#### SYSTEMATIC DESCRIPTIONS

#### Monique Feist and Nicole Grambast-Fessard

[Université Montpellier II, France]

# Phylum CHAROPHYTA Migula, 1897

[Charophyta Migula, 1897, p. 94] [=order Charales Mattox & Stewart, 1984, p. 50]

Oogamous chlorophyte algal group with gametangia surrounded by a multicellular cover and verticillate thallus made of alternating giant coenocytic cells and short uninucleate nodal cells where whorls of branchlets originate. Main part found as fossils is female fructification (gyrogonite), representing oogonium that contained egg; resistant oospore (zygote) membrane made of sporopollenin and more or less calcified enveloping tube cells and basal plate. Antheridia, preserved as casts, rarely represented, and remains of thallus generally fragmentary and not taxonomically significant. Classification based mainly on gyrogonite. Silurian (?Llandovery-?Wenlock, Ludlow)-Holocene.

# Class CHAROPHYCEAE Smith, 1938

[Charophyceae SMITH, 1938, p. 127] [=Charophycophyta Papenfuss, 1946, p. 218]

Description as for phylum. Silurian (?Llandovery-?Wenlock, Ludlow)-Holocene.

# Order MOELLERINALES Lu, Soulié-Märsche, & Wang, 1996

[Moellerinales Lu, Soulié-Märsche, & Wang, 1996, p. 8]

Gyrogonites with 5 to 12 dextrally spiralled cells without transverse ridges. *upper Silurian (Ludlow)–Permian.* 

#### Family MOELLERINACEAE Feist & Grambast-Fessard, 1991

[Moellerinaceae Feist & Grambast-Fessard, 1991, p. 198; *emend.*, Lu, Soulië-Märsche, & Wang, 1996, p. 8] [=Karpinskyaceae Z. Wang & Lu, 1980, p. 196, *partim*]

Gyrogonites with 7 to 12 dextrally spiralled cells, without transverse ridges; equa-

torial angle of the spiral cells above 20°. upper Silurian (Ludlow)–Permian.

Moellerina Ulrich, 1886, p. 34, non Schellwien, 1898 [\*M. greenei Ulrich, 1886, p. 34, pl. 3,8; OD] [=Calcisphaera WILLIAMSON, 1880, p. 521, partim (type, C. robusta, OD); Saccammina Dawson, 1883, p. 5 (type, *S. eriana* Dawson, 1883, p. 5, fig. 3, OD), non SARS in CARPENTER, 1869; Trochiliscus Karpinsky, 1906, p. 123 (type, T. ingricus Karpinsky, 1906, p. 112), partim; Trochiliscus subgenus Eutrochiliscus CROFT, 1952, p. 209 (type, Trochiliscus ingricus KARPINSKY, 1906, p. 123), partim; Weikkoella Summerson, 1958, p. 548 (type, W. sphaerica Summerson, 1958, p. 548, pl. 81,1-2, OD)]. Gyrogonites with 8 to 12 dextrally spiralled cells, with no coronula cells; shape subglobular, apical area rounded, pointed, or elongated to form a neck. Apical pore small. Spirals not divided by transverse ridges; basal area rounded, apical pore larger than basal pore. [Nomenclatural history of Moellerina was given by PECK and Mo-RALES, 1966. To date, M. laufeldi Conkin & CONKIN, 1992 is the oldest charophyte species.] upper Silurian (Ludlow)-Upper Devonian (Frasnian): Ukraine, Sweden, China, USA, Australia. FIG. 44,1a-e. \*M. greenei ULRICH, Middle Devonian, USA, neotype; a, lateral view; b, basal view, ×35 (Grambast-Fessard, Feist, & Wang, 1989, fig. 2, 1); c, lateral view, CF.2915-3/3, ×45; d, apical view, ×45; e, longitudinal section, CF.2915-3/4, ×50 (new).—Fig. 44,1f. M. laufeldi Conkin & CONKIN, Ludlow, Gotland, Sweden; lateral view, CF.3012-1, ×120 (new).

Gemmichara Z. WANG, 1984, p. 55 [\*G. sinensis Z. WANG, 1984, p. 55, pl. I, 1-7; OD]. Gyrogonites with 8 to 9 dextrally spiralled cells and no coronula cells. Shape bulbiform. Apical area drawn into an elongated neck; apical pore small or closed. Basal area rounded, basal pore large. [Gemmichara is the youngest known Moellerinales. WANG regarded this genus as the final step in a lineage starting in the Devonian with Moellerina. The lineage is defined by both the decrease in cell number and the closure of the apical pore. The latter feature seems to be linked to the tightness of the spiral cells, which are strongly stretched at the apex. A space (possibly a pore) between the apical ends of the spiral cells is visible on an internal mold of G. sinensis (Z. WANG, 1984, pl. I,3)]. Carboniferous (Mississippian)-upper Permian: China. FIG. 44,2a-c. \*G. sinensis WANG, upper Permian; a, holotype, lateral view, NIGP PB11279, ×50; b, apical view, ×60; c, basal view, ×50 (Z. Wang, 1984, pl. I,2,1,5).

Primochara ISHCHENKO & SAIDAKOVSKY, 1975, p. 42 [\**P. calvata* ISHCHENKO & SAIDAKOVSKY, 1975, p. 43, pl. I–III; OD]. Gyrogonites pear shaped, with dex-

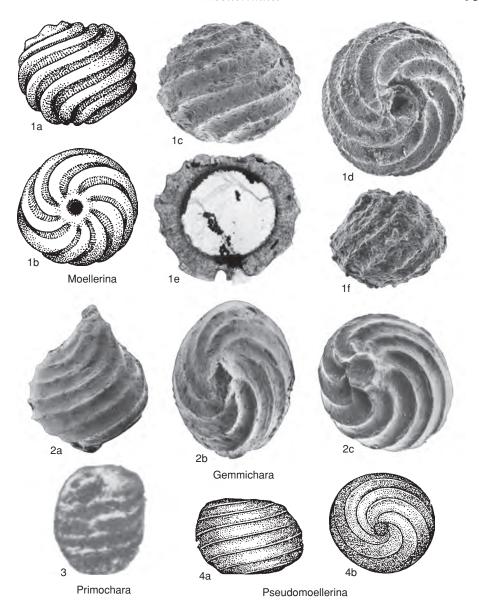


Fig. 44. Moellerinaceae and Pseudomoellerinaceae (p. 92-94).

trally spiralled cells. Cell number unknown. Size very large, up to 3 mm. [Tentatively attributed to the Moellerinaceae due to the incomplete state of preservation.] This genus is one of the oldest known charophytes. Gyrogonites of *P. calvata* sometimes occur on well-preserved vegetative parts. *Silurian (Pridoli):* Ukraine.——Fig. 44,3. \**P. calvata* ISHCHENKO & SAIDAKOVSKY; lateral view, ×25 (Shaikin, 1987, pl. XXIII,4).

### Family PSEUDOMOELLERINACEAE Z. Wang, 1984

[nom. transl. Feist & Grambast-Fessard, herein, ex Pseudomoellerinoideae Z. Wang, 1984, p. 54 (59)]

Gyrogonites with 5 to 7 dextrally spiralled cells, equatorial angle of spirals less than 20°. *Upper Devonian*.

Pseudomoellerina Z. WANG, 1984, p. 54 [\*Trochiliscus maslovi SAMOILOVA, 1955, p. 911, fig. 3; OD]. Gyrogonites with 5 to 7 spiral cells, with no coronula cells, shape oblate or subglobular, apical and basal areas rounded to flat, apical pore smaller than basal pore. Upper Devonian: Russia.——Fig. 44,4a-b. \*P. maslovi (SAMOILOVA) Z. WANG, holotype; a, lateral view; b, apical view, x60 (Samoilova, 1955, fig. 3a-b).

#### Order SYCIDIALES Mädler, 1952

[Sycidiales MÄDLER, 1952, p. 13; emend., FEIST & GRAMBAST-FESSARD, herein] [=Chovanellales CONKIN & CONKIN, 1977, p. 178, partim]

Gyrogonites incompletely known. Presence of a utricle, composed of vertical or dextrally spiralled cells, or ramified branches. Silurian (?Llandovery-?Wenlock, Ludlow)—Carboniferous (Mississippian).

#### Family SYCIDIACEAE Karpinsky, 1906

[nom. transl. PECK, 1934a, p. 116, ex Sycididae KARPINSKY, 1906, p. 83; emend., FEIST & GRAMBAST-FESSARD, herein] [=class Sycidiphyceae LANGER, 1976, p. 217]

Utricle made of numerous long cells that may be vertical or dextrally spiralled and are divided or not by numerous horizontal ridges creating polygonal pits. Silurian (?Llandovery-?Wenlock, Ludlow)-Carboniferous (Mississippian).

Sycidium Sandberger, 1849, p. 671; emend., Feist & GRAMBAST-FESSARD, herein [\*S. reticulatum SANDBERGER, 1849, p. 672, pl. VIIIB, a-d; OD] [=Pseudosycidium KARPINSKY in HACQUAERT, 1932, p. 10, fig. 5, 7, nom. nud.; Praesycidium T. A. Ishchenko & A. A. Ishchenko, 1982, p. 24 (type, P. siluricum T. A. ISHCHENKO & A. A. ISHCHENKO, 1982, p. 26, pl. V-VI, OD)]. Utricles bilaterally symmetrical, with 12 to 22 vertical cells divided into small polygonal pits by transverse ridges; division of vertical units around base follow determinate pattern. General shape subglobular to ovoid, apical pore large. Small pores representing apertures of internal canals present at utricle surface. [LANGER (1991) established two subgenera according to the position of the pore canals: S. (Sycidium), with pore canals in the angles of the polygonal units, and S. (Centroporus), with pore canals in the center of the polygonal units; the distribution of Sycidium species within these subgenera has not been established. Pseudosycidium, which is one of the oldest charophytes, is known only from thin sections; HACQUAERT (1932) noted that the laminate wall structure and the numerous outer polygonal units are typical of Sycidium and suggested assignment to that genus. The precise stratigraphic locality of the upper Silurian Turkestanian locality is unknown.

MASLOV (1961, 1963b) suggested that forms referred to this family may be utricles. The specimens from the lower Silurian of Anticosti Island (Quebec, Canada), consisting of thin sections, are attributed with doubt to Sycidium; and they may not be charophytes (MAMET & others, 1992).] Silurian (?Llandovery-?Wenlock, Ludlow)-Carboniferous (Mississippian): Russia, Ukraine, Germany, China, Turkestan, Iran, Zaire, USA, Canada, Australia. Fig. 45a. \*S. reticulatum Sandberger, Eifelian, Middle Devonian, Germany; lateral view, ×33 (Sandberger, 1849, pl. 8a).—Fig. 45b-d. S. foveatum PECK, basal Mississippian, USA, topotypes; b, lateral view, C.1237-1, ×50; c, apical view, C.1237-2, ×40; d, longitudinal section, C.1237-3, ×30 (new).——Fig. 45e-k. S. xizangense f. turbineum Z. WANG, Middle Devonian, China; e, topotype, lateral view, CF.2985-1; f, topotype, basal view, CF.2985-1, ×15; g, internal basal view of utricle with four branches, external layers removed, CF.3057-1, ×39 (new); h, longitudinal axial section with two-layered utricle wall, CF.3056-2, ×15 (new); i, internal view of utricle with casts of presumed vertical and undivided long cells of gyrogonite, ×40 (new); j, basal view with symmetrical disposition of utricular cells around basal pore (adapted from Wang, 1976, pl. 2,7); k, schematic reconstruction of utricular system of ramifications; A-C and D-F, basal cells of ending ramifications; a1-f3, basal cells of vertical calcified rows of polygons; G-J, basal cells of internal branches (new).

#### Family TROCHILISCACEAE Karpinsky, 1906

[nom. transl. Peck, 1934a, p. 104, pro Trochiliscidae Karpinsky, 1906, p. 83; emend., Feist & Grambast-Fessard, herein]

Utricle with numerous, often 18, dextrally spiralled cells that are simple or subdivided by numerous transverse ridges; apical pore usually open. *Lower Devonian (Emsian)—Carboniferous (Mississippian).* 

Trochiliscus Karpinsky, 1906, p. 112; emend., Feist & Grambast-Fessard, herein [\* T. ingricus Karpinsky, 1906, p. 112, pl. II,23-28; OD; lectotype, pl. II,23-24, designated FEIST & GRAMBAST-FESSARD herein] [= Trochiliscus KARPINSKY, 1906, p. 123, obj., partim (including Miliola panderi Ehrenberg, 1858, p. 311, partim); Trochiliscus subgenus Eutrochiliscus CROFT, 1952, p. 209 (type, Trochiliscus ingricus KARPINSKY, 1906, p. 112, partim)]. Utricles with 18 dextrally spiralled cells, with no coronula cells; spirals occasionally divided by transverse ridges, shape subglobular to oblate, apical region flattened or depressed, apical pore larger than basal; basal pore sometimes surrounded by 2 bisymmetrical, lip-shaped protuberances. [The most important characters are the number of spiral cells (18) as well as the occasional transverse ridges, which recall Sycidium.] Lower Devonian (Emsian)-

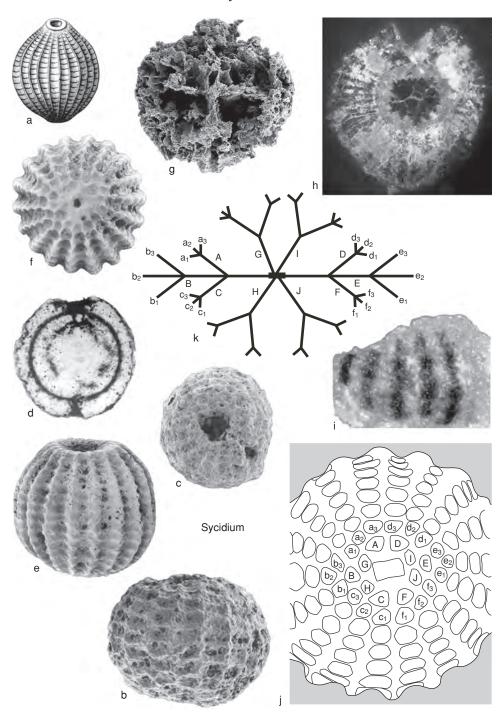


Fig. 45. Sycidiaceae (p. 94).

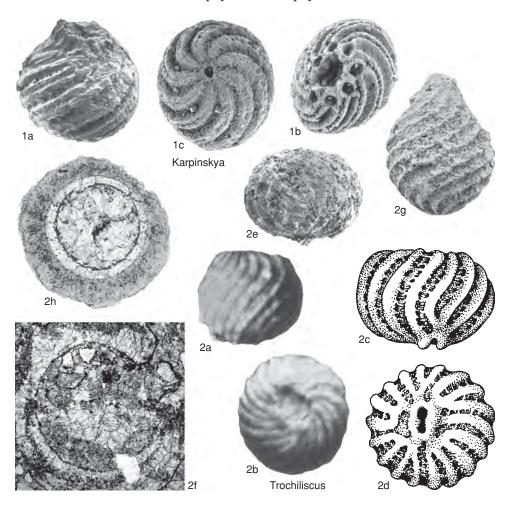


Fig. 46. Trochiliscaceae (p. 94-97).

Middle Devonian, ?Upper Devonian: United Kingdom, Poland, Ukraine, Russia, China, Iran.-Fig. 46,2a-d. \*T. ingricus Karpinsky, ?Devonian, Russia; a-b, lectotype, lateral, apical views, ×60 (Karpinsky, 1906, pl. II,23-24); c-d, lateral, basal views, ×70 (Grambast-Fessard, Feist, & Z. Wang, 1989, fig. 4, 3).——Fig. 46,2e. T. sp. cf. ingricus, Middle Devonian, Iran; lateral view, ×60 (Feist & Grambast-Fessard, 1985, fig. 8).—Fig. 46,2f. T. sp., Emsian, Wales; thin rock section with two-layered utricle wall, CF.2770, ×48 (new).-46,2g-h. T. podolicus CROFT, Emsian, Ukraine, topotypes; g, lateral view, ×60 (Feist & Grambast-Fessard, 1985, pl. I,4); h, transverse section with two-layered utricle wall and black oospore membrane, CF.2717-5, ×66 (new).

Karpinskya (Croft) Grambast, 1962b, p. 65; emend., FEIST & GRAMBAST-FESSARD, herein [\* Trochiliscus laticostatus PECK, 1934a, p. 109, pl. 11,1-23; OD] [= Trochiliscus KARPINSKY, 1906, p. 123, partim (type, T. ingricus Karpinsky, 1906, p. 112); Trochiliscus subgenus Karpinskya CROFT, 1952, p. 209, obj.]. Utricles with 7 to 10 dextrally spiralled cells and an equal number of calcified coronula cells. Multilayered wall of utricle visible in thin sections. General shape globular, coronula units forming erect, parapet-like ring around large summit opening. Middle Devonian-Carboniferous (Mississippian): Poland, Russia, USA.—Fig. 46,1a. \*K. laticostata (PECK) GRAMBAST, Mississippian, USA; topotype, lateral view, C1237-2, ×30 (new).-Fig. 46, 1b-c. K. bilineata (Peck) Peck & Morales, Upper Devonian, USA; *b*, apical view, CF.2915-3/1; *c*, basal view, CF.2915-3/2, ×50 (new).

#### Family CHOVANELLACEAE Grambast, 1962

[Chovanellaceae Grambast, 1962b, p. 64; emend., Feist & Grambast-Fessard, herein] [=Xinjiangocharaceae Lu, Soulié-Märsche, & Wang, 1996. p. 8]

Utricles with 3 to 14 vertical units that are simple or divided only at apical end. *Lower Devonian–Carboniferous (Mississippian)*.

Chovanella Reitlinger & Jarzewa, 1958, p. 1,114; emend., Feist & Grambast-Fessard herein [\*C. kovalevii; OD; lectotype, Reitlinger & Jarzewa, 1958, p. 1,114, pl. 1,1–3, designated Feist & Grambast-Fessard herein]. Utricles with 5 to 8 long vertical units, basal pore closed by discoid plate; summit opening occasionally surrounded and extended by short neck composed of separate apical cells equal in number to vertical cells. Apical cells occasionally missing. Long vertical units bifurcating into 2 secondary parts. Upper Devonian: Russia.

—Fig. 47,1a-c.\*C. kovalevii Reitlinger & Jarzewa, 1958, pl. I,1–3).

Ampullichara YANG & ZHOU, 1990, p. 272; emend., FEIST & GRAMBAST-FESSARD, herein [\*A. talimuica YANG & ZHOU, 1990, p. 272, pl. II, *I*–14; OD]. Utricles with 3 to 4, long and thick, slightly dextrally spiralled units, not reaching apex; apical pore large, basal pore closed by discoid plate. Gyrogonites visible from exterior, at summit and laterally, between utricle units. Gyrogonites of Moellerina type with 10 to 12 dextrally spiralled cells and no coronula cells. Gyrogonite pyriform or bottle shaped, with basal and apical areas truncated. Carboniferous (Mississippian): China.—Fig. 47,2a-d. \*A. talimuica YANG & ZHOU, gyrogonites; a-c, holotype, lateral, apical, basal views, BPNWC XC-015; d, specimen with elongated neck, lateral view, ×180 (Yang & Zhou, 1990, pl. II, 4b, 4a, 4c, 1b). ——Fig. 47, 2e-f. A. talimuica forma crassa YANG & ZHOU, utricles; e, lateral view; f, apical view with 12 gyrogonite cells, ×70 (Yang & Zhou, 1990, pl. II, 15b, 15a).

Xinjiangochara Yang & Zhou, 1990, p. 270; emend., Feist & Grambast-Fessard herein [\*X. rosulata Yang & Zhou, 1990, p. 271, pl. I, 1–7; OD] [=Nucella Yang & Zhou, 1990, p. 271 (type, N. bella Yang & Zhou, 1990, p. 272, pl. I, 14–15, OD)]. Vertical units, simple or bifurcating, up to 9 to 14 in number, going up to apical pore without intermediate apical cells. Basal plate rounded, slightly projecting. [Differs from Chovanella in having a higher cell number and by the apex, which is truncated instead of prominent. Nucella, which dif-

fers only in its more elongated utricle shape, is a synonym of Xinjiangochara (YANG Guodong, personal communication, 1996).] Lower Devonian-Carboniferous (Mississippian): USA, Canada, FIG. 47,3a-c. \*X. rosulata YANG & Zhou, Mississippian, China; a, holotype, lateral view; b, apical view; c, basal view, ×60 (Yang & Zhou, 1990, pl. I, 1b, 1a, 1c).——Fig. 47,3d-f. X. burgessi (Peck & Eyer) Lu, Soulié-Märsche, & Q. F. WANG, Middle Devonian; d, holotype, lateral view with coronula cells, western Canada, ×58 (Peck & Eyer, 1963a, pl. I,7); e, basal view with external basal plate, C.1238-1, Cooper Quarry, Missouri, USA, ×60 (new); f, longitudinal section with two-layered utricle, C.1386-1, Richfield, western Canada, ×64 (new).—Fig. 47,3g. X. complanior YANG & ZHOU; longitudinal section, ×60 (Yang & Zhou, 1990, pl. I,13).—Fig. 47,3h. X. (Nucella) bella YANG & ZHOU; lateral view, ×60 (Yang & Zhou, 1990, pl. I,14b).

#### Family PINNOPUTAMENACEAE Z. Wang & Lu, 1980

[Pinnoputamenaceae Z. Wang & Lu, 1980, p. 197; emend., Feist & Grambast-Fessard, herein]

Utricles with vertical units arranged in a symmetrical branching sequence. Lower Devonian–Middle Devonian.

Pinnoputamen Z. WANG & Lu, 1980, p. 197 [\*P. yunnanensis Z. WANG & Lu, 1980, p. 198, pl. 1,1-6; OD; lectotype, NIGP PB8680, WANG & LU, 1980, pl. 1, 1a-c; designed Feist & Grambast-FESSARD herein]. Utricles bilaterally symmetrical; each face bearing one group of long vertical furrows and four branching short furrows obliquely directed upward; adjacent branching furrows overlapping each other and forming sawtooth ridges at their junction. [The species from the Emsian of southern France (FEIST & FEIST, 1997), which has the same basic structure but with antheridia, is the oldest representative of Pinnoputamen. Costacidium Langer was referred by Langer (1991) to the Pinnoputamenaceae; however, the differences from Pinnoputamen remain unclear.] Lower Devonian (Lochkovian)-Middle Devonian (Givetian): Europe, China.—Fig. 48a-c. \*P. yunnanensis Z. Wang & Lu, Middle Devonian, southern China; a, lectotype, lateral view; b, apical view, ×60 (new, courtesy of Z. Wang & H. Lu); c, lateral view, schematic interpretation with bifurcated branch, ×70 (adapted from Feist & Grambast-Fessard, 1991, fig. 2-1). -Fig. 48d-f. P. sp., Lower Devonian, southern France; d, apical view; e, lateral view with a branch bearing antheridia, ×48 (Feist & Feist, 1997, fig. 1a, 1c); f, internal mold of a gyrogonite surrounded by its utricle, ×48 (new).

