Figure 47: Endoskeletal patterns in discoidal shells.

A-D: disposition of apertural axes. A: radial axes alternating in radial position from one stolon layer to the next. This is the most common disposition in imperforate forms with annular stages of growth. B: radial axes superposed in radial position on all stolon planes. C: crosswise-oblique stolon axes alternating in radial position from one stolon plane to the next. D: crosswise-oblique stolon axes superposed on all stolon planes. This pattern characterizes all members of the orbitolitid family. Schematic, not to scale. E-H: all endoskeletal elements are disposed in accordance with the basic patterns of the foraminal axes: E corresponds to pattern A, F to pattern B, G to pattern C and H to pattern D. Stereographs after HOTTINGER, 1967. Schematic, not to scale. In reality, the patterns are often disturbed by intercalary elements generated as the diameter of the annuli increases during growth. This maintains on the apertural face the mean distances between apertures and their mean diameter constant during ontogeny. Examples:

E1-2: Pseudotaberina malabarica, megalospheric generation, from Iran. Middle Miocene. E1: oblique-centered section of spiral-involute stage showing radial disposition of pillars. Laterally, there is a layer of short septula. E2: a transverse section tangential to a septum shows the alternating disposition of the foramina and the pillars. F1-2: New genus (possibly related to Pastrikella) from the Pyrenean Upper Cretaceous in Northern Spain. The endoskeleton consists only of septula. There is but one median annular preseptal passage and it occupies the total radial extension of the annular chamber. There are only two planes of stolons. F1: an oblique section at a low angles with respect to the equatorial plane shows the radial disposition of the apertural axes and of the septula. F2: a transverse section parallel to the shell axis shows that the stolon axes on the two stolon planes are superposed. G1-3: Amphisorus from Rottnest Island near Perth, Australia. Recent. G1: the detail of an equatorial section demonstrates the crosswise-oblique disposition of the pillars on neighboring stolon planes. G2, an equatorial section, demonstrates that pillars are restricted to the equatorial zone of the disc. G3: a transverse section parallel to the shell axis and tangential to an annular septum shows the disposition of the median foramina and pillars alternating in radial position on successive stolon planes. They are flanked by two annular preseptal passages separating them from a lateral layer of septula subdividing the annular chamber. H1-2: Orbitolites spp. from the region of Tremp, Lerida prov., Northern Spain. Pyrenean Lower Eocene (Ilerdian). H1: the comparatively regular disposition of the ramps in sections parallel to the equatorial plane reveals their superposition in consecutive stolon planes. H2: in the transverse section parallel to the axis of the shell this superposition is clearly visible where the section is tangential to an annular septum.

Abbreviations: b: beam; f: foramen; pi: pillar; prp: preseptal space; ra: ramp; s: septum; sl: septulum.
Figure 48: Faces (coloured red) in biserial and spiral forms. SEM graphs (if not specified otherwise) of specimens from the Gulf of Aqaba, Red Sea. Recent.

A-C: Textularia aff. goesi CUSHMAN, apertural and lateral views of intact specimens and frontal view of broken specimen showing septal face. Note the smooth surfaces characteristic of the faces of many agglutinated forms. D-E: Discorbinoïdes sp. A in HOTTINGER et alii, 1993. Plastogamic pair and plastogamic umbilical face with radial grooves. F-G: Glabratrullina sp. A in HOTTINGER et alii, 1993. Ventral view showing plastogamic ventral face with radial grooves and lateral view showing shell whorls with their sutures. H-I: Bolivinella elegans PARR, a lamellar-perforate, biserial form with known plastogamic reproduction, that has radial grooves on its face. J: Floresina spicata (CUSHMAN et PARKER) has a smooth face with few radial grooves and in addition grooved septal sutures. A (plastogamic?) plate covers the narrow umbilicus. As yet, plastogamy has not been observed in vivo in this species. K-L: Amphistegina lobifera LARSEN, Megalospheric specimen in incident light micrograph, ventral view and detail of apertural face. Note the extension of the ornamented surface for a notable distance over peripheral-ventral parts of the previous whorl. M-N: Amphistegina bicirculata LARSEN, megalospheric specimen in incident light micrograph, ventral view and detail of apertural face. Note comparatively much smaller ornamented surface corresponding to lower water energy in its deeper habitat.

a: aperture; af: apertural face; f: foramen; p: pore; plp: plastogamous (?) plate; pp: parapore; rgr: (plastogamous) radial grooves; sfa: septal face; stch: stellar chamberlet; stsut: stellar suture; sut: (chamber) suture; wsut: whorl suture.

