PART L
MOLLUSCA

CEPHALOPODA
AMMONOIDEA

By W. J. Arkell, W. M. Furnish, Bernhard Kummel, A. K. Miller, R. C. Moore, O. H. Schindewolf, P. C. Sylvester-Bradley, and C. W. Wright

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INTRODUCTION TO AMMONOIDEA

By A. K. Miller and W. M. Furnish

The clymenias, goniatites, ceratites, and ammonites, which together constitute the order Ammonoidea, have long been extinct, but their fossilized shells are common in all continents and many oceanic islands. Numerous specimens are remarkably well preserved, even spectacular, and their exceptional value as a basis for stratigraphic correlations has been recognized for well over a century. Accordingly, they have attracted the attention of both layman and scientist for generations, and the literature in regard to them is voluminous. Almost all our knowledge of these creatures comes from studies of the shells and the enclosing matrices, but a few opercula are also preserved. The shells are comparable to that of modern *Nautilus,* a presumed relative of the group.

The nautiloids and ammonoids, which together constitute the subclass Tetrabranchiata, were widespread and abundant in the past but are now almost extinct, being represented by only a few species of the single genus, *Nautilus.* All members of the entire group are characterized by the possession of an external univalved camerate shell. Typically this shell is bilaterally symmetrical, being straight, curved, or coiled in one plane; but helicoid and irregular forms are not rare. Some authors have expressed the opinion that at least certain of the ammonoid shells were internal. However, the presence of color markings and the absence of surficial deposits indicate that they were external.

Living representatives of *Nautilus* differ from all other present-day cephalopods in that they have 4 gills, rather than a single pair, and the 2 flaps which form the hyponome overlap ventrally, rather than being fused together. Whether or not their fossil relatives possessed these features is a matter of conjecture; the shape of the body chamber and the aperture indicate only the general nature of the soft parts of the animal.

Conventionally, tetrabranchiate cephalopod illustrations are oriented with the peristome above the phragmocone. *Nautilus,* however, is well stabilized in the reverse manner and cannot change its position materially. Most ammonoids had a comparable low center of gravity. Nevertheless, certain forms with body chambers about a volution in length may have been able to invert themselves.

The present-day representatives of the subclass live in the moderately shallow waters of the southwest Pacific Ocean. However, their ancient relatives ranged in the oceans and the seas all over the world, most of the known fossil remains coming from rocks that represent shallow-water marine deposits. The subclass made its debut in the Cambrian. It developed and evolved so rapidly that in the Ordovician it was perhaps the pre-eminent group of animals, some of its members attaining enormous proportions and being the largest creatures of the time. It continued unabated in the Silurian, and very early in the Devonian the ammonoids evolved from the nautiloids. Both these groups flourished until near the close of the Triassic, when they almost became extinct, only to be revitalized in the Jurassic. Throughout the Mesozoic, ammonoids were more numerous than nautiloids. During the Cretaceous, ammonoids were the largest and among the most abundant of the invertebrates, and nautiloids were not rare. However, at the end of that period, the former became extinct, and after the early Tertiary the nautiloids dwindled rapidly. Few if any are known from the Pliocene and none from the pre-Recent Pleistocene, though, of course, the ancestors of modern *Nautilus,* a relic, must have been in existence during those times.

The tetrabranchiate cephalopods are among the very best of our guide or index fossils. The ammonoids in particular are good stratigraphic indices, and the marine strata of the later Paleozoic and the Mesozoic are zoned with reference to them.

Order AMMONOIDEA Zittel, 1884

Tetrabranchiate cephalopods characteristically tightly coiled in a plane and symmetrical, with a bulbous calcareous protoconch, septa that form angular sutural flexures, and a small marginal siphuncle. *L. Dev.-U.Cret.*

MORPHOLOGICAL TERMS APPLIED TO AMMONOIDEA

By W. J. Arkell, Bernhard Kummel, A. K. Miller, and C. W. Wright

The preparation of a glossary of morphological terms applied to Ammonoidea arranged in a single alphabetical list was advocated by the Editor at the outset of work undertaken by authors contributing to this volume. Surely, the availability of a glossary giving concise definitions or explanations of terms should be useful to readers and therefore Arkell, Kummel, Miller, and Wright accepted the task of reviewing terms to be included and of drafting definitions. Soon many difficulties appeared, several of these relating to terms such as camera, chamber, conch, shell, test, siphon, siphuncle, and others that belong also to nautiloid and dibranchiate cephalopods as well as to ammonoids. Authors concerned with these divisions were consulted. For some time a voluminous exchange of letters and memoranda seemed to bring out greater divergence than agreement on choice of terms and how to use them; eventually, however, decisions were made to accept some terms and to reject others, some measure of disagreement remaining also as to wording of definitions. The inclusion of many terms classed as obsolete was deemed inexpedient. As here published, the glossary contains no indication of the relative importance attached to various terms, some being classified as essential, others as important because commonly used, and still others as rather unimportant. By and large, terminology given in the glossary relates more to Mesozoic than Paleozoic ammonoids.—R. C. MOORE.

GLOSSARY OF MORPHOLOGICAL TERMS

accessory (lobe or saddle). Secondary or minor element of sutures.

acute (periphery). With sides of shell meeting at sharp angle without shoulders.

adapertural. *See* adoral.

adapical. Toward apex of shell; backward direction.

adoral. Toward mouth of ammonoid or aperture of shell; forward direction.

adventitious (or **adventive**) **lobe.** Lobe of suture formed secondarily by subdivision of 1st lateral saddle.

ammonitic (suture). With all lobes and saddles of suture denticulate or frilled.

anaptychus. Single plate closing aperture of some ammonoids.

aperture. Open end of body chamber of shell.

approximated (ribs). Crowded toward present or past position of aperture, usually associated with maturity of growth.

approximated (sutures). Crowded toward body chamber, usually indicating maturity of growth.

aptychus. Pair of plates serving for closure of aperture of some ammonoids (strict sense); single plate (anaptychus) or pair of plates (aptychus) (loose sense).

auxiliary (lobe or saddle). Lateral lobe or saddle of suture springing from umbilical lobe or saddle between 2nd lateral and umbilical seam.

bicarinate. With 2 keels on venter.

biconcave (rib). With 2 distinct portions concave toward aperture.

biconvex (rib). With 2 distinct portions convex toward aperture.

bifurcate (rib). Dividing into 2 branches toward venter.

biplicate. *See* bifurcate.

bisulcate. With 2 longitudinal grooves.

body chamber. Large undivided space in shell extending adapically from aperture, inhabited by living animal.

bulla. Tubercle elongated radially; adj. bullate.

bundled (ribs). United in bunches or sheaves at or near umbilical edge, usually at a tubercle (*see* fasciculate).

cadicone. Depressed barrel-shaped shell with more or less evolute coiling, wide venter, and crater-like umbilicus (as in *Cadoceras*).

caecum. Closed pouch or sac at apex of siphuncle; commonly termed siphuncular caecum.

camera. Compartment between 2 adjacent septa comprising one of the spaces into which entire shell between protoconch and body chamber is divided by the septa.

capricorn. Shell encircled by distant blunt ribs and subequal rounded interspaces, resembling a goat's horn (as in *Androgynoceras capricornus*).

carina. *See* keel; adj. carinate, bearing a keel.

ceratitic (suture). With rounded unbroken saddles and denticulate lobes (as in *Ceratites*).

chamber. *See* body chamber, camera.

chevron. V-shaped ridge on shell surface, commonly on venter.

clavus. Tubercle elongated in direction of coiling (longitudinally); adj. clavate.

collared (aperture). Encircled by flared rib and constriction close behind peristome.

compressed (whorl section). Higher than wide.

concave (side or venter). Broadly impressed. Concave rib, bowed away from aperture.

conch. Complete shell of ammonoid less the protoconch.

connecting ring. Porous segment of siphuncle between 2 adjacent septal necks, partly chitinous and partly calcareous spicular.

constricted (aperture). Encircled by constriction close behind peristome. Constricted conch, with several constrictions.

constriction. Depression encircling a whorl.

contracted (peristome). With diameter smaller than that of body chamber.

convergent (whorl sides). Converging toward venter.

convex (rib). Bowed toward aperture.

coronate. With whorl section resembling a crown viewed from side.

costa. *See* rib.

cruciform. Cross-shaped.

cuneiform. Wedge-shaped.

cyrtocone. Shell curved without completing a single whorl.

dense (ribs). Closely spaced.

dependent. *See* retracted.

depressed (whorl section). Wider than high.

distant (ribs). Widely spaced.

divergent (whorl sides). Diverging toward venter.

dorsal lobe. Median primary lobe of suture on dorsum (internal in normally coiled conchs).

dorsolateral area. Side of impressed area on each flank of dorsum in involute shells.

dorsum. Dorsal side of conch (opposite ventral), generally grading into dorsolateral areas; in slightly involute shells equivalent to impressed area but in deeply involute shells refers only to portion of conch adjacent to venter of preceding whorl.

ellipticone. Shell with elliptical coiling of last whorl or half whorl which slightly breaks regularity of spiral form.

endogastric. Shell curved or coiled so that venter is on inner (concave) area of whorls.

evolute. With whorls overlapping little or not at all and therefore having a wide umbilicus. (As commonly used, evolute and involute are relative terms, since a shell form called evolute in one family may be classed as involute in another.)

excentric (umbilicus). Type characterized by abrupt opening up of spiral described by umbilical seam or tendency to closing of this spiral while the peripheral spiral is relatively unchanged.

excentrumbilicate. *See* excentric umbilicus.

exogastric. Shell curved or coiled so that venter is on outer (convex) area of whorls; nearly all ammonoids are exogastric.

external lobe. *See* ventral lobe.

external saddle. *See* lateral saddle (1st) and ventral saddle.

external suture. Part of suture (in coiled forms only) which is exposed on outside of whorls between the umbilical seams.

falcate (rib). Sickle-shaped.

falcoid (rib). Approaching sickle-shaped.

fasciculate (ribbing). With ribs bunched or bundled to form sheaves.

fastigate. With roof-shaped venter, periphery of shell being sharpened but not keeled.

fillet. Longitudinal raised smooth band on venter or whorl side.

flank. *See* whorl side.

flare. Random annulation or very distinct rib that usually marks location of a former peristome and denotes a temporary halt in growth.

flared peristome. With diameter larger than that of body chamber.

flared rib. Swollen so as to stand in higher relief than average ribs.

floored (hollow keel). Divided from chambers by a partition (septum) external to the siphuncle.

foliole. Minor element of saddle of a suture.

goniatitic (suture). With most or all lobes and saddles of suture entire (not denticulate or frilled), the only common exception being the ventral lobe, which is subdivided.

growth lines. Striae encircling whorl, in some shells separating lamellae, marking repeated minor halts in growth.

gyrocone. Loosely coiled shell which completes only a single whorl approximately.

helicoid. Coiled in regular 3-dimensional spiral form with constant spiral angle, as in most gastropods.

heteromorph. Ammonoid shell of any form except plane spiral with whorls in contact.

hyponomic sinus. Ventral notch or re-entrant in peristome through which the hyponome protrudes, useful for orienting shells because it is invariably ventral where present.

impressed area. Concave dorsal part of shell and in some including dorsolateral part of coiled shell; comprises part of whorl between umbilical seams that is in contact with preceding whorl.

intercalatory (rib). Secondary rib not attached to primary rib, at least on one side of whorl.

intercosta. *See* interspace.

internal lobe. *See* dorsal lobe.

internal suture. Part of suture located within impressed area and extending between umbilical seams.

interspace. Area between adjacent ribs.

involute. With whorls overlapping considerably and hence with narrow umbilicus (*see* evolute).

keel. Continuous distinct longitudinal ridge on venter; may be either solid or hollow, those of hollow type being floored (septicarinate) or without floor so as to open inward to chambers.

labial ridge. Linear elevation of shell corresponding to former apertural border (peristome).

lanceolate. Spear-shaped, referring to form of suture lobes or cross section of acute periphery of shell.

lappet. Simple or necked (spatulate) projection of peristome on whorl sides or venter (called ventral lappet when located on venter); also called ear or auricle.

last septum. Septum separating body chamber from adjoining camera at any stage of growth; adoral septum.

lateral lobes. Primary lobes of external suture other than ventral lobe: **1st lateral lobe** next to ventral lobe, usually on whorl side but in depressed whorls commonly on venter; **2nd lateral lobe** next to 1st lateral, commonly on whorl side and morphogenetically part of umbilical lobe.

lateral saddles. Primary saddles of external suture other than ventral saddle: **1st lateral saddle** (external saddle) separating ventral lobe from 1st lateral lobe; **2nd lateral saddle** (often called 1st lateral saddle) separating 1st and 2nd lateral lobes.

lateral sinus. Notch or re-entrant in peristome on whorl sides.

lateral sulcus. Spiral groove on whorl sides.

lipped (peristome). With liplike extension of shell set at an angle to the apertural rim.

lira. Fine raised line on shell surface.

lobe. Element of suture directed backward (adapically).

lobule. Minor element of sutural lobe.

longitudinal. In direction of shell growth, generally equivalent to spiral.

looped (ribs). United on ventrolateral angle, usually at a tubercle.

median saddle. *See* ventral saddle.

mouth. *See* aperture.

node. Large blunt or formless tubercle.

oblique whorl height. *See* whorl height.

occluded (umbilicus). So narrow or closed that inner whorls are not visible.

ornament. Features of shell exterior such as ribs, tubercles, bullae, clavi, spines, and strigations.

oxycone. Discoidal shell with acute periphery and very narrow or occluded umbilicus (as in *Oxynoticeras*).

parabola. Collective term for rib, node, or constriction of parabolic form.

parabolic node. Small node or tubercle near ventrolateral angle of whorl, associated with an earlier growth halt and independent of ordinary tuberculation.

peristome. Edge of aperture of body chamber; mouth border.

phragmocone. Camerated part of shell.

phylloid. Leaf-shaped, commonly referring to saddle endings (folioles) of sutures.

pila. *See* rib.

planulate. Moderately evolute compressed shell with open umbilicus and bluntly rounded venter (as in *Perisphinctes*).

platycone. Shell with flattened form, without implication as to width of umbilicus or shape of venter.

plicate (-d). With vague coarse radial folds, commonly denoting last stage in obsolescence of ribbing.

primary rib. Main stem or simple inward part of a branched rib.

prochoanitic (septal neck). Directed forward (adaperturally).

projected (rib). Swung forward (adaperturally) at or near venter.

prorsiradiate (rib). With general forward (adapertural) inclination from umbilical side toward venter.

prosepta. Initial partitions in apical part of shell.

prosiphon. Small structure extending from adapical part of caecum to wall of protoconch and having form of a partial cone.

prosiphonate. *See* prochoanitic.

prosuture. Line of junction of proseptum with walls of shell.

protoconch. First chamber of shell, closed by proseptum; sometimes called initial chamber or apical chamber.

pseudoceratitic (suture). Approximating ceratitic in form (but not related to ceratites).

radial. Direction outward from center of umbilicus, at right angles to axis of coiling and growth; transverse.

rectiradiate (rib). In straight radial position, bending neither forward nor backward.

retracted (suspensive lobe). Bent backward (adapically) on approaching umbilical edge and in umbilical area.

retrochoanitic (septal neck). Directed backward (adapically).

retrosiphonate. *See* retrochoanitic.

rib. Radially directed ridge on shell; sometimes called costa or pila.

rostrum. Pointed projection of peristome on venter; may continue spiral line of coiling or diverge from it.

runcinate. *See* tabulate.

rursiradiate (rib). Inclined backward (adapically) proceeding from umbilical area toward venter.

saddle. Element of suture directed forward (adaperturally).

secondary rib. Outer part of branched rib.

septal foramen. Opening in septum at siphuncle.

septal lobe. Lobe formed on adoral face of preceding septum.

septal neck. Tubular extension of septum around siphuncle, termed prochoanitic if directed forward (adaperturally) and retrochoanitic if directed backward (adapically).