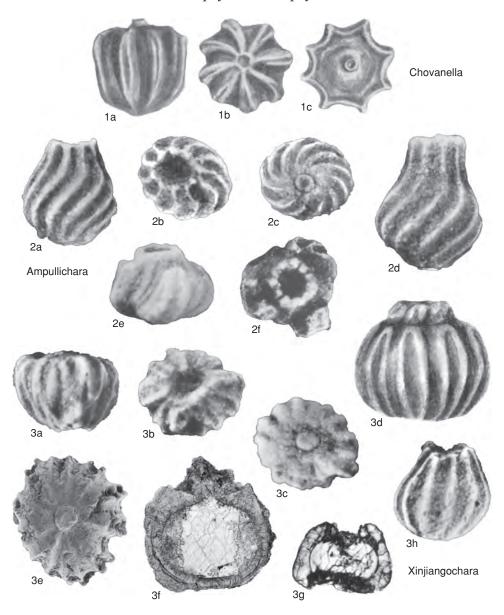


Fig. 47. Chovanellaceae (p. 97).

# Order CHARALES Lindley, 1836

[Charales LINDLEY, 1836, p. 414]

Gyrogonites composed of sinistrally spiralled cells. Apical structure variable. *Middle Devonian*<sup>1</sup>—*Holocene*.

<sup>1</sup>The assignment of *Palaeonitella cranii* (KIDSTON & LANG) PIA to the Eocharaceae extends the range of the Charales down to the Lower Devonian (Pragian; Kelman & others, 2004; see p. 120 herein for reference listing).

# Suborder PALAEOCHARINEAE Feist & Grambast-Fessard, 1991

[Palaeocharineae FEIST & GRAMBAST-FESSARD, 1991, p. 201]

Gyrogonites with more than 5 sinistrally spiralled cells. *Middle Devonian*<sup>1</sup>–*Middle Triassic*.

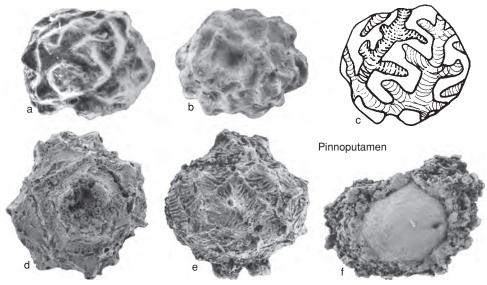


Fig. 48. Pinnoputamenaceae (p. 97).

#### Family EOCHARACEAE Grambast, 1959

[Eocharaceae GRAMBAST, 1959a, p. 559]

Gyrogonites with sinistrally spiralled cells variable in number from 8 to 13. Apical pore present. Apex flat. [The attribution of *Octochara* GESS & HILLER, 1995, p. 420, and *Hexachara* GESS & HILLER, 1995, p. 422, to the Eocharaceae, as suggested by GESS and HILLER (1995), is hypothetical due to the lack of data on the cell number and apical structure of gyrogonites. These genera have been reported from the Upper Devonian of South Africa. The presence of the family in the Triassic is attested by KISIELEVSKY (1996) based on the presence of an undescribed taxon.] *Middle Devonian*<sup>1</sup>–*Middle Triassic*.

Eochara Choquette, 1956, p. 1,373 [\*E. wickendenii Choquette, 1956, p. 1,373, fig. 1–7; OD]. 8 to 13 spiral cells in type species, and basal plate visible from exterior. Middle Devonian: Canada, USA, China.—Fig. 49,1a-c. \*E. wickendenii Choquette, Cooper Quarry, Missouri, USA; a, apical view, C.1238-2, ×75; b, lateral view, C.1238-3, ×70; c, basal view, C.1238-4, ×75 (new).

#### Family PALAEOCHARACEAE Pia, 1927

[Palaeocharaceae PIA, 1927, p. 90]

Gyrogonite with 6 to 7 sinistrally spiralled cells. Apical pore present. Apex protruding.

Carboniferous (Pennsylvanian)-lower Permian.

Palaeochara Bell, 1922, p. 160 [\*P. acadica Bell, 1922, p. 160, pl. I,3–9; OD; holotype, GSC 988, designated Peck & Eyer, 1963b, p. 843, pl. 101,10–12]. Apical part of gyrogonite protrudes into beak, conical to very elongated. Carboniferous (Pennsylvanian)–lower Permian: Canada, Germany, China.——Fig. 49,2a–c. \*P. acadica Bell, Pennsylvanian, Canada, holotype; a, apical view; b, lateral view; c, basal view, x125 (Peck & Eyer, 1963b, pl. 101,12,11,10).

# Suborder CHARINEAE Feist & Grambast-Fessard 1991

[Charineae Feist & Grambast-Fessard, 1991, p. 201]

Gyrogonite with 5 sinistrally spiralled cells. *Carboniferous* (*Pennsylvanian*)– *Holocene*.

#### Family POROCHARACEAE Grambast, 1962

[Porocharaceae Grambast, 1962b, p. 65]

Gyrogonites with 5 sinistrally spiralled cells, not enclosed in utricle; spiral cell endings delimit an apical pore generally open, although pore tends to be closed in some stellatocharoid genera. Basal plate undivided or with 2 to 3 pieces. [All the described species are without any ornamentation.]

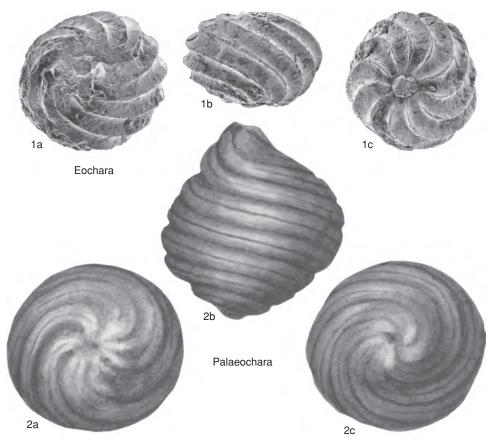


Fig. 49. Eocharaceae and Palaeocharaceae (p. 99).

Carboniferous (Pennsylvanian)—Paleogene (Paleocene, ?Eocene).

The Porocharaceae are mostly Mesozoic. Grambast (1962b) has divided the Porocharaceae into two subfamilies on the basis of the apex morphology: presence of an apical neck (Stellatocharoideae) or of a truncated or pointed apex (Porocharoideae). Kozur (1973) erected a third subfamily division, Clavatoritinae (later correctly named Clavatoritoideae by Bilan, 1988), grouping gyrogonites with a pointed apex not elongated into a neck; Cuneatocharoideae Z. Wang and Huang in Z. Wang (1978a), based on the same characters, is a junior synonym of the Clavatoritoideae.

Although Porocharaceae are characterized mainly by an open apical pore, some Permian Stellatocharoideae have a very small or even closed apex at the end of the apical neck. In such instances, the apical ends of the spiral cells join themselves at a point rather than along a broken line, as they do in the Characeae. On the other hand, the Permian representatives having a closed apex do not represent a distinct group, as specimens with open and closed apical pores may coexist in a given population (Z. WANG, 1984).

#### Subfamily POROCHAROIDEAE Grambast, 1961

[Porocharoideae Grambast, 1961, p. 200; emend., Z. Wang & Huang in Z. Wang, 1978a, p. 66]

Gyrogonite of Porocharaceae with a truncate summit. Apical pore sunken. *Carboniferous (Pennsylvanian)—Paleogene (Paleocene, ?Eocene)*.

The Porocharoideae are a homogeneous group, including approximately fifty species for only four genera. The inclination of the endings of the spiral cells into the center of the apex, which is the chief character of both *Euaclistochara* Wang, Huang, & Wang and *Jarzevaella* Shaikin, may occur in other genera, especially in *Porochara s.s.* These genera have been abandoned (Feist & Grambast-Fessard, 1982; Schudack, Turner, & Peterson, 1998).

Porochara Mädler, 1955, p. 271; emend., Schudack, 1986, p. 23 [\*Aclistochara kimmeridgensis MÄDLER, 1952, p. 26, pl. B,13–19; OD] [=Euaclistochara Z. Wang, Huang, & S. Wang, 1976, p. 71 (type, *E.* lufengensis Z. Wang, Huang, & S. Wang, 1976, p. 72, pl. 3,14–19, OD), partim; Jarzevaella Shaikin, 1977, p. 107 (type, J. boltiskaensis Shaikin, p. 107, fig. 1-2, OD), partim; Musacchiella Feist & Grambast-Fessard, 1984, p. 301 (type, M. douzensis Feist & Grambast-Fessard, 1984, p. 302, fig. 4a-c, OD)]. Apical opening small to medium; spiral ends sometimes bending toward center of apical pore; basal plate multipartite; general shape varying from ellipsoidal to subglobular. Size variable. [SCHUDACK (1986) described multipartite basal plates in type specimens of P. kimmeridgensis, and thus Musacchiella became superfluous as a junior synonym. Species whose basal plates have been recognized as multipartite extend from the Bathonian to the Berriasian. In addition, species attributed to Porochara but without indications on basal plate morphology are provisionally maintained in this genus.] ?upper Permian, Middle Jurassic-Lower Cretaceous, Paleogene (?Eocene): worldwide. FIG. 50,3a-b. \*P. kimmeridgensis (Mädler) Mädler, Kimmeridgian, Germany; a, topotype, lateral view, C.1234-1, ×60 (new); b, paratype, multipartite basal plate from inside gyrogonite, ×225 (Schudack, 1986, pl. 1,12).-Fig. 50,3c-e. P. (Musacchiella) douzensis (Feist & GRAMBAST-FESSARD) SCHUDACK, Bathonian, France; c, apical view, ×50; d, basal view, ×50; e, longitudinal section, ×54 (Feist & Grambast-Fessard, 1984, fig. 3B, 4C, 2A).

Feistiella Schudack, 1986, p. 23 [\*F. bijuescensis Schudack, 1986, p. 23, pl. 1,1–11; OD] [=Euaclistochara Z. Wang, Huang, & S. Wang, 1976, p. 71, partim (type, E. lufengensis Z. Wang, Huang, & S. Wang, 1976, p. 72, pl. 3,14–19, OD); Jarzevaella Shaikin, 1977, p. 107 (type, J. boltiskaensis Shaikin, 1977, p. 107, fig. 1–2, OD), partim; Porochara Mädler, 1955, p. 271 (type, Aclistochara kimmeridgensis Mädler, 1952, p. 26), partim]. Apical opening small or medium; basal plate undivided; general shape varying from ellipsoidal to subglobular. Size variable. [This genus is most similar to Porochara in its general shape and in the morphology of the somewhat sunken apical

opening. It differs in the particular character of an undivided basal plate and by the larger size of the Upper Cretaceous and Paleocene species.] ?upper Permian, Middle Jurassic—Paleogene (Paleocene, ?Eocene): worldwide.——Fig. 50,2a-d. \*F. bijuescensis SCHUDACK, Berriasian, Spain; a, holotype, lateral view, ×57; b-c, holotype, apical, basal views, ×60; d, basal plate, ×250 (Schudack, 1986, pl. 1,1,4,5,6).

Stomochara L. Grambast, 1961, p. 201[\*Gyrogonites moreyi PECK, 1934b, p. 54, pl. 1,1-3,5,6; OD; = Gyrogonites robertsi PECK, 1934b, p. 54] [=Catillochara Peck & Eyer, 1963b, p. 838, obj.; Horniella Shaikin, 1966, p. 158 (type, Gyrogonites robertsi R. PECK, 1934b, p. 54, fig. 10-12, OD), non A. Traverse, 1955, p. 55 (type, H. clavaticostata A. Traverse, 1955, p. 55, pl. 48,65, OD); Altochara SAIDAKOVSKY, 1968, p. 103 (type, A. continua Saidakovsky, 1968, p. 104, pl. 15,22-23, OD)]. Apical opening fairly large and ranging from strongly stellate to almost round; gyrogonites taper and may possess beak with small, truncate, apical area; basal plate undivided (PECK & EYER, 1963b, pl. 101,6). [Peck & Eyer (1963b) restudied the types of Gyrogonites moreyi PECK and G. robertsi PECK with approximately 600 gyrogonites from the Pennsylvanian and Permian of the central United States. They concluded that all the Pennsylvanian and Permian gyrogonites studied should be placed in a single species, G. moreyi, thus placing G. robertsi into synonymy.] Carboniferous (Pennsylvanian)-Triassic: Bulgaria, Germany, Poland, Ukraine, USA, China. Fig. 50, 1a-e. \*S. moreyi (PECK) GRAMBAST, Pennsylvanian, USA; a-b, holotype, lateral and apical view, ×54 (Peck, 1934b, fig. 1–2); c, lateral view, C.1235-1; d, apical view, C.1235-2, ×105; e, basal plate in situ, C.1235-3, ×325 (new).

Vladimiriella Saidakovsky, 1971, p. 122 [\* Tolypella globosa Saidakovsky, 1960, p. 56, pl. I,4a; OD] [=Porosphaera Z. WANG & HUANG, 1978, p. 273, obj., non Dumortier, 1822, p. 91]. Apical opening small; general shape spherical, with rounded apex and base; size medium. [SAIDAKOVSKY (1971) erected a new Porocharaceae genus for species previously assigned to Tolypella or Sphaerochara (Characeae), as they possess an apical pore. The genus Porosphaera, based on the same type, is a junior objective synonym of Vladimiriella.] Triassic: Bulgaria, Germany, Poland, Sweden, Ukraine, China.—Fig. 50,4a-b. \*V. globosa (Saidakovsky) SAIDAKOVSKY, Dnieper-Donets, Ukraine; a, lateral view, ×120 (Saidakovsky, 1960, fig. 4a); b, lateral view, ×108 (Bilan, 1988, pl. VIII, I).

#### Subfamily CLAVATORITOIDEAE Kozur, 1973

[nom. correct. KOZUR in BILAN, 1988, p. 107, pro Clavatoritinae KOZUR, 1973, p. 26] [=Cuneatocharoideae Z. WANG & HUANG in Z. WANG, 1978a, p. 66]

Gyrogonite of Porocharaceae with pointed summit that is not, however, drawn into a

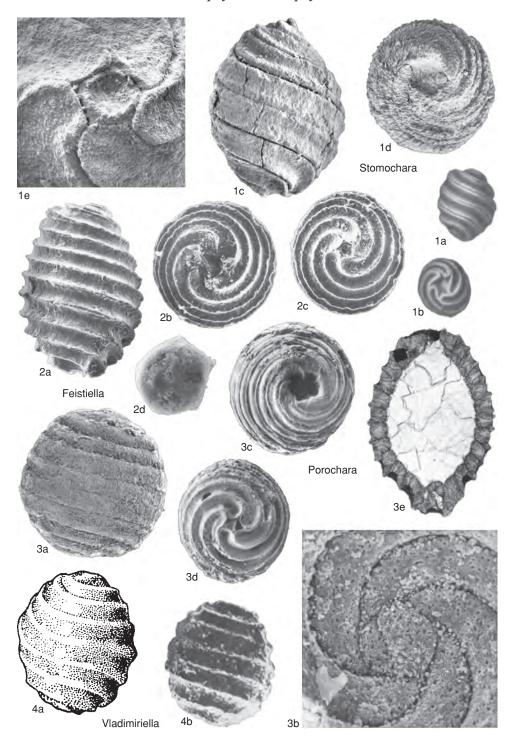


Fig. 50. Porocharaceae (p. 101).



Fig. 51. Porocharaceae (p. 103-104).

neck. Apical opening small. *Triassic–Lower Cretaceous*.

Clavatorites HORN AF RANTZIEN, 1954, p. 47 [\*Cl. hoellvicensis HORN AF RANTZIEN, 1954, p. 48, pl. IV,4; OD] [=Cuneatochara SAIDAKOVSKY, 1962, p. 1,144 (type, C. acuminata SAIDAKOVSKY, 1962, p. 1,144, pl. 1,1,7,8, OD)]. Apical part of gyrogonite forming cuneiform apical projection with small, circular aperture at its top; basal plate not described; general shape ovoid; size small to medium. [GRAM-BAST (1962b, p. 83) stated that the genus Clavatorites should be rejected because the type, based on a single badly preserved specimen, was not clearly established. KOZUR (1974) recognized the genus and considered Cuneatochara Saidakovsky as a junior synonym.] Triassic: Sweden, Bulgaria, Germany, Poland, Ukraine, China, Kazakhstan.-Fig. 51, 1a. \* C. hollvicensis Horn af Rantzien, Sweden; holotype, lateral view, SGS 1952-9-1762-2, ×70 (Horn af Rantzien, 1954, pl. IV,4).—Fig.

51,1b-c. C. (Cuneatochara) acuminatus SAIDA-KOVSKY, Lower Triassic, Ukraine; b, holotype, lateral view, PMUK 570; c, apical view, ×110 (Saidakovsky, 1962, pl. I,7-8).——Fig. 51,1d-f. C. (Cuneatochara) wuerttembergensis BREUER, Triassic, Germany; d, holotype, lateral view, MNS P1456, ×80; e, apical view, ×100; f. basal view of oospore, ×100 (Breuer, 1988, fig. 2a-2c).

Stenochara Grambast, 1962b, p. 66, nom. nov. pro Praechara Horn af Rantzien, 1954, p. 57, non Birina, 1948 (type, Praechara chovanensis Birina, 1948, p. 154, pl. 1,1–2) [\*Praechara mädleri Horn af Rantzien, 1954, p. 62, pl. 5,6–8; OD]. Apical part of gyrogonite forming low projection, with small, star-shaped or rounded aperture at its top. General shape ovoid, with apex slightly conical and base rounded. Basal plate unknown. Size small to medium. [Differs from Cuneatochara in its apical part, which is less protruding and does not form an acute angle.] Triassic–Lower Cretaceous: Bulgaria, Germany, Poland, Portugal, Sweden, Ukraine,

China, Kazakhstan.—Fig. 51,2a. \*S. maedleri (HORN AF RANTZIEN) GRAMBAST, Triassic, Sweden; holotype, lateral view, x70 (Horn af Rantzien, 1954, pl. V,6).—Fig. 51,2b–d. S. zavialensis GRAMBAST-FESSARD, Lower Cretaceous, Portugal; b, holotype, lateral view, x70; c, paratype, apical view; d, basal view, x80 (Grambast-Fessard, 1980, pl. 3,10,12,11).

#### Subfamily STELLATOCHAROIDEAE Grambast, 1962

[Stellatocharoideae Grambast, 1962b, p. 68] [=Maslovicharoideae Saidakovsky, 1966, p. 114; Stellatocharaceae Conkin & Conkin, 1977, p. 181]

Gyrogonite of Porocharaceae with apical part drawn into neck that is conical or truncated at distal end; apical pore variable in diameter; in some genera very small or even closed. Apical pore rounded, pentagonal, or stellatiform. Basal plate multipartite or unknown. *Carboniferous (Pennsylvanian)—Paleogene (Paleocene)*.

Stellatochara HORN AF RANTZIEN, 1954, p. 26 [\*S. sellingii HORN AF RANTZIEN, 1954, p. 33, pl. 1,1-3; OD] [=Maslovichara SAIDAKOVSKY, 1962, p. 1,143 (type, M. gracilis SAIDAKOVSKY, 1962, p. 1,143, pl. 1,1-2, OD)]. Spiral cells progressively bent at rim of apex, forming wide apical neck, less than onethird of gyrogonite length. Apical neck truncated at extremity; apical pore rounded, pentagonal, or star shaped, generally small; basal plate multipartite. General shape frequently ovoid, occasionally ellipsoid or subglobular. Size small to medium. [The genus is well characterized by its apical elongated neck; however the trait is not well marked in the type species S. sellingii. The Jurassic and Cretaceous species, which present a truncated apex and were assigned to Stellatochara by PECK (1957) and BHATIA and Mannikeri (1977), belong to Porochara. HORN AF RANTZIEN (1954) noted the similarities in the gyrogonites of Stellatochara and Clavatoraceae genera; in both instances, the gyrogonite is bottle shaped with a cylindrical apical neck. Grambast (1962b) agreed with HORN AF RANTZIEN (1964) and expressed the opinion that the ancestors of the Clavatoraceae are to be sought among the Stellatocharoideae. Transitional forms between the Triassic Stellatocharoideae and the Upper Jurassic Clavatoraceae, however, are presently unknown. The Upper Jurassic S. rostrata (MÄDLER) SCHUDACK, 1993b, as well as the Lower Cretaceous S. reyi GRAMBAST-FESSARD, 1980, and S. nehdensis SCHUDACK, 1987, have an apex with apical projection abruptly turning upward, which is typical of Stellatochara. These taxa most likely represent clavatoracean gyrogonites, exceptionally calcified when the utricle was, for some reason, uncalcified, and they therefore should not be referred to Stellatochara.] Triassic: Germany, Poland, Sweden, Ukraine, China, Kazakhstan.—Fig. 52,4a-d. \*S.

sellingii HORN AF RANTZIEN, Triassic, Sweden; *a*, holotype, lateral view RMS-1952-9-1805-44, ×70 (new); *b–c*, paratype, apical, basal views, RMS-1952-9-1805-48, ×120 (new); *d*, longitudinal section, ×90 (Horn af Rantzien, 1954, pl. II,4).—FIG. 52,4*e*. *S. germanica* KOZUR, Triassic, Germany; lateral view, ×110 (Breuer, 1988, fig. 2d).

Auerbachichara Kisielevsky, 1967, p. 37; emend., SAIDAKOVSKY, 1968, p. 102 [\*A. saidakovskyi KISIELEVSKY, 1967, p. 38, pl. 1,1-2; OD] [=Shaikinella KISIELEVSKY, 1993b, p. 87 (type, S. consummata Kisielevsky, 1993b, p. 89, pl. VIII, 1-2, OD)]. Spiral cells progressively bent at summit, forming short and broad apical neck; apical ends of spiral cells forming more or less developed denticles around apical aperture; apical aperture large, pentagonal or star shaped. Basal plate unknown. General shape ovoid. Size small. [Differs from Stellatochara in its less protruding neck and in its larger apical pore.] Permian-Triassic: Germany, Poland, Ukraine, Russia, China, Kazakhstan.-Fig. 52,1a. \*A. saidakovskyi KISIELEVSKY, Lower Triassic, Russia; lateral view, ×105 (adapted from Saidakovsky, 1968, pl. XV, 18). ——Fig. 52, 1b-c. A. starozhilovae Kisielevsky, Triassic, Poland; lateral, apical views, ×108 (Bilan, 1988, pl. X,1a-1b).