Figure 49: Equitant chambers in Frondicularia sp. from the Prerif, Northwestern Morocco, Lower Miocene. Transmitted light micrograph of section in the sagittal plane of a microspheric specimen. Note the denticulate margin of the single, stellar foramen in terminal position (f) and the extremely fine perforation of the septal wall that is characteristic of most nodosariids.
Figure 50: Feathered grooves. All specimens figured as SEM graphs.
A-B: *Ammonia beccarii* (LINNÉ), Adriatic Sea, Recent. Peripheral and oblique - umbilical views. Note the ridges on the apertural face that initiate the feathering when the next chamber is added during ontogeny. C-D: *Neorotalia calcar* (d’ORBIGNY), Keij Island, Indonesia. Recent. Ventral view of an entire specimen and detail of a ventral feathered groove covered by a folded outer lamella. Note the imperforate nature of the cover and the orifices of the canal system. Compare: enveloping canal systems in Fig. 44. E-G: Unfeathered grooves in *Ammonia ikebei* (INOUE et NAKASEKO), Eastern Kalimantan, Borneo, Upper Miocene. Peripheral view of entire specimen and details in oblique-umbilical and in dorsal views. Note the hemispherical attachment of the septal flap and the undivided umbilical plug that correspond to unfeathered septal grooves.
af: apertural face; f: foramen; fea: feathered grooves; ol: (folded) outer lamella covering a septal groove that is converted to an interlocular space; or: canal orifice; pil: pile; s: septum; sgr: septal groove (unfeathered); spgr: spiral groove (unfeathered); upl: umbilical plug.

Figure 51: Fistulose chamberlets. All specimens from the Gulf of Aqaba, Red Sea, Recent.
A-C: *Sahulia kerimbaensis* (SAID). A: Detail of an edge view, SEM graph; B: side view, X-ray graph, black background removed. Note the narrowness and the irregularity of the fistulose chamberlets in this species. C: edge view, SEM graph. D-H: *Spirotextularia floridana* (CUSHMAN). D: paraporous partition separating the chamber lumen from a fistulose chamberlet. SEM graph. E: Detail of sectioned paraporous partition. SEM graph. Note the organic lining that closes off the parapores from the chamber lumen. SEM graph. F: Shell fragment broken in a direction perpendicular to the shell axis, showing paraporous partition between the chamber lumen and the fistulose chamberlet. SEM graph. G: Lateral view, X-ray graph. H: lateral view of an entire specimen. SEM graph. Note the spiral arrangement of the nepionic chambers.
a: aperture; af: apertural face; ch: chamber lumen; f: foramen; fis: fistulose chamberlet; OL: organic lining; pp: parapore; ppa: paraporous partition; pr: proloculus; pv: pavement; s: septum.
Figure 52: The flange (double arrow) in *Nephrolepidina* sp., axial section, transmitted light. Oligocene, Sarawak, Borneo.

*lchl*: lateral chamberlets; *mchl*: median chamberlet layer. Scale bar 0.2 mm.
Figure 53: The folium and its apertures. All specimens from the Gulf of Aqaba, Red Sea, Recent. SEM graphs.
A-D: Rosalina bradyi (CUSHMAN). A: detail of dissected specimen, oblique-ventral view. The approximate position of the breakage surface (arrows A-A) is indicated by the line A-A in Fig. B. B: ventral view showing the folium at its maximum development, with anterior and posterior apertures. C-D: peripheral and dorsal views. Note the restriction of the perforation to the dorsal surface of the shell, an indication that the face extends from the umbilical side of the shell over its periphery. E-H: Asterorotalia gaimardi (d’ORBIGNY). E-F: dissected specimens showing details of advanced umbilical architecture covered by the folia: foraminal and coverplates (compare Fig. 34). G: oblique-ventral view showing the folia that cover the ventral part of the interlocular space. H: dorsal view showing the spiral arrangement of the chambers.

a: aperture; ch: chamber lumen; cp: coverplate; f: foramens; fo: folium; foa: foliar aperture; fochl: foliar chamberlet lumen; fp: foraminal plate; is: interlocular space; li: lip (of foramen); n: notch; sf: septal flap; u: umbilicus.

