators.

The distribution of charophyte floras in different European regions (France, Belgium, Great Britain) having shown that common species were present in correlative strata, the establishment of a biozonation appeared possible. Owing to the fact that the fossiliferous deposits were at first few and scattered, the first biozonations (CASTEL, 1968; GRAMBAST, 1972a) were named after local reference levels comparable to mammalian stages (THALER, 1965). They are assemblage zones, and their precise range is not defined.

Later, new biozonations were published: biochronological zones based on the succession of evolutionary stages within phylogenetic lineages (GRAMBAST, 1971, 1974; BABINOT & others, 1983) and interval zones (RIVELINE, 1986; RIVELINE & others, 1996). The latter, named after guide fossils, correspond theoretically to the interval between two succeeding first occurrences of guide fossils. In some cases the interval zone corresponds to the range of a species. The guide fossils present characters that facilitate easy identification and have short stratigraphic

ranges, as well as a wide geographic distribution, such as *Atopochara trivolvris*, a cosmopolitan species of the upper Barremian and Aptian.

With the exception of some intervals, such as the Frasnian, the Rhetian–middle Oxfordian, and Coniacian–Turonian where data are too fragmentary, the charophyte biozonation constitutes a reliable biostratigraphical tool for dating and correlation in continental areas. Today this biozonation covers nearly all the fossil record of charophytes.

## PALEOZOIC

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The zonation of the Paleozoic has been established recently in China (WANG, YANG, & LU, 2003). Paleozoic charophytes have been reported from various levels in different areas of China. Due to their frequent occurrence in marginal-marine paleoenvironments, these charophyte floras are often associated with diverse organisms (spores, molluscs, conodonts) that are stratigraphically significant and ensure their correlation. Thus, the charophyte distribution, although relatively sporadic, has been taken into consideration for a preliminary biozonation of the Paleozoic. The following succession (Table 4) is based on the biozonation recently published by WANG, YANG, and LU (2003).

The charophyte assemblages comprise 11 different biozones. Three of them are not significant enough stratigraphically; nevertheless their occurrence furnishes clues for further research. The Paleozoic charophyte biozones are described below with the assemblages of their charophyte-yielding units. For the sake of brevity, locality information is given only at the level of county or province.

TABLE 4. Late Paleozoic charophyte biozonation of China (new).

Stage		Charophyte Assemblage
upper Permian	11	Stomochara kunlunshanensis–Porochara moyuensis–Leonardosia jinxiensis–L. jimsarensis–Gemmichara sinensis
upper Permian	10	Gemmichara pingdingshanensis–Leonardosia sp.
middle Permian	9	Leonardosia yongchengensis
lower Permian	8	Leonardosia sp.
Visean	7	Gemmichara hunanensis–Palaeochara sp.
Tournaisian	6	Ampulichara talimuica–Xinjiangochara rosulata–Palaeochara chinensis
Famennian	5	Karpinskya? sp.
Givetian	4	Sycidium lagenarium–Xinjiangochara burgessi
Eifelian	3	Trochiliscus ingricus–Pinnopotamen yunnanensis–Sycidium spinuliferum
upper Emsian	2	Sycidium sipaiense–Trochiliscus lipuensis–Xinjiangochara sp.
lower Emsian	1	Trochiliscus? sp.

The charophyte localities, more than 50 all together, are distributed differently through time: those referred to the Emsian and Eifelian (Biozones 1 to 3) have been found exclusively in South China, but for the Givetian (Biozone 4) they extend northward to central areas, and for the interval from Famennian to upper Permian (Biozones 6 to 11), the charophyte localities are all found in northern or north-central China. This change in distribution probably results from different paleogeographic conditions.

The oldest fossil charophyte is from the Lower Devonian of southwestern China. It is taken herewith as the beginning of the present list in decreasing age.

## DEVONIAN

### Lower Emsian

*Trochiliscus?* sp. biozone.—The only record of lower Emsian charophytes is the doubtful *Trochiliscus?* from the Ertang Formation of the Xiangzhou County in Guangxi. This record is, however, insufficient as a reliable criterion for the geological age of the fossil-bearing unit. It is based on brachiopod evidence that Biozone 1 has been referred to the lower Emsian (Z. WANG & others, 1980).

### Upper Emsian

*Sycidium sipaiense*–*Trochiliscus lipuensis* biozone.—Charophytes occur in the Sipai Formation of Guangxi, which is more or less correlated with the Dacaozi Formation of

Yunnan. Both formations contain rich faunas of brachiopods, corals, ostracodes, and conodonts on which is based the assignment to the upper Emsian. The charophyte assemblage includes *S. sipaiense* (Z. WANG & LU) Z. WANG and others, *Trochiliscus lipuensis* Z. WANG, *Sycidium miniglobosum* Z. WANG and others, *S. cf. panderi* KARPINSKY, and *Xinjiangochara* sp. The two guide fossils have been recorded also from the correlative beds of Lipu County (J. ZHANG & others, 1978; Z. WANG & others, 1980; Z. WANG & LU, 1980); furthermore, the Dacaozi Formation has yielded *Xinjiangochara* sp. in Ninglang (Yunnan).

## Eifelian

*Trochiliscus ingricus*–*Pinnopotamen yunnanensis*–*Sycidium spinuliferum* biozone.—This biozone (Table 5) is based on the assemblages from the Yingtang Formation of Guangxi and correlative beds of Yunnan and Hunan. On evidence of brachiopods and conodonts, the charophyte-

TABLE 5. Charophyte distribution in the Eifelian of China (new).

charophyte	Guangxi	Yunnan	Hunan
<i>Trochiliscus ingricus</i>	×	×	
<i>Pinnopotamen yunnanensis</i>		×	×
<i>Sycidium spinuliferum</i>	×		
<i>Eochara changshanensis</i>			×
<i>Sycidium haikouensis</i>		×	
<i>Sycidium anhuaense</i>			×

TABLE 6. Charophyte distribution in the Givetian of China (new).

charophyte	Guangxi	Yunnan	Guizhou	Hunan	Sichuan	Xizang
<i>Sycidium lagenarium</i>	x	xx	x	x	x	x
<i>Xinjiangochara burgessi</i>		xx				
<i>Moellerina convoluta</i>		x				
<i>Sycidium anhuaeense</i>				x	x	
<i>Sycidium beiliuense</i>	x			xx		
<i>Sycidium haikouensis</i>		xxx	x		xx	
<i>Sycidium xizangense</i>	x				xx	x
<i>Trochiliscus zhanyiensis</i>		x				
<i>Trochiliscus</i> sp.					x	

yielding beds have been attributed to the Eifelian (Z. WANG, 1976; J. ZHANG & others, 1978; ZENG & HU, 2001).

The charophyte assemblages are well diversified, with four genera and six species. The two most widely distributed species in South China are *Trochiliscus ingricus* KARPINSKY and, to a lesser extent, *Pinnopotamen yunnanensis* WANG & LU. *Sycidium spinuliferum* Z. WANG & LU, *Sycidium haikouensis* Z. WANG, *Sycidium anhuaeense* Z. WANG, and *Eochara changshaensis* Z. L. ZHANG have each been reported from only one locality.

Among the mentioned species, *Trochiliscus ingricus* has been recorded also from the Givetian of Russia (KARPINSKY, 1906), Poland (RACKI & SOBON-PODGORSKA, 1992), and Iran (FEIST & GRAMBAST-FESSARD, 1985); and *Sycidium spinuliferum* resembles *Sycidium volborthi eifelicum* LANGER from the Eifelian Mountains in Germany (LANGER, 1976). These resemblances suggest easy communication between close paleogeographic landmasses (see chapter on Paleobiogeography, herein p. 39).

#### Givetian

*Sycidium lagenarium*–*Xinjiangochara burgessi* biozone.—Records of charophytes of Givetian age (Table 6) extend northward to the Guizhou and Sichuan Provinces as well as to the Xizang Zang Autonomous Region (Tibet). *Sycidium lagenarium* Z. WANG is the most widely distributed species, extending through the southern, central, and northwestern areas of China. *Xinjiangochara*

*burgessi* (PECK & REKER) LU, SOULIÉ-MÄRSCHÉ, and Q. WANG has been reported from only two localities in Yunnan, from the lower part of the Xichong Formation in Zhanyi and Luquan as well from the Haikou Formation in Kunming, but this species is widespread in the Middle Devonian of North America (PECK & EYER, 1963a; PECK & MORALES, 1966). Another cosmopolitan species present in this assemblage is *Moellerina convoluta* (PECK) PECK, described from the Middle Devonian of Missouri (PECK, 1936; PECK & MORALES, 1966). The Givetian charophyte flora includes six other species, among which the most common are *Sycidium xizangense* WANG, *S. haikouensis* WANG, *S. anhuaeense* WANG, and *S. beiliuense* WANG. *Trochiliscus zhanyiensis* Z. WANG & LU and *Trochiliscus* sp. have been reported from only a single locality each (WANG & CHANG, 1956; WANG, 1976; ZHANG & others, 1978; WANG & LU, 1980; CHEN & YANG, 1992; LU, 1997; ZENG & HU, 2001).

#### Frasnian

No charophytes have been reported from strata of this age in China.

#### Lower Famennian

*Karpinskya?* sp. biozone.—In China, the charophyte record of the Famennian is very poor. The single record is *Karpinskya?* sp. from a unit in Xinjiang questionably correlated with the Hongguleleng Formation of Hoboksar County, which is attributed to the lower Famennian on conodont evidence. The finding of Famennian charophytes has

TABLE 7. Charophyte distribution in the upper Permian of China (new).

charophyte	southern Xinjiang	northern Xinjiang	Gansu	Liaoning
Leonardosia jinxiensis			×	×
Leonardosia jimsarensis		×		
Gemmichara sinensis				×
Stomochara kunlunshanensis	×			
Stomochara sp. cf. moreyi	×			
Porochara moruensis	×			
Leonardosia bellatula		×		
Leonardosia bellatula f. longa		×		
Leonardosia elliptica		×		
Leonardosia gansuensis			×	
Leonardosia nanpiaoensis				×
Leonardosia turpanensis		×		
Leonardosia xinjiangensis		×		

been taken as a provisional reference for Zone 5; further investigations will be necessary to correlate the the Xinjiang sequences precisely.

CARBONIFEROUS

Tournaisian

*Ampullichara talimuica*–*Xinjiangochara rosulata*–*Palaeochara chinensis* biozone.—Tournaisian charophytes are known from

northwestern China exclusively. *Xinjiangochara rosulata* YANG & ZHOU, *Ampullichara talimuica* YANG & ZHOU, and *Palaeochara chinensis* LU & LUO have been recorded from boreholes in a sequence ranging from the Bachu to the Kalasay Formations in the Tarim basin (Xinjiang) (YANG & ZHOU, 1990; GAO & others, 2002). The occurrence of *Xinjiangochara rosulata* YANG & ZHOU in the Tournaisian is confirmed by outcrop samples from the Qianheishan Formation of Zhongwei County in Ningxia (LU, SOULIÉ-MARSHE, & WANG, 1996).

Visean

*Gemmichara hunanensis*–*Palaeochara* sp. biozone.—In Hunan, *Gemmichara hunanensis* LU & ZHANG and *Palaeochara* sp. occur in the upper member of the Tseishui Formation of Lengshuijiang City (LU & S. ZHANG, 1990), which has been attributed to the Visean on palynological and floral evidence. This assemblage is also represented in the Yangjiazhangzi and Gaotai Formations of Liaoning (LIU & ZHANG, 1994).

PERMIAN

Lower Permian

*Leonardosia* sp. biozone.—*Leonardosia* sp. is the only charophyte record for the lower Permian. Only one gyrogonite has been obtained from the Kangkelin Formation of Kalping County in Xinjiang (LU & LUO, 1990). It is on faunal evidence (conodonts,

Triassic	stages	substages	charophyte zones (Polish Lowland) Bilan, 1988	
Upper	Rhaetian	upper Rhaetic	not determined	
		Norian	Sevastian	Auerbachichara rhaetica
		Alaunian		
		Lacian		
	Carnian		Tuvalian	Stellatochara thuringica
			Julian	
Middle	Ladinian	Longobardian	Stellatochara hoellvicensis	
		Fassanian		
	Anisian		Illyrian	Stellatochara drjeprviviformis
			Pelsonian	
			Bithynian	
			Aegean	
Lower	Scythian	Spathian	Porochara triassica	
		Nammalian	Porochara globosa	
		Griesbachian	?	

FIG. 25. Triassic charophyte biozonation (new, courtesy of W. Bilan).