septal funnel. *See* septal neck.

septate (whorl). Divided into camerae by transverse septa.

septicarinate. Having a hollow floored keel.

septum. Transverse partition dividing shell into camerae, attached to inside of shell wall along suture line.

serpenticone. Very evolute many-whorled shell with whorls hardly overlapping, like coiled snake or rope (as in *Skirroceras*): sometimes called tarphycone.

serrated (keel). Toothed or notched.

shell. Complete hard parts of ammonoid, including protoconch and conch (but excluding aptychus and beaks or jaw structures, which generally are separated from the conch if preserved at all).

shoulder. Ventrolateral blunt angle of whorl.

sigmoid (rib). S-shaped, sinuous, flexuous.

simple (peristome). Devoid of lappets or rostrum.

simple (rib). Unbranched.

simple (suture). Not appreciably subdivided.

sinus. Re-entrant curve or notch in any part of peristome.

sipho, siphon. *See* siphuncle.

siphuncle. Narrow longitudinal tube passing through camerae and septa from protoconch to base of body chamber.

spatulate (lappet). Spoon-shaped, stalked, bud-shaped.

sphaerocone. Involute globular shell with small or occluded umbilicus which commonly opens out suddenly along last whorl (as in *Sphaeroceras*).

stria. Minute groove on shell surface, especially on otherwise smooth shell.

strigate. Shell surface finely ridged or furrowed longitudinally (as in *Strigoceras*).

sulcate. With longitudinal groove on venter.

sulcus. Groove on shell surface, usually referring to longitudinal groove on venter.

suspensive lobe. Visible external part of umbilical lobe of suture on exposed part of whorl, comprising portion from which auxiliaries spring.

sutural elements. Major undulations of suture alternately directed forward (adaperturally) as saddles and backward (adapically) as lobes.

suture. Line of junction of septum with walls of shell, visible only when this wall is removed; sometimes termed septal suture, suture line.

tabulate (venter). Truncate or flattened; sometimes termed runcinate (planed off).

tarphycone. *See* serpenticone.

test. Fossil shell substance; material of the shell as opposed to the fossil as an object.

torticone. Shell coiled in irregular 3-dimensional spiral with progressive twisting of conch.

transverse. *See* radial.

tricarinate. Bearing 3 keels on venter.

trifurcate (rib). Dividing into 3 branches.

triplicate. *See* trifurcate.

tubercle. Projection or pimple on shell surface, or on internal mold (cast) commonly representing base of a spine.

umbilical angle. Generally blunt angle between whorl side and umbilical area.

umbilical area. Inner part of whorl on each side, separating umbilical angle from umbilical seam; called umbilical wall if it rises somewhat vertically from spiral plane and umbilical slope if it rises gently.

umbilical border. *See* umbilical angle.

umbilical callus. Plug of test that more or less fills umbilicus.

umbilical edge. *See* umbilical angle.

umbilical lobe. Large primary lobe of suture centered on or near umbilical seam and forming part of both external and internal sutures.

umbilical perforation. Vacant space around axis of coiling and connecting umbilici.

umbilical seam. Helical line of overlap of successive whorls, comprising "line of involution" analogous to suture of gastropods.

umbilical shoulder. *See* umbilical angle.

umbilical suture. *See* umbilical seam.

umbilical width. Diameter of umbilicus measured either between umbilical angles (outside diameter) or between umbilical seams (inside diameter).

umbilicus. External depression on each side of shell centered on axis of coiling, its rim being the umbilical angle or edge.

unipolar. *See* ceratitic.

venter. Peripheral wall of whorl comprising part of shell radially farthest from protoconch; in heteromorphs, the homologous wall.

ventral area. *See* venter.

ventral lappet. *See* lappet.

ventral lobe. Median primary lobe of suture located on venter, external in normally coiled shells and therefore sometimes called external lobe.

ventral saddle. Median saddle of suture located on venter, external in normally coiled shells and therefore sometimes called external saddle.

ventrolateral angle. Angle between venter and whorl side, called shoulder if blunt.

ventrolateral edge (or margin). *See* ventrolateral angle.

virgatotome. Type of ribbing in which 3 to 6 straight secondaries may branch off in succession from forward (adapertural) side of a primary rib (as in *Virgatites*).

volution. *See* whorl.

whorl. Complete turn of shell through 360 degrees.

whorl flank. *See* whorl side.

whorl height. Height of whorl measured at right angles to maximum width, comprising distance from middle of venter to middle of dorsum plus depth of impressed area; in practice, oblique whorl height commonly is used, consisting of distance from umbilical seam to middle of venter.

whorl section. Transverse section of a whorl.

whorl side. Lateral wall of whorl between umbilical seam and venter.

whorl thickness. *See* whorl width.

whorl width. Maximum horizontal distance between points located between ribs or spines on opposite whorl sides.

SUMMARY OF CLASSIFICATION

By W. J. Arkell, W. M. Furnish, Bernhard Kummel, A. K. Miller, O. H. Schindewolf, and C. W. Wright

An outline of the classification of ammonoids as developed by authors working on this group of fossils for the *Treatise* is introduced here for the purpose of summarizing taxonomic relationships, stratigraphic distribution, and numbers of genera and subgenera which now are known in each family-group and higher-rank taxon. Where a single number is recorded, this refers to genera, and where 2 numbers are given, the first indicates genera and the second indicates subgenera (for example, "4; 6" signifies 4 genera and 6 subgenera). The outline furnishes also a convenient means of explicit statement of the authorship of systematic descriptions given in following parts of the volume, which is made by recording with each division the initial letters of the author's name (as A for Arkell, F for Furnish, K for Kummel, M for Miller, S for Schindewolf, and W for Wright).

This section on summary of Classification has been compiled by R. C. Moore from the typescript submitted by the several authors.

Suprageneric Divisions of Ammonoidea[1]

Ammonoidea *(order)* (1,554; 384) (incl. genera of aptychi, 1,570; 384). *L.Dev.-U.Cret.* (A-F-K-M-S-W)
  Anarcestina *(suborder)* (34; 2). *L.Dev.-U.Dev.* (F-M)
    Anarcestaceae *(superfamily)* (16; 2). *L.Dev.-U.Dev.* (F-M)
      Mimoceratidae (4). *L.Dev.-M.Dev.* (F-M)
        Mimoceratinae (1). *L.Dev.-M.Dev.* (F-M)
        Mimosphinctinae (3). *L.Dev.* (F-M)
      Agoniatitidae (3). *L.Dev.-M.Dev.* (F-M)
      Anarcestidae (9; 2). *L.Dev.-U.Dev.* (F-M)
        Anarcestinae (4; 2) *L.Dev.-U.Dev.* (F-M)
        Pinacitinae (5). *L.Dev.-M.Dev.* (F-M)
    Prolobitaceae *(superfamily)* (6). *M.Dev.-U.Dev.* (F-M)
      Prolobitidae (6). *M.Dev.-U.Dev.* (F-M)
        Prolobitinae (3). *M.Dev.-U.Dev.* (F-M)
        Sandbergeroceratinae (3). *U.Dev.* (F-M)
    Pharcicerataceae *(superfamily)* (12). *U.Dev.* (F-M)
      Gephuroceratidae (5). *U.Dev.* (F-M)
      Pharciceratidae (4). *U.Dev.* (F-M)
      Beloceratidae (3). *U.Dev.* (F-M)
  Clymeniina *(suborder)* (30; 5). *U.Dev.* (S)
    Gonioclymeniaceae *(superfamily)* (16; 2). *U.Dev.* (S)
      Hexaclymeniidae (3). *U.Dev.* (S)
      Acanthoclymeniidae (1). *U.Dev.* (S)
      Gonioclymeniidae (5; 2). *U.Dev.* (S)
      Wocklumeriidae (5). *U.Dev.* (S)
      Glatziellidae (2). *U.Dev.* (S)
    Clymeniaceae *(superfamily)* (11; 3). *U.Dev.* (S)
      Clymeniidae (6; 3).*U.Dev.* (S)
      Cyrtoclymeniidae (3). *U.Dev.* (S)
      Rectoclymeniidae (2). *U.Dev.* (S)
    Parawocklumeriaceae *(superfamily)* (3). *U.Dev.* (S)
      Parawocklumeriidae (3). *U.Dev.* (S)
  Goniatitina *(suborder)* (93; 14). *M.Dev.-U.Perm.* (F-M)
    Cheilocerataceae *(superfamily)* (17; 7). *M.Dev.-M.Perm.* (F-M)
      Tornoceratidae (4; 4). *M.Dev.-U.Dev.* (F-M)
      Cheiloceratidae (13; 3). *M.Dev.-U.Perm.* (F-M)
        Cheiloceratinae (3; 3). *U.Dev.* (F-M)
        Raymondiceratinae (1). *U.Dev.* (F-M)
        Sporadoceratinae (3). *U.Dev.* (F-M)
        Imitoceratinae (6). *U.Dev.-M.Perm.* (F-M)
    Agathicerataceae *(superfamily)* (8). *L.Penn.-M.Perm.* (F-M)
      Agathiceratidae (2). *L.Penn.-M.Perm.* (F-M)
      Shumarditidae (4). *U.Penn.* (F-M)
      Perrinitidae (2). *L.Perm.-M.Perm.* (F-M)
    Cyclolobaceae *(superfamily)* (8). *M.Penn.-U.Perm.* (F-M)
      Popanoceratidae (5). *M.Penn.-U.Perm.* (F-M)
        Popanoceratinae (2). *L.Perm.-M.Perm.* (F-M)
        Marathonitinae (2). *M.Penn.-U.Perm.* (F-M)
        Hyattoceratinae (1). *M.Perm.* (F-M)
      Cyclolobidae (3). *M.Perm.-U.Perm.* (F-M)
    Goniatitaceae *(superfamily)* (44; 7). *L.Miss-U.Perm.* (F-M)
      Goniatitidae (22; 7). *L.Miss.-L.Perm.* (F-M)
        Goniatitinae (9). *L.Miss.-M.Penn.* (F-M)
        Neoglyphioceratinae (2). *U.Miss.* (F-M)
        Pericyclinae (2; 7). *L.Miss.-U.Miss.* (F-M)
        Girtyoceratinae (3). *U.Miss.* (F-M)
        Bisatoceratinae (3). *U.Miss.-U.Penn.* (F-M)
        Gonioloboceratinae (3). *M.Penn.-L.Perm.* (F-M)
      Neoicoceratidae (12). *L.Penn.-U.Perm.* (F-M)
      Metalegoceratidae (4). *L.Perm.-M.Perm.* (F-M)
      Schistoceratidae (6). *L.Penn.-L.Perm.* (F-M)
        Schistoceratinae (5). *L.Penn.-L.Perm.* (F-M)
        Welleritinae (1). *M.Penn.* (F-M)

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[1] The group of bactritids, comprising the suborder Bactritina Miller & Furnish, 1954, and component divisions, is excluded from description and discussion in this volume of the *Treatise*, although it has been accepted generally as belonging to the Ammonoidea. By agreement of authors who are working to prepare the *Treatise* text and illustrations for the nautiloid cephalopods, the Bactritina are to be included in Part K.—Editor.

- Adrianitaceae *(superfamily)* (8). *M.Penn.-M.Perm.* (F-M)
  - Adrianitidae (8). *M.Penn.-M.Perm.* (F-M)
    - Adrianitinae (5). *L.Perm.-M.Perm.* (F-M)
    - Dunbaritinae (2). *M.Penn.-U.Penn.* (F-M)
    - Clinolobinae (1). *M.Perm.* (F-M)
- Dimorphocerataceae *(superfamily)* (8). *U.Miss.-M.Perm.* (F-M)
  - Dimorphoceratidae (3). *U.Miss.-U.Penn., ?L.Perm.* (F-M)
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  - Prolecanitaceae *(superfamily)* (9). *U.Dev.-M.Perm.* (F-M)
    - Prolecanitidae (5). *U.Dev.-U.Miss.* (F-M)
    - Prodromitidae (1). *L.Miss.* (F-M)
    - Daraelitidae (3). *U.Miss.-M.Perm.* (F-M)
  - Medlicottiaceae *(superfamily)* (18). *U.Miss.-U.Trias.* (F-M)
    - Pronoritidae (6). *U.Miss.-M.Perm.* (F-M)
    - Medlicottiidae (8). *L.Penn.-L.Trias.* (F-M)
      - Uddenitinae (3). *L.Penn.-U.Penn.* (F-M)
      - Medlicottiinae (5). *U.Penn.-L.Trias.* (F-M)
    - Sageceratidae (4). *L.Trias.-U.Trias.* (F-M)
- Ceratitina *(suborder)* (390; 36). *M.Perm.-U.Trias.* (K)
  - Otocerataceae *(superfamily)* (17; 9). *M.Perm.-L.Trias.* (K)
    - Xenodiscidae (6). *M.Perm.-U.Perm.* (K)
    - Otoceratidae (5; 2). *U.Perm.-L.Trias.* (K)
    - Ophiceratidae (5; 7). *L.Trias.* (K)
    - Dieneroceratidae (1). *L.Trias.* (K)
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      - Gyronitinae (6). *L.Trias.* (K)
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    - Flemingitidae (6). *L.Trias.* (K)
    - Xenoceltitidae (5). *L.Trias.* (K)
      - Xenoceltitinae (3). *L.Trias.* (K)
      - Inyoitinae (2). *L.Trias.* (K)
    - Paranoritidae (6). *L.Trias.* (K)
    - Proptychitidae (8). *L.Trias.* (K)
      - Proptychitinae (6). *L.Trias.* (K)
      - Owenitinae (2). *L.Trias.* (K)
    - Paranannitidae (15). *L.Trias.* (K)
      - Paranannitinae (7). *L.Trias.* (K)
      - Columbitinae (8). *L.Trias.* (K)
    - Ussuriidae (3). *L.Trias.* (K)
    - Hedenstroemiidae (12). *L.Trias.-M.Trias.* (K)
      - Hedenstroemiinae (7). *L.Trias.* (K)
      - Lanceolitinae (1). *L.Trias.* (K)
      - Aspenitinae (3). *L.Trias.* (K)
      - Beneckeinae (1). *L.Trias.-M.Trias.* (K)
    - Kashmiritidae (4). *L.Trias.* (K)
    - Meekoceratidae (10). *L.Trias.* (K)
      - Meekoceratinae (3). *L.Trias.* (K)
      - Arctoceratinae (5). *L.Trias.* (K)
      - Dagnoceratinae (2). *L.Trias.* (K)
    - Noritidae (5). *L.Trias.-M.Trias.* (K)
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    - Tirolitidae (6). *L.Trias.* (K)
    - Dinaritidae (4). *L.Trias.* (K)
    - Hellenitidae (1). *L.Trias.* (K)
    - Acrochordiceratidae (2; 3). *M.Trias.* (K)
    - Beyrichitidae (5; 2). *L.Trias.-M.Trias.* (K)
    - Ceratitidae (16). *M.Trias.* (K)
    - Danubitidae (4). *M.Trias.* (K)
    - Balatonitidae (3). *M.Trias.* (K)
    - Hungaritidae (9). *L.Trias.-U.Trias.* (K)
    - Carnitidae (7). *M.Trias.-U.Trias.* (K)
    - Proteusitidae (1). *M.Trias.* (K)
    - Aplococeratidae (6). *M.Trias.* (K)
  - Clydonitaceae *(superfamily)* (70; 12). *M.Trias.-U.Trias.* (K)
    - Trachyceratidae (8; 6). *M.Trias.-U.Trias.* (K)
    - Clydonitidae (2). *U.Trias.* (K)
    - Clionitidae (8; 4). *U.Trias.* (K)
    - Arpaditidae (14). *M.Trias.-U.Trias.* (K)
    - Heraclitidae (1). *U.Trias.* (K)
    - Lecanitidae (2). *M.Trias.-U.Trias.* (K)
    - Cyrtopleuritidae (4). *U.Trias.* (K)
    - Tibetitidae (10). *M.Trias.-U.Trias.* (K)
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    - Distichitidae (3). *U.Trias.* (K)
    - Choristoceratidae (4; 2). *U.Trias.* (K)
    - Cochloceratidae (1). *U.Trias.* (K)
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    - Tropiceltitidae (6). *U.Trias.* (K)
    - Celtitidae (8). *M.Trias.-U.Trias.* (K)
    - Metasibiritidae (2). *U.Trias.* (K)
    - Haloritidae (29; 2). *U.Trias.* (K)
      - Haloritinae (25). *U.Trias.* (K)
      - Sagenitinae (1; 2). *U.Trias.* (K)
      - Episculitinae (3). *U.Trias.* (K)
    - Didymitidae (30; 2). *U.Trias.* (K)
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    - Lobitidae (6). *M.Trias.-U.Trias.* (K)
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    - Arcestidae (1; 6). *M.Trias.-U.Trias.* (K)
    - Joannitidae (3). *M.Trias.-U.Trias.* (K)
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    - Cladidiscitidae (5). *M.Trias.-U.Trias.* (K)
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    - Ptychitidae (12). *M.Trias.-U.Trias.* (K)
    - Isculitidae (4). *M.Trias.* (K)