Figure 54: Fossette, parafossette, ponticulus and retral process in advanced elphidiids from the Gulf of Aqaba, Red Sea. Recent. SEM graphs except D and H.
A-F: Elphidium striatopunctatum (FICHTEL et MOLL). A: lateral (umbilical) view of the surface of the shell. B: detail showing the orifices of the canal system. Note the heavy spiking of the orifices, a device to fend off inedible particles such as diatom frustules. C: the detail of an orifice of a parafossette. Note its alignment with the axis of the adjacent ponticulus. D: axial section of megalospheric specimen, transmitted light micrograph. Note the row of foramina at the base of the chamber and the row of retral processes in the chamber roof. E: epoxy resin cast of the cavities of the shell showing the narrow spiral of the umbilical canal and the double row of fossettes and parafossettes representing the septal interlocular space. F: detail of a cast showing the disposition of fossettes and parafossettes and their connection to the intraseptal canal system. G-L: Elphidium craticulatum (FICHTEL et MOLL). G: oblique-peripheral view of entire shell. H: axial section of megalospheric specimen. Transmitted light micrograph. Note the single row of foramina at the bottom of the chamber and the broad umbilical pile with its funnels. I: apertural face showing the masked apertures. Note the imperforate keel, an important specific character. J: detail of G: the orifices of the fossettes in the last chamber alternate with tiny parafossettes. These disappear when they are covered by subsequent secondary lameliation in later stages of growth. K: epoxy resin cast showing umbilical cavities including the foliar chamberlets at the tips of the alar prolongation of the chamber. The foliar chamberlets are transformed during ontogeny into a spiral umbilical canal. L: epoxy resin cast showing detail of septal architecture: the alternation of retral processes and fossettes. Note the tiny pores on the cast of the main chamber lumen and the traces of the spikes on the walls of a fossette.

a: aperture; af: apertural face; f: foramens; fo: folium; foa: foliar aperture; foc: foliar chamberlet; fs: fossette; k: keel; m: mask; mc: main chamber lumen; pfs: parafossette; po: ponticulus; rp: retral process; s: septum; suc: spiral umbilical canal; upil: umbilical pile; vc: vertical canal (funnel). Scale bars: 0.1 mm, double scale bars: 0.05 mm.
Figure 55: An umbilical architecture dominated by funnels: *Dictyokathina simplex* SMOUT, megalospheric specimens from Qatar, Paleocene. Transmitted light micrographs.

A: subaxial section showing funnels in their longitudinal extension. B: transverse section near the axis of the shell with the positions of sections A & C-D indicated. C-E: sections more or less perpendicular to the axis of the shell showing the vast umbilical area crowded with funnels. Note the chamber arrangement in multiple spirals. The start of supplementary spirals is indicated by arrows. The material does not allow resolution of the question: is the first chamber of a supplementary spiral fed from a foramen or from a canal?

ch: chamber lumen; f: foramen; fu: funnel (vertical canal); isp: intraseptal interlocular space; ssp: spiral interlocular space; up: umbilical plate.
Figure 56: The Golgi apparatus and mitochondria in the cytoplasm of Alveolinella quoyi (d’ORBIGNY) from the Maldive Islands, Indian Ocean. Transmission electron micrograph, x 44,500. Courtesy S REBER-LEUTENEGGER.

G: Golgi apparatus with its cisternae (cist); M: mitochondrion with its cristae (cr).
Figure 57: Glomerulus (coloured) in *Glomalveolina lepidula* (SCHWAGER) from Tremp, Northern Spain, Ilerdian. Approximately equatorial section with small, ?microspheric proloculus and axial section with large, ?megalospheric proloculus. Incident light.

*f*: foramen; *icf*: intercalary foramen; *pop*: postseptal passage; *prp*: praeseptal passage; *s*: septum; *sl*: septulum; *wsut*: whorl suture (enlarged by slight deformation).
Figure 58: Hemiseptula in *Amphistegina lessonii* d'ORBIGNY from the Gulf of Aqaba, Red Sea. Recent. 
**A:** the dorsal surface of a megalospheric specimen. Incident light. **B:** the inner surface of a fragment of dorsal chamber walls showing septa and hemiseptula broken at a short distance from the level of the eggholders. Note the three-layered texture of the septa (a primary bilamellar wall plus a septal flap) and the two-layered nature of the hemiseptula that results from the folding of the inner lamella. SEM graph. 
*egh:* eggholder; *hs:* hemiseptula; *s:* septa.
**Figure 59**: Intercalary chamberlets in *Borelis curdica* (REICHEL). Qum Basin, Iran. ALLEMANN collection 229. Lower Miocene. Axial section.