Latochara Mädler, 1955, p. 271; emend., Feist in FEIST & CUBAYNES, 1984, p. 595 [\*Aclistochara latitruncata PECK, 1937, p. 89, pl. 14,1-4; OD] [=Minhechara WEI in HAO & others, 1983, p. 173 (type, M. columelaria WEI in HAO & others, 1983, p. 174, pl. 43,11-17, OD)]. At rim of summit, spiral cells level off, turn inward, then turn abruptly upward into almost vertical position to form small pyramidal projection in center of summit (PECK, 1957); apical pore very small. Basal plate multipartite. General shape varying from subglobular to ovoid. Size small to medium. [Minhechara, based only on the wider apical pyramidal projection, is not distinguishable from Latochara (FEIST & GRAMBAST-FESSARD, 1991).] Triassic-Paleogene (Paleocene): France, Ukraine, USA, China.-52,2a-c. \*L. latitruncata (PECK) MÄDLER, Upper Jurassic, USA; a, lateral view, C.1236-1; b, multipartite basal plate from inside gyrogonite, C.1236-3, ×145; c, apical view, C.1236-2, ×80 (new).

Leonardosia Sommer, 1954, p. 186; emend., Saidakovsky, 1989, p. 91 [\*L. langei Sommer, 1954, p. 187, pl. 16,12; OD] [=Paracuneatochara Z. WANG, 1984, p. 55 (type, P. jinxiensis Z. WANG, 1984, p. 56, pl. I, 1-15, OD); Acutochara SAIDAKOVSKY, 1993, p. 78 (type, A. chinensis SAIDAKOVSKY, 1993, p. 79, fig. 4, OD; holotype, NIGP PB 11298, WANG, 1984, pl. II,8); Leonidiella Kisielevsky, 1993c, p. 98 (type, L. embensis Kisielevsky, 1993c, p. 98, pl. XII,1-2, OD); Luichara Kisielevsky, 1993c, p. 100 (type, L. molostovskae Kisielevsky, 1993c, p. 100, pl. XII,5-6, OD)]. Apical neck very long, more than onethird of gyrogonite length; Apical neck broad at base, then decreasing in width toward top. Apical pore small or closed. Basal plate unknown. General shape subglobular. Size large. [In the apical neck,

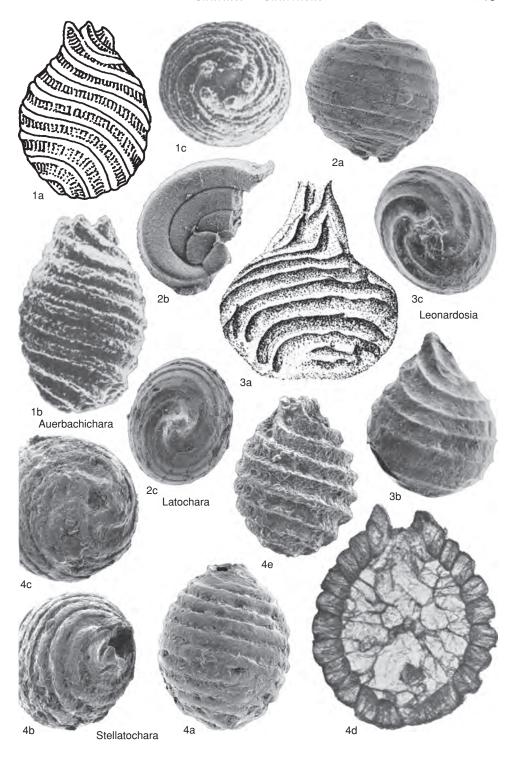


Fig. 52. Porocharaceae (p. 104-106).

cells are so tightly conjoined that the small pore at their apical ends tends to disappear. This condition differs from the closure of the apex in the Characeae. Original description by SOMMER (1954), based on impressions, shows a reverse course of the spiral cells. Acutochara SAIDAKOVSKY, 1993, which is defined only by the wavy outline of the apical neck that may be due to the preservation as a cast, is not distinct from Leonardosia.] Carboniferous (Pennsylvanian)-upper Permian: Russia, Brazil, Paraguay, China, Kazakhstan. FIG. 52,3a. \*L. langei SOMMER, Permian, Brazil; holotype, lateral view of dextrally spiralled impression of enveloping cells, ×45 (Sommer, 1954, pl. 16,12).——Fig. 52,3b-c. L. (Paracuneatochara) jinxiensis (Z. WANG) FEIST & GRAMBAST-FESSARD, upper Permian, China; b, lateral view; c, basal view, ×60 (Z. Wang, 1984, pl. II,5–6).

#### Family CLAVATORACEAE Pia, 1927

[Clavatoraceae Pia, 1927, p. 91]

Gyrogonites with 5 sinistrally spiralled cells, enclosed in utricle, made of generally calcified cells of vegetative origin. Gyrogonites with apical pore at end of neck or collar. [Gyrogonites resembling those of the Porocharaceae Stellatocharoideae, from which the Clavatoraceae probably evolved. Characters of particular importance are the symmetry and the number of layers in the utricle. Reported only from the Mesozoic.] Upper Jurassic—Upper Cretaceous (Maastrichtian).

The family Clavatoraceae was established by PIA (1927) after the genus Clavator REID & Groves, 1916. PECK (1938), who described the genus Atopochara, placed it in a new family, the Atopocharaceae, which has since been abandoned. GRAMBAST (1969) created three subfamilies within the Clavatoraceae, based upon utricle symmetry and number of layers of the utricle wall: Echinocharoideae, Clavatoroideae, and Atopocharoideae. Z. WANG and LU (1982) subdivided the Atopocharoideae into two tribes, the Atopocharae and Globatorae, and the Clavatoroideae into Clavatorae and Clypeatorae; the latter was divided into two subtribes, the Clypeatorinae and Septorellinae. These subdivisions, however, do not appear needed; and they have not generally been followed. SCHUDACK (1993b) has shown that the structure of the utricle in the Echinocharoideae was of the same type as that in the Atopocharoideae; the former subfamily has thus been abandoned.

In the classification of the Clavatoraceae proposed by Martin-Closas and Serra-Kiel (1991), the evolutionary lineages are interpreted as evolutionary species, in the sense of Wiley (1978). Although attractive in correctly reflecting progressive evolution within the phylum, this interpretation would however entail a total turnover of the taxonomy not completely in agreement with the rules of nomenclature (Feist & Z. Wang, 1995).

#### Subfamily CLAVATOROIDEAE Pia, 1927

[nom. transl. Grambast, 1969, p. 880, ex Clavatoraceae Pia, 1927, p. 91; emend., Grambast, 1969, p. 880]

Gyrogonite enclosed in utricle typically bilaterally symmetrical and composed of inner nodular layer and external structural layer formed of elongated units. External layer not developed in some genera. Some specialized genera develop secondary triradiate or four-rayed symmetry. *Upper Jurassic–Upper Cretaceous*.

Clavator Reid & Groves, 1916, p. 253, pl. 8; emend., HARRIS, 1939, p. 14 [\*C. reidii Groves, 1924, p. 116; SD Groves, 1924, p. 116]. Utricle bilaterally symmetrical with 2 calcified layers, inner smooth or nodular, outer made of 12 or fewer elongated vertical or spiralled units. Vegetative apparatus strongly calcified, with central tube surrounded by 12 dextrally coiled cortical tubes composed of alternate long and short units, latter giving rise to clusters of spines that more or less completely cover cortex. Upper Jurassic (Tithonian)-Lower Cretaceous (Aptian): USA, Germany, United Kingdom, Switzerland.—Fig. 53,2a-b. \*C. reidii Groves, Berriasian, United Kingdom; utricles, lateral views, MPK 8892 and 8895, ×45 (Feist, Lake, & Wood, 1995, pl. I,11-12).

Ascidiella GRAMBAST, 1966b, p. 2,210 [\*A. iberica GRAMBAST, 1966b, p. 2,210, pl. I, I–3; OD]. Utricle with strong bilateral symmetry and lateral expansion resembling a horn on shoulder near apex. A pore opening at end of horn. Numerous accessory pores present, with units of outer layer of utricle radiating from them. Pores are outlets for internal canals. Internal nodular layer of utricle well developed. [GRAMBAST (1966b) indicated that Dictyoclavator may have been ancestral type of Ascidiella.] Lower Cretaceous (Barremian—Aptian): United Kingdom, Portugal, Spain, Lebanon.—FIG. 54, Ia–b. \*A. iberica GRAMBAST, Barremian,

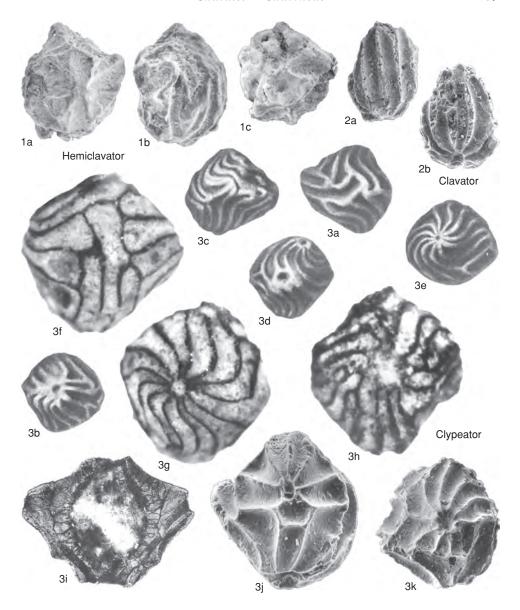


Fig. 53. Clavatoraceae (p. 106-110).

Spain; *a,* holotype, lateral view, C.6333-6, ×38 (new); *b,* longitudinal section, ×35 (Grambast, 1966b, pl. I,4).—Fig. 54, *Ic. A. irregularis* Grambast-Fessard, Aptian, Portugal; paratype, lateral view, ×28 (Grambast-Fessard, 1986, pl. I,5).—Fig. 54, *Id. A. inflata* Grambast-Fessard, Barremian, Spain; paratype, apical view, ×25 (Grambast-Fessard, 1986, pl. I,3).

Clypeator Grambast, 1962b, p. 69; emend., L. Grambast, 1970, p. 1,967 [\*Perimneste corrugata Peck, 1941, p. 295, pl. 42,15–24; OD]. Utricle

bilaterally symmetrical, with 2 opposite shields, each composed of 9 to 13 superficial units radiating from 2 lateral pores. Pores at end of internal canals, generally opening at tip of lateral projections. On 1 or 2 sides, 2 or 3 cells are intercalated between basal cell and lateral pore. *Upper Jurassic–Lower Cretaceous (Albian):* North America, Bulgaria, Germany, United Kingdom, Portugal, Romania, Russia, Spain, China, South Korea.—FIG. 53,3a-i. \*C. corrugatus (PECK) GRAMBAST, Aptian, North America; a-e, different views of one specimen, ×40

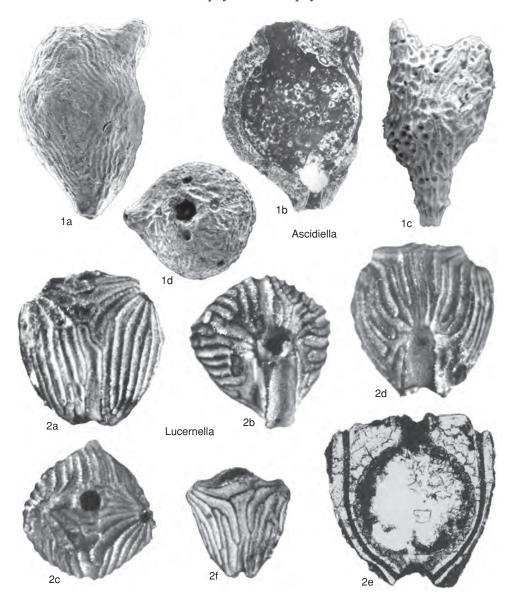


Fig. 54. Clavatoraceae (p. 106-110).

(Peck, 1957, pl. 3,1–5); f–g, topotype, ventral, lateral views of same specimen; h–i, basal view, longitudinal section, ×70 (Grambast, 1970, pl. IV,3a–3b,2d,4).——Fig. 53,3j. C. discordis Shaikin, Berriasian, Germany; lateral view, CF.2003c-1, ×75 (new).——Fig. 53,3k. C. combei Grambast, Hauterivian, United Kingdom; lateral view, MPK 8906, ×50 (new).

Dictyoclavator Grambast, 1966b, p. 2,210 [\*Clavator fieri Donze, 1955, p. 288, pl. XIII,4–5; OD]. Utricle globular, with a well-marked adaxial furrow

underlining bilateral symmetry. Outer layer not developed. Inner layer composed of irregularly disposed short units. *Upper Jurassic (Kimmeridgian)–Lower Cretaceous (Valanginian):* France, Portugal, Spain, Switzerland. ——FIG. 55, *1a–b. \*D. fieri* (DONZE) GRAMBAST, Berriasian, France, topotypes; a, lateral view, C.1218-1; *b*, apical view, C.1218-2, ×30 (new). ——FIG. 55, *1c. D. ramalhoi* GRAMBAST-FESSARD, Kimmeridgian, Portugal; adaxial view with median furrow, ×40 (Grambast-Fessard & Ramalho, 1985, pl. I,4).

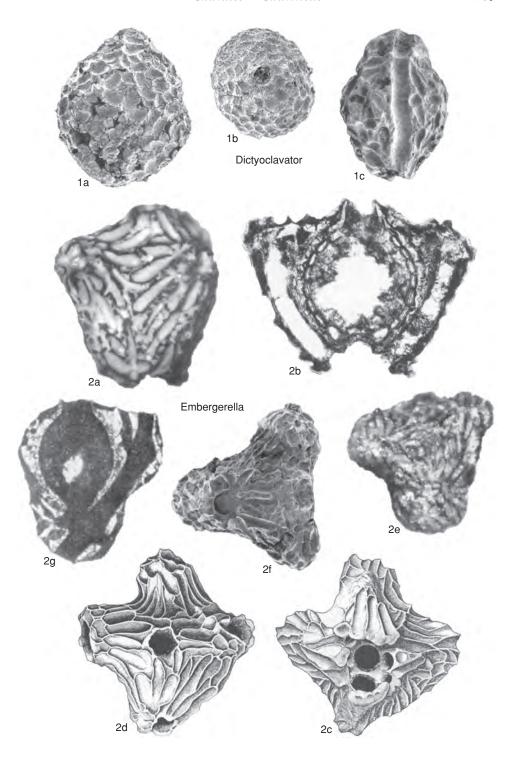


Fig. 55. Clavatoraceae (p. 108–110).

Embergerella GRAMBAST, 1969, p. 881 [\*E. cruciata Grambast, 1969, p. 881, pl. II,8–14; OD]. Utricle quadrangular to triangular from apex to base, composed in upper part of 3 or 4 strongly developed projections. At ends of projections are openings of canal system, canals originating near base. Surface units short and consisting of asymmetrical rosettes radiating from openings. [Embergerella differs from Triclypella in shape, development of surface units, and development of canal system.] Upper Jurassic-Upper Cretaceous (Cenomanian): France, Spain, Russia.—Fig. 55,2a-d. \*E. cruciata Grambast, Barremian, Spain; a, holotype, lateral view; b, longitudinal section, ×55 (Grambast, 1969, pl. II,8a,13); c, basal view; d, apical view, C.747-7, ×55 (new).—Fig. 55,2e-g. E. triquetra Grambast, Barremian; e, holotype, lateral view; f, apical view; g, longitudinal section with main canal and gyrogonite, ×60 (Grambast, 1969, pl. III, 18a, 15b, 20).

Flabellochara Grambast, 1959a, p. 559 [\*Clavator harrisi Peck, 1941, p. 292, pl. 42,28–34; OD]. Utricle bilaterally symmetrical with 2 opposite fans originating from a basal vertical unit. Fans each composed of 7 to 11 radiating cells. On adaxial side, single elongated cell intercalated between 2 fans. Lower Cretaceous: USA, Argentina, Bulgaria, France, Germany, United Kingdom, Italy, Spain, Switzerland, Ukraine, China, Uzbekistan.—Fig. 56,3a–b. \*F. harrisi (Peck) Grambast, Aptian, North America; a, topotype, lateral view, ×40 (Peck, 1957, pl. 2,9); b, topotype, lateral view, C.1240-1, ×45 (new).—Fig. 56,3c. F. grovesi (Harris) Grambast, Berriasian, United Kingdom; lateral view, C.1219-1, ×45 (new).

Hemiclavator Z. WANG & Lu, 1982, p. 98 [\*H. nei-mongolensis Z. WANG & Lu, 1982, p. 98, pl. IV, 1–5; OD; lectotype, PB8738OD, pl. IV, 1b, 1c, 1d, designated Feist & Grambast-Fessard herein]. Utricle with 2 different sides: 1 with vertical cells as in Clavator species, the other with long units radiating from central pore. Nodular layer generally visible laterally as well as in apical part of utricle. Lower Cretaceous (Barremian): Spain, China.—Fig. 53,1a-c. \*H. neimongolensis Z. Wang & Lu, China; lectotype; a, lateral side with radiating units; b, lateral side with vertical units; c, basal view, ×50 (Z. Wang & Lu, 1982, pl. IV,1b-1d).

Heptorella Feist & Grambast-Fessard, nom. nov. herein, nom. nov. pro Septorella Grambast, 1962b, p. 69, non Allescher in Hennings, 1897, p. 242, Fungi (type, S. salacia, OD) [\*Septorella brachycera Grambast, 1962b, p. 69, pl. I,a-d; OD]. Utricle with 6 to 9 lateral pores, superficial or at ends of projections. Lateral pores are outlets for internal canals originating from basal chamber. Outer layer with numerous vertical, long units in basal part of utricle. Apical part composed of shorter units converging to apical pore. A horizontal corticated tube, weakly developed in H. campylopoda, joined to basal part of utricle. [Septorella Grambast, 1962b, is a junior homonym of Septorella Allescher, 1897.

Derivatio nominis: Heptorella, from the Greek hepta (seven), referring to the frequent number of lateral horns of utricles in the type species.] Upper Cretaceous (Campanian–Maastrichtian): France, Spain.—Fig. 56, 1a-c. \*H. brachycera Grambast, Maastrichtian, southern France; a, holotype, lateral view, ×50 (Grambast, 1962b, fig. 1b); b, paratype, apical view, ×40; c, longitudinal section, ×45 (Grambast, 1971, pl. III,3b, pl. II,4).—Fig. 56,1d-f. H. ultima Grambast, southern France; d, holotype, lateral view; e, paratype, basal view, ×30 (Grambast, 1971, pl. VI,1a, pl. VII,1c); f, dwarf form, ×30 (Grambast, 1977b, fig. 4b).

Lucernella Grambast & Lorch, 1968, p. 48 [\*L. ampullacea Grambast & Lorch, 1968, p. 48, pl. I, 1-3, pl. II, 1-9; OD]. Utricle bilaterally symmetrical, with 2 accessory pores located at top of shoulders of apex. Accessory pores are outlets for 2 internal canals originating at basal chamber. Adaxial face of utricle joined to fragment of branch or with prominent furrow marking its place. Internal nodular layer of utricle well developed. External layer made of vertical units except in apical zone where furrows radiate from accessory pores. Lower Cretaceous (Aptian): Lebanon.—Fig. 54,2a-e. \*L. ampullacea Grambast & Lorch, holotype; a, dorsal (abaxial) view, ×49; b, basal view, ×47; c, apical view, ×44; d, ventral view, ×49; e, longitudinal section, ×50 (Grambast & Lorch, 1968, pl. I, 1a, 1d, 1c, 1b, pl. II,8).—Fig. 54,2f. L. deltea Grambast & Lorch; paratype, dorsal view, ×60 (Grambast & Lorch, 1968, pl. III, 1a).

Nodosoclavator MASLOV, 1961, p. 679; emend., Grambast, 1966c, p. 269 [\*Clavator nodosus Peck, 1957, p. 15, pl. 8,3–18; OD]. Utricle with external layer restricted to basal portion of gyrogonite, nodular layer with tubercles well developed and irregularly disposed or more or less aligned with spirals and covering gyrogonite. Gyrogonites strongly beaked by abrupt upturn of spiral units at distal ends. Vegetative parts commonly preserved at base of utricle. [Nodosoclavator differs from Clavator in that outer structural layer is restricted to the basal part of the utricle or even missing. Nodosoclavator is one of the oldest representatives of the Clavatoraceae family. The nodosoclavatoroid utricles (SCHUDACK, 1989) are incompletely developed utricles of other Clavatoroideae, which may represent the Nodosoclavator stage and do not put the validity of the genus in question.] Upper Jurassic (Oxfordian)-Lower Cretaceous (Aptian): USA, France, Germany, United Kingdom, Portugal, Spain, Switzerland, Ukraine, China, Algeria.-Fig. 57,1a-b. \*N. nodosus (Peck) Maslov, Aptian, North America; a, holotype, lateral view; b, paratype, lateral view, ×60 (Peck, 1957, pl. 8,5-6).—Fig. 57,1c-d. N. adnatus Martin-Closas & GRAMBAST-FESSARD, Barremian, Spain; c, lateral view with part of branchlet, ×50; d, interpretation of external utricle structure in connection with branchlet, ×50 (Martin-Closas & Grambast-Fessard, 1986, pl. II, 10, text-fig. 4).

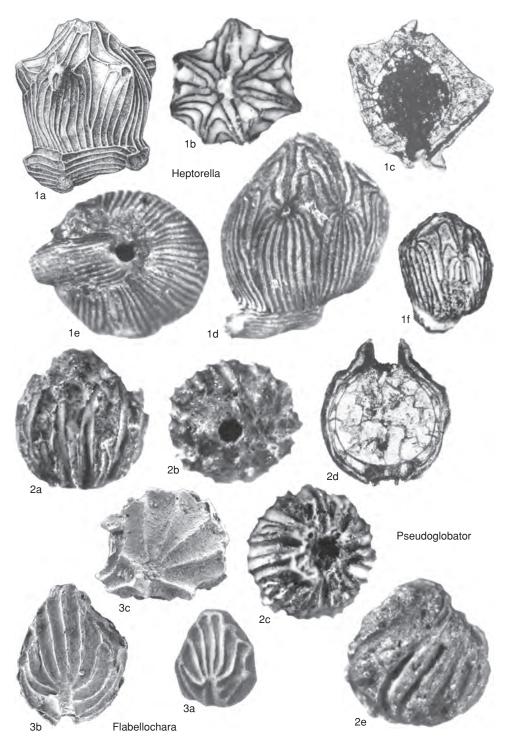


Fig. 56. Clavatoraceae (p. 110-112).