- ?Nannitidae (1). *U.Trias.* (K)
- Pinacocerataceae *(superfamily)* (16). *L.Trias.-U. Trias.* (K)
    - Pinacoceratidae (8). *M.Trias.-U.Trias.* (K)
    - Gymnitidae (8). *L.Trias.-U.Trias.* (K)
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    - Phyllocerataceae *(superfamily)* (34). *L.Trias.-U. Cret.* (A-K-W)
        - Ussuritidae (7). *L.Trias.-U.Trias.* (K)
        - Discophyllitidae (4). *U.Trias.* (K)
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            - Phylloceratinae (8). *L.Jur.-U.Cret.* (A-W)
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        - Juraphyllitidae (8). *L.Jur.* (A)
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            - Analytoceratinae (1). *L.Jur.* (A)
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            - Villaniinae (1). *M.Jur.* (A)
            - Alocolytoceratinae (4). *M.Jur.* (A)
        - Nannolytoceratidae (2). *L.Jur.-M.Jur.* (A)
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            - Tetragonitinae (4; 2). *L.Cret.-U.Cret.* (W)
        - Macroscaphitidae (3). *L.Cret.* (W)
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            - Crioceratinae (12). *L.Cret.* (W)
            - Ancyloceratinae (16). *L.Cret.* (W)
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        - Hemihoplitidae (3). *L.Cret.* (W)
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        - Ptychoceratidae (5). *L.Cret.* (W)
        - Hamitidae (5; 3). *L.Cret.-U.Cret.* (W)
        - Baculitidae (6). *L.Cret.-U.Cret.* (W)
        - Anisoceratidae (7) *L.Cret.-U.Cret.* (W)
        - Phlycticrioceratidae (2). *U.Cret.* (W)
        - Turrilitidae (10; 7). *L.Cret.-U.Cret.* (W)
        - Nostoceratidae (11; 2). *U.Cret.* (W)
        - Diplomoceratidae (9; 2). *U.Cret.* (W)
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        - Scaphitidae (13). *L.Cret.-U.Cret.* (W)
            - Scaphitinae (11). *L.Cret.-U.Cret* (W)
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            - Psiloceratinae (8; 3). *L.Jur.* (A)
            - Alsatitinae (8). *L.Jur.* (A)
        - Schlotheimiidae (9). *L.Jur.* (A)
        - Arietitidae (25; 2). *L.Jur.* (A)
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            - Arnioceratinae (3). *L.Jur.* (A)
            - Asteroceratinae (8). *L.Jur.* (A)
            - Cymbitinae (1; 2). *L.Jur.* (A)
        - Oxynoticeratidae (10). *L.Jur.* (A)
        - Echioceratidae (7). *L.Jur.* (A)
    - Eoderocerataceae *(superfamily)* (43; 12). *L.Jur.* (A)
        - Eoderoceratidae (16; 2). *L.Jur.* (A)
            - Xipheroceratinae (4). *L.Jur.* (A)
            - Eoderoceratinae (5; 2). *L.Jur.* (A)
            - Phricodoceratinae (2). *L.Jur.* (A)
            - Coeloceratinae (5). *L.Jur.* (A)
        - Polymorphitidae (9; 2). *L.Jur.* (A)
            - Polymorphitinae (7; 2). *L.Jur.* (A)
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        - Sonniniidae (13; 5). *M.Jur.* (A)
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        - Haploceratidae (9; 2). *M.Jur.-L.Cret.* (A)
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            - Ochetoceratinae (5; 3). *U.Jur.* (A)
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- Phlycticeratinae (1). *M.Jur.* (A)
- Streblitinae (9; 2). *U.Jur.* (A)
- Mazapilitinae (2). *U.Jur.* (A)
- Aconeceratinae (5; 2). *L.Cret.* (W)
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  - Stephanoceratidae (7; 7). *M.Jur.* (A)
  - Thamboceratidae (3). *M.Jur.* (A)
  - Clydoniceratidae (4; 2). *M.Jur.* (A)
  - Sphaeroceratidae (4). *M.Jur.* (A)
  - Tulitidae (7; 2). *M.Jur.* (A)
  - Macrocephalitidae (12; 7). *M.Jur.* (A)
  - Oecoptychiidae (2). *M.Jur.-U.Jur.* (A)
  - Pachyceratidae (2; 6). *M.Jur.-U.Jur.* (A)
  - Mayaitidae (5; 2). *U.Jur.* (A)
  - Kosmoceratidae (7; 10). *M.Jur.* (A)
  - Cardioceratidae (10; 27). *M.Jur.-U.Jur.* (A)
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    - Peltoceratinae (10; 3). *M.Jur.-U.Jur.* (A)
    - Aspidoceratinae (7; 8). *M.Jur.-U.Jur.* (A)
    - Simoceratinae (11). *U.Jur.* (A)
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    - Hauericeratinae (2). *U.Cret.* (W)
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[1] MOORE & SYLVESTER-BRADLEY, in last chapter of Part L, recognize 17 generic units classed as valid.—EDITOR.

PALEOZOIC AMMONOIDEA

By A. K. MILLER, W. M. FURNISH, and O. H. SCHINDEWOLF

CONTENTS

The systematic descriptions of the Clymeniina and its subdivisions, limited to the Upper Devonian, are by O. H. SCHINDEWOLF. Those of the other Paleozoic taxa were prepared by A. K. MILLER and W. M. FURNISH, who, as a matter of expediency, contributed also the text on Triassic medlicotiids and sageceratids. BERNHARD KUMMEL has included a systematic treatment of the Permian constituents of the Otocerataceae together with the Triassic representatives of that superfamily. Thus, the divisions of Ammonoidea occurring near the Paleozoic-Mesozoic boundary have been allocated to authors on a systematic basis rather than a strictly stratigraphic basis.

MORPHOLOGY

The early ammonoids are intermediate between their ancestral nautiloids and ammonites of the Upper Paleozoic and Mesozoic. The latter, in general, are much more specialized in being diverse in form and having complex sutures. Several phylogenetic groups, with fundamental sutural differences, can be recognized in the Paleozoic, and only one of these continued into the Mesozoic. Therefore, more taxonomic significance is attributed to the sutures in the earlier than in later ammonoids. Otherwise, construction of the shells is relatively uniform throughout the order.

PROTOCONCH

The ammonoid shell consists of a small **protoconch** and a much larger **conch,** both of which were calcified and were therefore commonly preserved as fossils. Typically, the conch consists of a circinate spiral tightly coiled about the protoconch, and it is involute, as the whorls are impressed dorsally by the ventral portion of the preceding volution (Fig. 1). However, in a very few of the early members of the group there is an **umbilical perforation.** In rare specimens the coiling is subtriangular or subquadrangular; modifications at maturity are fairly common. For the most part the shells are of modest proportions, with maximum overall measurements of only a few centimeters; the largest Paleozoic forms attained diameters of only about a tenth that of huge Cretaceous species more than 2.5 m. across.

The protoconch, though spheroidal in some primitive ammonoids, is generally ellipsoidal, with its longer axis normal to the plane of coiling. It is distinctly wider than the extreme adapical part of the conch and is therefore rather conspicuous despite its small size. In its adoral portion are located the structures that are antecedent to the siphuncle (Fig. 4).

CONCH

The conch comprises all of the shell except the protoconch. In typical mature individuals it is several volutions in length. It consists of a camerate **phragmocone** and a **body chamber;** presumably the former served as a float, whereas the latter housed almost all of the soft parts of the living animal. The subdivisions of the phragmocone are sometimes called "air chambers" or "gas chambers," but it seems better to use the noncommittal term **camerae** for them. In general, their length increased progressively during ontogenetic development; but when the animal had attained full maturity it tended to form very short camerae, a fact which makes it possible to distinguish mature individuals. The partitions of the conch, which bound each camera adorally and adapically, are termed **septa.** Typically, at least, their peripheral portions are crenulate, presumably to increase the strength of the conch without adding unduly to its weight. A small conchiolin tube, the **siphuncle,** extends from the protoconch to the body chamber.

The ventral portion of the conch of many ammonoids is modified near the adoral end of the 1st volution. In some shells this modification takes the form of a constriction, whereas in others it is an expansion. This feature may be analogous to the so-called nepionic line of modern *Nautilus,* which has been interpreted as indicating the size of the individual when it hatched from the large egg, some 25 mm. in diameter. The embryogeny of *Nautilus* is still not known. However, the apical portion of the test is small in comparison to size of the egg, and presumably the embryonic development takes place within the attached egg capsule. In *Nautilus* there is no counterpart of the ammonoid protoconch, which may have served as an efficient buoying apparatus for a newly hatched animal.

The material of which the shell is composed, the **test,** is rarely if ever preserved in the original condition, but almost certainly it was largely aragonite, as in modern *Nautilus.* It consists of 3 main layers, a thin **periostracum,** a relatively thick **ostracum,** and a thin **hypostracum.** The growth lines and color markings are limited to the outer layer, the periostracum. Characteristically there are fine ridges or nodes (or both) on the surface of the hypostracum, which is therefore commonly designated the **runzelschicht** or "wrinkle-layer." The shell walls are remarkably thin for the most part, and therefore light in weight, suggesting that these animals were active and the shell buoyant. Color markings are unknown on Paleozoic ammonoids but have been recorded on a few Mesozoic forms; longitudinal, transverse, and zigzag bands have been found on nautiloids of various ages. As would be expected of creatures adapted for swimming, the surface of the shell tends to be rather smooth and the **growth lines** are generally fine and not very prominent.

Nevertheless, many ammonoids bear keels, lirae, ribs, nodes, and spines, and such protuberances are more common in the ammonites and the ceratites than in the nautiloids and the primitive ammonoids. Furthermore, in many cases the conch bears transverse **constrictions** which are more prominent on the internal mold than on the exterior of the test and which tend to be more or less parallel to the growth lines and to strengthen the shell. Characteristically they are limited to the phragmocone at maturity, except for an apertural constriction, which reinforces the peristome. In *Agathiceras* the constrictions of the phragmocone are not discernible on the exterior of the test, and they consist exclusively of internal thickenings of the ostracum.

The **shape of growth lines** in most ammonoids can be expressed briefly by a nomenclature propounded by WEDEKIND in 1918 but not widely used. Growth lines that are straight or nearly so on both the lateral and ventral areas of the conch are said to be **linear;** those that form a single broad rounded salient on each of the lateral areas and a sinus on the venter are said to be

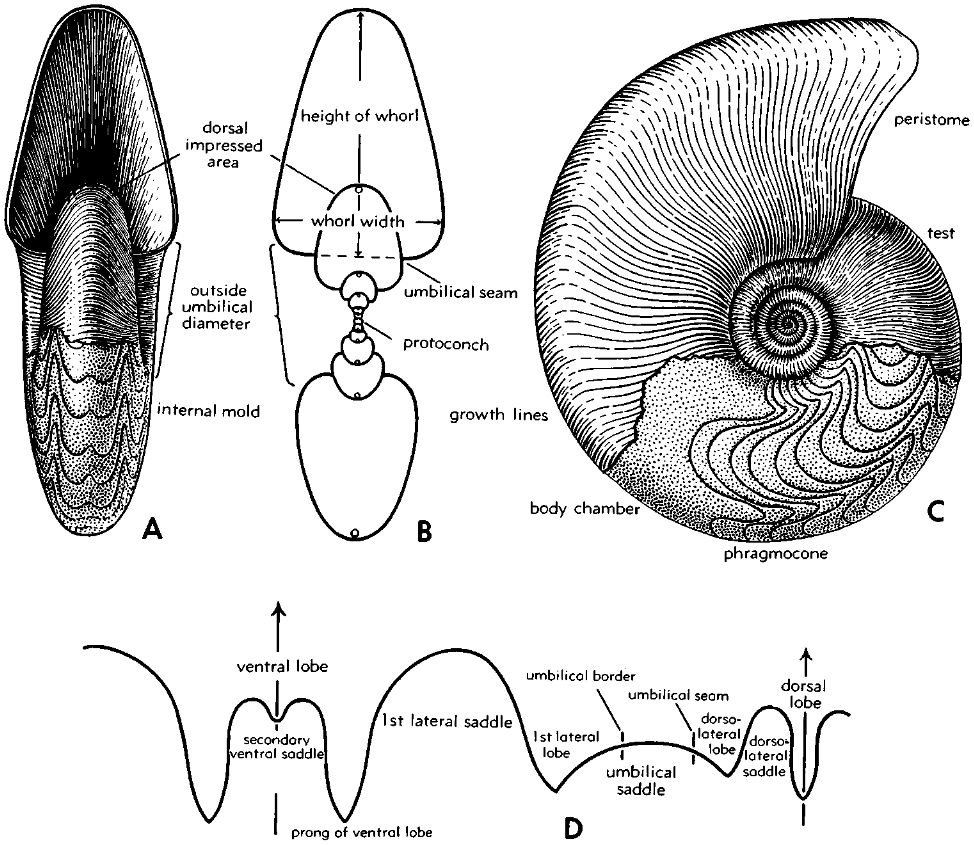


FIG. 1. Diagrammatic ventral *(A)*, cross-sectional *(B)*, and lateral *(C)* views of a typical goniatite, *Manticoceras*, about natural size; and *(D)* enlarged representation of a suture of the same. The upper part of *A* and *C* portrays the exterior of the test and shows the growth lines, whereas the lower part represents the internal mold with the sutures (110).

convex; those that form a single broad sinus on each of the lateral areas and a salient on the venter are said to be **protractive;** and those that form salients on both the umbilical margins and ventrolateral areas of the conch are said to be **biconvex** (Fig. 1*C*). In the last type, the growth lines, of course, form sinuses on the venter and on the median portion of the lateral areas. Biconvex growth lines are comparable to those of *Nautilus* in which the lateral re-entrants of the peristome are designated ocular sinuses as they enable the animal to see when the body is partially retracted.

The **aperture** or **peristome** of the ammonoid conch was not appreciably modified until maturity had been attained, and its shape is indicated by the growth lines. However, during late ontogenetic stages many forms contracted the adoral portion of the conch, and in some cases it was modified greatly by the development of lappets. In many forms the fully mature shell was strengthened by the formation of an adapertural constriction. The development of these modifications at full maturity suggests a change in the living habits of the individual. The presence of constricted apertures or short adoral camerae or both of these features is not indicative of gerontism, as has been believed.