- **chl**: chamberlet; **f**: foramen; **ichl**: intercalary chamberlet; **if**: intercalary foramen; **prp**: preseptal passage; **s**: septum; **sl**: Y-shaped septulum.
Figure 60: Surface of attachment with supplementary apertures in *Planorbulina mediterranensis* d’ORBIGNY. Elba Island, Mediterranean. Recent.

**A:** Free surface with apertures in subperipheral position. SEM graph. **B:** Equatorial section showing the nepionic, keeled spiral chambers followed by early chamberlet cycles with their oblique foramina and supplementary apertures where the section passes immediately below or within the attached chamber walls. Note the straight septa between the proconch and the two following chambers forming together a triconch. Transmitted light micrograph. **C:** Detail of surface of attachment with its tiny supplementary apertures in sutural position. Note the keeled nepiont. SEM graph.

*a*: aperture; *f*: foramen; *k*: keel of the nepiont; *p*: pore; *pr*: proloculus; *sa*: supplementary aperture.
Figure 61: Infundibulum and marginal prolongation.

A: Neoeponides bradyi (LE CALVÉZ), oblique-ventral view showing infundibulum. SEM graph; Gulf of Aqaba, Red Sea; Recent. B: Eponides repandus (FICHTEL et MOLL), ventral view showing marginal prolongation, SEM graph; Gulf of Aqaba, Red Sea; Recent. C: Schematic drawing showing position of marginal prolongations in respect to ventral and dorsal test morphology in the last whorl of Eponides repandus.

Gray: dorsal view with raised sutures; red: outline of chamber walls at level ventrally below periphery; green: ventral outline of chambers below level of marginal prolongation. a: aperture; inf: infundibulum; mpr: marginal prolongation; per: (imperfotate) periphery; s(d): (oblique) septum (as seen in dorsal view); s(per): position of septum at level of periphery; ss(v): (radial) septal suture in ventral view.
Figure 62: Keriotheca (double arrow) in equatorial section of unidentified Triticites and as plasticine model by M. REICHEL (unpublished, modified).

**cho:** choma; **kalv:** keriothecal alveoles; **k ex:** extern keriotheca; **k in:** intern keriotheka; **s:** septum; **s₁:** septum belonging to whorl bearing the keriotheka; **s₂:** septum of following whorl; **te:** tectum.
Figure 63: Comparison of foraminiferal skeletons. Schematic, not to scale. Lamellation, perforation and canal orifices omitted.
A: a planispiral-evolute shell without skeletal structures, composed of simple primary chamber walls with multiple apertures, such as that of *Peneroplis*. B: a planispiral-evolute shell with an alveolar exoskeleton, such as *Pseudocyclusmmina*. C: a planispiral shell with a pillared endoskeleton such as *Archaias*. Note that in the axial sections of shells with peneropliform, flaring chambers the periphery of the shell and the apertural face are on opposite sides. Consequently, the pillars extending from chamber bottom to chamber roof appear in the axial plane on the side cutting the apertural face as longitudinal and on the other side cutting the periphery as more or less perpendicular sections. D: a spiral shell with a supplemental skeleton restricted to the periphery of the shell, as in nummulitids with a marginal cord. E: a spiral shell with an enveloping canal system and a marginal crest as in *Pellatispira*. Note the primary lateral chamber walls "emerging" from the supplemental skeleton. These primary chamber walls are covered by secondary lamellae but are perforated in continuation of the primary bilamellar wall. Therefore they are not a part of the supplemental skeleton. The supplemental chamberlets have perforate lateral walls but do not communicate directly with the spiral chambers by retral stolons. They are fed by canal orifices.

a: aperture; af: apertural face; alv: alveole; bl: basal layer; ch: chamber; chsut: chamber suture; f: foramen; lh: loophole; mc: marginal cord; mcr: marginal crest; per: periphery; pi: pillar; pr: proloculus; s: septum; schl: supplemental chamberlet; spc: spiral canal; spsut: spiral suture; sulc: sulcus; t: tunnel; up: umbilical plate.