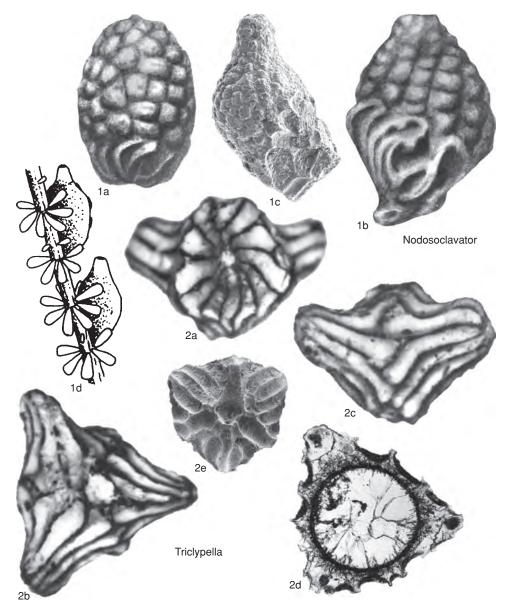


Fig. 57. Clavatoraceae (p. 110-113).

Pseudoglobator Grambast, 1969, p. 881 [\*P. fourcadei Grambast, 1969, p. 881, pl. IV,22–28; OD]. Utricle globular, not bilaterally symmetrical, without lateral expansions or canals. Internal layer formed of large nodules, external layer of numerous units, not articulated, long, vertical, or slightly spiralled. Lower Cretaceous (Barremian): Spain.—Fig. 56,2a–e. \*P. fourcadei Grambast; a–c, holotype, lateral, apical, basal views; d, longitudinal section; e,

paratype, lateral view, ×40 (Grambast, 1969, pl. IV,22a-c,27,23a).

Triclypella Grambast, 1969, p. 881 [\**T. calcitrapa* Grambast, 1969, p. 881, pl. I, *I*–*T;* OD]. Utricle with 3 laterally directed projections developed in upper half. At ends of projections are openings of internal canals that originate near base. Surface units forming shields radiate from ends of projections. [Differs from *Clypeator* by presence of a third

projection developed in the symmetry plane.] Lower Cretaceous (?Hauterivian, Barremian): Argentina, United Kingdom, Spain, China.——Fig. 57,2a–e. \*T. calcitrapa Grambast; a, holotype, lateral view with 1 shield, Barremian, Spain; b–c, holotype, apical, lateral views, Barremian, Spain; d, transverse section, Barremian, Spain, ×70 (Grambast, 1969, pl. I,1c,1a–1b,7); e, basal view, ?Hauterivian, United Kingdom, ×45 (Feist, Lake, & Wood, 1995, pl. II,2).

# Subfamily ATOPOCHAROIDEAE Peck, 1938

[nom. transl. Grambast, 1969, p. 880, pro Atopocharaceae Peck, 1938, p. 173; emend., Schudack, 1993b, p. 93]

Utricle with a well-developed, 3-rayed symmetry. Utricle composed of 2 superposed groups of branched units. 3 or 6 similarly branched units of internal group trifurcately ramified, whereas external group more variable or even completely reduced. *Upper Jurassic–Upper Cretaceous*.

Atopochara PECK, 1938, p. 173; emend., PECK, 1941, p. 289 [\*A. trivolvis PECK, 1938, p. 174, pl. 28,8-12, text-fig. 1; OD]. Utricle composed of 3 equivalent groups of units. Each group composed of 3 short vertical units originating near basal opening and ending near equator; 2 to 5 small units grouped on or near equator and several sinistrally spiralled units extending distally from equator to apex. Gyrogonite thin walled, fragile. [GRAMBAST (1967) stated that Atopochara developed directly from Perimneste by suppression of primordial basal cells of each ramulus and of all vestigial antheridia except that in right-hand fork.] Cretaceous: world-—Fig. 58,1a-c. \*A. trivolvis Peck, Aptian, North America; a, holotype, lateral view, ×33 (Peck, 1938, pl. 28,12); b-c, topotype, basal view, apical view, ×40 (Grambast, 1968, pl. III, 16b, 1c).-Fig. 58,1d-e. A. triquetra (Grambast) Feist, Lower Cretaceous, Spain; d, paratype, lateral view; e, paratype, basal view, ×50 (Grambast, 1968, pl. II, 13a, 12b). ——Fig. 58, 1f. A. multivolvis Peck, Cenomanian, southern France; lateral view, ×35 (Feist, 1981, fig. 1f). FIG. 58, 1g-h. A. trivolvis PECK; interpretations of cellular structure of utricle (white, antheridia) (Grambast, 1967, fig. d,f).

Diectochara Musacchio, 1971, p. 29 [\*D. andica Musacchio, 1971, p. 31, text-fig. 4, pl. I,8–10, pl. II,24–29, pl. III,30–38; OD]. Utricle made of long, noncontiguous, unbranched tubes forming 2 superposed series of 6 cells each, outer being more elongated. Vegetative apparatus preserved, composed of vertical, long units. [The utricle structure in this genus is even less distinctive than in Echinochara.] Lower Cretaceous (Barremian): Argentina.—Fig. 59,2a–c. \*D. andica Musacchio; a, topotype, acidized specimen, C.1217-1, ×25 (new); b, paratype, gyrogonite and antheridia, ×54

(Musacchio, 1971, pl. I,9); *c*, topotype, internal view of half of whorl of utricles with 3 gyrogonites and 1 antheridium, C.1217-2, ×23 (new).

Echinochara PECK, 1957, p. 21; emend., SCHUDACK, 1993b, p. 94 [\*E. spinosa Peck, 1957, p. 22, pl. I,1-22, pl. 2,21-25; OD]. Utricle made of short, contiguous, branched or not branched cortical tubes, more or less fused to gyrogonite; these tubes form 2 groups of units: internal ones, 3 or 6 in number, trifurcately ramified; external units (also 3 or 6) more variable. Vegetative apparatus preserved, with external filaments more or less dextrally coiled. [In E. pecki (MADLER) GRAMBAST, the tubes are contiguous and joined to the gyrogonite and constitute a true utricle completely enclosing the gyrogonite.] Upper Jurassic-Lower Cretaceous: North America, Germany, Switzerland, Spain.—Fig. 58,2a-c. \*E. spinosa PECK, Kimmeridgian, North America; a, paratype, 3 fertile nodes with spiral internal fillings of gyrogonites (etched specimen), ×16; b, section through 2 fertile nodes of branchlet, ×18 (Peck, 1957, pl. 1,2, 6); c, holotype, lateral, view of gyrogonite filling and utricle cells (etched specimen), ×40 (Peck, 1957, pl. 1,2,6, pl. 2,23).-Fig. 58,2d-e. E. pecki (Mädler) Grambast, upper Kimmeridgian, Germany, topotypes; d, apical view of utricle whorl around central axis, CF.2950-1, ×40; e, internal view of utricle with casts of spiral cells, CF.2950-2, ×60 (new).

Globator L. GRAMBAST, 1966a, p. 1,932 [\*G. trochiliscoides L. GRAMBAST, 1966a, p. 1,932, fig. 1-3; OD]. Utricle composed of 3 equivalent groups of units. Each group composed of 3 units at base, with 5 units resting on them. Type species unique in having only 15 units, 3 basal units not represented. Upper Jurassic (Tithonian)-Lower Cretaceous (Barremian): France, Germany, United Kingdom, Italy, Spain, Switzerland, Algeria.—Fig. 59, 1a-d. \*G. trochiliscoides GRAMBAST, Barremian, Spain, topotype; a, lateral view; b, basal view; c, apical view, ×35 (L. Grambast, 1966a, fig. 1-3); d, longitudinal section, ×45 (Grambast, 1966b, pl. III,6).—Fig. 59,1e. G. rectispirale Feist, Tithonian, United Kingdom; holotype, lateral view, MPK 8919, ×45 (Feist, Lake, & Wood, 1995, pl. —Fig. 59,1f–g. G. protoincrassatus Mojon, Berriasian, United Kingdom; f, lateral view, MPK 8921; g, apical view, MPK 8890, ×45 (Feist, Lake, & Wood, 1995, pl. I,8,4).

Perimneste Harris, 1939, p. 54 [\*P. horrida Harris, 1939, p. 54, text-fig. 80-q, 9-13, pl. 13-15, pl. 16,6,8,9; OD]. Utricle consisting of 3 similar groups of branching ramuli bearing antheridia. Each right-hand side branch of ramulus bearing fork of 2 long units with antheridium in angle. Supplementary antheridia may occur at any point where 2 cells form sufficiently open angle. Utricle units not contiguous. Lower Cretaceous (Berriasian–Barremian): Germany, United Kingdom, Spain, Switzerland, China.—Fig. 60a-e. \*P. horrida Harris, Berriasian, Germany; a, lateral view, CF.2003, x45 (new); b, specimen with outer wall dissolved by acid to show utricular ramulus, x40;

# Charophyta—Charophyceae

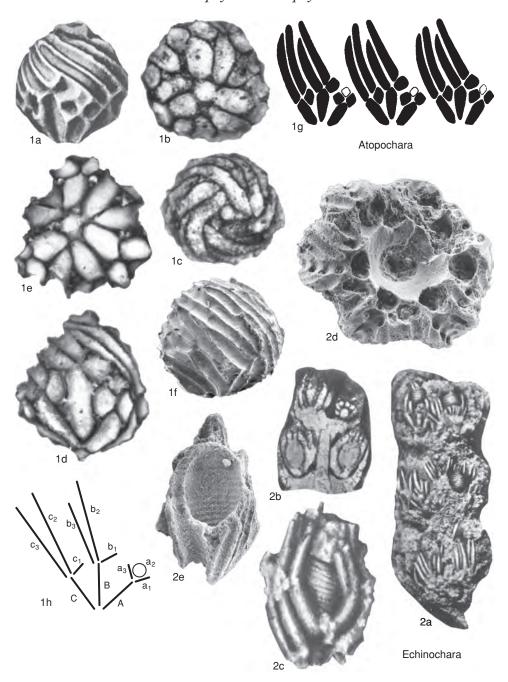


Fig. 58. Clavatoraceae (p. 113).

c–d, analysis of cellular structure of utricle (antheridia: white) (Grambast, 1967, pl. I,2; text-fig. a,e); e, detail of antheridial cast, CF.2003, ×90 (new).

——Fig. 60f. P. vidua Grambast, Barremian, Spain;

transverse section of utricle, ×35 (Grambast, 1967, pl. IV,20).——Fig. 60g. *P. ancora* Grambast, lower Barremian, Spain, holotype; lateral view, ×50 (Grambast, 1967, pl. III,13a).

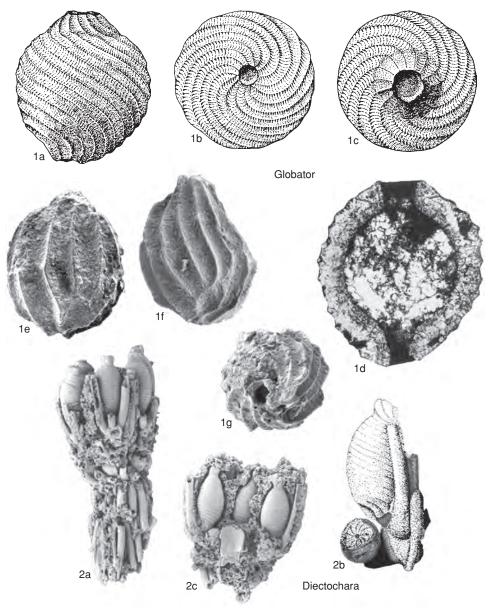


Fig. 59. Clavatoraceae (p. 113).

## Family RASKYELLACEAE L. Grambast & N. Grambast, 1955

[nom. transl. Grambast, 1957, p. 357, ex Raskyelloideae L. Grambast & N. Grambast, 1955, p. 1,001] [=Raskyellae Z. Wang, 1978a, p. 67]

Gyrogonite with 5 sinistrally spiralled cells, not enclosed in utricle; spiral endings bearing 5 apical cells, joined in apex center and constituting deciduous operculum. Loss

of operculum creates rose-shaped apex opening. Spirals smooth or with tubercles. *Upper Cretaceous–Neogene (lower Miocene)*.

MÄDLER (in MÄDLER & STAESCHE, 1979) and Z. WANG (1978b) compared the 5-celled operculum of the Raskyellaceae with nodules present at apical ends of spirals in some genera, such as *Nitellopsis* and

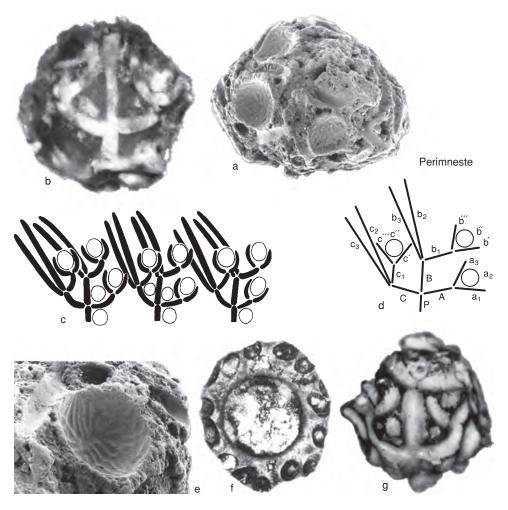


Fig. 60. Clavatoraceae (p. 113-114).

Gyrogona, in the family Characeae; however, actual apical nodules have never been reported in the Raskyellaceae. The opercular units are separated from the spirals by true walls, as visible on the inside of the apex of a gyrogonite of *Raskyella*. The 5 apical cells are separated from the spirals and from one another by undulating walls similar to those separating the spirals.

Raskyella L. Grambast & N. Grambast, 1954, p. 669 [\*R. peckii L. Grambast & N. Grambast, 1954, p. 670, fig. 1; OD]. Gyrogonites with opercular apical cells in most instances superficial and alternating

with spirals in position. General shape spheroidal to prolate, with apex truncated and base rounded or tapered. Spirals smooth or with nodules. Internal cellular folds present. Basal plate not well calcified and not visible from exterior. Size medium to large. Paleogene (Eocene): France, Hungary, Spain, Algeria, —Fig. 61*a-d.* \*R. peckii L. & N. GRAMBAST, France, topotypes; a, apical view with opercular cells, C.33-18; b, lateral view, C. 33-19; c, base, C.33-20, ×35 (new); d, apical view without opercular cells, ×40 (Grambast, 1957, pl. V,9).-Fig. 61e-g. R. vadaszi (RASKY) Grambast, France; e, ×40, lateral view (Grambast, 1957, pl. V,3); f, exterior apical view, ×90; g, interior apical view showing folded sutures between apical and spiral cells, ×110 (Anadón & Feist, 1981, pl. 2,1-2).

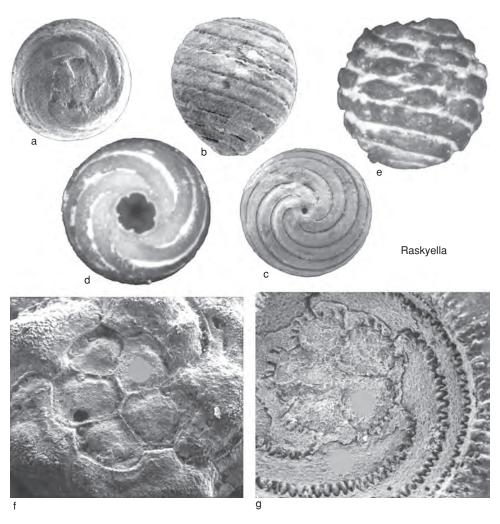


Fig. 61. Raskyellaceae (p. 116).

Rantzieniella Grambast, 1962b, p. 72 [\*R. nitida Grambast, 1962b, p. 74, fig. 3a-c; OD]. Gyrogonites with superficial or slightly inserted opercular apical cells positioned in alignment with spiral ends. General shape perprolate, with apex and base truncated. Spirals smooth. Internal cellular folds present. Basal plate weakly calcified, wider than high, and not visible from exterior. Size medium to large. [Differs from Raskyella chiefly in cylindrical shape of gyrogonite and position of opercular units.] Neogene (lower Miocene): France, Switzerland, China. Fig. 62,2a-d. \*R. nitida Grambast, France; a, holotype, lateral view, C.536-1; b, apical view, C.536-8; c, basal view, C.536-9, ×50 (new); d, internal view of gyrogonite showing folded sutures between spiral cells, ×250 (Feist-Castel, 1973, pl. 15,5).

Saportanella Grambast, 1962b, p. 72 [\*S. maslovi Grambast, 1962b, p. 72, fig. 2a-f; OD]. Gyrogonites with superficial or slightly inserted opercular apical cells positioned in alignment with spiral ends. General shape prolate-spheroidal to prolate, with apex truncated and base truncated or tapered. Spirals smooth. Internal cellular folds absent. Basal plate generally thick, higher than wide, visible from the exterior. Size small to large. Upper Cretaceous: France, Spain, Peru, Mongolia.-62, 1a-f. \*S. maslovi Grambast, France, topotypes; a, lateral view, C.450-49; b, apical view, C.450-450; c, base, C.450-51, ×35; d, basal plate, C.754-1, ×155 (new); e, longitudinal section, ×50; f, longitudinal section of basal part, with basal plate in situ and lamellar structure of calcified wall, ×90 (Grambast, 1971, pl. XIII,2,10).

# Charophyta—Charophyceae

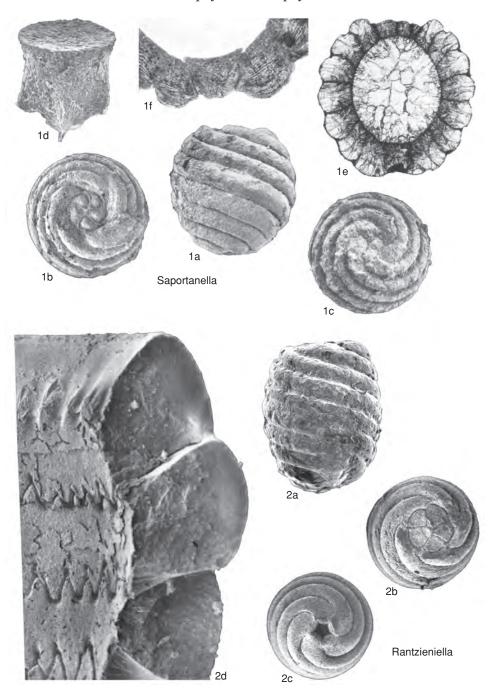


Fig. 62. Raskyellaceae (p. 117).

#### Family CHARACEAE Agardh, 1824

[Characeae AGARDH, 1824, p. XXVII]

Gyrogonite with 5 sinistrally spiralled cells, not enclosed in utricle; spiral cells joined at apex along a broken line. Pore of dehiscence wide, in form of a cog wheel. Spiral cells smooth or variously ornamented. *Upper Triassic—Holocene*.

#### Range

The Aclistochara species reported by LIU and CHEN (1992) from the Upper Triassic of Western China are the oldest known Characeae. Previously, all the Triassic species placed in the Characeae had been attributed to the family Porocharaceae (GRAMBAST, 1963; SAIDAKOVSKY, 1971).

The Characeae were rare until the Late Cretaceous, the time of their first great diversification. After the end of the Cretaceous extinctions, a new stage of diversification occurred in the Paleocene, and their development continued through the Tertiary. From the late Miocene onward the Characeae is the only remaining family; this includes 7 extant genera represented by 77 species (WOOD & IMAHORI, 1965 in 1964–1965).

#### Classification

The Characeae presently include 43 genera, more than all the other charophyte families. All the extant genera have been recorded as fossils with certainty. Even the noncalcified Nitella seems to have been in existence since the Jurassic, as suggested by the characters of the oospore membrane of N. sahnii Horn af Rantzien, 1957. The Characeae are divided into two subfamilies. Charoideae and Nitelloideae, sometimes considered at the family or tribe level. This subdivision, first established in living species, is based on characters that are not always preserved in the fossils. The uncalcified coronula cells, whose number is invariably 10 in the Nitelloideae and 5 in the Charoideae, have been recorded only by casts in early Tertiary species of Microchara and Peckichara. The vegetative parts, which also characterize well the two subdivisions in the living forms, are not of great utility since fossil gyrogonites are rarely connected to the fragments of thallus that are found with them in the sediments. The basal plate, corresponding to the calcified sister cells of the oosphere (GRAMBAST, 1956a), is the only relatively significant character that is represented in extant as well as frequently in fossil members; in the Nitelloideae, the basal plate is multipartite in both Nitella and Tolypella (section Tolypella) but simple in Sphaerochara (synonym of Tolypella section Rothia in the classification of extant forms). The inclusion of Sphaerochara in the Nitelloideae is based on morphological characters of the subfamily and on molecular data that place the two Tolypella sections in the same clade (McCourt, Karol, & others, 1996). In the Charoideae, the basal plate is simple, but it is multipartite in Aclistochara and related genus Songliaochara (LU & LUO, 1990). The inclusion of both genera in the Charoideae is based on the apical structure and postulated relationships of Aclistochara with Lamprothamnium (Soulié-Märsche, 1989; Feist & Grambast-Fessard, 1991). That the two types of basal plates are represented in both subfamilies suggests that Charoideae and Nitelloideae are less distinct than suggested by the morphological cladistic analysis that was based mainly on the basal plate morphology (MARTIN-CLOSAS & SCHUDACK, 1991). The attribution to one of these subfamilies is possible only in two instances: when fossil species may be attributed with certainty to an extant genus and when the fossils have significant characters of a particular subfamily. Such are the corticated fragments of thallus-bearing oogonia of the Oligocene Gyrogona, allowing their inclusion among the Charoideae. Similarly, the uncalcified, uncorticated, and bifurcated

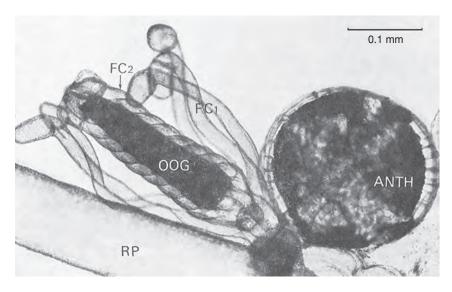


Fig. 63. Modifications of oogonial bud of *Chara vulgaris* L. after isolation of young plagiotropic branchlet, setting up two successive stages of spiral cells of oogonium; *ANTH*, antheridia; *FC*, spiral cells of oogonium; *FC1*, *FC2*, spiral cells belonging to successive whorls; *OOG*, oogonium; *RP*, plagiotropic branchlet (Ducreux, 1975, pl. VIII, 3).

branchlets of the Devonian *Palaeonitella* (KIDSTON & LANG, 1921; KELMAN & others, 2004<sup>1</sup>) suggest affinities with the Nitelloideae. Among the fossil Characeae, all species with a simple basal plate (except *Sphaerochara*) are assigned to the Charoideae; those with a multipartite basal plate are included in the Nitelloideae (except *Aclistochara*). The Characeae do not have utricles, but under experimental conditions involving extant species they produce supernumerary vegetative whorls that evoke this organ (Fig. 63; see also discussion on p. 23 herein).