Our knowledge of modifications at maturity in Paleozoic ammonoids is very incomplete. None seem to be present in the Ceratitina or the Prolecanitina. As early as the Devonian, certain of the Anarcestina and Clymeniina showed a tendency toward uncoiling after full maturity was attained. During the late Paleozoic other prominent traits were evolved (Fig. 2). For example, some forms became ellipsoidal (Fig. 2*C,D,E*), and some developed prominent ribs and spines. A few genera (e.g., *Eumorphoceras* and some thalassoceratids) evolved ventrolateral grooves that were associated with apertural lappets. These modifications tended to strengthen the body chamber, protect the soft parts of the animal, lower the center of gravity, and streamline the shell. Many species attained a remarkably uniform size. No differences attributable to sexual dimorphism can be recognized. As in *Nautilus,* neither the rate of growth nor the life span is known, but presumably the individuals attained maturity in a relatively short period of time.

APTYCHI

Aptychi, together with **anaptychi,** are now regarded as ammonoid opercula, though there has been much difference of opinion as to their biologic affinities (Fig. 3). A few of these plates have been found just inside and even closing the aperture of ammonoids, and therefore corresponding to the hood of *Nautilus* and the opercula of certain gastropods. It is readily apparent that they would fit into the apertural portion of the ammonoid shell, for they are more or less cordate in outline. There are 2 general types. Some (anaptychi) are simple arched chitinoid disks. Others (aptychi) consist of a symmetrical pair of calcareous plates, either in juxtaposition or coalesced along a median dorsoventral line. Both anaptychi and aptychi appear in the Devonian but are rare in the Paleozoic and the Triassic. Aptychi are more common in the Jurassic and the Cretaceous; locally they are so abundant that they characterize certain strata. In some of these beds, ammonoid shells are rare, suggesting that, as in the case of certain present-day gastropods, the opercula were more readily preserved. Although some anaptychi and aptychi can be associated with ammonoid genera that are based on conchs, these opercula are generally treated as biologic entities. TRAUTH has published comprehensive studies of them and classified them in form genera, the taxonomic status of which is indefinite. Because of the uncertainties, we are not listing these "genera."

(see facing page)

FIG. 2. Middle Permian ammonoids showing various mature modifications.——*1a,b, Waagenoceras guadalupense* GIRTY, Texas; ×1 (110).——*2a-c, Hyattoceras abichi* GEMMELLARO, Sicily; ×1.25 (24).——*3a,b, Adrianites kingi* GEMM., Sicily; ×1.25 (24).——*4, A. ensifer* GEMM., Sicily; ×1.25 (24).——*5a,b, A. distefanoi* GEMM., Sicily; ×1.25 (24).——*6, Doryceras spinosum* (MILLER), Coahuila; ×2 (110).——*7a,b, Hyattoceras geinitzi* GEMM., Sicily; ×1.25 (24).——*8a,b, Popanoceras scrobiculatum* GEMM., Sicily; ×1 (24). Lappets are portrayed in *3a, 4, 5b;* spines in *6;* flattened venters in *5a, 6, 7a;* an accentuated ventral sinus in *8a.*


1a

Waagenoceras


2b

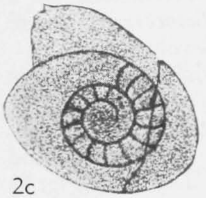

3b

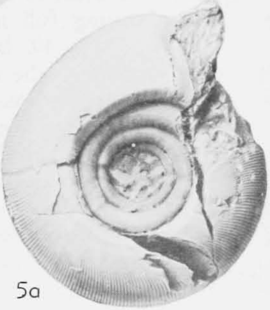
Adrianites

Hyattoceras


1b

Waagenoceras


2c

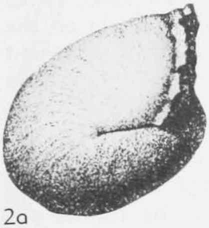

5a


5b

Adrianites


4

Adrianites

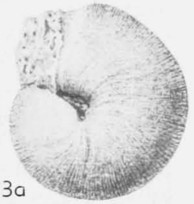

2a

Hyattoceras


7b

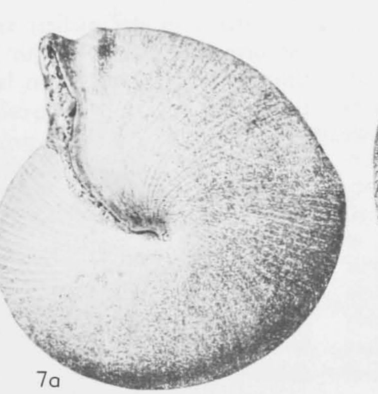

6

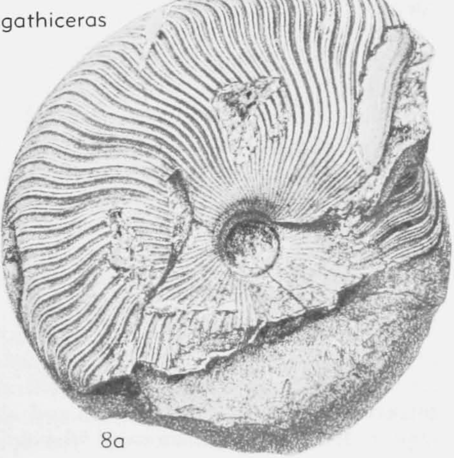
Pseudagathiceras


3a

Adrianites


8b


7a


8a

Popanoceras

Hyattoceras

Popanoceras

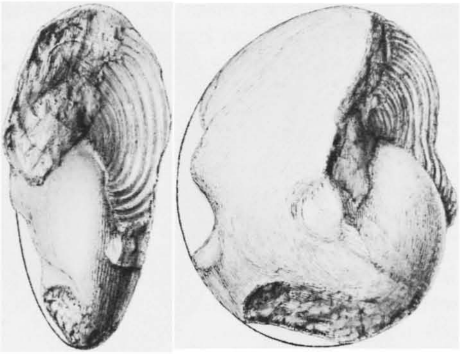


FIG. 3. The aptychus in place in *Manticoceras,* Upper Devonian, Germany, ×1 (21).

BODY CHAMBER

The body chamber is not generally preserved in its entirety, for it bears no such internal supports (septa) as does the phragmocone. Typically its length varies from about half a volution to a little more than a full volution, but in some forms at least the outer one and a half whorls are nonseptate. During ontogenetic development there was a tendency for the relative length of the body chamber to decrease. However, the volume ratio of that chamber to the phragmocone remained fairly constant. Furthermore, forms with a relatively large cross-sectional area had a proportionately short body chamber. It seems clear that the length of this chamber is of only secondary taxonomic value. Traces of the **contact areas** of the shell muscles and possibly aponeurotic bands, comparable to those of modern *Nautilus,* have been observed in some specimens.

SEPTA AND SUTURES

The **septa** were secreted periodically at the adapical end of the body chamber during the development of the individual. Adjacent septa reveal only such differences as were permitted by the growth that took place during the interval between their formation. The septa appear to have been constructed of the same material as the shell walls, to which they were cemented. In at least some forms, 2 **prosepta** (Fig. 4) occur in the extreme adapical portion of the conch. As a general rule these are considerably thicker than the adapical septa, and they appear to be continuous with the spiral shell wall, rather than cemented to it. A small adjacent structure, called a **flange,** is an adapical extension of the shell wall.

The **number of septa** per volution, though variable, tended to increase during ontogenetic development. This tendency was marked in form which, in the 1st volution, had a small number of septa, as few as 4. Tabulation in several late Paleozoic genera has shown that by the 5th to 7th volution the number of septa per volution tended to stabilize at some 15 to 20. However, in many forms, during full maturity, it became as high as 35 to 40, largely because of very close spacing in the adoral quarter-volution of the phragmocone. Nevertheless, in a unique Devonian genus, *Beloceras,* there are as many as 100 septa to a volution.

In the early ammonoids, the septa were convex adapically, much as in the nautiloids. However, in later forms this general shape was obscured by numerous inflections and was even reversed. **Septal diagrams** (Fig. 5) have been employed to show configuration.

The **sutures** (junctions of the septa with the shell wall) are of high taxonomic value. They can be observed readily only on the internal mold. In involute forms, the portion of the suture that extends across the ventral and lateral areas to the umbilical seams is designated the **external suture,** and its continuation across the dorsal impressed area is called the **internal suture** (Fig. 1).

Terminology applied to the **sutural element** varies. However, it is generally agreed that the basis of nomenclature should be ontogenetic development rather than morphologic resemblance. Furthermore, adapical inflections of the sutures are invariably known as **lobes** and adoral inflections as **saddles.**

In many of the earliest ammonoids, the **1st-formed suture** tends to be virtually a simple circle. However, in later representatives, this suture (the so-called **prosuture**) characteristically shows a prominent ventral saddle. The **2nd suture,** which is located close to the 1st, forms a slight ventral lobe (Fig. 6). This lobe is accentuated in the later-formed sutures. The unique shape of the 1st suture does not seem to suggest a phylogenetic relationship to any known form, whereas the remainder of the sutures show a normal progression in complexity.

The closely spaced 1st 2 sutures presumably represent the edges of the prosepta.

During early **ontogenetic development** the sutures characteristically form lobes on the venter, dorsum, and lateral zones, and then in the umbilical regions. All 6 of these lobes appear in certain species as early as the 2nd suture. These 3 pairs are commonly regarded as more or less fundamental, as are also the pair of dorsolateral lobes. The primary lobe on the venter is referred to by some authors as the "siphonal lobe" or the "external lobe," but it seems preferable to designate it the **ventral lobe,** as is commonly done. Similarly, the lobe on the dorsum is best termed the **dorsal lobe,** rather than the "antisiphonal lobe," the "internal lobe," or the "columellar lobe," though all of these are to be found in the literature. In some of the clymenias the ventral lobe is obliterated during early adolescence, and its place is taken by a secondary saddle; but in all other

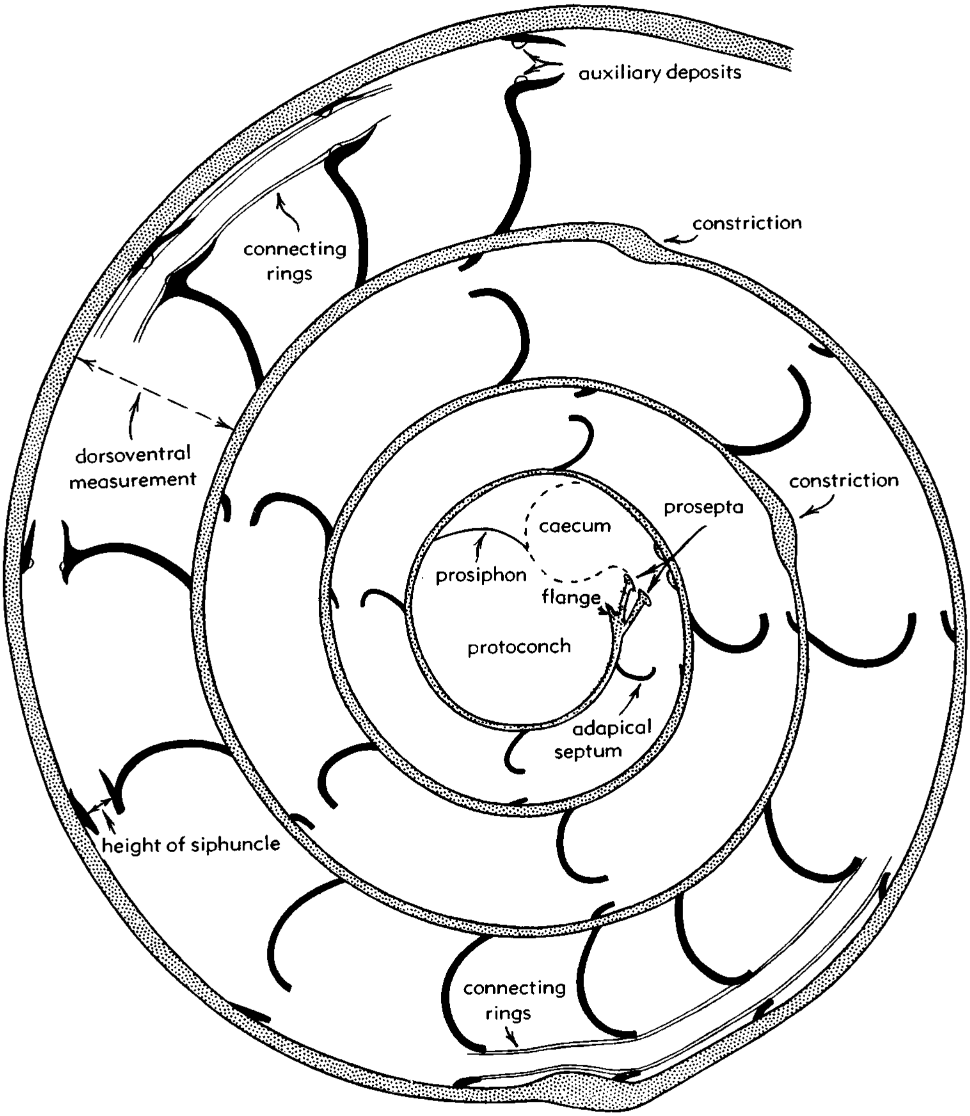


Fig. 4. Enlarged median dorsoventral section of the adapical portion of the shell of a typical ammonoid, showing diagrammatically the various internal structures (54).

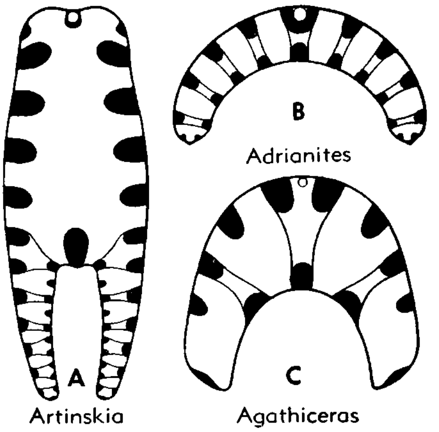


FIG. 5. Septal diagrams of *Artinskia (A), Adrianites (B),* and *Agathiceras (C);* all from Permian of Urals (65,66).

ammonoids it persists and is typically quite conspicuous.

Primary lobes, other than the fundamental ones, were added in the umbilical regions during ontogenetic development, and from there they migrated toward both the venter and dorsum. The saddles adjacent to the ventral lobe, though called "external saddles" by some authors, are better termed the **1st lateral saddles,** and the lobes that follow them the **1st lateral lobes.** The subsequent elements are then the **2nd lateral saddles** and **2nd lateral lobes.** If additional primary inflections are present between the 2nd lateral saddle and the umbilicus, they are termed **auxiliaries.** Prominent inflections that evolved secondarily from ventral and lateral elements of the suture are said to be **adventitious.** Auxiliary and adventitious lobes may be as large as primary lobes (Fig. 11*E*). The elements of the internal suture, other than the dorsal lobe, bear comparable names, but the term **dorsolateral** is employed instead of lateral (Fig. 1).

Ammonoids in which all or most of the lobes of the sutures are undivided are called **goniatites;** those in which the great majority of the lobes (but not the saddles) are serrate are termed **ceratites;** whereas those in which both lobes and saddles are finely subdivided are known as **ammonites.** These terms originated as generic names when classification was primitive. As knowledge advanced, many intermediate forms were found and the latitude allowed genera diminished. Nevertheless, the terms are still useful in a broad way, as well as in a very restricted sense for genera with relatively narrow limits.[1] Goniatites are more or less characteristic of the Paleozoic, ceratites of the Triassic, and ammonites of the later Mesozoic. However, goniatites range well up into the Triassic, typical ceratites (e.g., *Prodromites*) appear as early as the Early Mississippian, and well-developed ammonites (e.g., *Perrinites*) are known from the Middle Permian. Many representatives of all 3 of these categories occur in the Permian (Fig. 7). In the later Mesozoic, most of the ammonites developed extremely complex sutures, but owing to atavism some of them resemble goniatites and ceratites—the last are called **pseudoceratites.**

Commonly ammonoid sutures are portrayed diagrammatically, as shown by Fig. 1*D*. Such drawings are attempts to represent in a single plane a suture pattern that, as a general rule, is developed on a coiled expanding cone which is modified by being impressed dorsally. Accordingly, they are projections, subject to the limitations of the method employed and affected by the preservation of the specimens and the interpretation of the investigator. For these reasons, drawings prepared under different circumstances are not precisely similar, but it is generally possible to compensate for the slight deviations. It should, of course, be kept in mind that a suture is generally portrayed as a line, whereas in reality it is a narrow zone of varying width. Inasmuch as almost all ammonoids are bilaterally symmetrical, the drawings usually depict only a little more than half a suture. However, individuals of certain species may reveal conspicuous asymmetry.