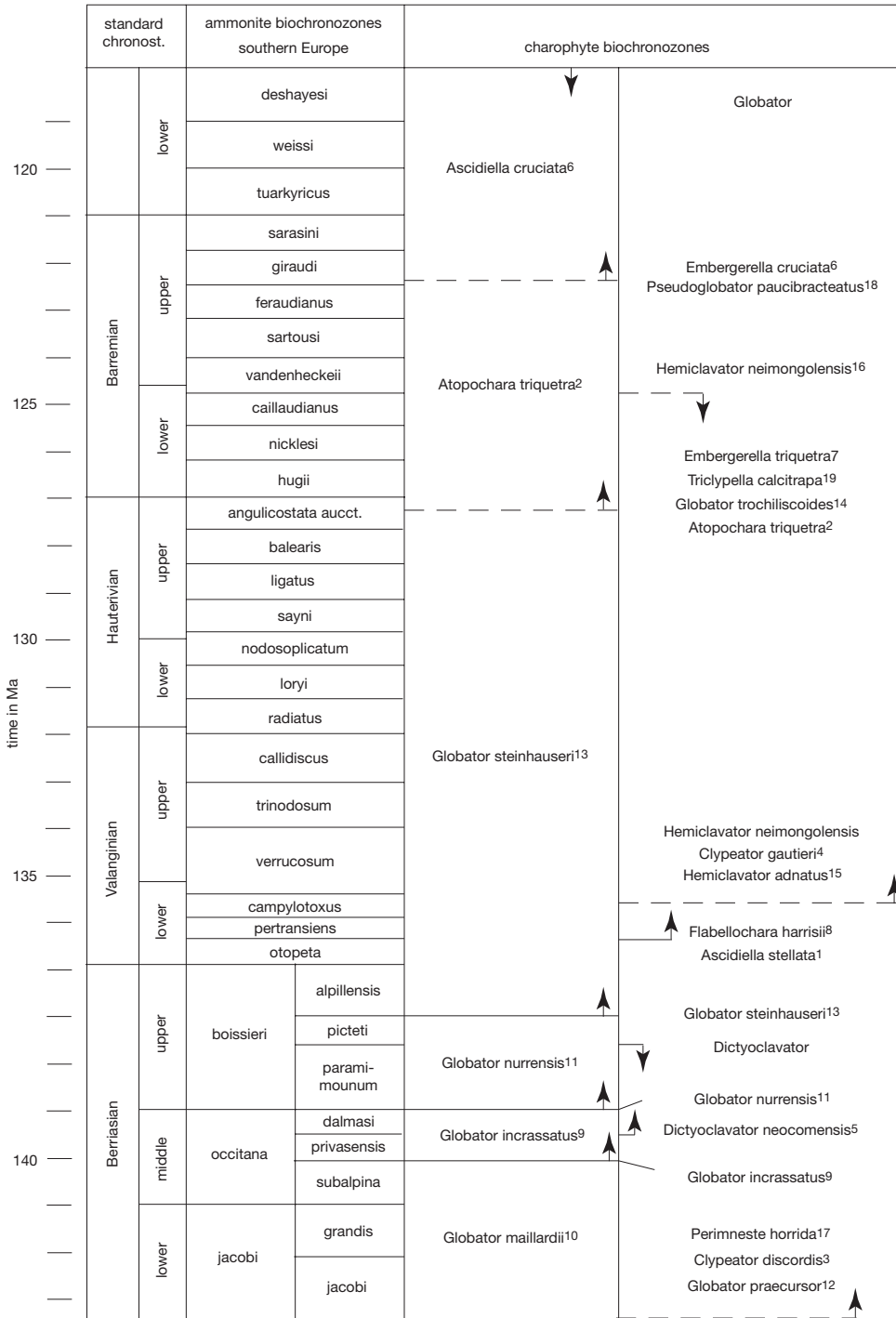


FIG. 27. For explanation, see facing page.

*Leonardosia yongchengensis* (Z. WANG & R. N. WANG) LU & ZHANG from Yongcheng County is the only taxon reported here (Z. WANG & R. N. WANG, 1986), with a stratigraphic range extending from the middle to the upper part of the Lower Shihhotse Formation (third and fourth coal formations, respectively). The two successive formations have been attributed to the Kuhfenginan ( $P_2^3$ ) and Lengwan respectively, according to floral data and magnetostratigraphy.

### Lower Upper Permian ( $P_3^1$ )

*Gemmichara pingdingshanensis*–*Leonardosia* sp. biozone.—This assemblage has been described from the third member of the Upper Shihhotse Formation (sixth and seventh coal formations) of Henan, Anhui, and Jiangsu provinces.

In Henan, *Gemmichara pingdingshanensis* Z. WANG & R. N. WANG has been obtained from boreholes from the middle part of the Upper Shihhotse Formation of Xiangcheng County, and *Leonardosia?* sp. has been found in Pingdingshan and Yingshang. Remains of *Gemmichara* sp. occur in the correlated horizons in Huainan (Anhui), and *Leonardosia* sp. occurs in Feng County (Jiangsu). The assemblage is assigned to the Wuchiapingian ( $P_3^1$ ) by floral data (Z. WANG & R. N. WANG, 1986).

### Upper Upper Permian ( $P_3^2$ )

*Leonardosia jinxiensis*–*L. jimsarensis*–*Gemmichara sinensis* and *Stomochara kunlunshanensis*–*Porochara moyuensis* biozones.—Late Permian charophytes are well represented in northern China (Table 7). They have been reported from three provinces. In the Tarim basin in southern

Xinjiang, the assemblage includes *Stomochara kunlunshanensis* LUO, which has been described from the Duwa Formation in Pishan and Hotan; *S. cf. moreyi* (PECK) GRAMBAST from Hotan only; and *Porochara moyuensis* LUO from Moyu County (LU & LUO, 1990). On evidence from ostracodes, the Duwa Formation is attributed to the Changhsingian ( $P_3^2$ ). Data from fossil vertebrates and flora indicate the same age for the following occurrences.

In northern Xinjiang, *L. turpanensis* LU & ZHANG occurs in the lower part of the Guodikeng Formation of the Turpan basin (LU & ZHANG, 1990). In addition, *Leonardosia bellatula* (LU & LUO) LU & ZHANG, *L. bellatula* f. *longa* (LU & LUO) LU & ZHANG, *L. elliptica* (LU & LUO) LU & ZHANG, *L. jimsarensis* (LU & LUO) LU & ZHANG, and *L. xinjiangensis* (LU & LUO) LU & ZHANG have been described from the Guodikeng Formation of the Junggar basin (LU & LUO, 1984).

In Liaoning, *Gemmichara sinensis* Z. WANG, *Leonardosia jinxiensis* (Z. WANG) LU & ZHANG, and *Leonardosia nanopiaensis* Z. WANG occur in the lower part of Hongla Formation of Jinxi County (Z. WANG, 1984).

In Gansu, *Leonardosia jinxiensis* (Z. WANG) LU and ZHANG and *Leonardosia gansuensis* (Z. WANG) LU and ZHANG have been recorded from the Sunan Formation of Sunan County (Z. WANG, 1984).

The distribution of charophyte species during the late Permian shows two distinct assemblages: in northern Xinjiang, Gansu, and Liaoning, the assemblage that is dominated by *Leonardosia* and includes the last representative of the Moellerinales, *Gemmichara*, has a typically Paleozoic aspect, while

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FIG. 27. Cretaceous (Berriasian-lower Aptian) charophyte biochronozones, after cladistic nomenclature; 1, *Asciadiella stellata*; 2, *Atopochara trivolvis triquetra*; 3, *Clypeator grovesii discordis*; 4, *C. grovesii gautieri*; 5, *Dictyoelavator fieri neocomensis*; 6, *Asciadiella cruciata*; 7, *Asciadiella triquetra*; 8, *Clavator harrisii*; 9, *Globator maillardii incrassatus*; 10, *G. maillardii maillardii*; 11, *G. maillardii nurrensis*; 12, *G. maillardii praecursor*; 13, *G. maillardii steinhauseri*; 14, *G. maillardii trochiliscoides*; 15, *Pseudoglobator adnatus*; 16, *Hemiclavator neimongolensis*; 17, *Atopochara trivolvis horrida*; 18, *Pseudoglobator paucibracteatus*; 19, *Clavator calcitrapus* (Martin-Closas & Schudack in Riveline & others, 1996; time, chronostratigraphy, ammonites, and biochronozones, adapted from Hardenbol & others, 1998).

in the Tarim basin (southern Xinjiang), there occur only the newly evolved Porocharioideae. The two assemblages may suggest the existence of two paleobiogeographic provinces or a slight diachronism.

## MESOZOIC–CENOZOIC

MONIQUE FEIST

A detailed account of the Mesozoic–Cenozoic biozonation was published by RIVELINE and others (1996). Herein only the main references are indicated as well as information on new zones introduced in the charophyte zonal scheme based on new data. At present, this biozonation is applicable only to Europe, but the general stratigraphic subdivisions can be recognized everywhere at the generic level. For example, *Auerbachichara* was common to Europe and China during the Triassic; most genera of the Clavatoraceae characterize the Cretaceous, and *Peckichara* as well as *Maedleriella* are universal markers of the Upper Cretaceous and Eocene. Exceptionally some stratigraphic markers allow the identification of stages, for example *Globator rectispirale*, which dates the Tithonian in two different continents, Europe and Africa (FEIST, LAKE, & WOOD, 1995).

### TRIASSIC

The biozonation established by BILAN (1988) in the continental Triassic of Poland (Fig. 25) includes six partial range zones, each of which corresponds to the interval between the last occurrences of two guide species. The stratigraphic attributions are based on well-dated marine intercalations or on data on spores, molluscs, and ostracodes of continental origin present in levels with charophytes or intercalated between them. Most of the analyzed material comes from boreholes situated at the margin of the upper Silesian coal basin.

### LOWER AND MIDDLE JURASSIC

No biozonation has yet been developed for the Rhaetian–middle Oxfordian interval, due to the rarity of charophytes, probably

related to the scarcity of calcareous nonmarine deposits. Some well-dated occurrences of species, however, show that a potential exists for subdivision of this interval. The Planioles Limestone of the southwestern Massif Central (France), with *Latochara durand-delgai* FEIST, has been correlated with the lower Sinemurian *Arnioceras semicostatum* ammonite zone (FEIST & CUBAYNES, 1984). For the middle Bathonian, the Hampen Marly Formation of Oxfordshire (England), which has yielded *Porochara palmerii* (FEIST & GRAMBAST-FESSARD) SCHUDACK, is considered to be an equivalent of the *Procerites progradilis* ammonite zone (COPE & others, 1980; FEIST & GRAMBAST-FESSARD, 1984). *Porochara sublaevis* (PECK) GRAMBAST, which has been described from the Middle Jurassic Piper Formation of Montana (PECK, 1957) and is also present in the Comblanchien Limestone of Bourgogne (east-central France), referred to the lower to middle Bathonian (MOJON, 1989), could be viewed as a widely distributed guide fossil of the Middle Jurassic.

### UPPER JURASSIC–UPPER PLIOCENE

The Meso-Cenozoic charophyte biozonation of RIVELINE and others (1996) is based on interval zones or range zones. The Jurassic and Cretaceous include 16 zones, the Paleogene 20, and the Neogene 4.

These zones have been established in different western European areas; their duration, variable according to periods, reduces in an ascending way. It varies from 4.3 Ma for the Upper Jurassic to 1.5 Ma for the Neogene. Correlations with marine stages are based on direct correlations, where charophytes are associated with marine markers at the same levels or on indirect correlations where charophytes and other markers occur in stratigraphically correlated layers. In some instances, correlations are deduced from the general biostratigraphic framework of a studied area. In addition, charophyte zones of the Upper Cretaceous have been related to the standard stages by direct correlation with the magnetostratigraphic scale (GALBRUN & others, 1993).



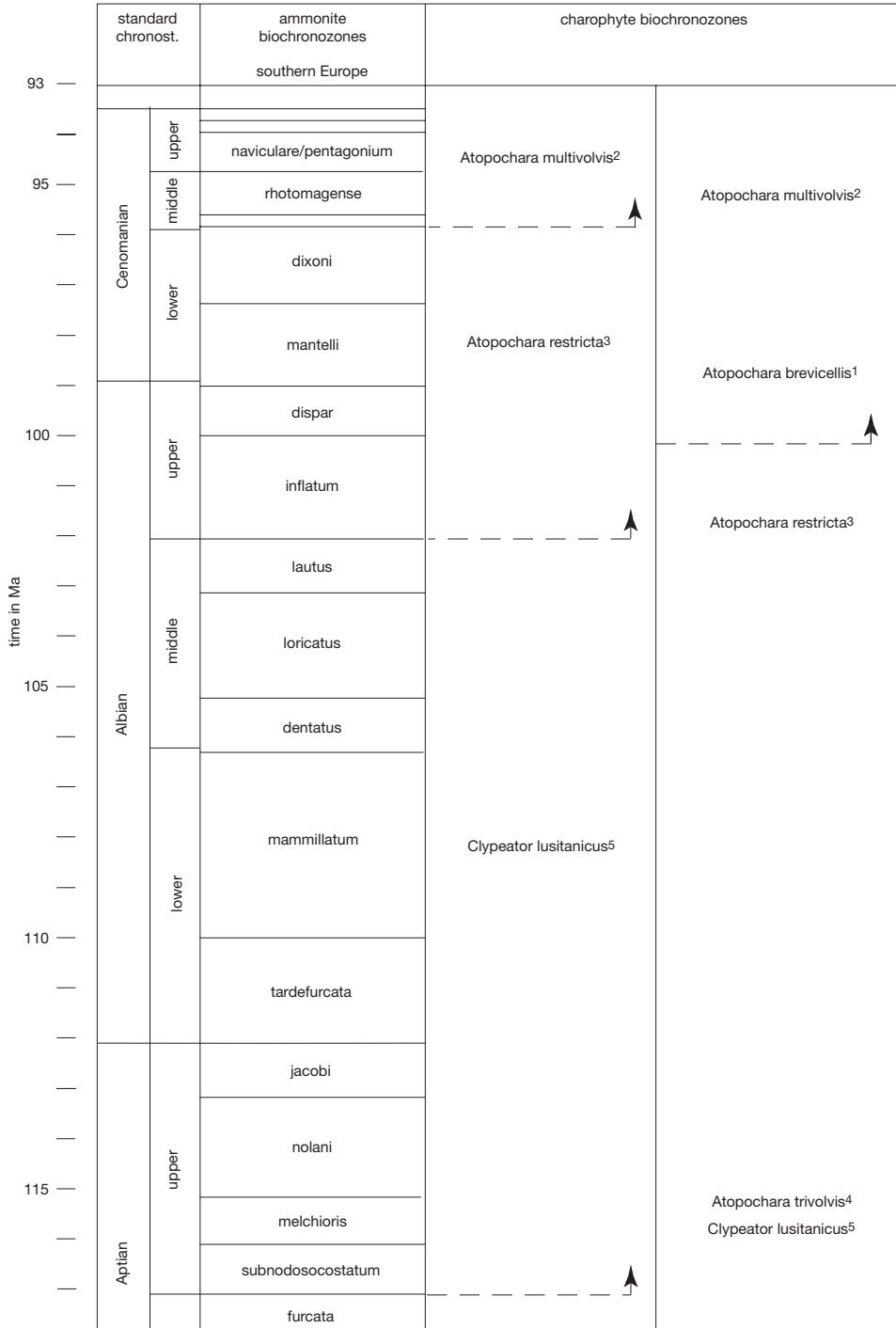


FIG. 28. Cretaceous (upper Aptian–Cenomanian) charophyte biochronozones. After cladistic nomenclature: 1, *Atopochara trivolis brevicellis*; 2, *A. trivolis multivolis*; 3, *A. trivolis restricta*; 4, *A. trivolis trivolis*; 5, *Clypeator grovesii lusitanicus* (Martin-Closas & Schudack in Riveline & others, 1996; time, chronostratigraphy, ammonites, and biochronozones, adapted from Hardenbol & others, 1998).