With three extant genera, the Nitelloideae represent a small, well-characterized group. On the other hand, the Charoideae contain 40 genera, 4 of which are still living, and they have a great diversity.

#### Subfamily CHAROIDEAE Braun, 1897

[nom. correct. FEIST & GRAMBAST-FESSARD, herein, pro subfamily Chareae Braun in Migula, 1897, p. 94]

Gyrogonite of Characeae with undivided basal plate, except *Aclistochara*. In extant species, 5 large noncalcified coronula cells in 1

tier; thallus corticated or not corticated. *Upper Triassic–Holocene*.

The subdivision of the Charoideae into 3 morphological types (FEIST & GRAMBAST-FESSARD, 1982), adopted herein, is based mainly on the detailed structure of the apex of the gyrogonites. It is worth noting that specimens may contain characters dissimilar to the generic criteria, due to variable degrees of calcification in the gyrogonites. At the present time, the groupings listed below (Table 8), although useful in practice for identifying the genera, do not seem to be based on phylogenetic relationships.

Chara Linnaeus, 1753, p. 1,156; emend., Agardh, 1824, p. 27; emend., A. Braun, 1849, p. 292 [\*C. tomentosa; OD; see also Horn af Rantzien & Olsen, 1949, p. 99] [=Chara Vaillant, 1719, partim (type, Chara vulgaris foetida, OD); Chara Linnaeus, 1753, p. 1,156, obj. (includes the family Characeae); Characias Rafinesque, 1815, p. 209, nom. nud., non Gray, 1821, p. 259 (type, C. purpurea, OD); Characella Gaillon, 1833, p. 33 (type, C. vulgaris, OD); Charopsis Kützing, 1843, p. 319 (type, Chara braunii Gmelin, 1826, p. 646, OD); Characeites Tuzson, 1913, p. 209 (type, C. verrucosa Tuzson, 1913, p. 210, OD); Protochara Womersley & Ophel, 1947, p. 311 (type, P. australis, OD); Grambastichara Horn af Rantzien,

<sup>1</sup>Kelman, Ruth, Monique Feist, Nigel H. Trewin, & Hagen Hass. 2004. Charophyte algae from the Rhynie Chert. Transactions of the Royal Society of Edinburgh (series IV) 4:445–455.

TABLE 8. Apical features in the genera of the Characeae (new).

Types of apex	Lamprothamnoid	Psilocharoid	Nitellopsidoid
apex outline	prominent in center	flat or convex	convex, rounded
periapical depression		absent, except in Lychnothamnus and Pseudoharrisichar	generally present
periapical narrowing	absent	absent	generally present
apical nodules	absent	absent or weak	present
Het Me	clistochara, Grovesichara, aochara, Lamprothamnium, ongolichara, Nemegtichara, eudolatochara, Stylochara, Wangichara	Amblyochara, Chara Collichara, Dughiella Harrisichara, Henanochara, Hornichara, Linyiechara, Lychnothamnus, Maedleriella, Mesochara, Microchara, Multispirochara, Nothochara, Peckisphaera, Pseudoharrisichara, Psilochara, Rhabdochara, Saidakovskyella, Shandongochara, Strobilochara	Bysmochara, Gyrogona, Neochara, Nitellopsis, Nodosochara, Peckichara, Platychara, Songliaochara, Stephanochara, Zhejiangella

1959b, p. 68 (type, Chara tornata Reid & Groves, 1921, p. 187, pl. V,1-3, OD); Charites HORN AF RANTZIEN, 1959b, p. 57 (type, Chara molassica Straub, 1952, p. 466, pl. A, 1-3, OD); Amphorochara Krassavina, 1978, p. 227 (type, A. grambasti Krassavina, 1978, p. 227, pl. 1, OD); Granulachara Lu & Luo, 1990, p. 142 (type, Kosmogyra ovalis MÄDLER, 1955, p. 302, pl. 26,28-30, OD)]. Apex psilocharoid, convex, with cellular apical ends enlarged, generally shaped into a cap without apical nodules; in ornamented species (occurring as fossils) apical tubercles present, similar to those of lateral parts of gyrogonite. General shape of gyrogonite ellipsoid to cylindroid, sometimes very elongated. Basal plate pyramidal, its thickness being more than half of width. Size small to medium. [A great number of species were designated formerly under the name Chara without any real taxonomic significance, meaning roughly Characeae or charophytes. VAILLANT (1719) published the name Chara and gave a type and an illustration, but the genus was officially and validly published by LINNAEUS in 1753.] Upper Cretaceous-Holocene: worldwide. Fig. 64, 1a-d. \*C. tomentosa L., Holocene, Sweden; a, lateral view; b, apical view; c, basal view, ×44; d, basal plate, ×350 (Soulié-Märsche, 1989, pl. XXI,2,4,5, pl. XV,1).—Fig. 64, 1e. C. notata Grambast & Paul, lower Miocene, France; lateral view, ×80 (Feist & Ringeade, 1977, pl. XII,7).—Fig. 64,1f. C. antennata Grambast, upper Eocene, United Kingdom; lateral view, ×80 (Feist-Castel, 1977a, pl. 22,1).—Fig. 64,1g. C. microcera GRAMBAST & PAUL, upper Oligocene, France; longitudinal section, basal plate upside down, ×70 (Castel, 1967, pl. XXI, 13).

Aclistochara PECK, 1937, p. 86; emend., PECK, 1957, p. 24 [\*A. bransoni PECK, 1937, p. 87, pl. 14,8-11; OD] [=Obtusochara MÄDLER, 1952, p. 36, partim (type, O. prima Mädler, 1952, p. 36, pl. B,53-55); Jurella Kyansep-Romaschkina, 1974, p. 28 (type, J. abshirica Kyansep-Romaschkina, 1974, p. 28, pl. 2,2,6, OD); Caucasuella Kyansep-Romaschkina, 1980, p. 81 (type, C. gulistanica KYANSEP-Romaschkina, 1980, p. 82, pl. I,4–7, pl. II,1–3, OD); Xinjiangichara Lu & Luo, 1990, p. 80 (type, X. wuqiaensis Lu & Luo, 1990, p. 81, pl. 10,10–16, OD)]. Apex lamprothamnoid with deep periapical furrow. Diameter of apical zone varying from 100 to 160 µm. Spirals turn onto truncate apex to form its outer rim, then bend down into central depression, finally turning sharply into center of summit depression and expanding to fill space; horizontal part of apex thin and transparent to swollen and bulbous. Abrupt downward turning and thinning producing circular furrow around expanded ends of spirals (PECK, 1957). General shape of gyrogonite ovoid to ellipsoid, with truncate apex. Spirals smooth, concave to gently convex. Size small. Basal plate generally not described; in some species, basal plate multipartite (Lu & Luo, 1990). [Aclistochara resembles Porocharaceae and Raskyellaceae in some respects, the periapical zone with a small diameter and being located within a depression; Aclistochara has an apical opening closed by the calcified tips of the spiral cells, which differs from the Porocharaceae (where this zone is open) and from the Raskyellaceae (where it is closed by an operculum composed of five supplementary cells). Because of similarities in periapical morphology some Aclistochara were referred to Raskyellaceae (Jurella

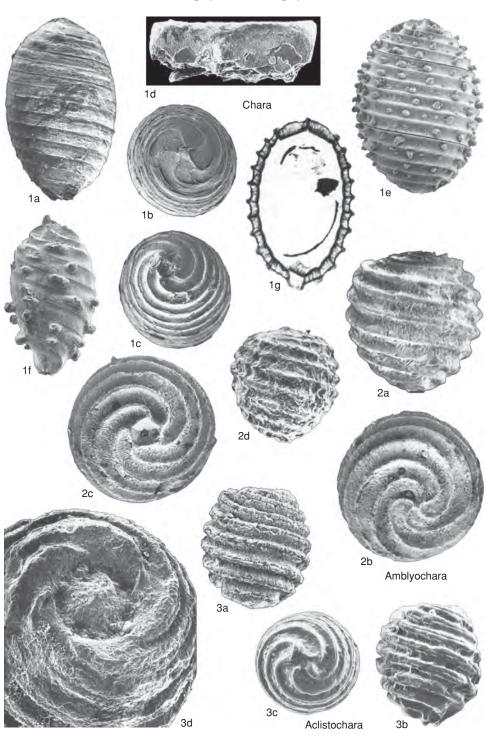


Fig. 64. Characeae (p. 120-123).

and Caucasuella Kyansep-Romaschkina; Kyansep-ROMASCHKINA, 1974); or, on the contrary, some Porocharaceae were ascribed to the genus Aclistochara (Bhatia & Mannikeri, 1977). Schudack (1990) put Obtusochara into synonymy with Aclistochara; however, several species are referable to different genera (Lamprothamnium, Mesochara, Mongolichara), and thus they have not been considered here for the range of Aclistochara.] Upper Triassic-Upper Cretaceous: USA, Armenia, Germany, United Kingdom, China, Kazakhstan, Mongolia, Tanzania.— —Fig. 64,3a–d. \*A. bransoni Peck, Middle Jurassic, USA, topotypes; a, lateral view, C.1212-1; b, lateral view, C.1221-1; c, basal view, C.1221-2, ×72; d, apical view, detail, C.1222-1, ×130 (new).

Amblyochara Grambast, 1962b, p. 79 [\*A. begudiana Grambast, 1962b, p. 79, fig. 4; OD]. Apex psilocharoid, with spirals retaining their width but tending to flatten as they turn onto summit. General shape subovoid with apical part gently rounded or slightly projecting; base tapered, basal pore at end of funnel-shaped depression; basal plate parallelepidal shaped, being generally less high than onequarter of width. Size medium to large. [Genus differs from Rhabdochara, which has a more flattened apex and a conical and hollow basal plate, and from Lychnothamnus, whose gyrogonites present a periapical groove and a thicker basal plate.] Cretaceous-Neogene (Pliocene): Europe, USA, South America (widespread), South Korea, Mongolia, China.-Fig. 64,2a-c. \*A. begudiana Grambast, Upper Cretaceous, France, topotypes; a, lateral view, C.450-46; b, apical view, C.450-47; c, basal view, C.450-48, ×40 (new).—Fig. 64,2d. A. rolli (KOCH & BLISSENBACH) GRAMBAST, Upper Cretaceous, Chile; lateral view, C.1223-1, ×40 (new).

Bysmochara Grambast & Gutiérrez, 1977, p. 10 [\*B. conquensis Grambast & Gutiérrez, 1977, p. 11, pl. II, 10-14, pl. III, 1-4, pl. XIV, 4; OD]. Apex nitellopsidoid; at periphery of apex, spiral cells becoming markedly thinner and narrower, producing distinct furrow that surrounds prominent rosette made of swollen endings. General shape ovoid or ellipsoid; spirals smooth. Basal plate as thick as wide, lower face visible from exterior. Size medium to large. [Genus differs from Nitellopsis in having a thicker basal plate and no basal funnel.] Upper Cre--Fig. 65,3a-e. \*B. conquensis taceous: Spain.-GRAMBAST & GUTIÉRREZ; a, lateral view, holotype; b, apical view; c, basal view, ×30; d, basal plate, lateral view; e, basal plate, basal view, ×170 (Grambast & Gutiérrez, 1977, pl. II,11, pl. III,2,4, pl. II,13,14).

Coenoclavator Z. WANG & Lu, 1982, p. 99 [\*C. hubeiensis WANG & Lu, 1982, p. 99, pl. IV,13–15; OD]. Rejected genus. [Gyrogonites found in the Eocene, covered with calcified incrustation and bearing thallus fragments at their base, were designated under this name and attributed to the Clavatoraceae. The structureless covering and the absence of an apical pore (Z. WANG & Lu, 1982, pl. 4,13) do not correspond to a true utricle and are

referable to the Characeae (FEIST & COLOMBO, 1983). In the earlier classifications, taxa with similar structures were regarded as *Lagynophora*.]

Collichara S. WANG & ZHANG in S. WANG & others, 1982, p. 49 [\*C. taizhouensis S. WANG & ZHANG in S. Wang & others, 1982, p. 49, pl. 26,9–15; OD; lectotype, NIGP PB5827, S. Wang & Zhang in S. WANG & others, 1982, pl. 26, 1a-c, designated FEIST & GRAMBAST-FESSARD herein]. Apex psilocharoid; apical endings slightly thickened, without appreciable peripheral thinning and narrowing. Gyrogonite spheroidal to subprolate, with short, broad apical neck; number of convolutions high (more than 10); spirals smooth, concave to flat. Base rounded or slightly pointed. Basal plate conical, thickness being about half width. Size small to medium. Upper Cretaceous-Paleogene (Paleocene): Asia, China.—Fig. 65,2a-c. \*C. taizhouensis S. WANG & ZHANG, Upper Cretaceous, China, lectotype; a, lateral view; b, apical view; c, basal view, ×40 (new, courtesy of Z. Wang).

Dughiella Feist-Castel, 1975, p. 89 [\*D. bacillaris FEIST-CASTEL, 1975, p. 90, text-fig. 1-3; pl. I,1-9; OD]. Apex psilocharoid; spirals barely thinner as they pass onto summit then slightly thickened at center. Gyrogonite spheroidal; spirals smooth or in some species bearing well-calcified rods even in apical part. Basal plate prismatic, visible from exterior, thickness being more than half width. Size medium to large. [Genus differs from Gyrogona in lack of apical modification and having the basal plate visible from the exterior.] Upper Cretaceous-Paleogene (Paleocene): Belgium, France, Spain, Morocco, ?India. Fig. 65, 1a-f. \*D. bacillaris Feist-Castel, Paleocene; a-b, holotype, paratype, lateral views, France, ×30; c, longitudinal section, France, ×45; d-e, apical, basal view, France, ×30 (Feist-Castel, 1975, fig. 1-3, pl. I, 5, 8); f, apical view, Belgium, ×30 (Grambast-Fessard, 1980, pl. I,4).-65,1g-i. D. obtusa Grambast & Gutiérrez, Upper Cretaceous, Spain; g, holotype, lateral view; h, apical view, i, basal view, ×40 (Grambast & Gutiérrez, 1977, pl. XI,9,12,14).

Grovesichara HORN AF RANTZIEN, 1959b, p. 123 [\*Chara distorta Reid & Groves, 1921, p. 186, pl. V,6; OD]. Apex lamprothamnoid; spirals become thinner as they pass onto summit, then thicken again, ascending to center of apex. General shape irregular, oblate-spheroidal to subprolate; apex rounded, strongly prominent. Base rounded, in some species tapering. Basal plate strongly calcified, thickness being more than half of width; lower face of plate visible from exterior. Size medium to large. [Genus differs from Gyrogona in having less marked periapical modification as well as having the basal plate visible from the exterior and general shape more elongated.] Upper Cretaceous-Neogene (Miocene): Austria, France, United Kingdom, Spain, China, Mongolia. FIG. 66, 1a-c. \*G. distorta (REID & GROVES) HORN AF RANTZIEN, upper Eocene, United Kingdom; a, lateral view (Feist-Castel, 1977a, pl. 21,7); b, apical view, CF.1579-3; c, basal view, CF.1579-2, ×30 (new).

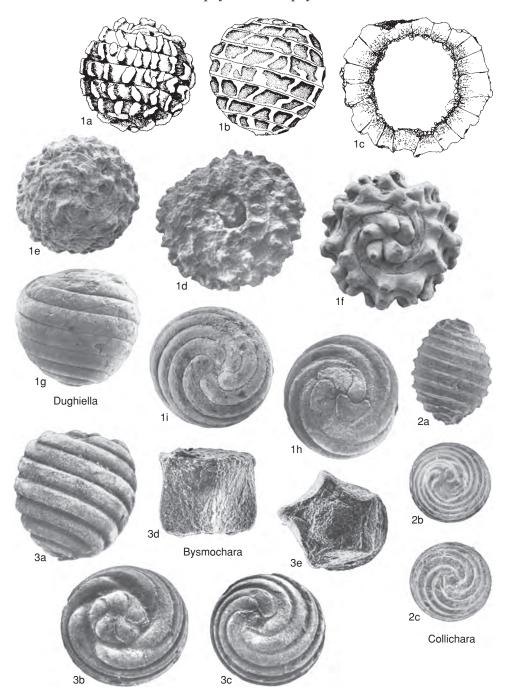


Fig. 65. Characeae (p. 123).

Gyrogona Lamarck, 1822, p. 613 (Lamarck, 1804, p. 355, nom. nud.); emend., Grambast, 1956b, p. 280 [\*Gyrogonites medicaginula LAMARCK, 1822, p. 614; OD; = Gyrogonites medicaginula LAMARCK, 1804, p. 356, nom. nud.] [=Gyrogonites LAMARCK, 1822, p. 613, obj. (LAMARCK, 1804, p. 355, nom. nud.), non PIA, 1927; Brachychara L. & N. GRAMBAST, 1954, p. 666 (type, Gyrogonites medicaginula LAMARCK, 1804, p. 356); Brevichara HORN AF RANTZIEN, 1956a, p. 245 (type, B. hordlensis, OD, nom. null.; =Chara wrightii Reid & Groves, 1921, p. 183, pl. IV,1, non Chara wrightii SALTER in FORBES, 1856, p. 160)]. Apex nitellopsidoid. Deep periapical furrow without notable narrowing of spirals, surrounding prominent rosette of well-marked nodules. Gyrogonite oblate to oblate-spheroidal; spirals smooth or variously ornamented. Base rounded; in some species, basal pore surrounded by widened funnel. Basal plate very thick, higher than wide, not visible from exterior. Size large. [Among the species reported by Z. WANG (1978a) from China, some, such as the Cretaceous G. hubeiensis, are more likely to be referable to Platychara.] Paleogene (lower Eocene)-Neogene (upper Miocene): Belgium, France, Germany, United Kingdom, Spain, China, India, ?USA; China (Xinxiang), upper Miocene (Lu & Luo, 1990).—Fig. 66,2a-c. \*G. medicaginula LAMARCK, Stampian, France; a, neotype, designated herein, lateral view, C.146-1, ×25 (new); b, apical view, ×25 (Grambast & Grambast-Fessard, 1981, pl. IV, 12); c, basal view, C.146-8, ×25 (new).-Fig. 66,2d-f. G. lamarcki Grambast, middle Eocene, France; d, basal plate, lateral view, ×100; e, basal plate, upper side,  $\times 100$ ; f, apical opening,  $\times 20$ (Grambast & Grambast-Fessard, 1981, pl. I,11,10,7).—Fig. 66,2g. G. caelata (Reid & GROVES) GRAMBAST, middle Eocene, France; lateral view, ×30 (Grambast & Grambast-Fessard, 1981, pl. IV,1).-–Fig. 66,2h. G. lemani lemani (Brongniart) Pia, middle Eocene, France; longitudinal section, ×40 (Grambast & Grambast-Fessard, 1981, pl. VI,2).

Harrisichara Grambast, 1957, p. 347 [\*Chara vasiformis Reid & Groves, 1921, p. 185, pl. IV,13; OD]. Apex psilocharoid. Gyrogonite subovoidal, apex truncated or broadly rounded, base forming narrow, projecting cone or columnar shaped; spirals generally with tubercles or crests; ornamentation interrupted at periphery of apex. Basal plate very thin, about ten times as wide as high. Size small to large. [Occurrence of this genus in the Upper Cretaceous is questionable, as H. cretacea KARCZEWSKA & ZIEMBINSKA-TWORZYDLO, 1970, and H. margaritata Z. WANG, 1978b, do not have the basal projection characteristic of Harrisichara.] ?Upper Cretaceous, Paleogene (Paleocene–lower Oligocene): Belgium, France, Germany, United Kingdom, Spain, China, India, Canada, USA, Peru.-67,1a. \*H. vasiformis (REID & GROVES) GRAMBAST,

upper Eocene, United Kingdom; lateral view, ×50 (Feist-Castel, 1977a, pl. 21,1).——Fig. 67,1b—f. H. tuberculata (Lyell) Grambast, lower Oligocene, United Kingdom; b, basal plate, ×300 (Grambast, 1957, text-fig. 2b); c, neotype, lateral view, spirals with nodules; d, lateral view, spirals with continuous crest, ×40 (Feist-Castel, 1977a, pl. 21,5,4); e, apical view, CF.1585-2; f, basal view, CF.1584-2, ×40 (new).

Hebeichara H. Lin, 1989, p. 76 [\*H. sphaerides H. Lin, 1989, p. 76, pl. 39,*I*–*T*; OD]. Incompletely known genus, referable either to *Sphaerochara* or *Tolypella*, according to the basal-plate morphology.

Henanochara ZHANG, JIANG, & MENG, in JIANG, ZHANG, & MENG, 1985, p. 164 [\*H. squalida JIANG, ZHANG & MENG, 1985, p. 164, pl. I,7,11,12, pl. II,30; OD]. Apex psilocharoid. Gyrogonite subprolate to prolate spheroidal with apex rounded or forming short neck; base rounded, truncated in center. Spirals numerous, unornamented, without modifications in apical part. Basal plug pentagonal, slightly wider than high, projecting out of basal pore. Size medium to large. [Whether this genus belongs to Characeae is questionable, and the described species might correspond to gyrogonites of Clavatoraceae without a developed utricle. H. squalida possesses an apical neck, a basal plate projecting out of the basal pore, and numerous convolutions of the spirals. Such features are present, for example, in Atopochara trivolvis gyrogonites (PECK, 1957, pl. 2,5).] Lower Cretaceous: China.—Fig. 66,3a-c. \*H. squalida ZHANG, JIANG, & MENG; a, holotype, lateral view; b, apical view; c, basal view, ×40 (Jiang, Zhang, & Meng, 1985, pl. 1,7b,7a,7c).-—Fig. 66,3*d–e. H. nitida* Zhang, JIANG, & MENG; d, lateral view; e, basal view, ×40 (Jiang, Zhang, & Meng, 1985, pl. 1,9,8c).