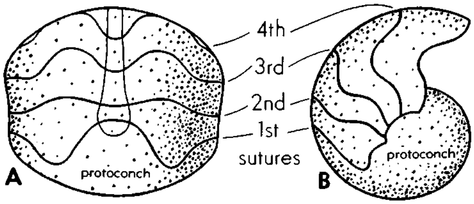


FIG. 6. Ventral *(A)* and side *(B)* views of protoconch and extreme adapical part of ammonoid phragmocone showing early sutures, greatly enlarged (10).

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[1] The generic name *Ammonites,* however, has been suppressed by the International Commission on Zoological Nomenclature (ICZN).—EDITOR.

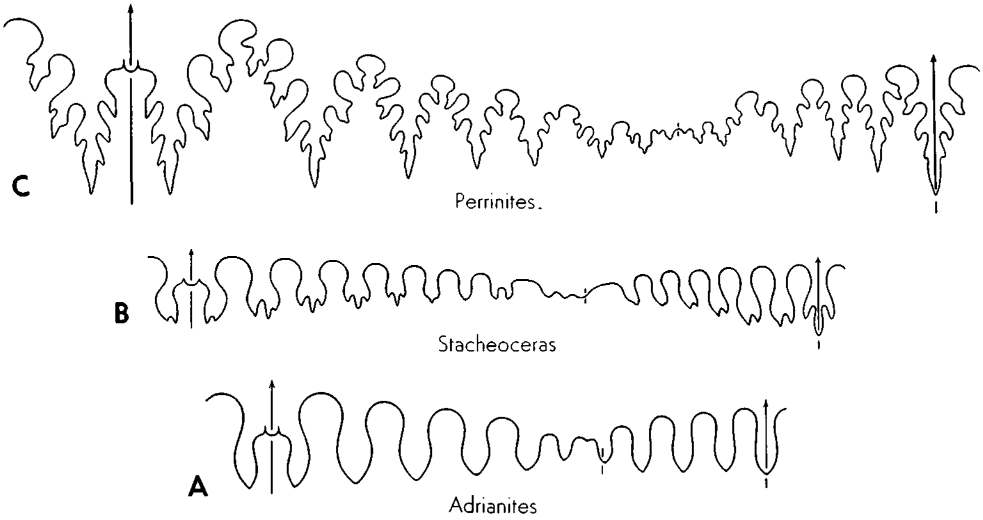

FIG. 7. Diagrams illustrating differences in types of ammonoid sutures, all based on Permian species: *A*, goniatitic, *Adrianites defordi* MILLER & FURNISH, ×1.3; *B*, ceratitic, *Stacheoceras toumanskyae* MILLER-F., ×2; *C*, ammonitic, *Perrinites hilli* (SMITH), ×2.7 (110).

Sutures which consist of many elements developed an **arcuate** shape in some groups of ammonoids. This feature is especially well illustrated by the cyclolobids of the late Paleozoic. In general, the sutures of the cyclolobids became strongly arcuate during late growth stages; peculiarly, however, specimens are known in which the adoral sutures became relatively straight. In some discoidal forms, such as the medlicottiids of the late Paleozoic and early Mesozoic, the amount of curvature of the sutures is greatly accentuated in the extreme adoral portion of the fully mature phragmocone.

Another **modification** of the **sutures** occurred in some forms during late ontogenetic development. When the septa became very closely spaced their edges overlapped at a few points and the details of the adapical portion of the lobes were altered.

In Europe, especially Germany, the configuration of the sutures is frequently expressed by means of **formulas.** In 1905 NOETLING propounded an elaborate system in which each lobe and saddle is designated by a symbol, but his formulas have never been used extensively. WEDEKIND subsequently proposed a simpler system in which a symbol is used for each lobe and the saddles are neglected, it being understood that in every suture lobes are separated by saddles. He used the letter **E** to refer to the ventral (external) lobe, **J** to the dorsal (internal) lobe, **L** to the 1st-formed lateral lobes, **U** to later-formed lateral (umbilical) lobes, and **A** to adventitious lobes. WEDEKIND's system of formulas has been employed rather widely in Germany, and by such authors as SPATH in England, BASSE in France, and RUZHENCEV in Soviet Russia. Unfortunately, most users have injected modifications of their own, so that, except to the specialist, their formulas are scarcely recognizable. For example, the suture formula of the well-known Devonian genus *Tornoceras* (Fig. 47*B*) was written "E. A_I Lu J" by WEDEKIND in 1918, "I L A_I" by SCHINDEWOLF in 1922, and "E A_1 L I" by MATERN in 1931. The use of these formulas obviously makes for brevity, but if they are not readily understandable they do not serve a good purpose.

SIPHUNCLE

The **siphuncle** of the ammonoids is not nearly so variable as is that of the nautiloids, and therefore it is of relatively little taxonomic value. Nevertheless, because at maturity it is marginal in position, it serves to differentiate the ammonoids from the great majority of nautiloids. Furthermore, it has been used to divide the ammonoids into 2 suborders: **Intrasiphonata** (clymenias), with dorsal siphuncles, and **Extrasiphonata,** which includes the host of other ammonoids with ventral siphuncles. In most ammonoids the siphuncle is ventral in position throughout ontogenetic development. However, in a few unrelated forms from various parts of the geologic column, it is subcentral or even subdorsal during early adolescence. The significance of this fact has been variously interpreted, but probably it means only that the position of the siphuncle was unstable during early growth stages.

The **structure of the siphuncle** in earliest ammonoids is reminiscent of that of the orthochoanitic nautiloids, for the **septal necks** or funnels extend adapically from the septa (**retrochoanitic** = "retrosiphonate"), and the connecting rings are small and cylindrical. In the more advanced ammonoids, during early adolescence the septal necks developed adoral projections and eventually became **prochoanitic** ("prosiphonate"), with the septal necks extending adorally. In the late Paleozoic at least, most of the prochoanitic forms developed small **auxiliary deposits** inside of the septal necks (Fig. 4). In a few fossils these deposits seem to consist of simple rings, but in others they are relatively complex. The siphuncle started in the adoral portion of the protoconch as a thin-walled bulbous **caecum.** An associated structure, the **prosiphon,** had the form of a partial cone and served to fasten the caecum to the inside surface of the protoconch. The adapical part of the siphuncle proper is relatively large, whereas in the mature portions of the conch it is invariably small; its cross-sectional area varies from more than a tenth to less than a thousandth that of the conch.

ONTOGENY

The development of the individual can be studied to particular advantage in the ammonoids. The immature portion of the shell was encompassed and therefore protected and preserved.

In general, the inner whorls of ammonoids are relatively broad and smooth. However, in some forms the reverse is the case, and there are inner whorls which are narower and more highly sculptured than the outer. SCHINDEWOLF has concluded that the latter types introduced evolutionary changes and are illustrative of **proterogenetic** development. Furthermore, in 1933 SPATH stated that he is "now accepting it as a matter of course that in ammonites at least ontogeny is not an epitome of phylogeny and that new characters appear in the young and only afterwards encroach on the later whorls."

Ontogenetic studies of the sutures may be of more value, however, for their shape is of basic taxonomic significance. The complexity of the sutures is known to have increased progressively with geologic time. Also, it can be seen that similar ammonoids added elements to their sutures in an orderly fashion. The changes which were first noted in a chronologic sequence of rocks were found to be more or less duplicated in the ontogenetic development of many ammonoids. This fact was noted as early as 1872 by HYATT, and soon BRANCA illustrated it precisely in a variety of materials of various ages. Then KARPINSKY used it as a basis for phylogenies and demonstrated clearly that one could correlate the early sutures with mature ones of ancestral genera. He was followed by HYATT, J. P. SMITH, and a host of others, and the work has continued to the present day. Thus, insofar as ontogenetic development of the sutures is an index, phylogenies have been established for all of the major groups of Paleozoic ammonoids and for some of those of the Mesozoic.

The **ontogeny** is, of course, only an approximation of the **phylogeny,** and the abbreviation of ancestral characters varies inversely with chronologic proximity. That is, in some Mesozoic forms even the most adapical sutures show only an obscure resemblance to Paleozoic ancestors, whereas the next sutures reveal a clear indication of the later progenitors.

Ontogenetic studies can be used for several purposes, as is elucidated by Figures 8-11. The first of these shows how a complicated suture evolved, passing through a sequence of stages that are characteristic of older, more primitive types. In it, *A* is reminiscent of *Goniatites* of the Upper Mississippian, *B* of *Proshumardites* of the Lower Pennsylvanian, *C* of *Shumardites* of the Upper Pennsylvanian, *D* of *Peritrochia* of the Upper Pennsylvanian and Lower Permian, *E* of *Properrinites* of the Lower Permian, and *F* is *Perrinites* of the Middle Permian. Figure 9 shows a comparable relationship in a **phylogenetic series** of forms varying in age from Mississippian to Permian.

Figure 10 offers direct comparison of an ontogenetic and phylogenetic sequence that should become classic. In 1897, J. P. SMITH observed that from ontogenetic studies one

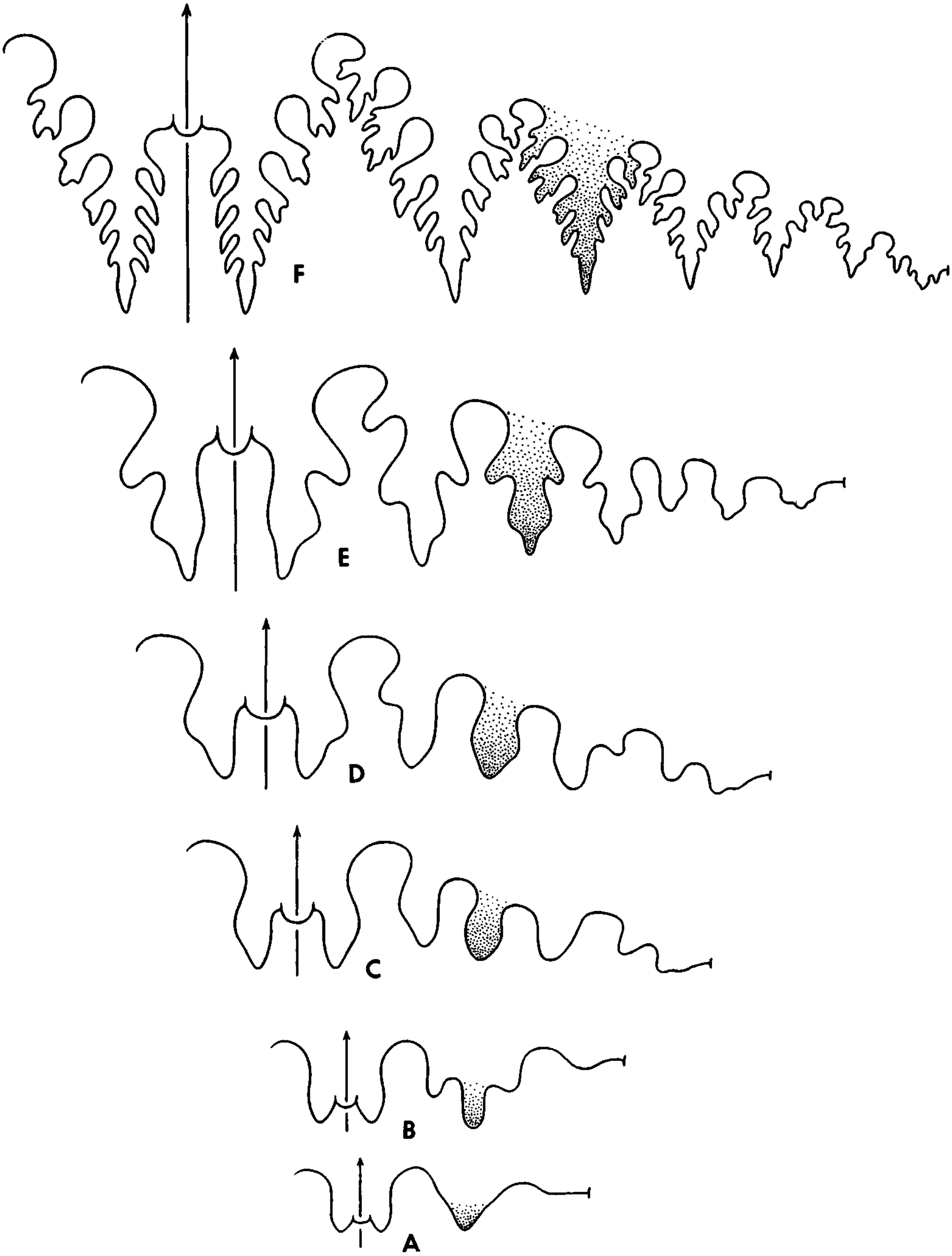

FIG. 8. Ontogenetic development of the external sutures in *Perrinites hilli* (SMITH) from the Permian of Texas.

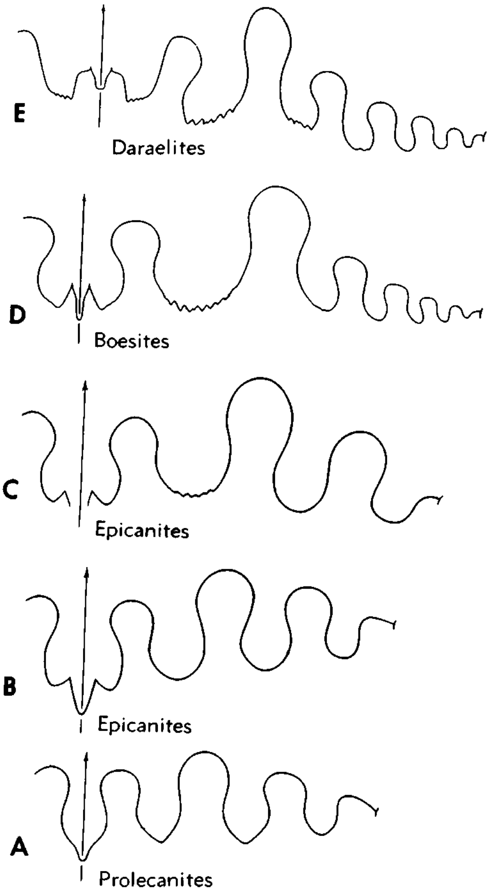

FIG. 9. Phylogenetic series of late Paleozoic ammonoids, showing development of daraelitids from prolecanitids: *A, Prolecanites hesteri* MOORE of the L.Carb., Eng.; *B, Epicanites sandbergeri* (SCHMIDT) of slightly younger Early Carb. age in Algeria; *C, E. culmiensis* (KOBOLD) of German strata of the same general age as *B; D, Boesites texanus* (BÖSE) from the Pennsylvanian of Texas; *E, Daraelites meeki* GEMMELLARO of the Sicilian Permian (110).

"can even prophesy concerning the occurrence of *unknown* genera in certain horizons when he finds their minute counterparts in youthful stages of later forms; in fact he could often furnish just as exact a description of the form as if he had the adult genus before him." In 1929 this same author noted that the medlicottiids, which are almost exclusively Permian, evolved from the Carboniferous *Pronorites,* which, however, he concluded is "separated from its descendants by at least one generic step." He then emphasized that *Uddenoceras* and *Uddenites* of the latest Pennsylvanian are intermediate forms, and by studying their early sutures he clearly demonstrated the nature of the "missing link" between them and *Pronorites.* The very next year that form was found in the Upper Pennsylvanian and was appropriately named *Prouddenites.*

EVOLUTION

Homeomorphy is not particularly rare in Mesozoic ammonoids and is known also in Paleozoic forms (Fig. 11). The range of possible variation in the ammonoid shell was somewhat limited. The causes of such variation were omnipresent and were locally recurrent. Therefore, morphologic types were repeated. Of course no phylogenetic significance is to be attributed to the resemblance of forms that are widely separated stratigraphically or to the similarity of contemporaneous species for which different ancestry can be established by ontogenetic studies.