Figure 64: Marginal cord in nummulitids.
A-B: *Assilina ammonoides* (GRONOVUS), Recent, Gulf of Aqaba, Red Sea. SEM graphs after HOTTINGER, 1977. A: Detail of marginal cord in a shell broken in the axial plane. Double arrow B - B indicates the approximate position of the cut in the cast of Fig. B. B: Detail of marginal cord in an epoxy resin cast that was cut approximately in the equatorial plane (as indicated in Fig. A), showing canal and chamber lumina after dissolution of shell. White arrows indicate direction of growth. C: Nummulitic limestone from Steinbach, Einsiedeln, Swiss Helvetic Alps, Lower Eocene (Cuisian). Transparent light micrograph of section perpendicular to bedding plane. 1: *Assilina* sp. of *A. ammonea-praeispira* phyletic line, with particularly large and prominent marginal cord; 2: *Nummulites* spp.; 3: *Assilina* sp. of *A. spira* phyletic line; 4: *Assilina* sp. of *A. exponens* phyletic line; 5: *Asterigerina* cf. *rotula* (KAUFMANN): no marginal cord.

ch: chamber lumen; isc: intraseptal canal system; mc: marginal cord; mcc: marginal cord canals; sf: septal flap; st: stolon; sulc: sulcus canal.
Figure 65: Supplemental skeletons including marginal crests.

A-G: *Pellatispira* group *provalei* YABE. H: *P. fulgeria* WHIPPLE. Both species from Kalimantan, Borneo, Indonesia. Middle-Upper Eocene. I-J: *Calcarina* sp., Kutei basin, Kalimantan. Pleistocene. A-D: SEM micrographs. G-J: transmitted light micrographs of oriented thin sections of free specimens. A: the free nepiont shows early spiral chambers not yet covered by a supplemental skeleton. An uncovered open interlocular space remains between the ultimate and penultimate chambers. B: detail of lateral view of a free nepiont revealing the early presence of canaliculate spines in the first volution of the spiral chambers and the modest extent of the marginal crest at this stage of growth. C: peripheral view of the margin of the second whorl. Note the strong radial spikes that support the thin imperforate walls of the marginal crest. D: septal face in oblique-peripheral view: the septal flap is reduced to a small area above the foramen. E: a lateral, flying cover of the interlocular space, with canal orifices at its margins, is produced by a free fold of an outer lamella and represents thus a primary element of the supplemental skeleton. F: in later growth stages, a first imperforate cover of the interlocular space may be bridged by supplementary chamberlets with a perforate, bilamellar wall. G: equatorial section. The primary bilamellar walls of the spiral chambers are coloured. All uncoloured constituents of the shell are part of the supplemental skeleton. H: Extreme development of the supplemental skeleton as a broad marginal crest covered with piles that are flanked by the canals of an enveloping system. I: the axial section of a trochospiral shell demonstrates the complex pattern of the umbilical cavities between umbilical piles of lamellae. The primary bilamellar walls of the spiral chambers are coloured. J: a section perpendicular to this axis of coiling shows that canaliculate spines grow outward from the supplemental skeleton that envelopes the primary bilamellar (coloured) wall of the spiral chambers.

Abbreviations: a: aperture; c: canals, canal orifices; ch: (spiral) chamber; chl: (supplemental) chamberlet; csp: canaliculate (pseudo)spine; f: foramen; is: intraseptal interlocular space; lh: loophole; mcr: marginal crest; p: pore; pil: pile (of lamellae); pr: proloculus; s: septum; schl: supplemental chamberlet; sf: septal flap; sk: supplemental skeleton; spi: spike; uc: umbilical cavity system; up: umbilical plate.

Figure 66: Septal and chomatal "pores" in *Triticites plummeri*, Graham Fm., Texas, Permian. Transmitted light micrographs.

A: subaxial section; B: details in equatorial section. Both pore-like features have nothing in common with true pores. Septal pores are tiny multiple foramina. The nature of chomatal pores, a wall texture particular to fusulinids, is not understood at present.

c: choma; c*p: chomatal "pores"; kth: keriotheka; sp: septal "pores". t: tunnel; te: tectum.
Figure 67: Microtubules (Mt) and tubulin paracrystals (T) in canal ectoplasm of *Assilina ammonoides* (GRONOVIUS). TEM micrograph, courtesy S. REBER-LEUTENEGGER, x 17,700. 
B: bacteria; M: mitochondria; Mt: microtubule; Pl: plasmalemma; T: tubulin paracrystals; V: vacuoles with or without fibrillar content (waste products?).

Figure 68: Milioline coiling. Schematic, not to scale. Note the coiling mode: only two chambers per whorl. Chamber lumina green, coiling axes black. Foramina aligned in the apertural axis (red). 
A: quinqueloculine mode of coiling: for each new chamber the coiling axis rotates 72° around the apertural axis. B: triloculine mode of coiling: for each new chamber the coiling axis rotates 120°. C: biloculine mode of coiling: the coiling axis does not rotate. 
a: aperture; cax: coiling axis; chs: chamber suture; mt: miliolid tooth.