Hetaochara Shu & Zhang, 1985, p. 68 [\*H. cupula SHU & ZHANG, 1985, p. 68, pl. 2,6-10; OD; lectotype, pl. 2,9a-c, designated FEIST & GRAMBAST-FESSARD herein]. Apex lamprothamnoid, with deep, periapical furrow and central part convex, not overtopping general surface. Gyrogonite stem shaped, lower part being abruptly narrowed and forming column with truncated ending. Summit truncated. Size small. Basal plate unknown. Differs from other genera by peculiar gyrogonite shape. [The validity of the genus is questionable as the atypical basal column, which comprises the entire lower half of the gyrogonite, could result from an abnormal calcification.] Lower Cretaceous: China.-67,2a-c. \*H. cupula SHU & ZHANG, Mongolia, lectotype; a, lateral view; b, apical view; c, basal view, ×140 (Shu & Zhang, 1985, pl. 2,9b,9a,9c).

Hornichara Maslov, 1963b, p. 444 [\* H. kazakstanica Maslov, 1963b, p. 445, fig. 1; OD; lectotype, Maslov, 1963b, fig. 1a–c, designated Feist & Grambast-Fessard herein] [=Krassavinella Feist in Feist & Ringeade, 1977, p. 346 (type, K. blayaci

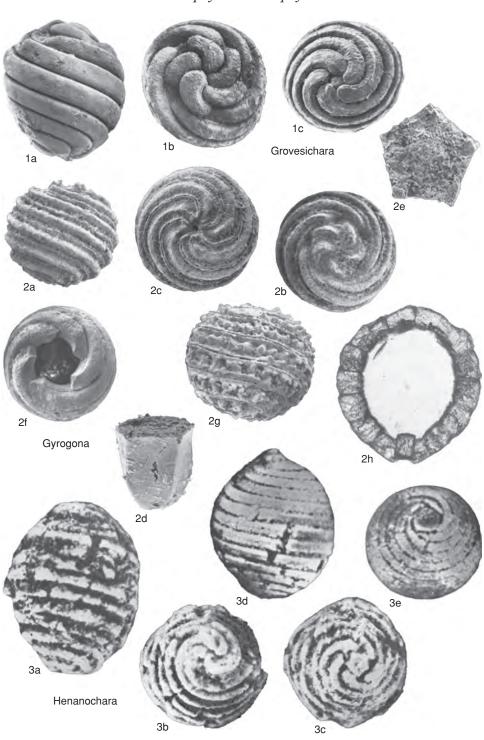


Fig. 66. Characeae (p. 123-125).

Feist in Feist & Ringeade, 1977, p. 346, pl. X, 1-5, OD)]. Apex psilocharoid with thinning of entire apical zone. General shape ovoidal with apex prominent and base tapered with tendency to form a broad column. Spirals unornamented; basal pore in some species at end of funnel-shaped depression. Basal plate thin. Size small. [Genus differs from Harrisichara in having a more protruding apex and a wider basal column, from Amblyochara in its apical characters and smaller size, and from Mesochara in having a tapered base and basal plate morphology.] Upper Cretaceous-Neogene (Pleistocene): France, Georgia, Germany, Russia, Spain, Switzerland, China, India, Kazakhstan.—Fig. 67,3a-c. \*H. kazakstanica MASLOV, middle Oligocene, Kazakhstan; a, lectotype, lateral view; b, apical view; c, basal view, ×88 (adapted from Maslov, 1963b, fig. 1a-c).—Fig. 67,3d-f. H. lagenalis (STRAUB) FEIST, upper Oligocene, Switzerland; d, lateral view; e, apical view; f, basal view, ×80 (Feist-Castel, 1977b, pl. 1,3,5,6).

Kosmogyra STACHE, 1889, p. 134 [\*K. superba STACHE, 1889, p. 134, pl. IV,2; OD] Genus based essentially on gyrogonite ornamentation. The artificiality of this taxon has been discussed by L. GRAMBAST (1957), and it is no longer acknowledged. The original material has been lost.

Lagynophora STACHE, 1889, p. 132 [\*L. liburnica STACHE, 1889, p. 132, fig. 9, 14; OD]. Rejected genus. Gyrogonites described as bottle shaped and enclosed by vegetative parts. [Such enclosed gyrogonites belong in fact to the Characeae (BIGNOT & GRAMBAST, 1969) and may represent several genera: Microchara (CASTEL, 1969), Peckichara (RIVELINE & PERREAU, 1979), our Harrisichara (GRAMBAST-FESSARD, 1980). Because the type material is lost, Lagynophora cannot be assigned to one or another of these genera, so this taxon cannot be maintained.]

Lamprothamnium GROVES, 1916, p. 336 [\*Chara papulosa Wallroth, 1833, p. 107; OD] [=Lamprothamnus Braun in Braun & Nordstedt, 1882, p. 100 (type, L. alopecuroides BRAUN in Braun & Nordstedt, 1882, p. 100, fig. 185-188, OD), non HIERN in OLIVER, 1877, p. 130; Yahuchara TANG & DI, 1991, p. 98 (type, Y. subcylindrica TANG & DI, 1991, p. 98, pl. 1,1-8, OD)]. Apex lamprothamnoid, with deep periapical furrow. Diameter of apical zone varying from 160 to 280 µm. Spirals thin or absent at apical center. When preserved, apical parts of spirals concave, turning up sharply into apex center. General shape subprolate to perprolate, with apex truncated and base slightly narrowed. Spirals unornamented and with Y-calcification (see p. 10 herein). Basal plate variable in thickness. Size small to medium. [Genus differs from Aclistochara in having the diameter of the apical zone notably wider and an undivided basal plate, and from Chara in having a strongly depressed periapical zone. Upper Cretaceous-Holocene: worldwide. Fig. 68,1a-f. \*L. papulosum (WALLROTH) GROVES, Holocene, France;

a, longitudinal section, ×50; b, lateral view, CF.2952-1, ×66 (new); c, apical view, ×150 (Feist & Grambast-Fessard, 1991, fig. 5b); d, basal view, CF.2952-2, ×66 (new); e, basal plate, lateral view, ×220 (Soulié-Märsche, 1989, pl. XXXII, 10); f, detail of wall of spiral cells, CF.2952-2, ×260 (new).——Fig. 68, 1g-i. L. priscum CASTEL & GRAMBAST, lower Eocene, France; g, lateral view, holotype; h, apical view, ×60 (Castel & Grambast, 1969, pl. XXXII, 4a, 4c); i, detail of the wall of spiral cells, ×300 (Feist & Grambast-Fessard, 1984, fig. 2G).

Linviechara XINLUN in WANG Shui & others, 1978, p. 23 [\*L. clara XINLUN in WANG Shui & others, 1978, p. 24, pl. 4,2–6; OD; lectotype, NIGP 390037, pl. 4,4a-c, designated FEIST & GRAMBAST-FESSARD herein] [=Guangraochara YANG, 1987, p. 159 (type, G. distincta YANG, 1987, p. 159, pl. 1,1–7, OD)]. Apex psilocharoid. Spirals narrowing at periphery of apex, then widening again toward center without thickening. General shape subprolate, with apex rounded and base truncated. Spirals smooth or with irregular nodules. Basal plate slightly wider than thick, visible from exterior. Size medium. Paleogene (Oligocene): China. FIG. 67,4a-d. \*L. clara XINLUN; a, longitudinal section, ×68; b-d, lectotype, lateral, apical, basal views, ×34 (Wang Shui & others, 1978, pl. 4,6a,4b,4a,4c).

Lychnothamnus (Ruprecht, 1845) von Leonhardi, 1863, p. 57; emend., A. BRAUN in BRAUN & Nordstedt, 1882, p. 100 [\*Chara barbata Meyen, 1827, p. 75; OD] [=Lychnothamnites MASLOV, 1966, p. 77 (type, L. narynensis MASLOV, 1966, p. 78, pl. IX,9-11, OD)]. Apex psilocharoid with periapical furrow. Apical ends of spirals concave, in some instances with poorly developed nodules. General shape subprolate to prolate with apex rounded and its central part slightly prominent; base rounded. Basal plate conical, its thickness being about half of width. Size medium to large. [Reminiscent of the genus Stephanochara.] Paleogene (upper Eocene)-Holocene: Europe, Mali, China, India, Australia. Fig. 69,3a-e. \*L. barbatus (MEYEN) VON LEONHARDI, Holocene, Germany; a, lateral view, ×50; b, apical view, ×47; c, basal view, ×47; d, basal plate, lower side, ×250 (Soulié-Märsche, 1989, pl. XXXV, 2,5,8,10); e, detail of the oospore membrane, CF.2953-5, ×580 (new).-Fig. 69,3f-g. L. longus CHOI, upper Eocene, Spain; f, holotype, lateral view; g, paratype, apical view, CF.VF/8-6, ×60 (new).

Maedleriella Grambast, 1957, p. 349 [\*Chara monolifera Peck & Reker, 1947, p. 4, fig. 12–18; OD]. Apex psilocharoid, without distinct differentiation. General shape oblate to oblate-spheroidal; apex and base rounded or truncated; spirals with tubercles or crests, continuing up to apex with small break in periapical zone. Basal plate prismatic, height and width approximately equal, visible from exterior. Size small to medium. Upper Cretaceous—Paleogene (upper Eocene): USA, Peru, France, Germany, Spain, China, Mongolia, Algeria.——Fig.

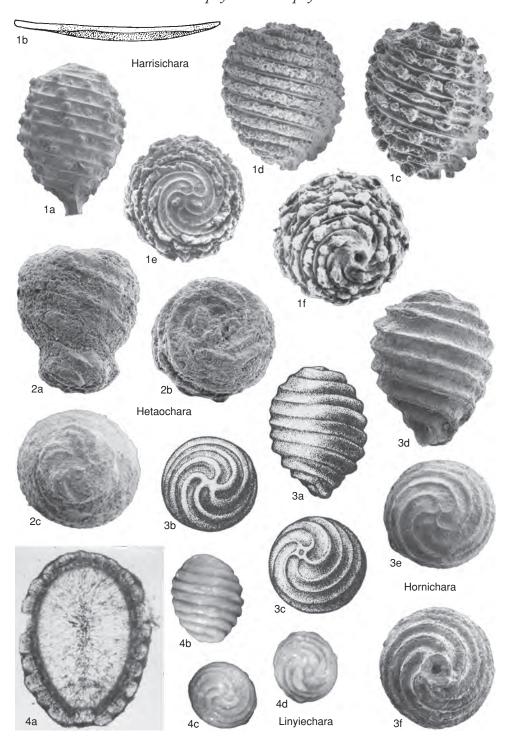


Fig. 67. Characeae (p. 125-127).

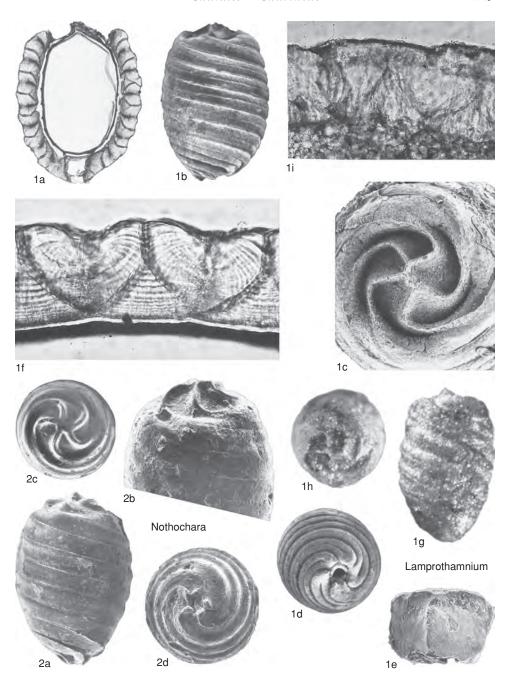


Fig. 68. Characeae (p. 127-136).

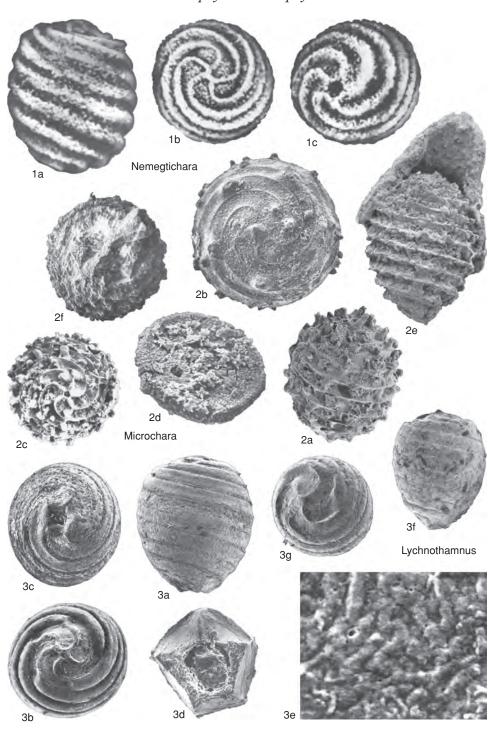


Fig. 69. Characeae (p. 127-134).

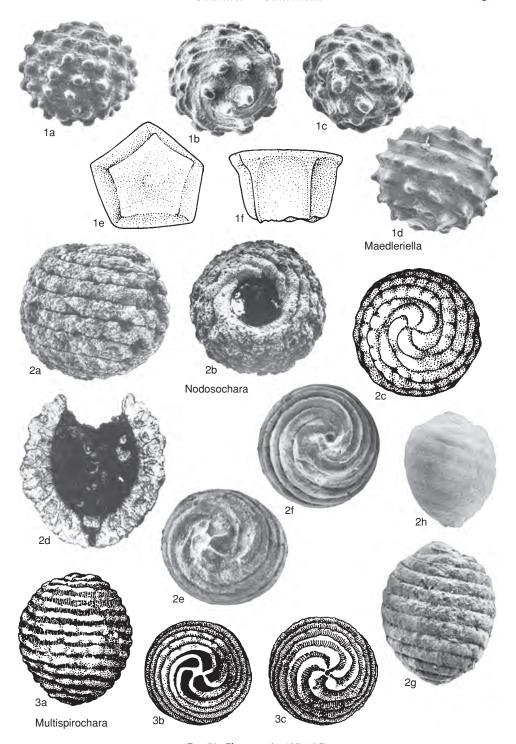


Fig. 70. Characeae (p. 127-136).

70,1*a*–*c.* \**M. monolifera* (PECK & REKER) GRAMBAST, Paleocene or lower Eocene, Peru, topotypes; *a*, lateral view, C.1224-1; *b*, apical view, C.1224-2; *c*, basal view, C.1224-3, ×60 (new).—Fig. 70,1*d. M. cristellata* GRAMBAST, Paleocene–lower Eocene, France; lateral view, C.1108-6, ×60 (new).—Fig. 70,1*e*–*f. M. mangenoti* GRAMBAST; *e*, basal plate, lower side; *f*, basal plate, lateral view, ×300 (Grambast, 1957, fig. 3a–b).

Mesochara Grambast, 1962b, p. 78 [\*Praechara symmetrica PECK, 1957, p. 39, pl. 7,13-16; OD] [=*Piriformachara* Liu & Ŵu, 1985, p. 147 (type, *P.* gumudiensis Liu & Wu, 1985, p. 148, pl. 3,5-6, OD)]. Apex psilocharoid, with apical spiral endings not enlarged or only slightly enlarged. General shape subprolate, with apex rounded or pointed and base thinner. Gyrogonites unornamented. Basal plate unknown. Size small to medium. [Differs from Amblyochara mainly in size and from Chara by absence of enlargement (or having only minor enlargement) of the apical spiral endings and having fewer convolutions. Piriformachara differs from Mesochara only by its spiral convexity, a character that may depend on the degree of calcification and cannot be alone considered as a generic criterion.] Cretaceous: USA, Argentina, France, Moldavia, Ukraine, China, Mongolia, Tanzania.—FIG. 71,2a-b. \*M. symmetrica (PECK) GRAMBAST, Lower Cretaceous, USA, topotypes; a, lateral view, C.1225-1; b, apical view, C.1225-1, ×80 (new). -Fig. 71,2c. M. fusiformis Feist, Upper Cretaceous, France, holotype; lateral view, ×80 (Feist, 1981, fig. 4g).

Microchara Grambast, 1959b, p. 6 [\*M. hystrix Grambast, 1959b, p. 7, fig. 1; OD] [=Gobichara Karczewska & Ziembińska-Tworzydło, 1972, p. 72 (type, G. deserta Karczewska & Ziembińska-Tworzydło, 1972, p. 73, pl. XIV, OD)]. Apex psilocharoid, with little or no modification. General shape subprolate, with apex rounded and base narrowed; in some species base projecting. Gyrogonites often with tubercles or crests, ornamentation reaching apex center. Basal plate very thin, not visible from exterior. Size generally small, in some species small to medium. [Gyrogonites of Microchara with tapered bases are difficult to distinguish from small specimens of *Harrisichara*. These resemblances may indicate a phylogenetic relationship between the two genera.] Upper Cretaceous-Paleogene (middle Eocene): Argentina, France, Spain, China, Mongolia, India. Fig. 69,2a-d. \*M. hystrix GRAMBAST, lower Eocene, France; a, holotype, lateral view, C.63-4, ×80; b, apical view, C.2-4, ×110; c, basal view, C.63-7, ×80; d, basal plate, C.63-8, ×660 (new).——Fig. 69,2e-f. M. vestita Castel, lower Eocene, France; e, lateral view of specimen, tunicate in upper part around site of missing coronula cells, ×124; f, apical view, with remains of 3 coronula cells, ×105 (Feist-Castel, 1975, pl. II,11,10).

Mongolichara Kyansep-Romaschkina, 1975, p. 200; emend., Karczewska & Kyansep-Romaschkina, 1979, p. 423 [\* Tectochara gobica Karczewska & ZIEMBIŃSKA-TWORZYDŁO, 1970, p. 137, pl. 33,1–2; OD]. Apex lamprothamnoid, with spirals narrowing and thinning on apex periphery, then slightly widening and thickening somewhat in apex center, without forming distinct nodules. General shape prolate spheroidal to subprolate, with apex center forming rounded or truncated cap; base rounded, in some species base slightly tapered. Spirals occasionally with surface ornamentation, especially secondary ridges or small cellular tubercles. Basal plate variable in thickness, generally thinner than wide. Size medium. [Differs from Peckichara in absence of apical nodules and weaker ornamentation.] Upper Cretaceous-Paleogene (lower Eocene): China, Mongolia. FIG. 71,3a-f. \*M. gobica Ziembińska-Tworzydło) (Karczewska & KARCZEWSKA & KYANSEP-ROMASCHKINA, Upper Cretaceous, Mongolia; a, holotype, lateral view; b, apical view; c, basal view; d, apical view, open summit, ×80 (Karczewska & Ziembińska-Tworzydło, 1970, pl. XXXIII, 1c, 1a, 1b, 2); e, longitudinal section, ×70 (Karczewska & Ziembińska-Tworzydło, 1981, pl. 35,6); f, lateral view, ×80 (Karczewska & Kyansep-Romaschkina, 1979, pl. 3,4).

Multispirochara HAO in HAO & others, 1983, p. 147 [\*M. subovalis HAO & others, 1983, p. 147, pl. 32,9–10; M]. Apex psilocharoid, without notable modifications. General shape prolate-spheroidal with apex truncated and base rounded. Convolutions numerous (11–14), without ornamentation. Basal plate unknown. Size small. Monospecific genus. Upper Jurassic–Lower Cretaceous: China.—FIG. 70,3a–c. \*M. subovalis HAO, Upper Jurassic or Lower Cretaceous, holotype; a, lateral view; b, apical view; c, basal view, x87 (adapted from Hao & others, 1983, pl. 32,9a–c).

Nanglingqiuchara TANG & D1, 1991, p. 99 [\*N. columelaria TANG & D1, 1991, p. 99, pl. 1,9–13; OD]. Rejected genus. Genus distinction based only on apical projections, which represent abnormal calcified apical cellular ends. Might be referable to Chara.

Neimongolichara Lu & Yuan, 1991, p. 386 [\*N. bayanhotensis Lu & Yuan, 1991, p. 386, pl. I,7–11; OD]. Rejected genus. Corresponds to nodosoclavatoroid utricles, as recognized from the nodular surface and from the presence of gyrogonite cells inside (Lu & Yuan, 1991, pl. I,11).

Nemegtichara Karczewska & Ziembińska-Tworzydło, 1972, р. 54 [\*N. prima Karczewska & Ziembińska-Тworzydło, 1972, р. 54, рl. 7; OD]. Apex lamprothamnoid, with shallow periapical depression; in apex center, spirals thin and turn up, forming conical protuberance. General shape variable, oblate-spheroidal to prolate, apex pointed and base rounded or truncated. Spirals generally unornamented; however, some species have thick,

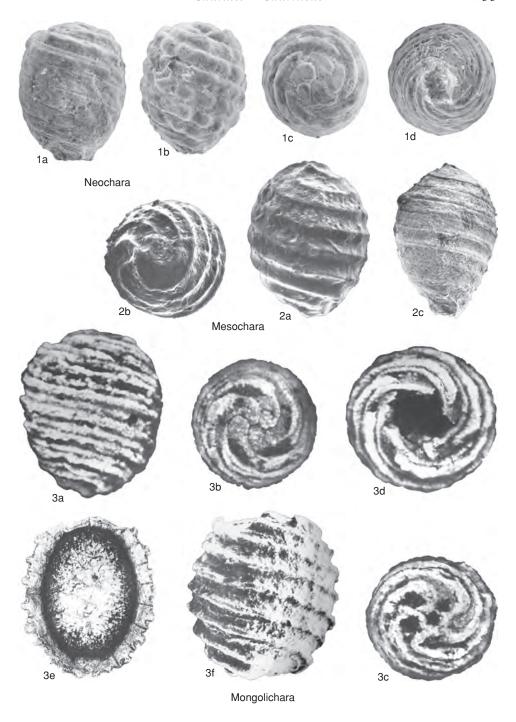


Fig. 71. Characeae (p. 132-134).

intercellular, prominent ridges. Basal plate twice as wide as high, generally visible from exterior. Size small. *Upper Cretaceous, Paleogene (?Paleocene):* China, Mongolia, India.——Fig. 69, 1a-c. \*N. prima Karczewska & Ziembińska-Tworzydło, Paleocene, Gobi desert; a, holotype, lateral view; b, apical view; c, basal view, ×70 (Karczewska & Ziembińska-Tworzydło, 1972, pl. VII,3b,3a,3c).

Neochara Z. WANG & LIN in Z. WANG, 1978b, p. 112 [\*N. huananensis Z. WANG & LIN in Z. WANG, 1978b, p. 113, pl. V,21-24,40-45; OD; holotype, NIGP PB5970, fig. 43-45]. Apex nitellopsidoid, with distinct periapical thinning and variable narrowing of spirals. General shape prolate to perprolate, with apex protruded and base tapered. Spirals generally smooth; in some species, spirals with wavy or nodular crest. Basal funnel present, basal plate thicker than half width, visible from exterior. Size small to medium. [Genus differs from Stephanochara in its periapical narrowing of the spirals. This character, however, is not strongly expressed in some species assigned to Neochara, such as N. taikengensis Z. WANG, Lu, & ZHAO, 1985.] Upper Cretaceous-Paleogene (Eocene): China .-FIG. 71,1a-d. \*N. huananensis Z. WANG & LIN, lower Eocene; a, lateral view; b, lateral view; c, apical view; d, basal view, ×60 (new, courtesy of Wang Zhen).