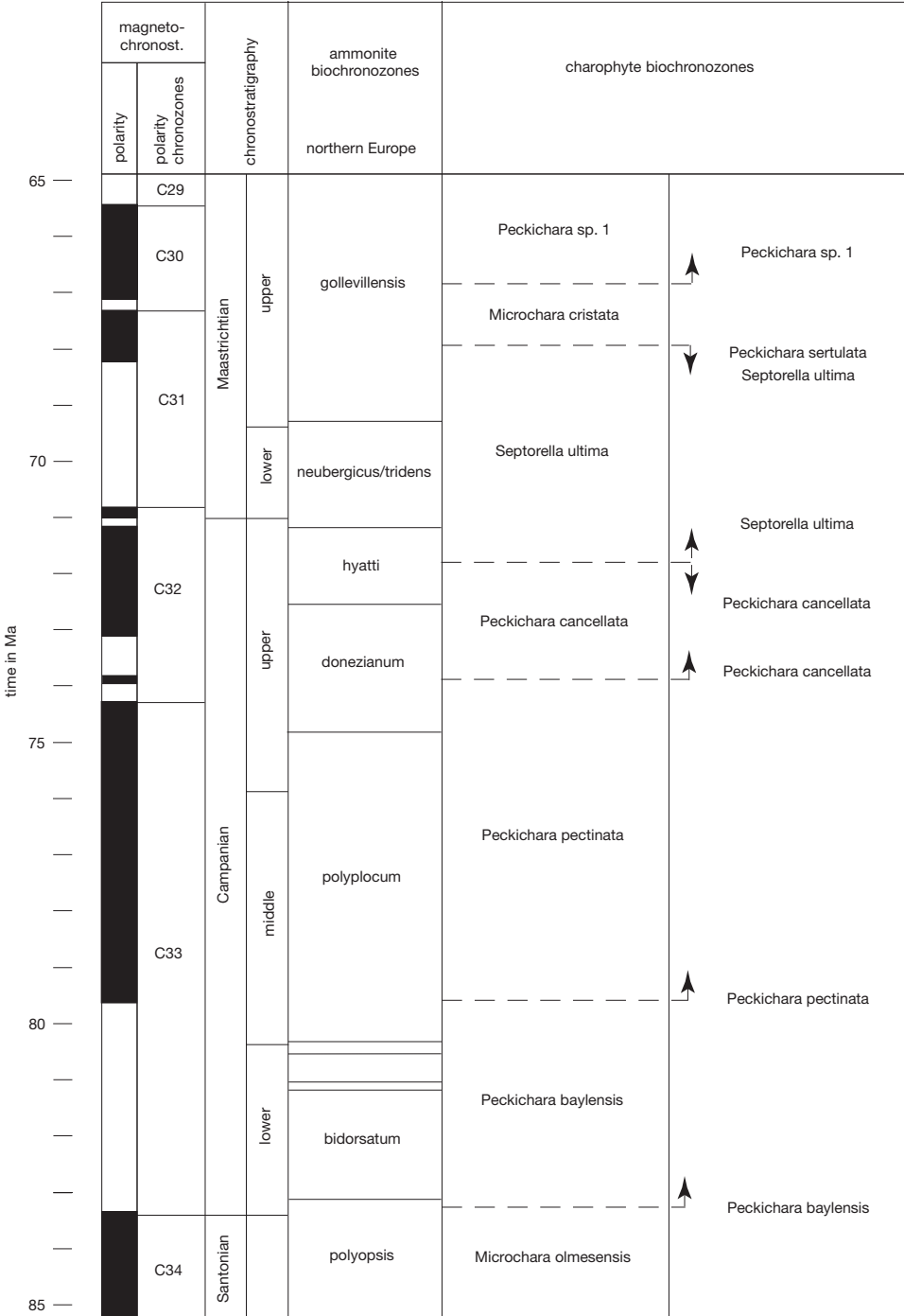


FIG. 29. Upper Cretaceous charophyte biochronozones (Feist in Rivelino & others, 1996; magnetostratigraphy and chronostratigraphy adapted from Gradstein & others, 1994).

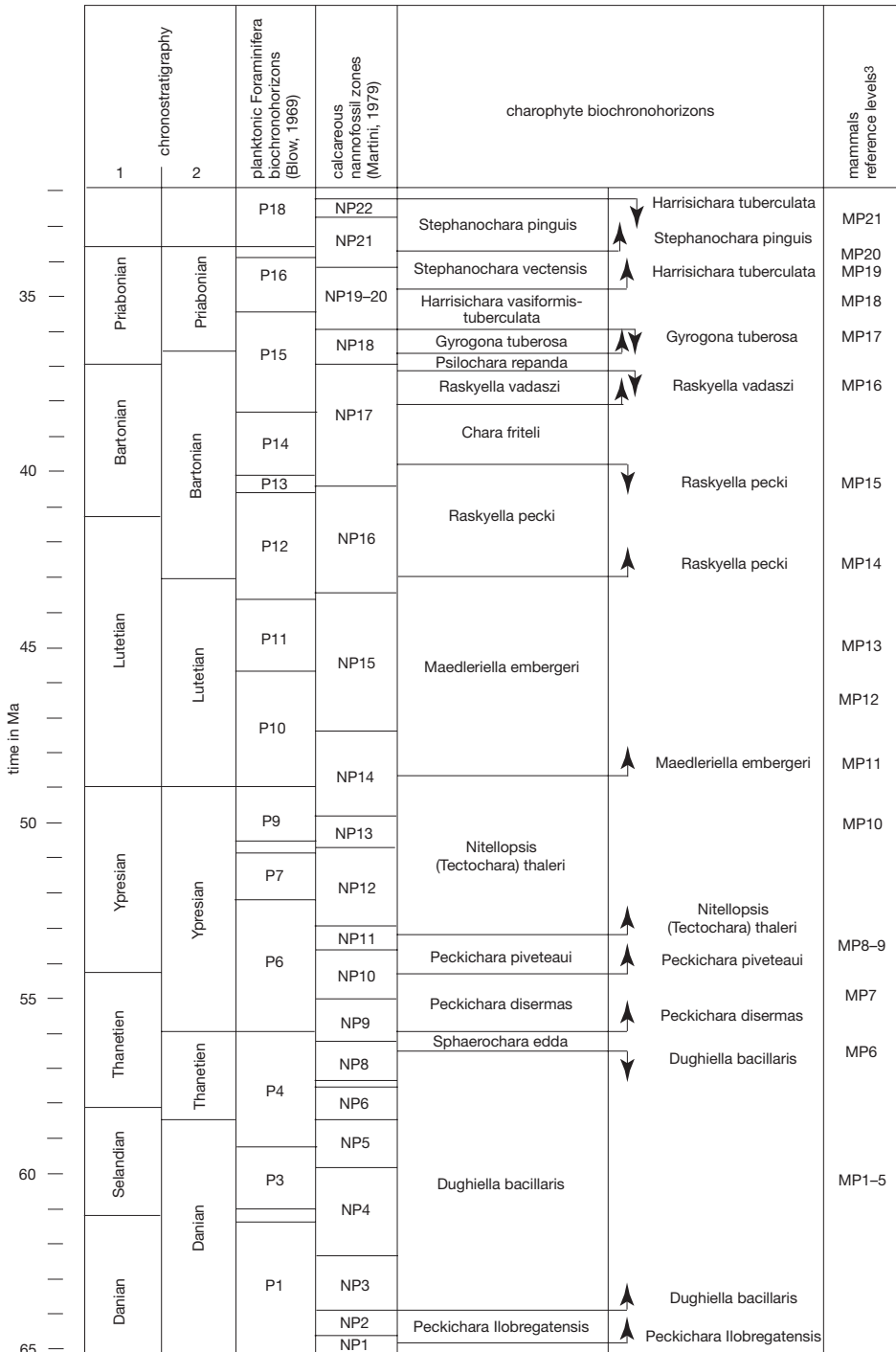


FIG. 30. Cenozoic (Paleogene: Danian–lower Rupelian) charophyte biochronozones (Riveline & others, 1996; time after Gradstein & others, 1994; chronostratigraphy: 1, adapted from Gradstein & others, 1994; 2, adapted from Cavalier & Pomerol, 1996; 3, Schmidt-Kittler, 1987; Mein, 1989).

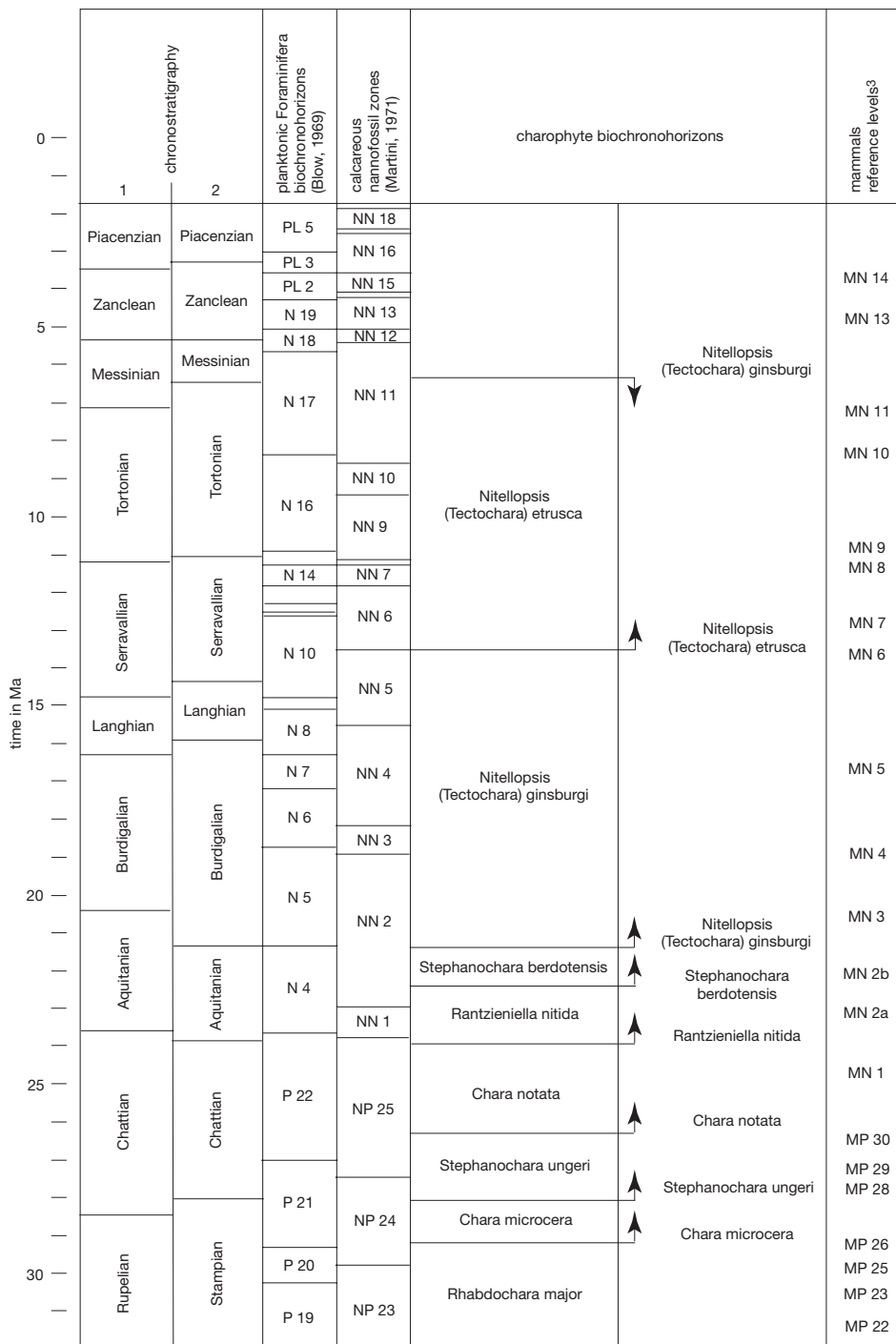


FIG. 31. Cenozoic (Paleogene–Neogene: upper Rupelian–Piacenzian) charophyte biochronozones (Riveline, Berger, & others in Riveline & others, 1996; time after Gradstein & others, 1994; chronostratigraphy: 1, adapted from Gradstein & others, 1994; 2, adapted from Cavalier & Pomerol, 1996; 3, Schmidt-Kitler, 1987; Mein, 1989).