PALEOECOLOGY

Ammonoids are confined to strata of marine origin. They occur in various lithologic types, but most of those that have been secured are from shales and marls, largely because of a natural concentration and ease of collecting. Locally, however, they are abundant in argillaceous and "detrital" limestones and in sandstones. Clearly a variety of sedimentary environments is represented.

Little or no paleoecologic significance can be attached to the occurrence of isolated specimens; these have been interpreted as individuals that drifted from their normal habitat. Presumably, assemblages containing various growth stages of the same species accumulated *in situ.* Those that consist exclusively of mature individuals probably indicate that the animals had changed their habitat during ontogenetic development. Concentrations of small individuals resulted from mechanical sorting by waves and currents. Concentrations of aptychi are believed to have resulted from the drifting away of the shells after separation from the decaying bodies.

The fact that ammonoid zones can be recognized all over the world indicates that these creatures were typically nektonic and were able to invade a variety of habitats.

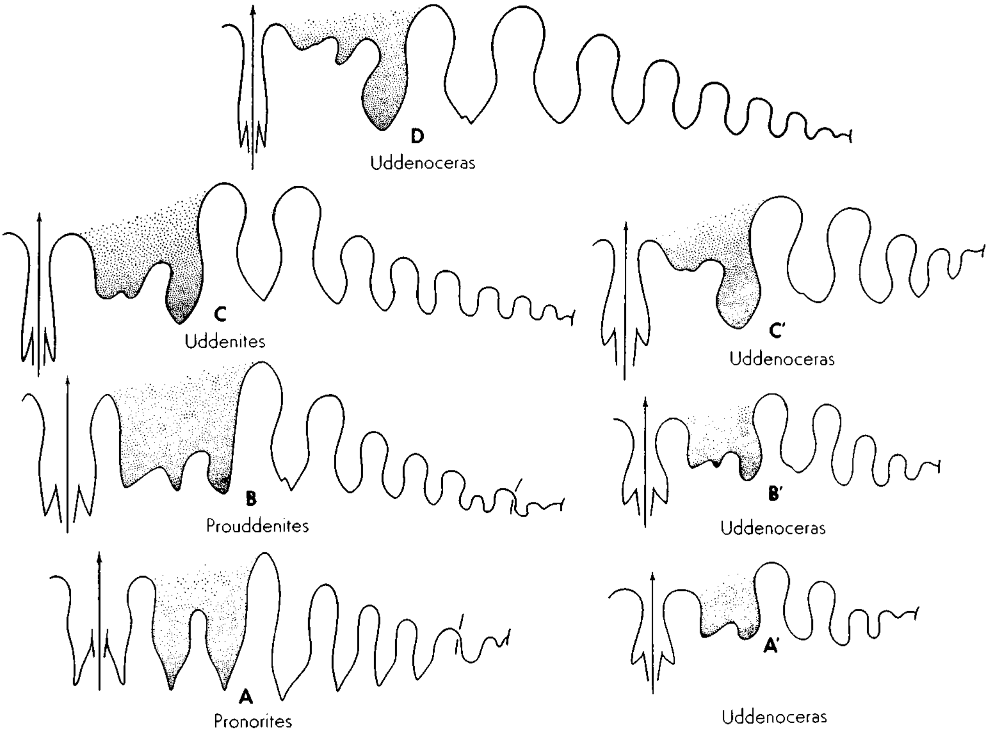

Fig. 10. Phylogenetic and ontogenetic development of *Uddenoceras*. Mature sutures of *Pronorites (A)*, *Prouddenites (B)*, *Uddenites (C)*, and *Uddenoceras (D)*, with comparable ontogenetic stages of *Uddenoceras (A'-C')*; all Pennsylvanian, southwestern United States (110).

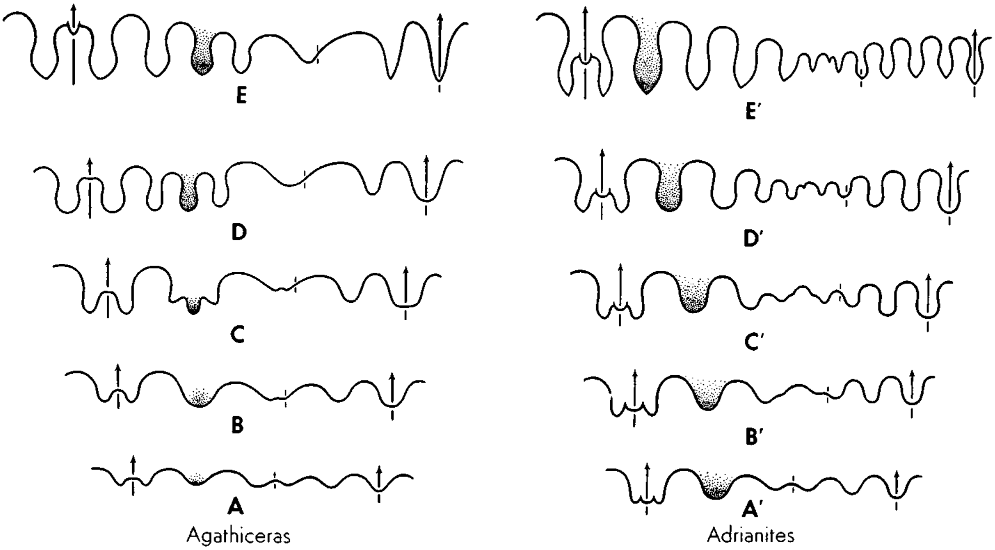

Fig. 11. The ontogenetic development of the sutures in 2 similar but not closely related Permian ammonoids: *A-E*, *Agathiceras uralicum* Karpinsky, from the Ural region, and *A'-E'*, *Adrianites dunbari* Miller & Furnish, from Mexico. The mature external suture of the former contains adventitious lobes; that of the latter, auxiliaries (110).

Certain black shales contain only ammonoids, pelagic foraminifers, and fish remains. The color marks, known on only a very few ammonoids, suggest that they were shallow-water dwellers.

The form and sculpture of the ammonoid shell may be a clue to the living habits. Bilateral symmetry and lenticular shape are presumably to be associated with mobility. Prominent sculpture would tend to retard locomotion, and irregular heteromorphs must have been benthonic.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

Many ammonoid genera seem to have been world-wide in distribution, and closely related, if not identical, species are known to occur on different continents. Even the same phylogenetic series can be recognized in widely separated localities. Furthermore, latitude does not seem to have been a controlling factor in geographic distribution. The often-cited geographic limitations of certain aberrant forms (e.g., *Prodromites*), like the scarcity of Paleozoic ammonoids in South America, is probably more apparent than real. However, peculiarities in distribution do exist; for example, the perrinitids, which are characteristic of the lower half of the Permian in the Americas, are not known in the related faunas of the Ural region, where most associates occur. Within recent years our knowledge of the geographic distribution of ammonoids has increased greatly, and comparable advances can be expected in the future. Some of the most significant faunas known represent "chance discoveries."

TABLE 1. *Distribution of Paleozoic Ammonoidea*

SYSTEM	SERIES	ZONE	TYPE AREA	OTHER IMPORTANT OCCURRENCES
PERMIAN	Upper	*Cyclolobus*	SaltR.	Himal.-Armenia-Madag.-Greenl.
	Middle	*Timorites*	Timor	USA(Tex.)-Mex.(Coah.)
		Waagenoceras	Sicily	Tunisia-Pamirs-China-Timor-USA(Tex.)-Mex.(Coah.)
		Perrinites	USA(Tex.)	Mex.-Colom.-USA-Can.-Urals-Crimea-AsiaM.-Timor.
	Lower	*Properrinites*	USA(Tex.)	USA(Kans.)-Timor-Urals-Crimea
PENNSYLVANIAN	Upper	*Uddenites*	SW.USA	Urals
		Prouddenites	SW.USA	USA(Ohio-Pa.)-Urals
	Middle	*Eothalassoceras*	SW.USA	Turkestan
		Wellerites	SW.USA	USA(Ohio)-Urals
		Owenoceras	SW.USA	?Argentina
	Lower	*Paralegoceras*	USA(Iowa)	SW.USA-C.USA-Peru-N.Afr.-S.China
		Gastrioceras	Eng.	
MISSISSIPPIAN	Upper	*Eumorphoceras*	USA(Okla.)	USA-W.Can.-Alaska-Eu.-N.Afr.
		Goniatites	Eng.	USA-W.Can.-Alaska-Eu.-N.Afr.
	Lower	*Beyrichoceras*	Eng.	Eu.-N.Afr.-C.USA
		Protocanites	USA(Ind.)	USA-Eu.-N.Afr.-Austral.(N.S.W.)
DEVONIAN	Upper	*Wocklumeria*	C.Eu.	N.Afr.
		Clymenia	C.Eu.	N.Afr.
		Platyclymenia	C.Eu.	N.Afr.-W.Austral.-USA(Mont.)
		Cheiloceras	C.Eu.	N.Afr.-W.Austral.-USA(Pa.)
		Manticoceras	USA(N.Y.)	USA-W.Can.-China-Austral.-N.Afr.
	Middle	*Maenioceras*	Ger.	USA-E.Can.-N.Afr.-Austral.
		Anarcestes	Ger.	USA-E.Can.-N.Afr.-Austral.
	Lower	*Mimosphinctes*	Ger.	

Ammonoids are commonly used as **index fossils** because of their widespread occurrence, easy recognition, and stable evolution. Many of the **faunal zones** recognized in intercontinental correlation are based on these fossils.

The oldest known ammonoids are from the European Lower Devonian (Fig. 159). During the remainder of that period, there was a progressive increase in numbers and complexity. In central Europe, where Devonian ammonoids are found in sequence, WEDEKIND and SCHINDEWOLF have shown that 2 or 3 zones can be recognized in the Middle and 5 in the Upper Devonian (Table 1). From the work in Europe, it is known that near the close of the Devonian several groups of ammonoids became extinct and the Goniatitina appeared. This suborder underwent a great development during the late Paleozoic, where it existed alongside the Prolecanitina.

Four ammonoid zones occur in the Mississippian. These are best known in Germany and England. The type Mississippian of central United States contains all 4 zones, but in this region the boundary with the Devonian has not been delimited on the basis of ammonoids. Furthermore, these cephalopods indicate that the dividing line between the American Mississippian and Pennsylvanian is stratigraphically higher than that between the European Lower and Upper Carboniferous.

In the well-known Pennsylvanian of the American Mid-Continent region, 7 ammonoid zones are recognized. Counterparts of most of these have been recorded from Europe, especially in the Ural region. The ammonoids of the Pennsylvanian are gradational with those of both the Mississippian and the Permian, though there are minor differences in stage of evolution.

Near the end of his long career, J. P. SMITH stated that the "Permian was the Golden Age for the ammonoids"; and the many forms known from that period are a culmination of the several Paleozoic stocks and therefore reveal a great amount of fundamental diversity. Five zones are differentiated. Peculiarly, the 1st 4 of these are well developed in 2 widely separate localities, Texas-Coahuila and Timor. The 5th, uppermost, is known from Greenland, Madagascar, and 3 areas in southwestern Asia; and in every place it is directly overlain by an early Triassic zone but is not underlain by older Permian ammonoid-bearing strata.

ORIGIN OF AMMONOIDEA

The ammonoids evolved from the nautiloids, but intermediate forms are not known. The only possible exception is the Bactritina, of uncertain affinities. Typically, ammonoids have a tightly coiled thin shell, a bulbous protoconch, and a small marginal siphuncle. *Bactrites* and its affines possess these characters except for their straight conchs. It has long been contended that they gave rise to the ammonoids by becoming coiled. This belief is conjectural. An alternative hypothesis postulates that the ammonoids arose from some Silurian coiled nautiloids of the general type of *Barrandeoceras*.

The oldest undoubted ammonoids, which are from the Lower Devonian, are reminiscent of certain contemporaneous and slightly older nautiloids. Nevertheless, it may be significant that some of the early Devonian goniatites are loosely coiled, and still others have an umbilical perforation. Thus, it appears that there are no preponderant supporting data to establish the identity of the ancestral form.

CLASSIFICATION

In taxonomy, previous authors have emphasized such characters as the shape of the conch, length of the body chamber, position of the siphuncle, and "ornamentation" of the test, as well as configuration of the sutures. All of these features are important, but in the Paleozoic ammonoids the one listed last is the best guide to phylogenetic relationships. The generic affinities of most forms can be determined from the shape of the sutures alone, a character in which homeomorphy is relatively rare and easily recognized.

Paleozoic ammonoid genera tend to be interpreted rather broadly. This attitude is responsible for the fact that many of the names proposed are placed in synonymy subjectively. In certain unstable groups, liberal subdivision would result in the number of genera being increased 10-fold or more. Some 425 generic names have been proposed for Paleozoic ammonoids, but less than half are now regarded as valid.

A tabular summary of suprageneric divisions permitting a survey of the whole Paleozoic assemblage of ammonoids is given on preceding pages. The number of genera and subgenera in each division is indicated by the figures enclosed in parentheses. A phylogenetic chart (Fig. 12) elucidates the major concepts on which the classification is based.

The suborder Anarcestina is the ancestral stock of the ammonoids. Its most primitive representatives are the Anarcestaceae. Forms with only slightly sinuous sutures, noninvolute whorls, and perforate umbilici are placed in the Mimoceratidae. Those with simple but nevertheless rather sinuous sutures, deeply involute conchs, compressed whorls, and imperforate umbilici are assigned to the Agoniatitidae. Similar forms with low whorls and relatively broad conchs constitute the Anarcestidae. The superfamily is known to be widespread geographically, but stratigraphically it is confined to the Devonian. All of the Lower Devonian representatives are from Europe.

The Prolobitaceae, which consist of a single family, are distinguished primarily by the sutures. These are characterized especially by the fact that the primary lateral lobes evolved on the flanks of the conch and remained there throughout ontogenetic development. The lobes of the sutures are few in number and are undivided. Stratigraphically the superfamily is limited to the latter half of the Devonian, and geographically it seems to be limited to the eastern hemisphere.

The Pharcicerataceae are a small compact unit that is characteristic of the lower Upper Devonian all over the world. The large prominently subdivided ventral lobe distinguishes its members from all other Devonian ammonoids but is superficially similar to that of the late Paleozoic goniatitids. The Beloceratidae evolved from the Gephuroceratidae by the addition of secondary elements to the sutures; the Pharciceratidae constitute a parallel development.

The Clymeniina have long been regarded as quite distinct from other ammonoids because of the dorsal position of their siphuncle. The group is quite diverse, limited to the Upper Devonian and world-wide in distribution. The oldest known representative, *Acanthoclymenia,* is from the lower Upper Devonian of New York, but clymenias are far more rare in the western than in the eastern hemisphere. They are generally regarded as excellent index fossils.

The Goniatitina constitute the great bulk of the Paleozoic ammonoids. During the latter part of the era, members underwent marked evolution and became quite varied. Among them are some of our best index fossils. The basic suture of the group consists of 4 pairs of lobes, though certain of the primitive representatives in the Cheilocerataceae did not attain that stage. The suborder is divided into superfamilies primarily defined by major modifications of basic elements of the sutures.