Nitellopsis Hy, 1889, p. 398 [\*Chara obtusa DESVAUX in Loiseleur-Deslongchamps, 1810, p. 136; OD] [= Tectochara L. Grambast & N. Grambast, 1954, p. 668 (type, Chara meriani Braun ex Unger, 1850, p. 34); Qinghaichara YANG in HAO & others, 1983, p. 156 (type, Q. ovalis YANG in HAO & others, 1983, p. 156, pl. 36,1-4, OD)]. Apex nitellopsidoid; spirals with distinct periapical narrowing and thinning, with ends thickening and expanding, forming prominent central rosette. General shape prolate-spheroidal to subprolate and subovoidal, with apex prominent and base rounded or tapered. Spirals smooth or with tubercles. Basal pore flaring, pentagonal, or star shaped. Basal plate very thin, not visible from the exterior. Size medium to large. [Krassavina (1971) established the identity of the extant Nitellopsis obtusa and of the Quaternary Tectochara diluviana. GRAMBAST and SOULIÉ-MÄRSCHE (1972) detailed the past history of Nitellopsis and established three subgenera, Nitellopsis, Tectochara, and Campaniella. FEIST-CASTEL (1977c) added a fourth subgenus, Microstomella.] Paleogene (Paleocene)-Holocene: worldwide.

N. (Nitellopsis) (HY, 1889, p. 398) GRAMBAST & SOULIÉ-MÄRSCHE, 1972, p. 3 [\*Chara obtusa DESVAUX in LOISELEUR-DESLONGCHAMPS, 1810, p. 136; OD]. General shape prolate-spheroidal to subprolate; basal region rounded, with basal funnel poorly developed or absent. Neogene (Pliocene)—Holocene: scattered in Europe and Asia, rare in Africa (Mali, Sudan) and South America (Argentina).——Fig. 72,1a-c. \*N. (N.) obtusa (DESVAUX) J. GROVES, Holocene, France; a, lateral view; b, apical view, ×47 (Feist &

Grambast-Fessard, 1991, fig. 4a, 4e); *c*, basal view, CF.2953-4, ×47 (new).

N. (Campaniella) Grambast & Soulié-Märsche, 1972, p. 3 [\* Chara helicteres Brongniart, 1822, p. 63, pl. VI,3; OD]. General shape prolate-spheroidal; basal part with protruding funnel surrounding basal pore. Paleogene (Paleocene—lower Eocene): Belgium, France, Spain.——Fig. 72,3a-c. \*N. (C.) helicteres (Brongniart) Grambast & Soulié-Märsche, lower Eocene, France; a, lateral view, C.7-1; b, apical view, C.6-10; c, basal view, C.6-11, ×30 (new).

N. (Microstomella) Feist-Castel, 1977c, p. 117 [\*M. aptensis Feist-Castel, 1977c, p. 118, pl. I, I-8, text-fig. 1; OD]. General shape subprolate; base rounded without distinct funnel, basal pore very small. Paleogene (upper Eocene): France, Spain.——Fig. 72,2a-c. \*N. (M.) aptensis Feist-Castel, upper Eocene, France; a, holotype, lateral view; b, apical view; c, basal view, ×30 (Feist-Castel, 1977c, pl. I, I, I, J, A).

N. (Tectochara) (L. & N. GRAMBAST, 1954, p. 668) Grambast & Soulié-Märsche, 1972, p. 3 [\*Chara meriani Braun, unpublished ms, ex UNGER, 1850, p. 34; OD; = Chara meriani Braun ex Heer, 1855, p. 24, pl. IV, 3] [=Tectochara (Sulcosphaera) MASLOV, 1966, p. 62 (type, S. nethoiensis MASLOV, 1966, p. 62, fig. 20)]. General shape subprolate, with contracted base and basal funnel well marked but not protruding. Paleogene (Paleocene)-Neogene (Pliocene): Mexico, Peru, Europe (widespread), China, India, Algeria, Senegal.— —Fig. 72,4*a*– e. \*N. (T.) meriani (Braun ex Unger) Grambast & SOULIÉ-MÄRSCHE, Oligocene, Belmont, Switzerland, topotypes; a, holoneotype, designated herein, lateral view, C.1226-1, ×30 (new); b, apical view, ×30; c, basal view, ×30; d, longitudinal section of basal part of gyrogonite, ×120 (Castel, 1967, pl. XIX, 3, 4, 14); e, basal plate, ×915 (Grambast, 1956b, text-fig. 3).— 72,4f. N. (T.) morulosa (Feist-Castel) Feist & GRAMBAST-FESSARD, middle Eocene, France; lateral view (Feist-Castel, 1972, pl. I,5).

Nodosochara Mädler, 1955, p. 276 [\*Aclistochara clivulata PECK & REKER, 1948, p. 88, pl. 21,1-7; OD] [= Turbochara Z. WANG, 1978a, p. 78 (type, T. specialis Z. WANG, 1978a, p. 78, pl. VI, 1–9, OD)]. Apex nitellopsidoid; spirals with distinct periapical narrowing and thinning, thickening and expanding at ends to form prominent central rosette. General shape prolate-spheroidal to prolate; apex rounded, prominent in center, base tapered. Spirals smooth or with tubercles. Basal plate thick, at least as thick as half of width, to thicker than wide, not visible from exterior. Size small to large. [Differs from Tectochara mostly in the characters of the basal part and not by the presence of an ornamentation as stated in Mädler diagnosis. The presence of this genus in the Neogene is questionable, the apical structure of ?N. globosa S. WANG, 1961, being unknown, and thus its attribution to Nodosochara is

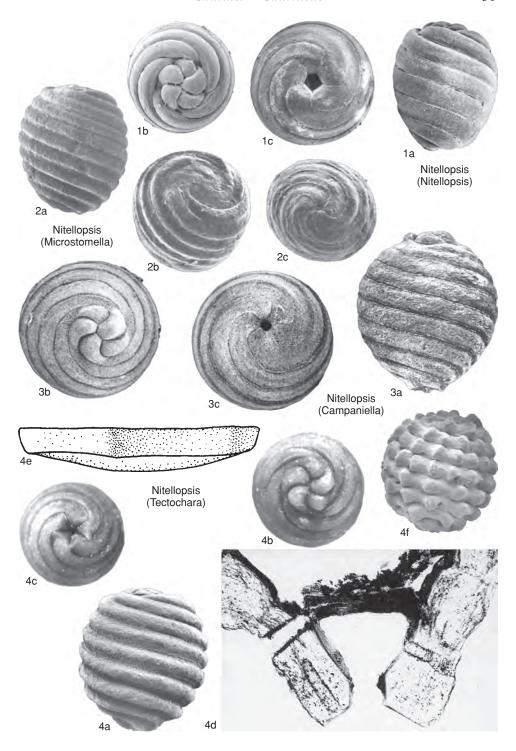


Fig. 72. Characeae (p. 134).

uncertain.] Upper Cretaceous-Paleogene (upper Eocene), ?Neogene: USA, Peru, France, Spain, −Fig. 70,2*a−d.* \**N. clivulata* (Peck & REKER) MÄDLER, middle Eocene, USA, topotypes; a, lateral view, C.1227-1, ×52 (new); b, apical view, open summit, C.1227-2, ×52 (new); c, apical view, ×42 (adapted from Peck & Reker, 1948, pl. 21,6); d, longitudinal section, ×62 (Horn af Rantzien, 1959b, pl. IX, 12). FIG. 70, 2e-g. N. thevallensis (DOLLFUS) RIVELINE, upper Eocene, France, topotypes; e, apical view, C.49-11; f, basal view, C.49-12; g, lateral view, C.49-10, ×32 (new).-Fig. 70,2h. N. (Turbochara) specialis (Z. WANG) FEIST & GRAMBAST-FESSARD, ?lower Eocene, China; holotype, lateral view, NIGP PB 4509, ×37 (Z. Wang, 1978a, pl. VI,2).

Nothochara Musacchio, 1973, p. 8 [\*N. apiculata Musacchio, 1973, p. 9, pl. II, 1, 4–5,7–12; M]. Apex psilocharoid; spirals convex, becoming concave with high, intercellular crests in apical zone and turning up in center. General shape prolate to subprolate, with apex strongly protruding; base rounded, with ends of spirals concave, sutures forming crests around pore. Spirals smooth. Basal plate nearly as thick as wide, generally visible from exterior. Size small. Monospecific genus. Upper Cretaceous: Argentina.—Fig. 68,2a–d. \*N. apiculata Musacchio; a, holotype, lateral view, ×117; b, upper part of gyrogonite, ×150; c, apical view, ×100; d, basal view, ×117 (Musacchio, 1973, pl. II,4,5,7,1).

Peckichara GRAMBAST, 1957, p. 352 [\*P. varians Grambast, 1957, p. 352, pl. VIII, 1-8; OD] [=Sinochara Lin & Z. Wang in S. Wang & others, 1982, p. 32 (type, S. rudongensis LIN & Z. WANG in S. WANG & others, 1982, p. 32, pl. 15,5–9, OD)]. Apex nitellopsidoid, with periapical furrow weakly marked and variable narrowing of spirals. Apical nodules present, generally elongated. General shape prolate spheroidal and often quadrangular, with rounded apex; base rounded or slightly tapering, with flaring funnel. Spirals generally with tubercles, rods, or crests. Basal plate as thick as about onethird width. Size small to large. [All the salient features of Peckichara are found in Sinochara. Only the apical tubercles of Sinochara are slightly more protruding. The differences in spiral ornamentation do not appear significant.] Upper Cretaceous-Paleogene (Eocene, ?Oligocene): USA, Peru, France, United Kingdom, Spain, Algeria, China, ?India, Mongolia.—Fig. 73, 1a-c. \*P. varians Grambast, lower Eocene, France, topotypes; a, lateral view, C.57-9; b, apical view, C.57-10; c, basal view, C.57-11, ×40 (new).—Fig. 73,1d-e. P. pectinata GRAMBAST, Upper Cretaceous, France; d, lateral view; e, apical view, ×46 (Grambast, 1971, text-fig. 9a-b).—Fig. 73, 1f. P. toscarensis Feist, Paleocene, Spain; longitudinal section, C.1124-8, ×40 (new).

Peckisphaera Grambast, 1962b, p. 78 [\*Chara verticillata Peck, 1937, p. 84, fig. 30–33; OD] [=Circonitella Watson, 1969, p. 214 (type, Chara knowltoni Seward, 1894, p. 13, text-fig. 1); Retusochara Grambast, 1971, p. 28 (type, R.

macrocarpa Grambast, 1971, p. 31, fig. 18, pl. XXIV-XXV, OD)]. Apex psilocharoid, without distinct apical modifications of spirals but with slight enlargement at ends. General shape prolate-spheroidal to subprolate with apex rounded. Spirals smooth. Basal plate thick, the thickness up to twice width, visible or not from exterior. Size small to large. [Retusochara and Peckisphaera have similar apical structures and thick basal plates; plate is sunken in Retusochara but in some species is still visible from the exterior.] Upper Jurassic-Cretaceous: USA, Argentina, France, Germany, Portugal, Spain, Ukraine, China, Lebanon.—Fig. 74,1a-c. \*P. verticillata (PECK) GRAMBAST, Upper Jurassic, USA, topotypes; a, lateral view, C.1228-1, ×80; b, basal view, C.1228-2, ×72; c, apical view, C.1228-3, ×72 (new).—Fig. 74,1d. P. (Retusochara) macrocarpa (GRAMBAST) FEIST & GRAMBAST-FESSARD, Upper Cretaceous, France; longitudinal section, ×40 (Grambast, 1971, pl. XXV,8).

Platychara Grambast, 1962b, p. 76 [\*Chara compressa KNOWLTON, 1888, p. 156, fig. 1-2; OD; non Kunth, 1815]. Apex nitellopsidoid; periapical zone variably thinned and slightly or not narrowed. Apical nodes convex and elongated; in some species, apical nodes absent. General shape oblate, suboblate to oblate-spheroidal, with apex rounded or truncated; base similar or, in numerous instances, spirals turned downward around basal pore to form small cone or distinct column. Spirals smooth or with tubercles or crests. Basal plate slightly calcified, not visible from exterior. Size small to large. [Differs from Gyrogona in being distinctly wider than high, in having wide spirals, continuous periapical furrow, and frequently a basal extension. In species with a protruding base, gyrogonite height may equal width or slightly exceed width, such as P. sahnii BHATIA & MANNIKERI, 1976, from the Paleocene of India. Some species described as Gyrogona from the Upper Cretaceous of China are in fact representatives of Platychara (GRAMBAST & GRAMBAST-FESSARD, 1981).] Upper Cretaceous-Paleogene (Paleocene): Canada, Mexico, USA, Argentina, Bolivia, Jamaica, Peru, Belgium, France, Spain, China, India.—Fig. 74,2a-e. \*P. compressa (KNOWLTON) GRAMBAST, Upper Cretaceous, USA, topotypes; a, lateral view, C.1229-1, ×40; b, lateral view, C.1229-2, ×40; c, wall structure of spiral cells, C.1229-5, ×300; d, apical view, C.1229-3, ×40; e, basal view, C.1229-4, ×40 —Fig. 74,2f. P. complanata Grambast & GUTIÉRREZ, Upper Cretaceous, Spain, holotype; lateral view, ×78 (Grambast & Gutiérrez, 1977, pl. VI,1).—Fig. 74,2g-h. P. stipitata Grambast & GUTIÉRREZ, Upper Cretaceous, Spain; g, lateral view, paratype; h, apical view, ×100 (Grambast & Gutiérrez, 1977, pl. VII,5a-b).

Pseudoharrisichara Musacchio, 1973, p. 10 [\*P. walpurgica Musacchio, 1973, p. 11, pl. III,9–16, pl. IV,3,6; OD]. Apex psilocharoid, with spirals somewhat thinned in apical zone, particularly on apex periphery. General shape prolate to subprolate, with apex rounded and base tapered; basal column

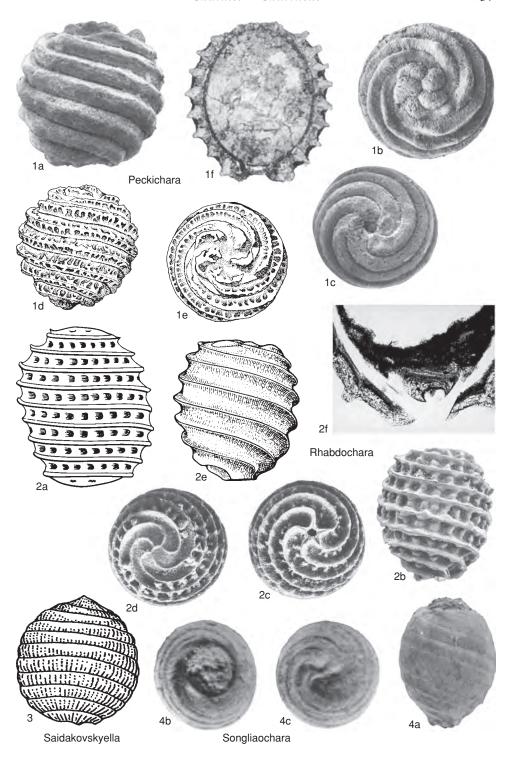


Fig. 73. Characeae (p. 136-141).

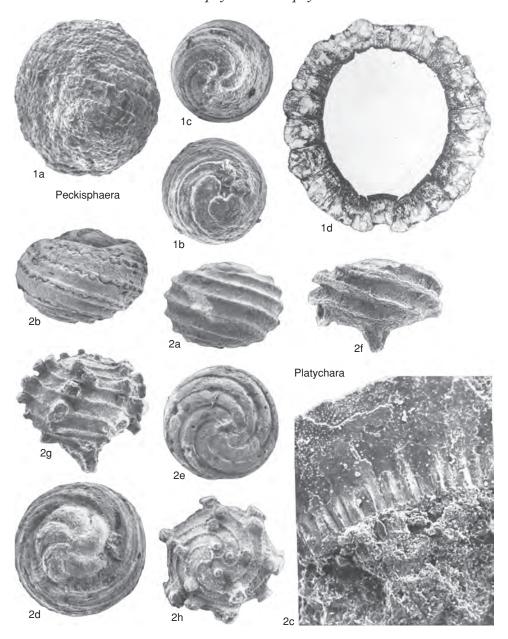


Fig. 74. Characeae (p. 136).

axis slightly curved with respect to polar axis. Spirals smooth or with nodular crests. Basal pore surrounded by distinct funnel. Basal plate wider than thick. Size small to medium. [Differs from Harrisichara in periapical thinning, oblique projecting base, and thicker basal plate.] Upper Cretaceous:

Argentina, Spain.——Fig. 75,1a. \*P. walpurgica Musacchio, Argentina; holotype, lateral view, ×67 (Musacchio, 1973, pl. III,13).——Fig. 75,1b–d. P. isonae Feist, Spain; b, apical view; c, basal view; d, lateral view, holotype, ×46 (Feist & Colombo, 1983, pl. I,10,9,6).

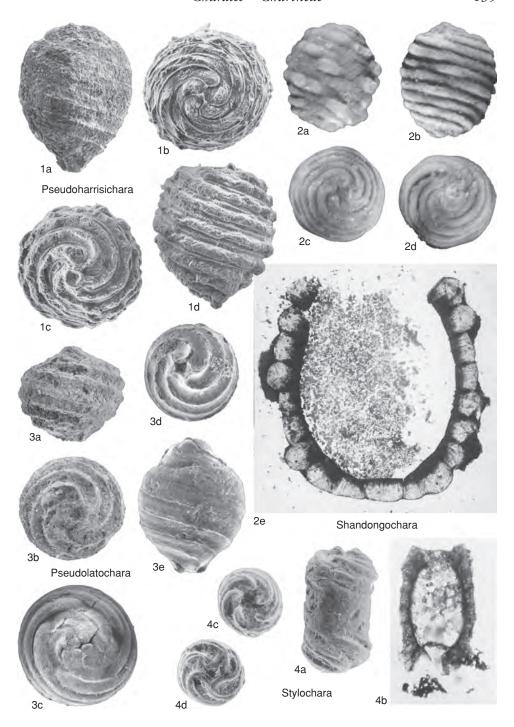


Fig. 75. Characeae (p. 136-142).

# Charophyta—Charophyceae

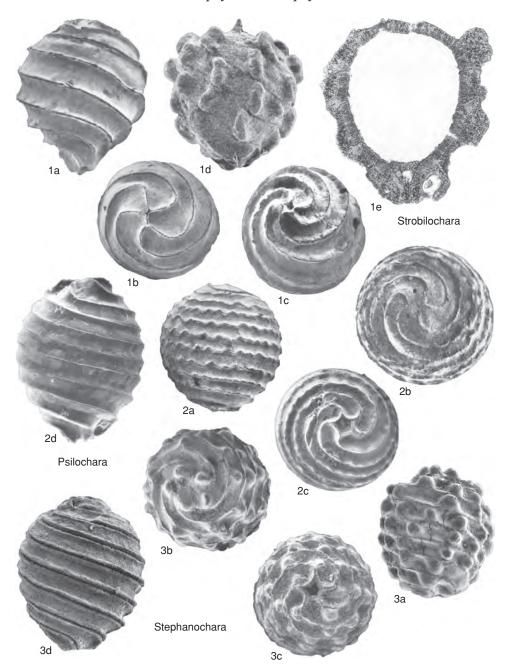


Fig. 76. Characeae (p. 141-142).

Pseudolatochara Z. Wang, 1978a, p. 74 [\*P. jianghanensis Z. Wang, 1978a, p. 74, pl. V,36–42; OD] [=Grambastiella Massieux in Massieux & Tambareau, 1978, p. 143 (type, G. acuta Massieux in Massieux & Tambareau, 1978, p. 144, pl. 1,1–

6, OD)]. Apex lamprothamnoid, with peripheral spiral thinning weak or absent. In apex center, spiral endings abruptly arise and form projecting cone. General shape prolate–spheroidal with apex protruded and base rounded; in some species base ta-

pered. Spirals smooth. Basal plate unknown. Size small. *Upper Cretaceous–Paleogene (Eocene):* France, China. ——FIG. 75,3a-b. \*P. jianghanensis Z. WANG, Upper Cretaceous, China; a, holotype, lateral view; b, apical view, ×95 (Z. Wang, 1978a, pl. V,38,40). ——FIG. 75,3c-e. P. (Grambastiella) acuta MASSIEUX, Paleocene, France; c, apical view, ×85; d, basal view, ×95; e, lateral view, holotype, ×85 (Massieux & Tambareau, 1978, pl. 1,2,3,1).

Psilochara Grambast, 1959b, p. 10 [\*Chara archiaci var. undulata Dollfus & Fritel, 1919, p. 252, fig. 14; OD]. Apex psilocharoid, convex, without periapical modification; spiral ends slightly enlarged. General shape prolate-spheroidal to perprolate, with apex rounded or pointed and base rounded or tapered. Spirals smooth, in numerous instances with sinuous spiral sutures. Basal pore at same level as lower surface, in some species surrounded by flaring funnel. Basal plate slightly calcified, about one-third as thick as wide, with upper face hollow. Size medium to large. [Differs from Grovesichara in its lack of periapical thinning, a basal plate that is not visible from the exterior, and presence of sinuous spiral sutures.] Paleogene (Eocene-Oligocene): Belgium, France, United Kingdom, Spain, China.—Fig. 76,2a-c. \*P. undulata (Dollfus & FRITEL) GRAMBAST, middle Eocene, France, topotypes; a, lateral view, C.121-17; b, apical view, C.121-19; c, basal view, C.121-18, ×35 (new).-Fig. 76,2d. P. bitruncata (Reid & Groves) Feist-CASTEL, upper Eocene, France; lateral view, C.F1509-6, ×50 (new).