### Upper Oxfordian–Upper Turonian

After the pioneering work of GRAMBAST (1974), MARTIN-CLOSAS and GRAMBAST-FESSARD (1986), SCHUDACK (1987), and DÉTRAZ and MOJON (1989), made important contributions to the biozonation of this interval. The scheme presented here is by MARTIN-CLOSAS and SCHUDACK (in RIVELINE & others, 1996), with addition of the *Globator rectispirale* Zone for the uppermost Jurassic (Fig. 26–28). The subdivisions of this interval are based on the Clavatoraceae, whose phylogenetic lineages are well suited for use in biozonation. Species have been named after the classification adopted in the charophyte *Treatise*. For the Upper Jurassic and Cretaceous, concordance with the cladistic nomenclature of the Clavatoraceae adopted by MARTIN-CLOSAS and SCHUDACK in RIVELINE and others (1996) is indicated in the captions of Figures 26–28.

### JURASSIC-CRETACEOUS BOUNDARY

In charophyte biozonation, this limit has been established within the Broadoak Calcareous Member of southern England (FEIST, LAKE, & WOOD, 1995). The guide fossil of the terminal Jurassic, *Globator rectispirale* FEIST, is the only representative of the genus *Globator* with perfectly vertical cells. In addition to this characteristic morphology, the

species has a wide distribution in northern Europe to northern Africa and until now has been the most precise marker for the end of the Jurassic. The Cretaceous begins with the first occurrence of spiral *Globator* species (FEIST & others, 1995).

### Upper Turonian–Lower Santonian

Up to now, no charophyte localities have been published for this interval; thus no succession can be established.

### Upper Santonian–Upper Maastrichtian

The biozonation of this interval (Fig. 29) was dealt with by FEIST in BABINOT and others (1983), FEIST and FREYTET (1983), and GALBRUN and others (1993), with an earlier account by GRAMBAST (1971). The succession was established in the south of France and northeastern Spain; it is calibrated with palynology and magnetostratigraphy.

### PALEOCENE–PLIOCENE

The Cenozoic biozonation (Fig. 30–31) comprises 24 zones that have been correlated with the marine stages owing to correlations with the zones of nanoplankton (ANADÓN & others, 1983; RIVELINE, 1986); they have been correlated also with mammal zones (FEIST & RINGEADÉ, 1977; ANADÓN & FEIST, 1981; BERGER, 1986; RIVELINE, 1986; SCHWARZ & GRIESSEMER, 1992).

# EVOLUTIONARY HISTORY

MONIQUE FEIST and NICOLE GRAMBAST-FESSARD

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The characters used to infer evolutionary trends in charophytes are primarily those of the fructification or postfertilization egg and associated cells and structures. Fossil fructifications comprise a gyrogonite (the enveloping cells, basal plate, and oospore membrane) and, in five families, a surrounding vegetative structure called a utricle. Details of gyrogonite and utricle structures are presented in the chapter on Morphology (herein, p. 1).

Characters useful in evolutionary reconstructions are both qualitative and quantitative. Qualitative characters include presence or absence of a utricle, shape and orientation of the enveloping cell (e.g., spiral or straight), apical-pore features, and basal-plate shape. Quantitative characters include size of the gyrogonite and utricle, number of enveloping cells, and number of basal-plate cells. The stratigraphic record of fossil charophytes provides a rationale for inferring primitive and derived character states (FEIST & GRAMBAST-FESSARD, 1991; MARTIN-CLOSAS & SCHUDACK, 1991; LU, SOULIÉ-MARSHE, & WANG, 1996). Based upon these inferences, a number of evolutionary trends are apparent and presented as hypotheses.

## TRENDS IN CHARACTER EVOLUTION

### ORIENTATION OF ENVELOPING CELLS

The direction of spiraling is visible from the base of the gyrogonites. In one of the oldest known charophyte species, the late Silurian *Moellerina laufeldi* CONKIN & CONKIN (Moellerinales), the gyrogonite is spiralled dextrally (clockwise spiralization; see *Pseudomoellerina*, Moelleriaceae, Fig. 44,4b, p. 93 herein). The sinistrally spiralled gyrogonites (Charales) appeared later during the Devonian in the Eocharaceae (counterclockwise spiralization; see *Rantzienella*, Raskeyellaceae, Fig. 62,2c, p. 118 herein).

Until recently, it was thought that the most primitive type of gyrogonite cell orientation was that of the vertical cells of the Sycidiales, but new data (see chapters herein on Classification, p. 83, and Systematic Descriptions, p. 92) show that these enveloping cells represent external layers of utricles, and the orientation and cell number of the enclosed gyrogonites are known incompletely. The utricular cells of the Sycidiaceae and most Chovanellaceae and dextrally coiled in the Trochiliscaceae. In *Ampullichara* YANG & ZHOU (Chovanellaceae) the utricular cells have a moderate dextral spiral.

### NUMBER OF ENVELOPING CELLS

Paleozoic gyrogonites have a variable number of enveloping cells, five to twelve in the Moellerinales; a trend toward reduction in cell number is evident by the Late Devonian (*Pseudomoellerina* has five to seven cells).

High numbers of enveloping cells occur only in the utricles of *Sycidium* and *Trochiliscus*; in both genera, the number of cells varies little: 18 in *Trochiliscus* and most *Sycidium* species; in the latter, however, different numbers have been found: 12 to 14 in *S. karpinskyi* SAMOILOVA & SMIRNOVA from the Frasnian of the Moscow region (SAMOILOVA, 1955) and 16 in *S. clathratum* PECK from the Lower Mississippian of Missouri (PECK, 1934a; PECK & MORALES, 1966). A tendency toward reduction in number of utricular cells is well illustrated by the Chovanellaceae where *Xinjiangochara*, known from the Lower Devonian onward, possesses 9 to 14 cells; *Chovanella*, approximately 10 Ma younger, has 5 to 8; and the most recent, *Ampullichara*, has only 3 to 5.

The Charales also have a trend toward reduction of the number of enveloping gyrogonite cells in more recent taxa. The number is relatively high at first in the

Devonian Eocharaceae with 8 to 13 cells. The number is reduced to 6 or 7 in the Palaeocharaceae, also during the Devonian, and is finally fixed at 5 cells in the Porocharaceae and in all post-Paleozoic families, with the exception of an isolated record of an Eocharaceae in the Triassic (KISIELEVSKY, 1996).

### APICAL PORE MORPHOLOGY

In the oldest charophyte fossils, the external cells of the fructification do not join at the apex, which leaves a small opening or pore that varies in size across taxa. An apical pore occurs in the Moellerinales, the Sycidiales, and the Palaeocharinae of the Charales. Among the Charinae, the Porocharaceae and Clavatoraceae also have an apical pore.

In the gyrogonites of the Raskyellaceae, the apex is closed by five small cells, which are missing in gyrogonites of germinated oospores. The complete closure of the apex, by junction of the enveloping cells, occurs in the Characeae, a condition that occurs first in *Aclistochara* from the Upper Triassic (LIU & CHEN, 1992).

### GENERAL EVOLUTION

The general evolution of Charophyta from Silurian to Holocene is summarized in Figures 32 and 33. Recent findings on the nature of the fructification in Paleozoic forms bring a new understanding of the early stages of charophyte evolution.

#### THE OLDEST CHAROPHYTES: HYPOTHESES ON THE ORIGIN OF THE GROUP

The most ancient charophyte is the presumed ancestor of *Sycidium* from the uppermost lower Silurian (Llandovery-Wenlock boundary) of Anticosti Island (MAMET & others, 1992). Although the three-dimensional shape of the species cannot be established from the thin sections shown in illustrated specimens, the microstructure of the wall with concentric lamellae as well as the dark, inner part resembling an oospore membrane (MAMET & others, 1992, fig. 12–13) bear a close resemblance to Charophyta.

Two layers composing the wall, apparent in their figures 12 and 13, show the structure of a utricle; the high number (more than 30) of the sectioned enveloping cells suggests a spiral utricle similar to that in the Trochiliscaceae. *Primochara calvata* ISHCHENKO & SAIDAKOVSKY is referred tentatively to this family and, among the Sycidiaceae, *Pseudosycidium* HACQUAERT, 1932 and *Praesycidium* T. A. ISHCHENKO & A. A. ISHCHENKO, 1982 (now included in *Sycidium*), which were both reported from the upper Silurian, could be the immediate descendants of the Anticosti species.

To determine the identity of the possible ancestor of the Sycidiales, the first step is to find the type(s) of gyrogonite that are enclosed inside the utricles of the four families, Sycidiaceae, Trochiliscaceae, Chovanellaceae, and Pinnopotamenaceae. In these families, the fructifications are utricles, inside of which gyrogonites are generally uncalcified and not fossilized or, when preserved, do not have the characters that relate them to a defined group. The Moellerinales seem to be possible candidates, although they postdate by 2 to 3 Ma the hypothetical Anticosti species. Given the near absence of material from the lower Silurian, their existence in this period cannot be ruled out. Thus, new collections (M. FEIST) from the upper Silurian of Gotland show that *Moellerina laufeldi* CONKIN occurs earlier than the type level (J. E. CONKIN & B. M. CONKIN, 1992) in the Ludlow sequences. With their small size, the gyrogonites of *Moellerina* (especially those of *M. laufeldi*, whose diameter does not exceed 350  $\mu\text{m}$ ) might have been contained inside utricles. In fact, a gyrogonite of *Moellerina* type is enclosed in the utricle of the Chovanellaceae, but a different type of gyrogonite is suggested for *Sycidium* by the casts of undivided vertical cells that are visible at the internal face of a utricle of *S. xizangense* WANG (see Fig. 45*i*, Systematics, herein p. 95). These elongated cells, however, could be part of the inner utricle wall instead of gyrogonite components.

GRAMBAST (1974) speculated that the different Paleozoic forms may have

independent origins from a primitive type in which the gyrogonite was not yet constituted, as the female organ (oosphere and egg) lacked sterile cells; the corresponding fructification would be a gametocyst rather than a gametangium. It seems probable that the gyrogonite first appeared by coalescence of unspecialized vegetative cells around a naked female cell; however, such a structure is unknown in charophytes.

The utricle of the Paleozoic families was probably elaborated progressively, as in the Clavatoraceae, and their origin is thus to be sought in former times. Molecular analyses of living charophytes suggest that they share a common ancestor with land plants (KAROL & others, 2001). Because fossil evidence for both charophytes and land plants is known from the Silurian (FEIST & GRAMBAST-FESSARD, 1991; KENRICK & CRANE, 1997), both groups diverged at some earlier time.

#### RELATIONSHIPS OF MODERN FORMS TO THEIR PALEOZOIC ANCESTORS

All post-Paleozoic taxa are grouped into the Charales; they have in common gyrogonites with sinistrally spiralled enveloping cells. The reversal of cell orientation that occurred first in the Eocharaceae may have arisen among the Moellerinaceae, which show a comparable gyrogonite cell number (8 to 13 in the former and 7 to 12 in the latter). Causes of this inversion remain enigmatic.

The oldest Charales, *Eochara wickendeni* CHOQUETTE (Eocharaceae) from the Middle Devonian of North America, has 8 to 13 cells. By reduction of the gyrogonite cell number, the Eocharaceae gave rise to the Palaeocharaceae and the latter to the Porocharaceae. The long time interval, ca. 40 Ma, between the first occurrences of Eocharaceae and Palaeocharaceae probably results from a gap in the fossil record, as a representative of the Eocharaceae has been found in the Middle Triassic (KISIELEVSKY, 1996).

#### EVOLUTIONARY TRENDS IN THE SYCIDIALES

Several evolutionary trends have developed in this group, mainly in the Devonian over a period of approximately 50 Ma.

##### *Sycidium* and *Trochiliscus*

The morphology of the basal pore, the long cells in comparably high number, and the cellular transverse ridges, which are common to *Sycidium* and *Trochiliscus*, suggest a close phylogenetic relationship between these genera (Z. WANG & LU, 1980; LU, SOULIÉ-MARSCHÉ, & WANG, 1996). *Trochiliscus*, which occurred first in the Early Devonian, was presumably derived from *Sycidium*, known possibly from the early Silurian but surely from the late Silurian onward, by spiral development of the long utricle cells.

##### *Pinnopotamen*

In the mid-Devonian *Pinnopotamen* WANG, the utricle presents two ramified, opposite branches (Z. WANG & LU, 1980) (see Fig. 48c, Systematics, herein p. 99) that in the Early Devonian *Pinnopotamen* sp. bear numerous antheridial casts (M. FEIST & R. FEIST, 1997) (see Fig. 48e, Systematics, herein p. 99). Although intermediate stages, probably including *Costacidium* LANGER, remain unclear, the evolution of the utricle, resulting in the coalescence of axes and in the reduction and loss of antheridia, is similar to the evolutionary trend in the Cretaceous *Perimneste-Atopochara* lineage.