The Cheilocerataceae consist of 2 families, Tornoceratidae and Cheiloceratidae. In both of these the sutures typically consist of 3 pairs of lobes, of which the external lateral pair arises adventitiously. According to WEDEKIND, the chief difference between the 2 families lies in the fact that in the Tornoceratidae growth lines are biconvex, whereas in the Cheiloceratidae they are convex. Members of the former family are widespread and locally abundant in the Middle and Upper Devonian, whereas cheiloceratids appear in the Upper Devonian, are abundant in the Lower Mississippian, and continue in the Middle Permian. This latter family is the stock that gave rise to the rest of the Goniatitina.

The Agathicerataceae contain forms in which the 3 pairs of external lateral lobes originated as subdivisions of a single pair of goniatitid lateral lobes. The superfamily made its debut in the Early Pennsylvanian, became fairly abundant during the latter part of the same period, and climaxed in the Permian. The Agathiceratidae, the most primitive family of the group, are a long-ranging stable unit. The Shumarditidae are quite variable in both form and occurrence. The Perrinitidae, a closely knit group confined to the first half of the Permian, have the same number of major sutural elements, which, however, are strongly digitate. Members of the last family are among the best index fossils.

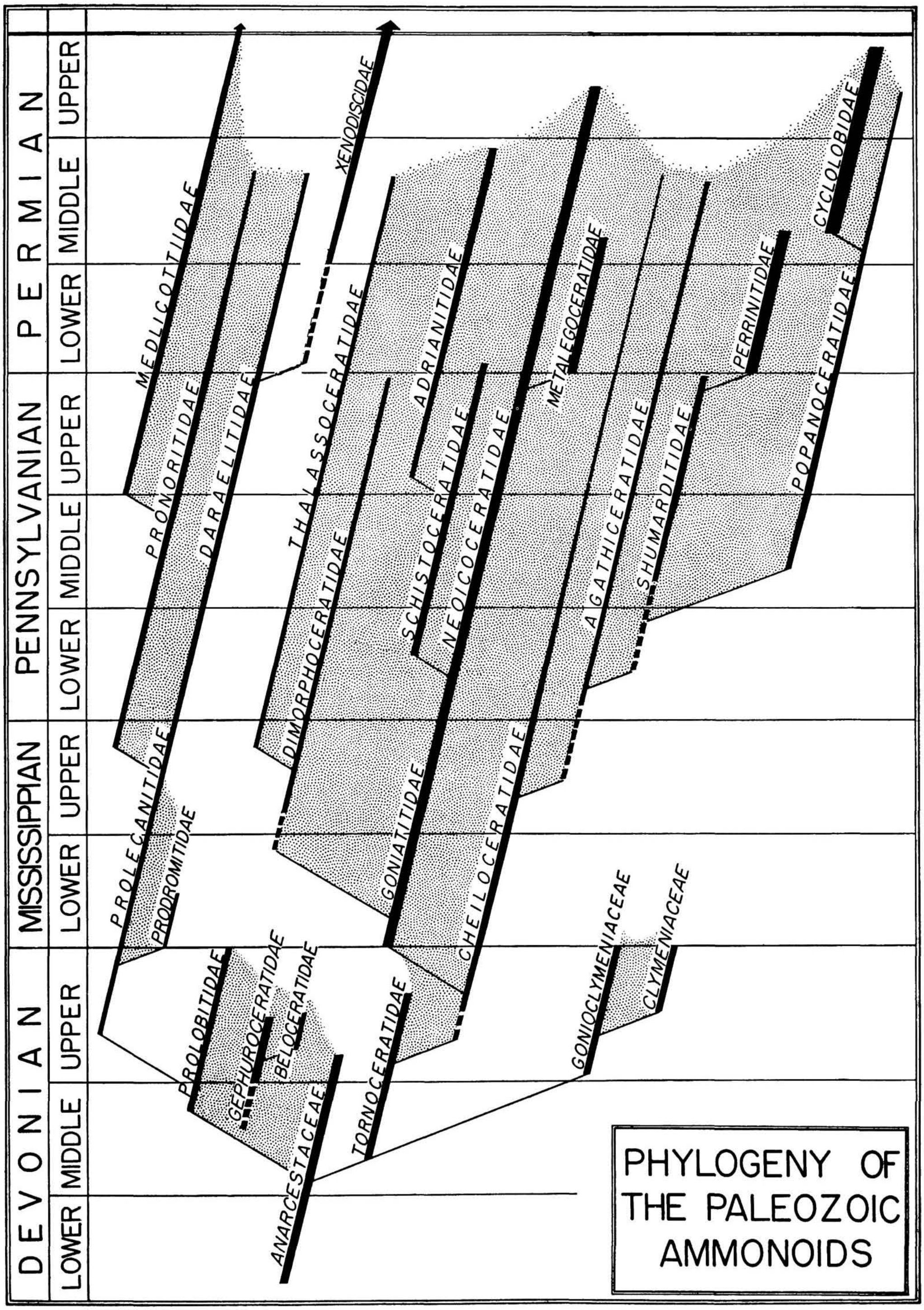
PHYLOGENY OF THE PALEOZOIC AMMONOIDS
PERMIAN
UPPER
MIDDLE
LOWER
PENNSYLVANIAN
UPPER
MIDDLE
LOWER
MISSISSIPPIAN
UPPER
LOWER
DEVONIAN
UPPER
MIDDLE
LOWER
MEDLICOTTIIDAE
XENODISCIDAE
CYCLOLOBIDAE
METALEGOCERATIDAE
PERRINITIDAE
PRONORITIDAE
DARAELITIDAE
THALASSOCERATIDAE
ADRIANITIDAE
SCHISTOCERATIDAE
NEOICOCERATIDAE
AGATHICERATIDAE
SHUMARDITIDAE
POPANOCERATIDAE
DIMORPHOCERATIDAE
PROLECANITIDAE
PRODROMITIDAE
GONIATITIDAE
CHEILOCERATIDAE
GONIOCLYMENIACEAE
CLYMENIACEAE
PROLOBITIDAE
GEPHUROCERATIDAE
BELOCERATIDAE
TORNOCERATIDAE
ANARCESTACEAE

Fig. 12.

The Cyclolobaceae are characterized especially by the possession of a series of auxiliary lobes in their sutures, which generally are ceratitic. Primitive members of both the Popanoceratidae and the Cyclolobidae did not develop many auxiliaries. However, in the more advanced representatives of these families the number of such lobes increased, culminating in *Cyclolobus* of the very late Permian. The Popanoceratidae appeared during mid-Pennsylvanian time and continued to the close of the Permian, being most abundant during the Late Pennsylvanian and the first half of the Permian. In general, these forms are not as good index fossils as are members of the Cyclolobidae, which represent a single phylogenetic sequence that evolved during the latter half of the Permian.

The Goniatitaceae include *Goniatites s.s.* and its affines, plus the neoicoceratids (=gastrioceratids) and their immediate descendants, the metalegoceratids and the schistoceratids. The Goniatitidae have received careful consideration over a period of many years, and the general evolutionary development is well known. Morphological details which are not believed to be particularly significant in other groups seem to have stratigraphic value in this family. The basic suture was evolved during early ontogenetic development, and then the number of lobes remained constant. Neoicoceratids are very widespread and abundant in the Pennsylvanian and the Permian, but, except in a general way, they are of limited stratigraphic value. The Metalegoceratidae, the last of the superfamily to be recognized, consist of a very few genera, which are limited to the Early Permian but are widespread geographically. The schistoceratids, with one exception, illustrate the development of a single evolutionary trend, viz., progressive increase in complexity of the suture by addition of lobes in the umbilical regions. The exception is *Wellerites,* in which a pair of adventitious lobes is developed as prominent subdivisions of the 1st lateral saddles of the external sutures, a difference of subfamily significance.

The Adrianitaceae, which comprise a single family, resemble superficially certain of the Agathicerataceae. However in the adrianitids the sutures, which are goniatitic, consist of elements that are added in the umbilical region. Stratigraphically the superfamily is limited to the upper Pennsylvanian and Permian, but typical forms are known from only the mid-Permian. Geographically, they are of world-wide distribution.

In the Dimorphocerataceae the sutures are basically the same as those of the Goniatitidae, but they are more or less ceratitic. Typical representatives of the Dimorphoceratidae have sutures in which the prongs of the ventral lobe are bifid. However, in advanced forms the lateral lobes of the external sutures are also bifid, and the prongs of the ventral and lateral lobes become more or less serrate. In the thalassoceratids the prongs of the ventral lobe and lateral and umbilical lobes are serrate; however, in the most advanced representative of this group all of the external suture is digitate and the internal lateral lobes are bifid. Both of the families of the Dimorphocerataceae are known from the Mississippian, and they range well up into the Permian.

The Prolecanitina, a relatively small suborder of discoidal Paleozoic ammonoids, are especially important because they are the stock from which all Mesozoic forms arose. Presumably the group evolved from the prolobitids during late Devonian times. With one minor exception, it continued as 3 stable trends through the late Paleozoic. One of these persisted into the Triassic, and another gave rise to the Ceratitina, of which the chief development was in the Triassic. Members of this suborder are of much more stratigraphic value in the Mississippian than in the later Paleozoic. Characteristically the sutures form a large number of lobes, which were added progressively in the umbilical regions. It may be significant that the siphuncle is simple and retrochoanitic, much as in the Devonian goniatites and in the most primitive members of the Goniatitina.

The Prolecanitaceae include the simplest members of the suborder. In the Prolecanitidae the sutures are goniatitic, whereas in the Prodromitidae and the Daraelitidae the lobes are serrate. The Prodromitidae consist of one unique species which is known from only the Lower Mississippian of central United States and which can be thought of as more or less "precocious" because of its similarity to the Ceratitina. The Daraelitidae are the classic example of a small compact group which exhibits an evolutionary trend that continued throughout the late Paleozoic. Both prolecanitids and daraelitids are world-wide in their distribution.

The Medlicottiaceae are widespread and abundant in the late Paleozoic and not particularly rare in the Triassic. However, only one genus crosses the Permo-Triassic boundary. The suture forms a number of subequal auxiliary lobes. Characteristically the 1st lateral lobes are modified; in the Pronoritidae they are bifid, whereas in the Medlicottiidae the changes are much more extreme. Most genera in this superfamily have a long range in the late Paleozoic. It has been thought that the typical medlicottiids evolved from the pronoritids through *Prouddenites, Uddenites, Propinacoceras,* and *Artinskia*. However, it seems more probable that during the late Pennsylvanian, *Artinskia* arose directly from *Uddenites* and then gave rise to *Propinacoceras* in the Permian.

Although the Ceratitina underwent their great development in the Triassic, they are known from strata as old as the Middle Permian. The shape of their conch, the nature of their sutures, and especially the structure of their siphuncle indicate that they arose from the Daraelitidae. The 1st superfamily of the suborder to appear, the Otocerataceae, includes the closely related Permian Xenodiscidae. However, except on a stratigraphic basis, it is difficult to differentiate many xenodiscids from Triassic ophiceratids, though the latter in general are farther advanced. The other 8 superfamilies of the Ceratitina are exclusively Triassic.

SYSTEMATIC DESCRIPTIONS[1]

Suborder ANARCESTINA Miller & Furnish, 1954

Primitive ammonoids with ventral retrochoanitic siphuncle and goniatitic sutures having a variable number of lobes. Some have only the basic minimum 3 or 4 lobes, whereas others possess auxiliaries or adventitious lobes or both. *L.Dev.-U.Dev.*

Superfamily ANARCESTACEAE Steinmann, 1890

[*nom. transl.* Miller & Furnish, 1954 (*ex* Anarcestinae Steinmann, 1890)]

Open umbilicus and sutures with small V-shaped ventral lobe. Characteristically, sutures form only 3 or 4 lobes, with all but ventral one rounded; but advanced representatives have 6 or even 8 lobes (73). *L. Dev.-U.Dev.*

Family MIMOCERATIDAE Steinmann, 1890

[*ex* Mimoceratinae]

Discoidal conch, whorls not impressed dorsally, with large umbilical perforation. Sutures form 3 lobes, a V-shaped ventral, and shallow laterals (19, 73). *L.Dev.-M.Dev.*

Subfamily MIMOCERATINAE Steinmann, 1890

No prominent sculpture; whorls in contact (19, 73). *L.Dev.-M.Dev.*

Gyroceratites Meyer, 1831 [**G. gracilis* Bronn, 1835] [=*Aphyllites* Mojsisovics, 1882; *Mimoceras* Hyatt, 1884]. *L.Dev.-M.Dev.,* Eu.-Fr.N.Afr.-SE. Austral.——Figs 13*A;* 14. **G. gracilis,* M.Dev., Ger.; enlarged (73).

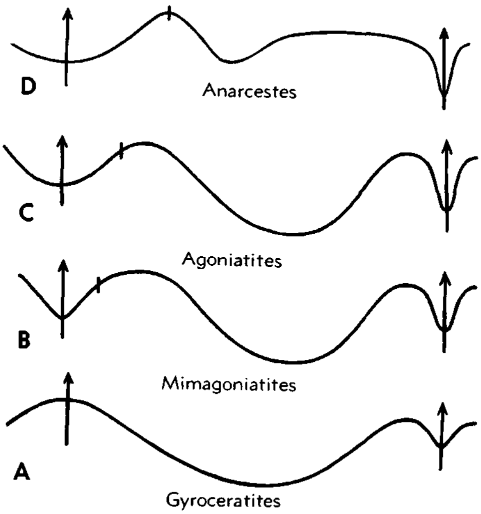

Fig. 13. Sutures of *Gyroceratites (A), Mimagoniatites (B), Agoniatites (C),* and *Anarcestes (D)* (110).

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[1] Miller & Furnish prefer to omit information concerning various sorts of nomenclatural alteration of family-group taxa and statement of synonymies applicable to these taxa because the preparation of such records would require too great labor and consumption of time, particularly in view of the inadequacy of literature readily at hand. Accordingly, only a few nomenclatural annotations are given and generally these do not specify authors and dates of original publication relating to altered family-group names.

Also, type species of genera and subgenera of Paleozoic ammonoids (other than Clymeniina), which are indicated invariably as defined by original designation, may include several established by subsequent designation (SD), for the manner of fixing type species has not been investigated comprehensively.—Editor.

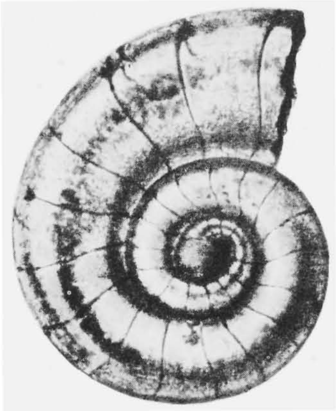

FIG. 14. *Gyroceratites gracilis* BRONN, M.Dev., Ger.; enlarged (73).

Subfamily MIMOSPHINCTINAE Erben, 1953

Characterized by prominent ribs that extend across the venter (19). *L.Dev.*

Mimosphinctes EICHENBERG, 1931 [**M. tripartitus*]. Whorls in contact; ribs bifurcate ventrally (19, 73). *L.Dev.*, Ger.——FIG. 15. **M. tripartitus;* ×2 (104).

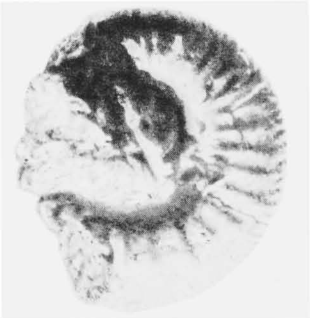

FIG. 15. *Mimosphinctes tripartitus* EICHENBERG, L. Dev., Ger.; ×2 (104).

Anetoceras SCHINDEWOLF, 1934 [**Cyrtoceratites arduennensis* STEININGER, 1853]. Loosely coiled with whorls not in contact, ribs prominent (19, 74). *L.Dev.*, Ger.

Paleogoniatites HYATT, 1900 [**Gon. lituus* BARRANDE, 1865]. Whorls subcircular and in contact, ribs moderately prominent. Sutures nearly straight laterally (1, 19,73). *L.Dev.*, Czech.——FIG. 16. **P. lituus* (BARRANDE); ×2 (1).