Rhabdochara MÄDLER, 1955, p. 299; emend., GRAMBAST, 1957, p. 357 [\*Chara langeri ETTINGSHAUSEN, 1872, p. 162, pl. 1,2-3; OD]. Apex psilocharoid; apical zone thin but convex; weakly marked apical nodules rarely present. General shape subprolate to ellipsoidal with summit truncated and base somewhat tapered. Spirals generally concave, smooth or with transverse rods. Basal plate conical and hollow. Size variable. [Differs from Stephanochara and Lychnothamnus in lacking periapical depression and having strongly developed nodules, hollow basal plate, and ornamentation consisting of rods instead of tubercles.] Paleogene (?lower Eocene, upper Eocene)-Neogene (Miocene): Europe (widespread), China.— -Fig. 73,2a-d. \*R. langeri (Ettingshausen) MÄDLER, lower Miocene; a, lateral view, Slovenia, ×40 (adapted from Ettingshausen, 1872, pl. I,3); b, lateral view, France, ×47 (Feist & Ringeade, 1977, pl. 23,9); c, basal view, France, C.536-9; d, apical view, France, C.536-8, ×40 (new).—Fig. 73,2e. R. stockmansi Grambast, lower Oligocene, France; lateral view, ×50 (Grambast, 1957, text-fig. 6). Fig. 73,2f. R. praelangeri Castel, upper Oligocene, France; longitudinal section, basal part, ×50 (Castel, 1967, pl. XX,11).

Saidakovskyella Shaikin, 1976, p. 83 [\*S. corpulenta Shaikin, 1976, p. 84, fig. 14–19; M]. Apex psilocharoid, with apical ends of spirals thickened. General shape spheroidal with apex pointed and base rounded. Spirals smooth. Basal funnel present.

Basal plate moderately thick. Size medium to large. Genus monotypic. *Lower Cretaceous*: Ukraine.—Fig. 73,3. \*S. *corpulenta* Shaikin; holotype, lateral view, ×33 (adapted from Shaikin, 1976, text-fig. 14).

Shandongochara XINLUN in WANG Shui & others, 1978, p. 46 [\*S. decorosa XINLUN in WANG Shui & others, 1978, p. 46, pl. 21, 1-7, pl. 22, 1-2, pl. 23,2; OD; lectotype, NIGP 390133, pl. 21,1a-c, designated Feist & Grambast-Fessard herein]. Apex psilocharoid, with distinct periapical narrowing and thinning; apical ends of spirals slightly pointed in center, without nodules. General shape prolatespheroidal to prolate; apex nearly flat to broadly conical, base truncated. Spirals flat to slightly convex with elongated, tumorlike decorations. Basal plate nearly twice as wide as thick, visible from exterior. Size large. Paleogene (Oligocene): China.-Fig. 75,2a-e. \*S. decorosa Xinlun; a, lectotype, lateral view; b, lateral view; c, basal view; d, apical view, ×34; e, longitudinal section, basal part, ×68 (Wang Shui & others, 1978, pl. 21,1b,2b,2c,2a,6a).

Songliaochara Z. Wang, Lu, & Zhao, 1985, p. 64 [\*S. heilongjiangensis Z. Wang, Lu, & Zhao, 1985, p. 65, pl. XXVIII,2-8; OD; holotype, NIGP 9836, fig. 3a-c]. Apex nitellopsidoid, with shallow periapical groove; apical nodules rounded, moderately thick. General shape ovoid with apex rounded, projecting above apical level. Spirals generally convex, smooth. Base tapering, sometimes forming wellmarked basal column. Basal pore small; basal funnel absent. Basal plate multipartite (Lu & Luo, 1990), as wide as thick, not visible from exterior. Size small. Immature specimens reminiscent of Aclistochara. [The recognition of the basal plate structure shows that Songliaochara can no longer be considered a synonym of Nodosochara (FEIST & Grambast-Fessard, 1991).] Upper Cretaceous: —Fig. 73,4a–c. \*S. heilongjiangensis Z. WANG, LU, & ZHAO, lower Upper Cretaceous, holotype; a, lateral view; b, apical view; c, basal view, ×120 (Z. Wang, Lu, & Zhao, 1985, pl. XXVIII,3b,3a,3c).

Stephanochara GRAMBAST, 1959b, p. 8 [\*S. compta Grambast, 1959b, fig. 3; OD] [=Croftiella Horn as RANTZIEN, 1959b, p. 104 (type, Chara escheri UNGER, 1850, p. 34); Eotectochara Hu & ZENG, 1982, p. 562 (type, E. hunanensis Hu & ZENG, 1982, p. 562, pl. 372,1-7, OD); Dongmingochara ZHAO & HUANG, 1985, p. 13 (type, D. concinna ZHAO & HUANG, 1985, p. 13, pl. I,4–10, pl. II,7– 9, OD)]. Apex nitellopsidoid, with deep depression and no constrictions at apical periphery; apical nodules strongly developed. General shape prolatespheroidal to prolate and perprolate with apex protruding and base tapered. Spirals smooth or with tubercles. Basal funnel star shaped, sometimes absent. Basal plate variable in thickness, about half as thick as wide. Size medium to large. [FEIST-CASTEL (1977c) documented the nonvalidity of Croftiella.] Upper Cretaceous-Neogene (Miocene): Europe (widespread), Mongolia, China.—Fig. 76,3a-c. \*S. compta GRAMBAST, lower Oligocene, United

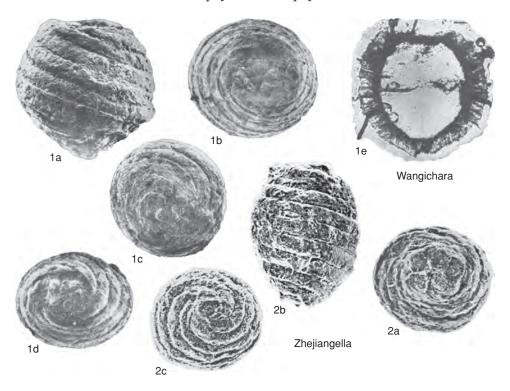


Fig. 77. Characeae (p. 142-143).

apical view, C.1230-2; c, paratype, basal view, C.1230-3, ×40 (new).—Fig. 76,3d. S. berdotensis FEIST, lower Miocene, western France; holotype, lateral view, ×43 (Feist & Ringeade, 1977, pl. XIII,1). Strobilochara Grambast, 1975, p. 72 [\*S. viallardi Grambast, 1975, p. 73, text-fig. 3, pl. II; OD]. Apex psilocharoid, with spirals unmodified at apex. General shape prolate-spheroidal to subprolate; apex rounded or truncated, central part variably prominent; base tapering to point or column. Spirals smooth or with tubercles. Basal plate thicker than wide, not visible from exterior. Size medium to large. [Differs from Hornichara in having apical zone normally calcified, thicker basal plate, larger size, and possible ornamentation.] Upper Cretaceous: Spain.—Fig. 76,1a-c. \*S. viallardi Grambast, topotypes; a, lateral view, C.1057-29; b, apical view, C.1057-30; c, basal view, C.1057-31, ×30 (new).—

Kingdom; a, holotype, lateral view; b, paratype,

pl. X, *I*, pl. XV, *5*). Stylochara Jiang & Zhang in Jiang, Zhang, & Meng, 1985, p. 162 [\**S. xitanlouensis* Jiang, Zhang, & Meng, 1985, p. 163, pl. II, *I*–*9*; M; holotype,

—Fig. 76,1d-e. S. diademata Grambast &

Gutiérrez; d, holotype, lateral view, ×53; e, longi-

tudinal section, ×80 (Grambast & Gutiérrez, 1977,

BGMRH Y00043, pl. II, 1a-c]. Apical zone sunken. General shape cylindrical with apex and base truncated. Spirals smooth, clearly widened and thickened in upper and lower parts. Basal plate multipartite, thick. Size small. Genus monotypic. [The swelling of apical and basal parts may represent a calcification anomaly. In spite of strong differences concerning the gyrogonite shape, Stylochara has been put in synonymy with Aclistochara by Lu & Luo (1990).] Lower Cretaceous: China.—Fig. 75,4a-d.\*S. xitanlouensis JIANG & ZHANG; a, holotype, lateral view, ×86; b, longitudinal section, ×82; c, apical view, ×86; d, basal view, ×86 (Jiang, Zhang, & Meng, 1985, pl. II, 1b, 9, 1a, 1c).

Wangichara Liu & Wu, 1985, p. 144 [\*W. tanshanensis Liu & Wu, 1985, p. 144, pl. 2,1–4; OD; holotype, BIG0225, pl. 2,1a–c]. Apex lamprothamnoid, with apical rosette in well-marked depression bearing slightly convex nodules in center. General shape of gyrogonite ovoid with truncated summit and tapering base. Spirals smooth, flat to convex. Size small. Basal plate nearly as wide as thick. [Differs from Aclistochara mainly by the presence of distinct apical nodules and from Stephanochara in its smaller size and apex not projecting above the general surface.] Lower Cretaceous: China.—Fig. 77,1a–e.

\*W. tanshanensis LIU & WU; a-c, holotype, lateral, apical, basal views; d, apical view; e, longitudinal section, ×80 (Liu & Wu, 1985, pl. II, 1b, 1a, 1e, 2a, 4).

Zhejiangella Lin, 1989, p. 5 [\*Z. tongxiangensis Lin, 1989, p. 5, pl. III, I–10; OD; holotype, NIGP PB1029, pl. III, I]. Apex nitellopsidoid, with slight narrowing and no depression of spiral cells in periapical zone. Apical nodules prominent, grouped into apical rose. Gyrogonite ellipsoid, with apex rounded and base tapering. Size small to medium. Basal plate wider than thick, visible from exterior. [Differs from Neochara by the absence of periapical depression.] Upper Cretaceous: China.——Fig. 77,2a–c. \*Z. tongxiangensis Lin; a, holotype, apical view; b, lateral view; c, basal view, ×80 (Lin, 1989, pl. III, I–3).

#### Subfamily NITELLOIDEAE Braun, 1890

[nom. correct. Feist & Grambast-Fessard, herein, pro subfamily Nitelleae Braun in Migula, 1890 in 1890–1897, p. 94]

Gyrogonite of Characeae with basal plate multipartite, except in *Sphaerochara* where basal plate is undivided. Uncalcified oogonia of *Nitella* and *Tolypella* are only occasionally fossilized. Extant species with 10 small uncalcified coronula cells in 2 tiers. Thallus not corticated, uncalcified. *Jurassic–Holocene*.

The Nitelloideae represent the tolypelloid morphological type (FEIST & GRAMBAST-FESSARD, 1982). This subfamily is characterized by gyrogonites with a prominent apex, either rounded or pointed, and without any periapical depression, except immediately around apical nodules when present, as in some *Sphaerochara* species. The origin of the Nitelloideae seems to go back to the Lower Devonian, as suggested by vegetative remains of *Palaeonitella* KIDSTON & LANG, resembling the extant *Nitella*.

Nitella Agardh, 1824, p. 123; emend., Braun, 1847, p. 5; von Leonhardi, 1863, p. 69 [\*N. opaca Agardh, 1824, p. 125; SD Horn af Rantzien & Olsen, 1949, p. 99] [=Nitellites Horn af Rantzien, 1957, p. 12 (type, N. sahnii Horn af Rantzien, 1957, p. 12, pl. 1,1–5, pl. II,1–2, OD)]. Enveloping cells do not secrete calcite, thus gyrogonites do not occur. Oogonia and oospore small, laterally compressed, with 3 basal sister cells. [The only substantiated fossil records of the genus are silicified materials. The oldest one is Palaeonitella Kidston & Lang (1921) from the Lower Devonian Rhynie Chert of Scotland, with uncorticated thallus very

similar to the extant *Nitella*. This structure is visible in the section given by TAYLOR, REMY, and HASS (1992, fig. 1). In *Nitellites* HORN AF RANTZIEN (1957), from the Jurassic of India, the resemblance with *Nitella* is in the reticulate membrane sculpture of the oospore: *J furassic—Holocene*: worldwide.——FIG. 78,2a-d. \*N. opaca AGARDH, Holocene, France, oospore; a, lateral view, CF.2955-1; b, apical view, CF.2955-2; c, basal view, CF.2955-3, ×96 (new); d, oogonium, without coronula, CF.2955-4, ×73 (new).——FIG. 78,2e. N. tenuissima (DESVAUX in LOISELEUR) KÜTZING; emend., WOOD & IMAHORI, Holocene, France, oospore; lateral view, ×225 (Soulié-Märsche, 1987, fig. 4A).

Sphaerochara Mädler, 1952, p. 6; emend., Soulié-Märsche, 1989, p. 172 [\*Chara hirmeri Rásky, 1945, p. 36, pl. I,10-12; OD] [=Maedlerisphaera HORN AF RANTZIEN, 1959b, p. 100 (type, Chara ulmensis Straub, 1952, p. 470, pl. A,19, OD); ? Raskyaechara HORN AF RANTZIEN, 1959b, p. 146 (type, Aclistochara pecki RASKY, 1945, pl. II,13-15); Tolypella section Rothia R. D. Wood, 1962, p. 23 (type, Chara intricata, TRENTEPOHL ex ROTH, 1797, p. 125, OD)]. Apex curved, with central rosette. In well-calcified specimens, spirals become thinner in periapical zone, then recover thickness at ends. General shape spheroidal to prolate-spheroidal. Spirals in most instances with granulate surface. When present, ornamentation consisting of constrictions and irregular, elongated nodules. Basal plate undivided, as thick as wide, with upper and lower faces commonly stellate, visible from exterior. Size generally small. [Identity of Maedlerisphaera and Sphaerochara established by HORN AF RANTZIEN & Grambast (1962). Raskyaechara doubtfully assigned to Sphaerochara as gyrogonite structure incompletely known (GRAMBAST, 1962b).] Cretaceous-Holocene: worldwide.—Fig. 78,1a. \*S. hirmeri (RÁSKY) MÄDLER, upper Oligocene, Hungary, topotype; lateral view, ×70 (adapted from HORN AF RANTZIEN, 1959b, pl. XVI, 1).—Fig. 78, 1b. S. hirmeri ssp. longiuscula Grambast & Paul, upper Oligocene, France; longitudinal section, basal part with basal plate in situ, ×150 (Castel, 1967, pl. —Fig. 78,1*c−e*. S. (Trentepohl ex Roth) Feist & Grambast-Fessard var. intricata f. prolifera R. D. WOOD, Holocene, Uruguay; c, lateral view, ×90; d, apical view, ×100; e, basal view, ×100 (Soulié-Märsche, 1989, pl. XLIII,2,4,7).—Fig. 78,1f. S. labellata Feist, upper Eocene, France; paratype, lateral view, ×95 (Feist & Ringeade, 1977, pl. XI,4).—Fig. 78,1g. S. senonensis FEIST, Upper Cretaceous, France; internal view of gyrogonite with microscopic waving of spiral cell walls, ×370 (Feist & Freytet, 1983, pl. I,14).

Tolypella (Braun, 1849) Braun, 1857, p. 338; emend., SOULIE-MÄRSCHE, 1989, p. 171 [\*Conferva nidifica MÜLLER, 1778, p. 761; OD] [=Tolypella section Tolypella WOOD, 1962, p. 23, obj.]. In extant species, oogonia uncalcified, not laterally compressed,

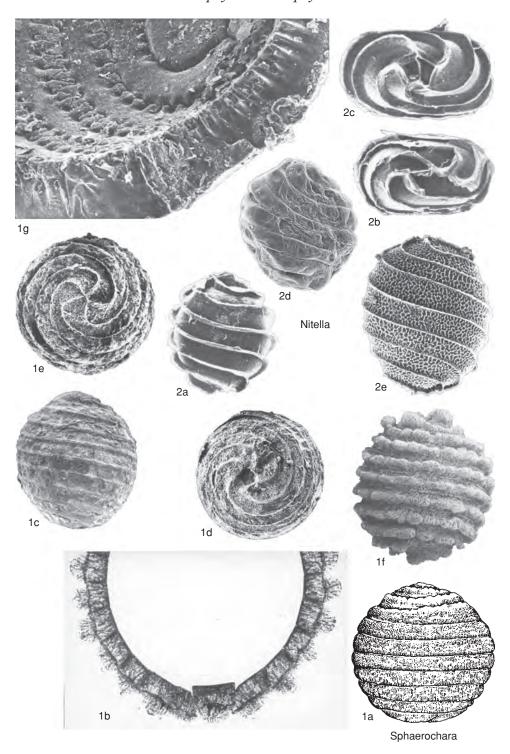


Fig. 78. Characeae (p. 143).

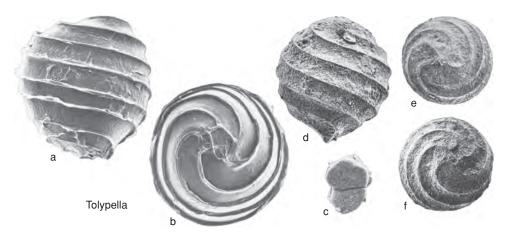


Fig. 79. Characeae (p. 143-145).

with 3 basal sister cells. In fossil species, uncalcified forms unknown; calcified gyrogonites with bipartite or tripartite basal plate. Apex without distinct modifications. General shape spheroidal with apex and base pointed. Spirals concave, smooth. Size very small. [Species with external characters of *Tolypella* but with basal plate unknown are questionably assigned to this genus, such as the Upper Jurassic *T. harrisi* MADLER, 1952.] *Upper Cretaceous—Holocene:* Alaska, Argentina, Belgium, France,

Germany, *Upper Cretaceous–lower Oligocene* (calcified); worldwide, *Holocene* (not calcified).—
FIG. 79*a–b.* \**T. nidifica* (O. MÜLLER) BRAUN, Holocene, Sweden; *a,* lateral view; *b,* basal view, ×120 (Soulié-Märsche, 1989, pl. XLI,2,1).——FIG. 79*c–f. T. pumila* GRAMBAST in STOCKMANS, upper Eocene, Belgium; *c,* isolated multipartite basal plate, ×325; *d,* lateral view, ×110 (Feist & Grambast-Fessard, 1991, fig. 5e, 5d); *e,* apical view, C.1231-2; *f,* basal view, C.1231-3, ×110 (new).

# NOMINA DUBIA AND GENERIC NAMES WRONGLY ATTRIBUTED TO CHAROPHYTES

Monique Feist and Nicole Grambast-Fessard

[Université Montpellier II, France]

#### NOMINA DUBIA

Algites SEWARD, 1894. Nomen nudum.

Astrocharas STACHE, 1872. Nomen nudum (Groves, 1933).

Barrandeina Stur, 1881. Vascular plant (Groves, 1933).

Bechera Sternberg, 1825. An artificial genus, conceived to include unlike charophyte plants (Groves, 1933).

Characeites Tuzson, 1913. Nomen nudum.
Cristatella Stache, 1889. Nomen nudum.
Kosmogyra Stache, 1889. Nomen nudum.
Kosmogyrella Stache, 1889. Nomen nudum.
Palaeoxyris Brongniart. Probably not vegetal (Groves, 1933).

Spirangium Schimper, 1869. Probably not vegetal (Groves, 1933).

# GENERIC NAMES WRONGLY ATTRIBUTED TO CHAROPHYTES

Uncatoella Li & Cai, 1978. Dasycladales (Kenrick & Li, 1998).

Munieria DEECKE, 1883. Dasycladales (FEIST, GÉNOT, & GRAMBAST-FESSARD, 2003).

Umbella MASLOV in BYKOVA & POLENOVA, 1955; emend., POYARKOV, 1965, and related genera. Microproblematica (PECK, 1974).

'New data on the utricles of the Sycidiales suggest that some umbellids could correspond to charophytes (Feist, Monique, Liu Junying, & Paul Tafforeau. In press. New insights on Paleozoic charophyte morphology and phylogeny. American Journal of Botany (in press).



### **RANGES OF TAXA**

The stratigraphic distribution of the Charophyta recognized in this volume is shown graphically in the range chart (Table 9).

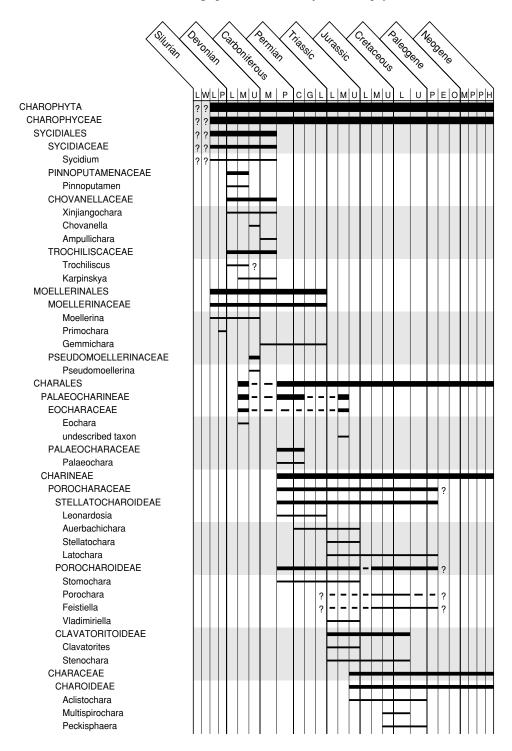
Because of the very long stratigraphic ranges of many higher taxa of Charophyta, ranges in the chart are rather broad in order to ensure that all periods are included. For more detailed stratigraphic information, refer to the systematic section of the volume, p. 92–145.

The following chart was compiled using software developed for the Paleontological Institute by Kenneth C. Hood and David W. Foster.

It must be emphasized that the order of taxa in this chart is governed entirely by their stratigraphic range and, within that, by alphabetical order and differs in some cases from the taxonomic order in the systematic part of the volume. No taxonomic conclusions should be drawn from the position of taxa in this chart.

Explanation for Table	9
PHYLUM	
CLASS	
ORDER SUBORDER	
FAMILY	
SUBFAMILY	
Genus	
Subgenus	
Occurrence questionable	????
Occurrence inferred	

Table 9. Stratigraphic Distribution of the Charophyta.



# Charophyta

Table 9. (Continued).

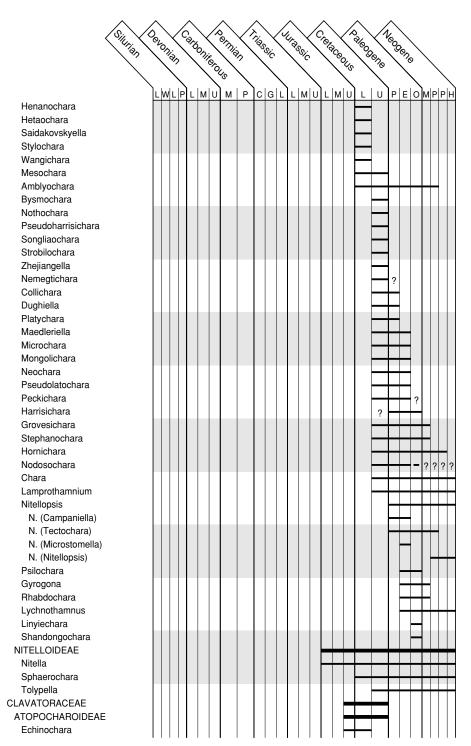


Table 9. (Continued).