##### *Xinjiangochara-Chovanella-Ampullichara* lineage

In these three genera, which comprise the Chovanellaceae, the utricle is composed of vertical long cells not reaching the apex. From the Early Devonian to the Mississippian, the cell number of the utricle reduces from 12 to 14 to 3 to 5. The utricle becomes spiral in the most recent of the three genera, *Ampullichara* from the Mississippian, which is the terminal member of the lineage.



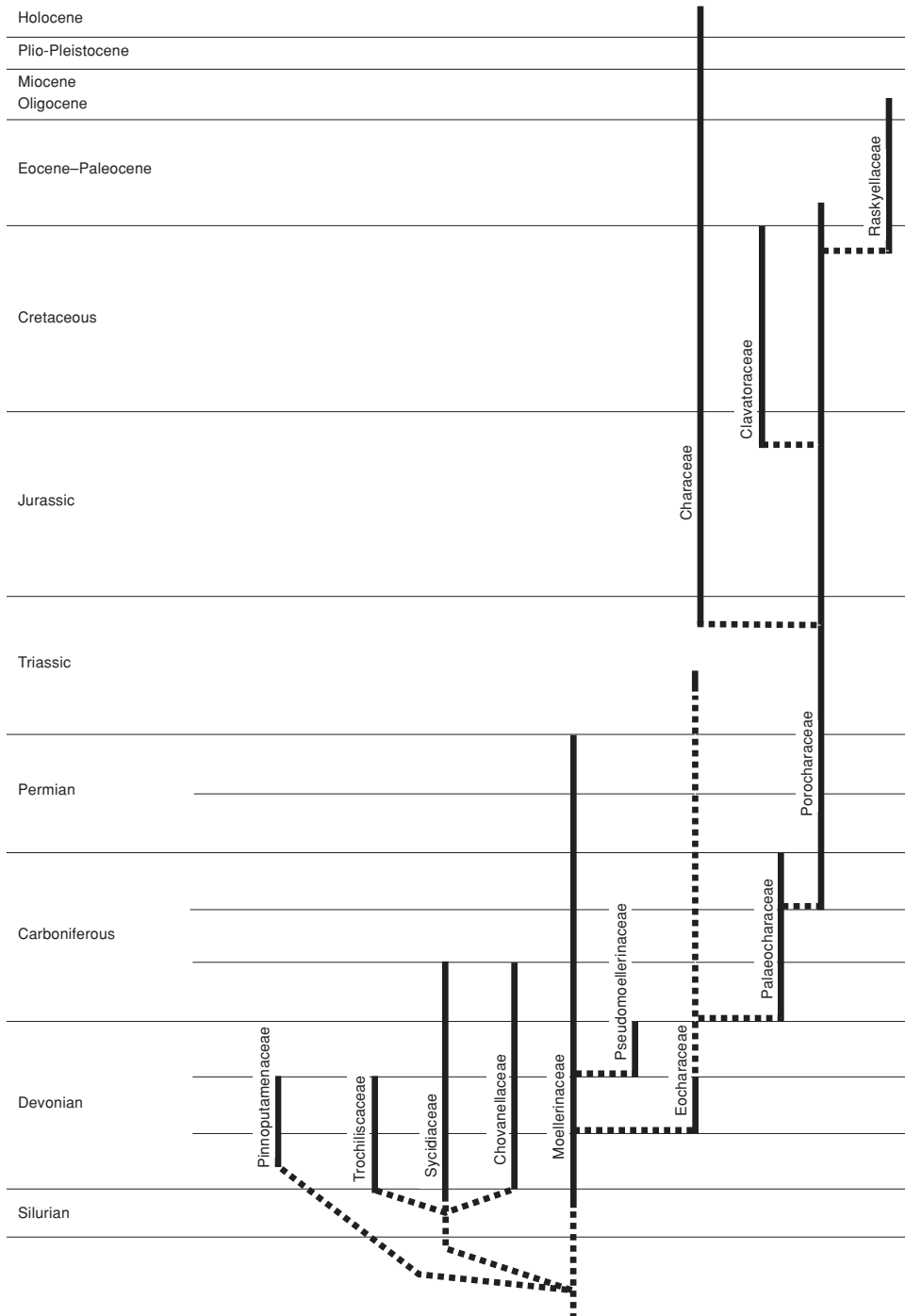
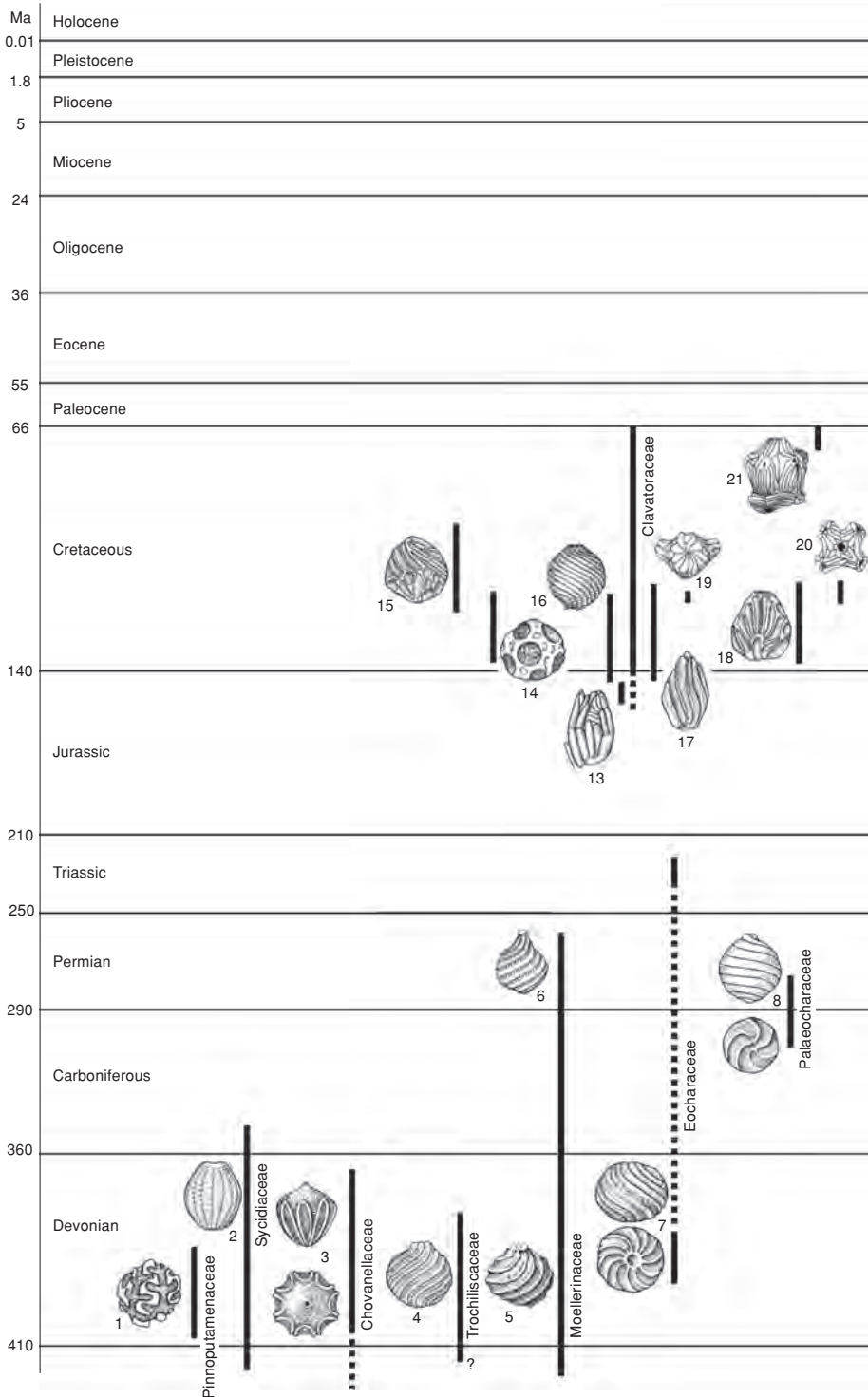


FIG. 32. Hypothesis of phylogenetic relationships between charophyte families (new).



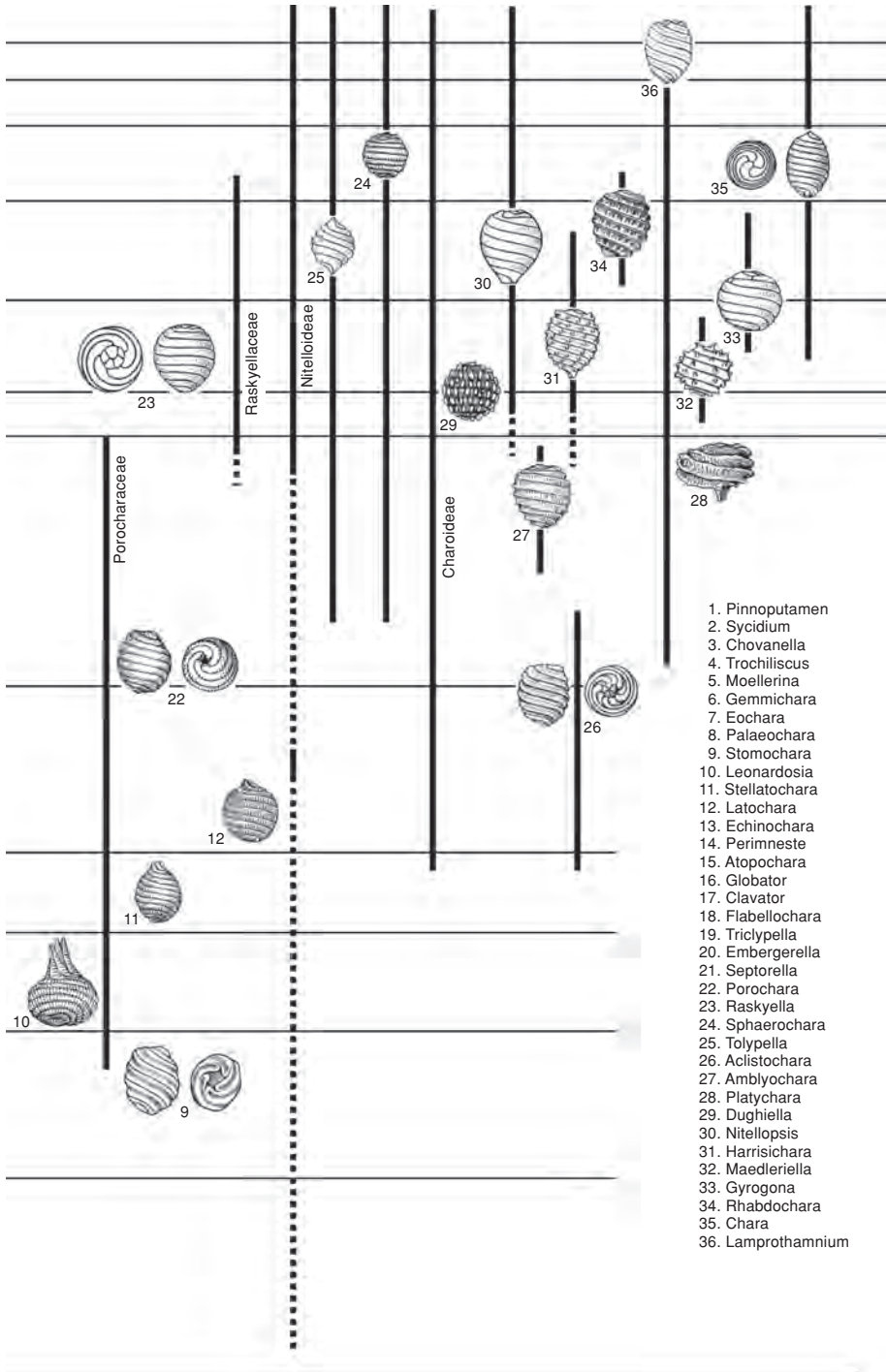


FIG. 33. Structural evolution of fructification in Charophyta (adapted from Grambast, 1974; Feist & Grambast-Fessard, 1991).

*A. talimuica* f. *crassa* YANG & ZHOU is the only specimen in which a gyrogonite can be observed in the utricle (see Fig. 47, 2e-f, Systematics, herein p. 98). We may assume that the other members of this lineage also possessed a *Moellerina*-type gyrogonite within the utricle.

#### THE RADIATION OF THE POROCHARACEAE

After the extinction of Paleozoic families, the Porocharaceae constituted the core of the charophyte flora during the Triassic and the Jurassic. Porocharaceae often have small gyrogonites devoid of any ornamentation, but this family is of major phylogenetic importance (GRAMBAST, 1974). Porocharaceae are thought to have given rise to the three other post-Paleozoic families, based on the time of their appearance. The first lineage to diverge gave rise to the Characeae through closure of the apical pore by junction of the spiral cells at the apex. In the early representatives of this family, the Triassic *Aclistochara* species, the gyrogonite morphology is very similar to that of the Porocharaceae. In particular, the narrow apical zone (see Fig. 64, 3d, Systematics, herein p. 122) resembles the small apical pore of the Porocharoideae (see Fig. 50, 2b, Systematics, herein p. 102). The second group to diverge was the Clavatoraceae, in which the gyrogonite inside a utricle has an apex stretched into a neck and a persistent apical pore analogous to the Stellatocharoideae. Finally, the Raskyellaceae diverged by closure of the apical pore by an operculum of five apical cells.

The evolutionary tendencies inside the Porocharaceae themselves are twofold: toward the closure of the apical pore, in *Leonardosia* SOMMER and *Latochara* MÄDLER (Stellatocharoideae), and toward an increase of dimensions, culminating in the Late Cretaceous and Paleocene species of *Feistiella* SCHUDACK (Porocharoideae).

#### THE RADIATION OF THE CLAVATORACEAE

In this large family, the gyrogonite is developed in a utricle made of whorls of vegeta-

tive origin. Barely modified through early forms from the Upper Jurassic, this utricle appeared to undergo a fast and variegated morphological differentiation, mostly during the Early Cretaceous. This makes the group particularly well suited for precise phylogenetic studies. Stages linking distinct and apparently totally different extreme types are illustrated below.

#### Atopocharoideae PECK, 1938; emend., GRAMBAST, 1969

Members of this subfamily have a triradial symmetry, the utricle being composed of three similar units and characterized by a single-layered utricle wall (GRAMBAST, 1974).

The *Perimneste-Atopochara* phylogenetic lineage.—This lineage (Fig. 34) is the best documented and also has the longest duration, extending for perhaps 70 Ma, from the Berriasian to the Campanian. First described by GRAMBAST (1967, 1974), it was later completed by KYANSEP-ROMASCHKINA (1975), GRAMBAST-FESSARD (1980), FEIST (1981), and WANG and LU (1982). The successive evolutionary stages and species of the *Perimneste-Atopochara* lineage are reported here following FEIST and WANG (1995).

*Perimneste horrida* HARRIS (Fig. 34.1) is the oldest representative of the lineage and also the most primitive. It shows clearly the vegetative origin of the utricle. Dissolving the calcite with weak acetic acid shows the position of the utricle cells, which are grouped in three distinct clusters. Each cluster contains one basal cell bearing three branches, each of which is ramified into three cells except for the right branch, which is ramified into only two cells. Four to six superficial hollows with antheridial structures are borne by every secondary branch (see Fig. 60, Systematics, herein p. 116). The total cell number is 48, plus on average, 14 antheridia.

From the Berriasian to the Cenomanian, the three clusters condense progressively and the number of antheridial casts decreases. The separation of the two genera has been placed at the appearance of *Atopochara trivolvis*, when the central basal cell of each

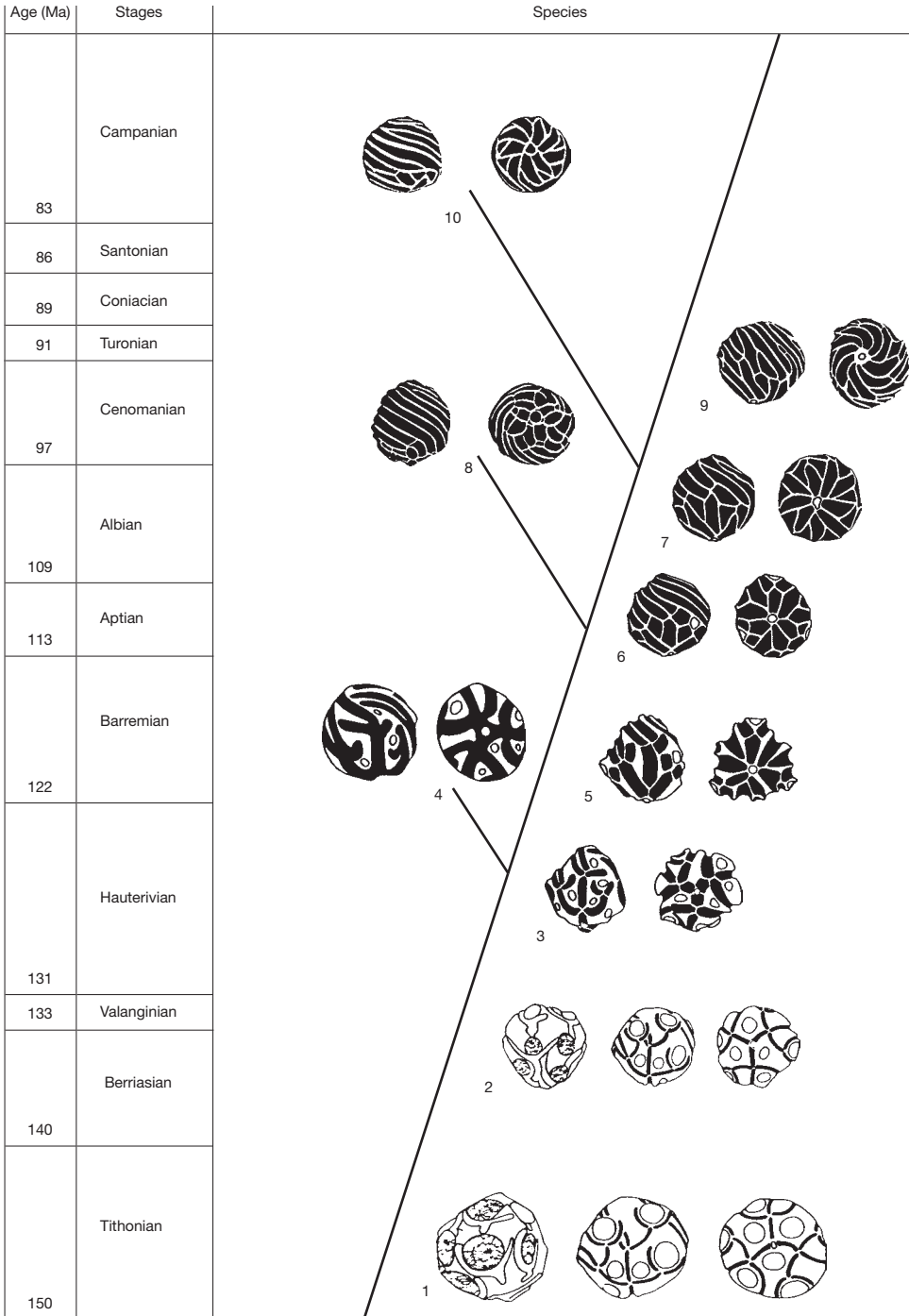


FIG. 34. Fossils of *Perimmeste-Atopochara* lineage; 1, *P. horrida*; 2, *P. micrandra*; 3, *P. ancora*; 4, *P. vidua*; 5, *A. triquetra*; 6, *A. trivolvis*; 7, *A. restricta*; 8, *A. brevicellis*; 9, *A. multivolvis*; 10, *A. ulanensis*. 1–2, left, surface of utricle with antheridia; center and right, lateral view, after etching of surface; 3–10, left, lateral view; right, basal view (Feist & Wang, 1995, fig. 1).

cluster disappeared and the antheridial sites were reduced to one sterile cell (Fig. 34.6, and see Fig. 58, *I*, Systematics, herein p. 114). From the Barremian to the Cenomanian, the cells of antheridial origin disappeared altogether, and the upper cells are strongly spiral. The most derived condition of this evolutionary progression occurs in *A. multivolvis* PECK (Fig. 34.9) and *A. ulanensis* KYANSEP-ROMASCHKINA. This progressive series of structural modifications has been viewed as an illustration of the evolutionary species concept (MARTIN-CLOSAS & SERRA-KIEL, 1991; SCHUDACK, 1993b; MARTIN-CLOSAS & SCHUDACK, 1997). The succession of all representatives of the *Perimneste-Atopochara* lineage, however, shows that they are not disposed in a single series. Two of them present an assemblage of primitive and derived features. In *Perimneste vidua* GRAMBAST (Fig. 34.4), the large size recalls the oldest representative, *P. horrida*; the vegetative origin of the utricle is still visible; and the cell number (36) is the same as in *P. ancora* GRAMBAST. In contrast, the basal cells are shorter than in the latter species and thus comparable with those of the contemporaneous *Atopochara triquetra* FEIST.

In *Atopochara brevicellis* GRAMBAST-FESSARD (Fig. 34.8), the strong reduction of all lower cells and the correlative lengthening and spiralling of the upper cells, as well as the low cell number (30), indicate the most condensed structure of the lineage, but without subdivision of the upper cells, which occurs in *A. multivolvis* PECK. The existence of several evolutionary divergences is incompatible with monophyly as postulated under the evolutionary species concept. The combination of primitive and derived characters found in both taxa can be interpreted as the result of heterochronic development. Heterochronic processes, corresponding to changes in the timing and rate of ontogenetic development, may account for the simultaneous presence of ancestral and derived characters as in *Perimneste vidua* and *Atopochara brevicellis*.

*Atopochara ulanensis* (Fig. 34.10), which is the last representative of the *Perimneste-*

*Atopochara* lineage, does not differ in its structure from *A. restricta*. In particular the lower cells of these taxa are triangular and relatively prominent. *A. ulanensis* has a lengthening and a spiralling of the upper cells that is comparable to that of *A. multivolvis*, although the upper cells are not divided in *A. ulanensis*. In Europe, *A. restricta* is succeeded by *A. multivolvis*, and the *Perimneste-Atopochara* lineage ends with the latter in the Turonian. In Asia (Mongolia and China) *A. restricta* subsequently gave rise to *A. ulanensis*, with dates ranging from Campanian to Maastrichtian. Allopatric speciation may explain the derivation of the two species from a common ancestor, *A. restricta*, during the Late Cretaceous.

The *Globator* lineage.—This series shows the evolution from the Tithonian *Globator rectispirale* FEIST to the Barremian and Aptian *G. trochiliscoides* GRAMBAST (Fig. 35). Initially reconstructed by GRAMBAST (1966a, 1974), this lineage was completed by the discovery of new stages and a reappraisal of the chronology (MARTIN-CLOSAS & GRAMBAST-FESSARD, 1986; MOJON & STRASSER, 1987; FEIST, LAKE, & WOOD, 1995; MARTIN-CLOSAS, 1996).

The utricle of *Globator rectispirale* is composed of three units of eight cells each: one basal cell bears three long upper cells and, on each side of the central units, a relatively long basal cell bears one upper cell. Altogether the 24 cells of a utricle have a vertical orientation. In *G. trochiliscoides*, only 15 strongly coiled long cells are present, and all the basal cells have disappeared. In successive localities of the Lower Cretaceous, intermediate species such as *Globator incrassatus* MARTIN-CLOSAS & GRAMBAST-FESSARD (upper Berriasian) and *G. mutabilis* MOJON (Barremian), show that the general trends of the succession are a progressive reduction of all the basal cells together with an increase in length and spiralling of the long cells.

*Globator nurrensis* PECORINI is separated from the main line by its utricle shape, which is elongated and fusiform and, above all, by the disposition of the basal part where only the central cell of each group is reduced.

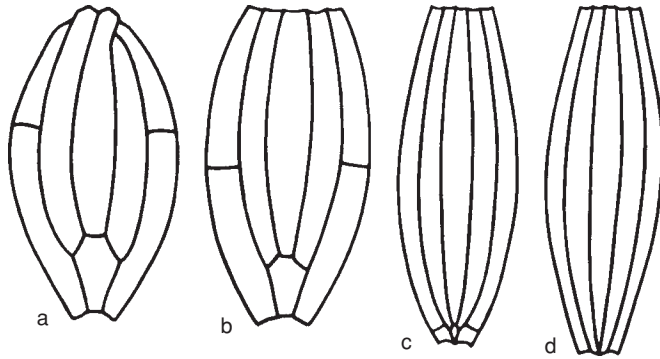


FIG. 35. Structure of utricular unit in *a*, *Globator maillardi* (SAPORTA) GRAMBAST; *b*, *G. incrassatus* MARTIN-CLOSAS & GRAMBAST-FESSARD; *c*, *G. trochiliscoides* var.; *d*, *G. trochiliscoides* GRAMBAST (Grambast, 1974, fig. 6).

GRAMBAST (1966a) interpreted this species as a side branch of the main line of the sequence.

**Clavatoroideae PIA, 1927;  
emend., GRAMBAST, 1969**

The Clavatoroideae are the Clavatoraceae with the longest range, from the Oxfordian with the genus *Clavator* REID and GROVES, to the uppermost Maastrichtian when the last *Septorella*, *S. ultima*, became extinct. This group has been interpreted as the result of extensive cladogenetic change, at least through the upper Barremian, and its members have the highest degree of specialization of the female reproductive structures in the Charophyta. Members of this subfamily have bilateral symmetry and are characterized by a bilayered utricule wall as well as by the presence of internal canals, representing small stems (stemlets) with a succession of nodes and internodes. Two examples illustrate the diversity displayed in this subfamily.

The *Clavator-Flabellochara-Clypeator* phylogenetic lineage.—GRAMBAST (1970, 1974) has established very precisely the successive stages of the *Flabellochara-Clypeator* lineage during the Early Cretaceous (Fig. 36). MARTIN-CLOSAS (1996) connected this lineage to its ancestral form from the Upper Jurassic, the genus *Clavator*. In this lineage the utricule is composed of two opposite lateral units separated by several cells in the ventral (adaxial) and dorsal (abaxial) sides.

*Flabellochara grovesi* (HARRIS) GRAMBAST presents a distinct bilateral symmetry; each of the two lateral fans includes a short median basal cell bearing six or more, often seven, radiating upper cells and two lower cells situated on each side of the median basal cell. As noted by HARRIS (1939) the utricles of this species are always laterally compressed. The first known occurrence of this species is in the lower Berriasian (FEIST, LAKE, & WOOD, 1995), although its putative descendant, *Clypeator discordis*, has been reported from the Upper Jurassic. Given the rarity of charophyte records for the Upper Jurassic, it is possible that *F. grovesi* may have evolved earlier.

*Clypeator discordis* SHAIKIN has a structure very similar to that of *Flabellochara grovesi*, but two or three additional cells are intercalated between the basal cell and the upper radiating cells of the still recognizable fans. Generally these cells are placed laterally, surrounding a lateral pore. In contrast to *F. grovesi*, the lateral sides are not flattened but curved, tending sometimes to have light, protruding expansions. The species has been reported from the Hauterivian to the lower Barremian (GRAMBAST, 1974; MARTIN-CLOSAS & GRAMBAST-FESSARD, 1986).

*Clypeator gautieri* GRAMBAST comprises the same essential elements as the preceding type, but the intermediate cells between the lateral pore and the basal cell are better developed, becoming similar to the fan cells.

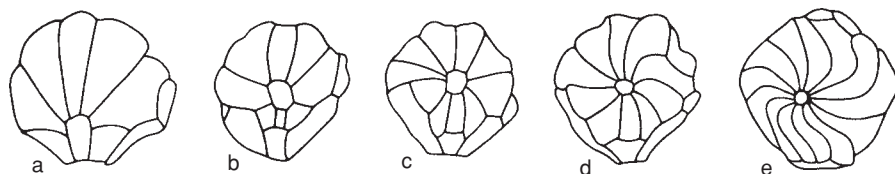


FIG. 36. Transition from lateral fan to shield structure in *Flabellochara-Clypeator* lineage; a, *Flabellochara grovesi* (HARRIS) GRAMBAST; b, *Clypeator discordis* SHAIKIN; c, *C. gautieri* GRAMBAST; d, *C. combei* GRAMBAST; e, *C. corrugatus* (PECK) GRAMBAST (Grambast, 1970, fig. a–e).

Moreover, the expansions bearing the lateral pores are here quite distinct. *C. gautieri* ranges from the Hauterivian to the upper Barremian (GRAMBAST, 1974; FEIST, LAKE, & WOOD, 1995).

*Clypeator combei* GRAMBAST is large, and the intermediate cells in contact with the basal cell tend to reach the same length as the upper cells. The disposition of the 10 to 11 cells radiating around the lateral pores that are borne by protruding expansions shows clearly the shield structure characteristic of the genus.

In *Clypeator corrugatus* (PECK) GRAMBAST, from the Aptian, the shields are made of 11 to 13 sinuous radiating cells among which the basal cells are not distinguishable from the upper ones.

In these five species, the adaxial side presents a rather constant disposition, resembling the opposing side, but two median lateral cells are present in *C. gautieri* and *C. combei*.

The *Ascidiella-Embergerella* phylogenetic lineage.—In this group, the utricle presents lateral expansions (horns) ending with central pores, which represent the protrusion of internal stemlets. Stemlets and horns are in equal numbers: only one in *Ascidiella*, three or four in *Embergerella*. The utricle was probably fixed at a node of a branchlet, as always occurs in the fructifications of the extant Characeae. The superficial layer of the utricle is made of cellular whorls, more or less imbricated one in another (Fig. 37). Every pore in the center of a whorl corresponds to the termination of internal long cells, which themselves originate from a stemlet connecting the basal pore to a lateral horn. Besides

the number of horns, the two genera differ in the morphology of the external whorls, which are single in the former and twofold in the latter.

MARTIN-CLOSAS (1996) proposed a quite different interpretation (Fig. 38). In *Embergerella*, he interpreted the stemlets as fixed at the base of the utricle on the branchlet (phylloid), but for *Ascidiella* it is the branchlet itself that is included in the utricle. Bracts were seen as ramifications leading to the external whorls. In this representation, the structure of the utricle appears different in these two genera.

The new approach of the Clavatoroideae by MARTIN-CLOSAS (1996), based mainly on cladistic analysis, allowed him to establish and connect together different lineages that were formerly isolated. Thus, *Lucernella* (*Clavator calcitrapus* and *C. ampullaceus*) and *Septorella* (*Clavator brachycerus* and *Clavator ultimus*) are related to the series *Clavator-Flabellochara-Clypeator* (genus *Clavator emend.* SCHUDACK, 1993b). *Pseudoglobator* and *Hemiclavator* were derived from *Nodosoclavator*.

## THE DEVELOPMENT OF THE CHARACEAE

### Origin

The oldest Characeae are the four *Aclistochara* species from the Upper Triassic of Sichuan Province (China; LIU & CHEN, 1992). These forms show the junction of the spiral cells at the summit of the gyrogonite that characterizes the family, but the features of the dehiscence pore, narrow and situated at the bottom of a depression (see Fig. 64, 3d, Systematics, herein p. 122), support the view



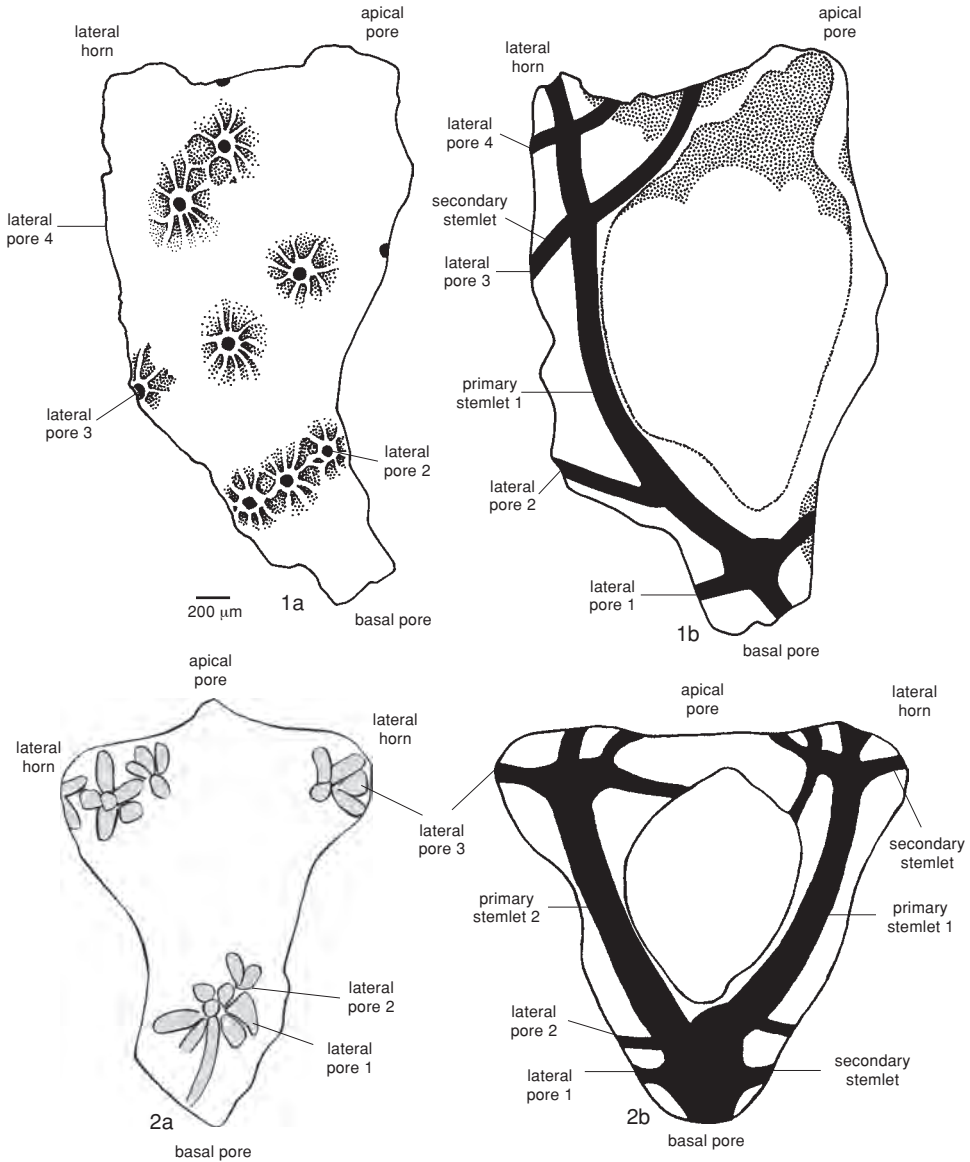


FIG. 37. Connections between external and internal structures of utricle; 1a–b, *Ascidiella irregularis* GRAMBAST-FESSARD (Grambast-Fessard, 1986, fig. 1); a, external view, b, longitudinal section; 2a–b, *Embergerella triquetra* GRAMBAST; a, external view, b, longitudinal section (new).

that the Characeae originated from the Porocharaceae.

### Evolutionary Tendencies

During the Late Cretaceous, such larger gyrogonites as *Peckisphaera macrocarpa* (GRAMBAST) FEIST & GRAMBAST-FESSARD appeared, as well as gyrogonites with diverse

types of ornamentation, such as *Peckichara pectinata* GRAMBAST and *Microchara punctata* FEIST. The Paleogene was the time of greatest diversification in the Characeae. The family has a great variety in the general shape, ornamentation, and apical features of the gyrogonites. From the Miocene onward, the family decreased in diversity and number

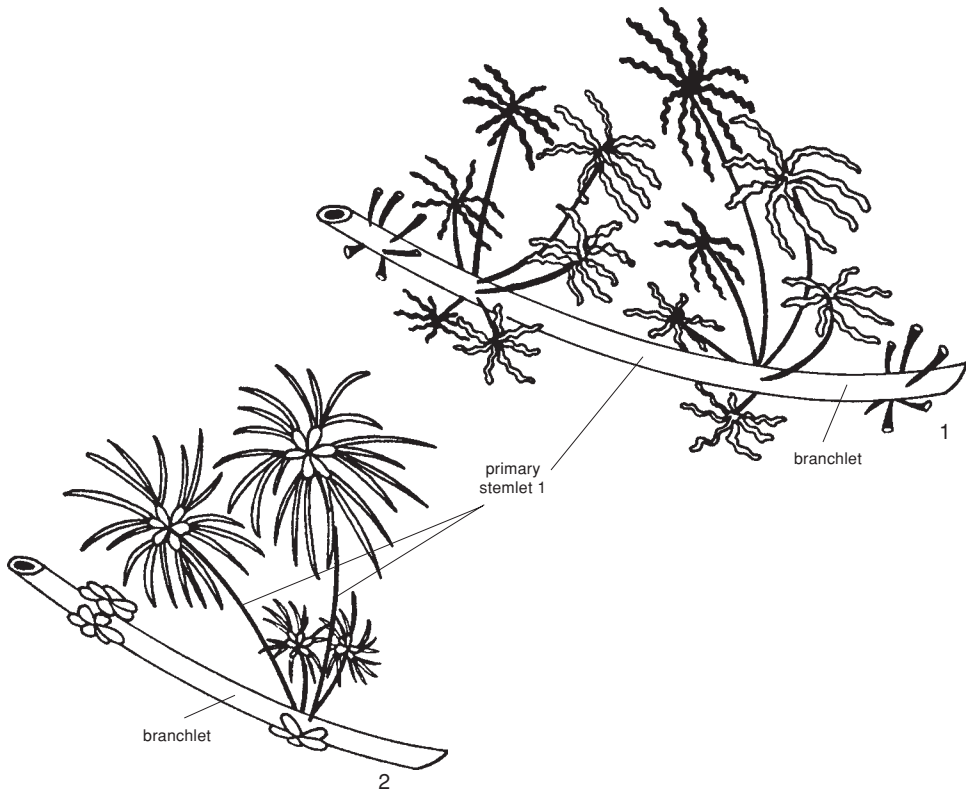


FIG. 38. Interpretation of utricle structure; 1, *Ascidiella iberica* GRAMBAST; 2, *Embergerella triquetra* GRAMBAST (*Ascidiella triquetra* in cladistic nomenclature) (Martin-Closas, 1996, fig. 13D, 13C).

of genera until the present day, when it is represented by seven unornamented genera including 80 species, according to WOOD and IMAHORI (1964–1965).

### Special Cases of Evolution

Phylogenetic lineages as complex as in the Clavatoraceae are unknown in the Characeae. A simple succession connecting *Aclistochara* to *Lamprothamnium* has, however, been recognized. SOULIÉ-MARSCHÉ (1979) noted the affinities of the two genera, according to their apical structure, in which the apex of the gyrogonite, prominent in the center, is surrounded by a periapical furrow. She proposed the inclusion of *Aclistochara* in *Lamprothamnium*. Apical views of both genera (see Fig. 64,3d and 68,1c, Systematics, herein p. 122 and p. 129 respectively), however, show that the apical zone is much

smaller in the former, in which it resembles the porocharacean ancestors. The variation curves of the apical pore diameter (Fig. 39) confirm these morphological data: the curve corresponding to *Aclistochara* is distinct from *Lamprothamnium* and closer to *Porochara*. The two genera are also distinguished by the general shape of their gyrogonites and by their basal plates: multipartite in *Aclistochara* and simple in *Lamprothamnium* (LU & LUO, 1990). The significance of the basal plate character is discussed in the chapter on Molecular Phylogeny, herein p. 81.

### Interspecific Relationships

An example of progressive evolution between species has been reported in the genus *Harrisichara* (FEIST-CASTEL, 1977a). *H. vasiformis* (REID & GROVES) GRAMBAST (see Fig. 67,1a, Systematics, herein p. 128) and

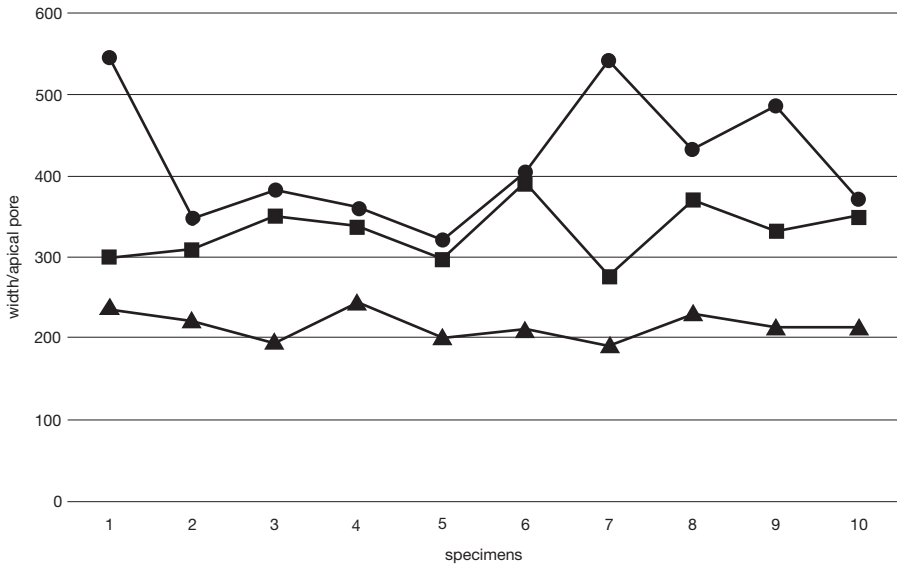


FIG. 39. Variation of apical pore in three species: curves for ratio of equatorial diameter of gyrogonite to diameter of apical pore; *Porochara douzensis* (FEIST & GRAMBAST-FESSARD) SCHUDACK, circles; *Aclistochara* aff. *jonesi* PECK, squares; *Lamprothamnium papulosum* GROVES, triangles (Feist, Bhatia, & Yadagiri, 1991, fig. 2).

*H. tuberculata* (LYELL) GRAMBAST (see Fig. 67, 1b, Systematics, herein p. 128) are two distinct and easily recognizable species. In the Isle of Wight (Hampshire, England) from the Lower Headon Beds upward and mainly in the series occurring between these and the Bembridge Beds, specimens of *Harrisichara* occur that are morphologically intermediate between the two species. Besides England, *H. vasiformis-tuberculata* is also relatively common in northern and southern Europe. Due to its wide geographical distribution and short vertical extension, this form is of great stratigraphical value; it is one of the guide fossils of the upper Eocene in the Paleogene biozonation (RIVELINE & others, 1996; and Biozonation, herein, Fig. 31, p. 58).

#### PHYLOGENY OF THE RASKYELLACEAE

The Raskyellaceae are a small group, characterized by the peculiar apical structure of the gyrogonite. In the three genera composing the family, the closure of the apex is brought about by a deciduous opercule of

five cells, which upon falling out of the pore leaves a rose-shaped opening (GRAMBAST, 1957). The shape and relative narrowness of this pore of dehiscence are similar in some Porocharaceae (see Fig. 50, 3c, Systematics, herein p. 102). These similarities suggest relationships between the families. The basal plate, which is simple in all the Raskyellaceae, suggests an origin in *Feistiella* SCHUDACK, which was, moreover, contemporaneous with the early genus *Saportanella* GRAMBAST during the Late Cretaceous.

The internal intercellular folds are another peculiar character common to *Raskyella* L. & N. GRAMBAST and *Rantzienella* GRAMBAST but not restricted to the Raskyellaceae. In both genera, the sutures between the spiral cells are strongly crenulated; such sutures also occur at the periphery of the apex between the tips of the spiral cells and the opercular cells. The internal folds are always visible at the internal face of the opercule (see Fig. 61g, Systematics, herein p. 117) but only rarely from the exterior, as in *Rantzieniella nitida* GRAMBAST (FEIST & GRAMBAST-FESSARD, 1984, fig. 3C).

The fossil record of the Raskyellaceae is relatively discontinuous: Upper Cretaceous (Campanian–Maastrichtian: *Saportanella*), Eocene (*Raskyella*), and Miocene (Aquitanian: *Rantzieniella*). According to NÖTZOLD (1965), Z. WANG (1978a), and SOULIÉ-MÄRSCHÉ (1989) the apical cells of the Raskyellaceae correspond to a thickening of the apical tips of the spiral cells and could have been derived in different periods from ancestors belonging to the Characeae. The individuality of the apical cells, however, cannot be questioned since the crenellated sutures differ from a straight dehiscence line or to a line of demarcation between differently calcified zones (ANADÓN & FEIST, 1981). Moreover, during the last two decades some gaps in the fossil record have been filled; for example, recent findings have contributed to completing the Eocene fossil record for the genus *Raskyella* (MARTIN-CLOSAS & others, 1999). The Raskyellaceae are thus deemed a valid family.

The characters used to detect affinities within the Raskyellaceae are the apex features, as well as the presence or absence of an ornamentation and of internal cellular folds. In *Saportanella* and *Rantzieniella*, the opercular cells occur as extensions of the spiral cells, and both genera are unornamented. In *Raskyella*, the opercular cells often alternate with the tips of the spiral cells; the genus is ornamented and shares with *Rantzieniella* the internal cellular folds. *Saportanella*, which is the oldest and has the most simple morphology, could be considered as the ancestor of *Saportanella* and *Raskyella*. The last occurrence of the Raskyellaceae is that of *Rantzieniella nitida* during the Aquitanian.

#### CONCLUDING REMARKS

The evolution of the fructification in Charophyta (Fig. 33) shows that the greatest morphological diversity occurred mainly in the Sycidiales and Clavatoraceae, groups that possess a utricle. A tendency to separation of sexes appears in two different lineages separated by nearly 300 Ma, the Devonian

*Pinnopotamen* and the Cretaceous *Perimneste-Atopochara* evolutionary lineages. It is surprising that analogous trends occur in both thalloid haplobiontic charalean algae and in vascular plants. In the latter dioecy tends to replace hermaphroditism, which may lead to self-sterility (MAYNARD SMITH, 1990).

Several general features also appear in charophyte evolution: the tendency toward becoming spiral and reduction of cell number, as well as improvements in enclosing and protecting the egg. This took place in one of two different ways, either by the closure of the apical pore of the gyrogonite in the Characeae and Raskyellaceae or by the acquisition of a supplementary cover (utricle) around the gyrogonite that occurred independently in the Sycidiales and in the Clavatoraceae.

#### EVOLUTION OF CHAROPHYTE BIODIVERSITY

The 420-million-year charophyte fossil record is well documented but varies in completeness according to periods and regions (see chapter on Paleobiogeography, herein p. 39). Charophytes from the Paleozoic have been reported mainly from North America and China and to lesser extent from Europe and some other parts of the world, whereas they occurred worldwide during the Mesozoic. During the Cenozoic, charophytes were most abundant in Europe and Asia (mainly China and India) and less common in North and South America. The fossil record of charophytes from Australia is still nearly nonexistent.

The succession of most genera (see Fig. 33, p. 65 herein) and a table of the range of families (see Stratigraphic Range Chart, herein p. 148) show that there were several phases of diversification and extinction.

#### PHASES OF DIVERSIFICATION

The oldest certain representatives of charophytes have been reported from upper Silurian Ludlow deposits of Europe:

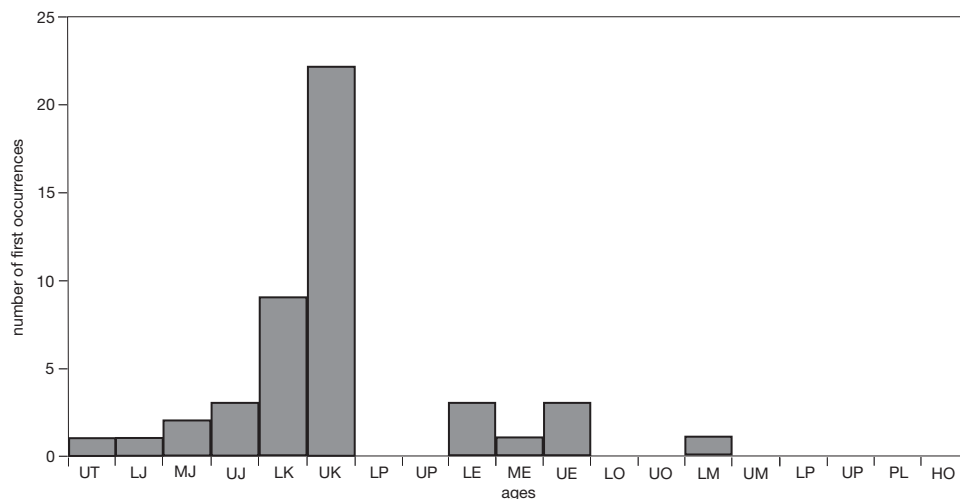


FIG. 40. First occurrences of charophyte genera, from Upper Triassic to Holocene (new).

*Moellerina laufeldi* CONKIN and *Praescydidium siluricum* T. and A. ISHCENKO, now regarded as a species of *Scydidium*. The form from Anticosti (Canada) figured in a section evoking a scyidiacean gyrogonite (in MAMET & others, 1992), however, suggests that the group may have appeared as early as the early Silurian (Wenlockian-Ludlowian transition). These occurrences coincide with the first records of land plants during the Silurian (KENRICK & CRANE, 1997). The Devonian, when six charophyte families were in existence, was the period of greatest diversity.

The second phase of major diversification corresponds to the appearance and development of the Clavatoraceae during the Late Jurassic and Early Cretaceous, whereas the Late Cretaceous was a time of the initial diversification phase of the Characeae (Fig. 40).

After numerous charophyte extinctions at the end of the Cretaceous, a new phase of diversification occurred during the Eocene, but it is detectable only at the generic and specific levels.

The last new charophyte genus to appear was *Rantzieniella* GRAMBAST (Raskyellaceae), the only Miocene origination.

## PHASES OF EXTINCTION AND RECOVERY

### Pennsylvanian Extinction

After the extinction at the end of the Devonian of two or three families (as the Eocharaceae are unknown between Late Devonian and Middle Triassic) and the drastic reduction in number of species in the Moelleriaceae, charophytes as a group would probably have become extinct if a new and important family, the Porocharaceae, had not evolved during the Pennsylvanian. The small family Palaeocharaceae, which appeared simultaneously, were extinct before the Triassic. The Porocharaceae represent the major part of the fossil record of the Triassic and Lower Jurassic. This family survived until the Paleocene.

### Cretaceous-Tertiary Boundary

The Cretaceous-Tertiary boundary represents a key period in charophyte history (Fig. 40). It marks the passage from the Cretaceous forms, dominated by the Porocharaceae and Clavatoraceae, to those of the Tertiary in which the radiation of the Characeae occurred. The small family Raskyellaceae apparently descended from the

Porocharaceae during the Late Cretaceous and persisted until the early Miocene.

If one compares the floras below and above the Cretaceous-Tertiary boundary, there is a sharp break between the Mesozoic and Cenozoic floras when approximately half of all charophyte species became extinct (FEIST, 1979). But this drastic decline in biodiversity did not cause the extinction of the group, most likely because it occurred during a diversification phase of one family, the Characeae. Thus the Cretaceous-Tertiary boundary marks a sharp decline within the charophytes, but not really a mass extinction. The most outstanding changes occurred after the K-T crisis. Indeed, the extinctions at the end of the Cretaceous were not balanced by an equivalent number of new genera. The result was a drastic reduction in diversity during the Cenozoic. The expansion of aquatic angiosperms may also have limited charophyte recovery.

#### PRESENT STATE AND PROSPECTS

Charophytes have shown remarkable resilience over the 420 million years of their existence. Their periods of greatest diversity and abundance occurred 300 to 400 million years ago. As shown by Figures 33 and 40, the present corresponds to a period of impoverishment of the Characeae, without any recent originations. Charophytes are cer-

tainly outcompeted by angiosperms in many habitats, but a kind of equilibrium appears in the biotopes where the two groups coexist. In spring, charophyte growth precedes that of aquatic angiosperms after which the vegetative parts of charophytes regress. Charophyte populations persist by means of fertilized oosporangia in the sediments of the water body until the next spring, when they germinate and give rise to a new vegetative thallus.

Probably most dangerous to the existence of charophytes are the various transformations that often eliminate bodies of water and, at the same time, the biotopes of Characeae. Chemical pollution, generally of agricultural or industrial origin, is responsible for the disappearance of species from some regions.

Protective measures, however, such as those applied to *Lamprothamnium* in Great Britain (MOORE, 1991) and *Lychnothamnus* (CASANOVA, 1997; McCOURT & others, 1999) in Australia as well as lake rehabilitation, for example in the Netherlands (SIMONS & others, 1994), have allowed the persistence of threatened species or the recovery of some species that had disappeared from their habitats. Such protective measures should be encouraged to preserve these interesting and scientifically important organisms.