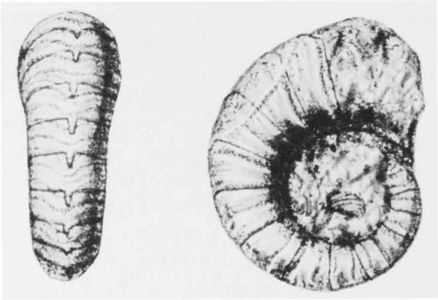

FIG. 16. *Paleogoniatites lituus* (BARRANDE), L.Dev., Czech.; ×2 (1).

Family AGONIATITIDAE Holzapfel, 1899

[= Agoniatitides HAUG, 1898 (invalid vernacular name)]

Conch discoidal, with moderate umbilici and biconvex growth lines. Sutures with small ventral and broad lateral and dorsal lobes (46, 73). *L.Dev.-M.Dev.*

Agoniatites MEEK, 1877 [**Gon. vanuxemi* HALL, 1879]. Imperforate umbilicus. Sutures form 4 lobes (46, 73). *?L.Dev.-M.Dev.*, widespread in Eurasia-N.Afr.-Austral.-N.Am.——FIGS. 17; 18. **A. vanuxemi* (HALL), M.Dev., N.Y.; 17,×0.3; 18, ×0.7 (107).——FIG. 13*C*. *A. costulatus* (D'ARCHAIC & DE VERNEUIL), M.Dev., Ger.; enlarged (73).

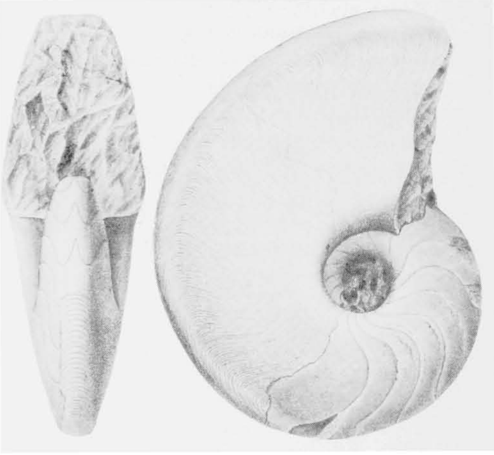

FIG. 17. *Agoniatites vanuxemi* (HALL), M.Dev., N.Y.; ×0.3 (107).

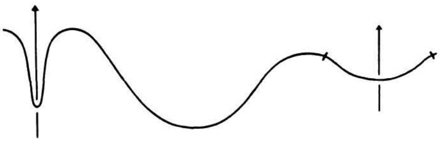

FIG. 18. Suture of *Agoniatites vanuxemi* (HALL), M. Dev., N.Y.; ×0.7 (107).

Mimagoniatites EICHENBERG, 1930 [**Gon. zorgensis* ROEMER, 1866]. Like *Agoniatites* but umbilicus perforate (19, 73). *L.Dev.-M.Dev.*, Ger.-N.Afr.——FIG. 13*B;* 19. **M. zorgensis* (ROEMER), L. Dev., Ger.; 13*B*, enlarged; 19, ×7.5 (73).

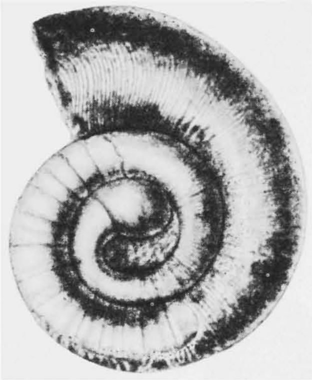

Fig. 19. *Mimagoniatites zorgensis* (Roemer), L. Dev., Ger.; ×7.5 (73).

Paraphyllites Hyatt, 1900 [**Gon. tabuloides* Barrande, 1865]. Like *Agoniatites* but suture with small umbilical lobe (1, 73). *M.Dev.,* Czech.-Turkey-N.Afr.——Fig. 20. **P. tabuloides* (Barrande), Czech.; 20, ×0.7 (1).

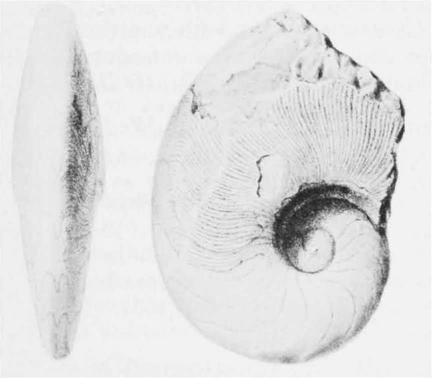

Fig. 20. *Paraphyllites tabuloides* (Barrande), M. Dev., Czech.; ×0.7 (1).

Family ANARCESTIDAE Steinmann, 1890

[*ex* Anarcestinae Steinmann, 1890]

Like Agoniatitidae but characteristically whorls broader and 1st lateral lobes appear in umbilical region rather than in lateral areas (73). *L.Dev.-U.Dev.*

Subfamily ANARCESTINAE Steinmann, 1890

Subglobular to thickly discoidal, widely umbilicate conchs. Sutures form 4 lobes (73). *L.Dev.-U.Dev.*

Anarcestes Mojsisovics, 1882 [**Gon. plebeius* Barrande, 1865] [=*Clarkeoceras* Wedekind, 1918]. Umbilicus perforate. Suture with lateral lobe variable in size and position (73, 100). *L.Dev.-M.Dev.*

A. (Anarcestes). Lateral lobe small and near umbilical shoulder. *L.Dev.-M.Dev.;* widespread Eurasia-N.Afr.——Fig. 21. **A. (A.) plebeius* (Barr.), M.Dev., Czech.; ×1 (117).——Fig. 13*D, A. (A.) lateseptatus* (Beyrich), M.Dev., Ger.; enlarged (73).

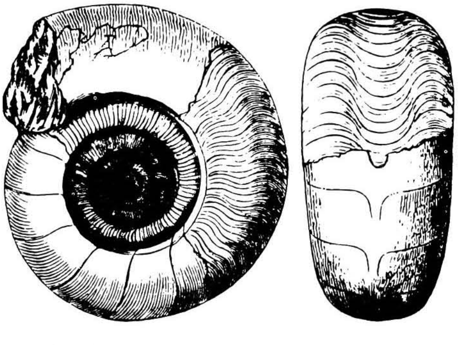

Fig. 21. *Anarcestes (Anarcestes) lateseptatus plebeius* (Barrande), M.Dev., Czech.; ×1 (1).

A. (Latanarcestes) Schindewolf, 1933 [**Am. noeggerati* von Buch, 1832]. Lateral lobe large and on lateral area. *M.Dev.;* Ger.-Czech.

Subanarcestes Schindewolf, 1933 [**S. macrocephalus*]. Conch subglobular, with imperforate umbilicus. Sutures as in typical *Anarcestes* (73). *M.Dev.,* Ger.——Fig. 25*A.* **S. macrocephalus;* enlarged (73).

Werneroceras Wedekind, 1918 [**Gon. ruppachensis* Kayser, 1879]. Like *Subanarcestes* but lateral lobe of suture on lateral area (46, 73, 100). *L.Dev.-U.Dev.,* Eu.-N.Afr.-E.USA.——Fig. 22. *W. ruppachense* (Kayser), M.Dev., Ger.; *A,B,* ×1 (108); *C,* ×1.5 (100).——Fig. 22*D. W. plebeiforme* (Hall), M.Dev., NY.; ×1 (107).

Sellanarcestes Schindewolf, 1933 [**Gon. wenkenbachi* Kayser, 1884]. Like *Werneroceras* but suture with secondary dorsal saddle (19, 73). *L.Dev.-M. Dev.,* Ger.

Subfamily PINACITINAE Schindewolf, 1933

[=Pinnacitidae Hyatt, 1900 (invalid name *ex Pinacites*)]

Subdiscoidal to lenticular conch with narrow imperforate umbilicus. Sutures from 6 to 10 lobes. *L.Dev.-M.Dev.*

Pinacites Mojsisovics, 1882 [**Gon. jugleri* Roemer, 1843]. Lenticular conch with acute venter. Sutures with 6 lobes and narrowly rounded 1st lateral saddle (73, 100). *M.Dev.,* Ger.-Czech.——Fig. 23. **P. jugleri* (Roemer), Ger.; ×0.7 (111).

Parodicerellum Strand, 1929 [**Tornoceras convolutum* Holzapfel, 1895] [=*Parodiceras* Wedekind, 1913 (*non* Hyatt, 1884); *Holzapfeloceras* Miller, 1932]. Like *Pinacites* but with wider conch and rounded venter (73). *M.Dev.,* Ger.

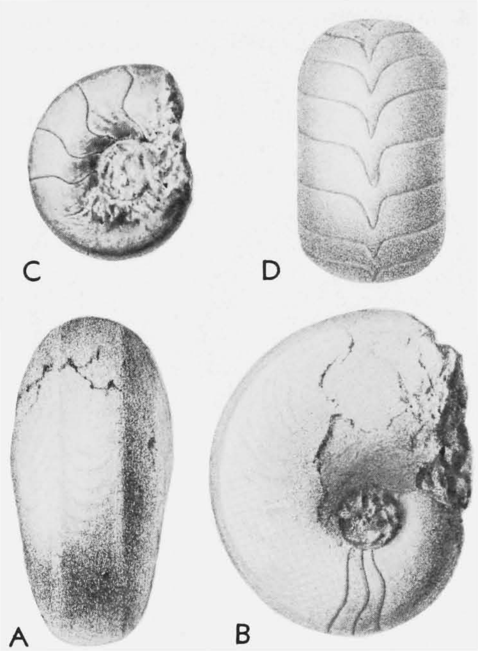

FIG. 22. *Werneroceras. A-C, W. ruppachense* (KAYSER), M.Dev., Ger.; *A,B,* ×1 (108); *C,* ×1.5 (100). *D, W. plebeiforme* (HALL), M.Dev., N.Y.; ×1 (107).

Wedekindella SCHINDEWOLF, 1928 [**Gon. retrorsus brilonensis* KAYSER, 1872]. Like *Parodicerellum* but suture with secondary dorsal saddle (73). *M. Dev.,* Ger.

Foordites WEDEKIND, 1918 [**Aphyllites occultus platypleura* FRECH, 1889]. Like *Parodicerellum* but flattened laterally and ventrally, and with ventrolateral sulci (73, 100). *M.Dev.,* Ger.

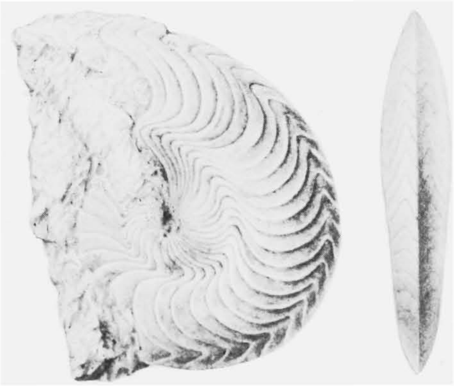

FIG. 23. *Pinacites jugleri* (ROEMER), M.Dev., Ger.; ×0.7 (111).

FIG. 24. *Maenioceras terebratum* (SANDBERGER & SANDBERGER), M.Dev., Ger.; ×1.5 (68).

Maenioceras SCHINDEWOLF, 1933 [**Gon. terebratus* SANDBERGER & SANDBERGER, 1851] [=*Maeneceras auctt.* (*non* HYATT, 1884)]. Like *Foordites* but suture with 10 lobes (73). *M.Dev.,* Eurasia-N.Afr.-?W.Austral.——FIG. 24. **M. terebratum* (SANDB.-S.), M.Dev., Ger.; ×1.5 (68).

Superfamily PROLOBITACEAE Wedekind, 1913

[*nom. transl.* MILLER & FURNISH, 1954 (*ex* Prolobitidae WDKD., 1913)]

Goniatitic sutures with undivided ventral lobe and primary lobes introduced in umbilical region (100). *M.Dev.-U.Dev.*

Family PROLOBITIDAE Wedekind, 1913

Characters of superfamily. *M.Dev.-U.Dev.*

Subfamily PROLOBITINAE Wedekind, 1913

[*ex* Prolobitidae WDKD., 1913]

Conch subglobular to subdiscoidal, with moderate to closed umbilicus. Sutures with no auxiliaries (41,68,96,100). *M.Dev.-U. Dev.*

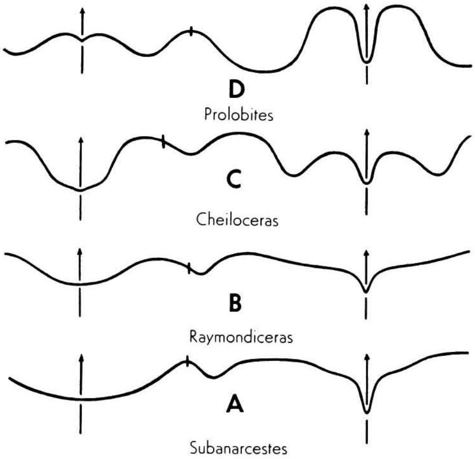

FIG. 25. Sutures of *Subanarcestes (A), Raymondiceras (B), Cheiloceras (C), and Prolobites (D)* (110).

FIG. 26. *Sporadoceras* and *Prolobites*. *A*, *S. biferum* (PHILLIPS), U.Dev., Ger.; ×1 (68). *B,C*, *P. delphinus* (SANDBERGER & SANDBERGER), Ger.; ×1 (68).

Prolobites KARPINSKY, 1885 [**Gon. bifer delphinus* SANDB.-S., 1851]. Conch subglobular, with closed umbilicus. Suture forms 6 lobes, lateral ones rounded (68,100). *U.Dev.*, Eu.-N.Afr.——FIGS. 25*D*; 26*B,C*. **P. delphinus* (SANDB.-S.), Ger.; 25*D*, enlarged (73); 26*B,C*, ×1 (68).

Sobolewia WEDEKIND, 1913 [**Gon. cancellatus* D'ARCHIAC & DE VERNEUIL, 1842]. Conch thickly subdiscoidal; with small to closed umbilicus. Suture forms 4 lobes, lateral ones shallow and rounded (100). *M.Dev.*, Ger.-N.Afr.

Clymenoceras SCHINDEWOLF, 1937 [**C. insolitum*]. Like *Prolobites* but with moderate umbilicus and suture with undivided dorsal saddle. *U.Dev.*, Ger.

Subfamily SANDBERGEROCERATINAE Miller, 1938

Conch discoidal, with transverse ribs, umbilicus large. Sutures form auxiliaries except in primitive forms (46). *U.Dev.*

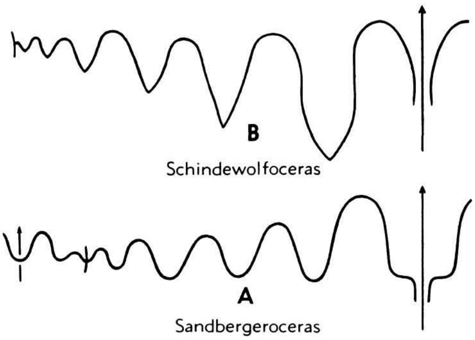

FIG. 27. Sutures of *Sandbergeroceras* (*A*) and *Schindewolfoceras* (*B*) (110).

Sandbergeroceras HYATT, 1884 [**Gon. tuberculosocostatus* SANDB.-S., 1850] [=*Triainoceras* HYATT, 1884 (*Triaenoceras auctt.*)]. Sutures form gradational series of rounded lobes and saddles, few auxiliaries (21,46,68). *U.Dev.*, Ger.-N.Y.——FIGS. 27*A*; 28. **S. tuberculosocostatum* (SANDB.-S.), Ger.; 27*A*, enlarged; 28, ×1 (68).

Pseudarietites FRECH, 1902 [**P. silesiacus*] [=*Pseudoarietites auctt.*]. Like *Sandbergeroceras* but sutures without auxiliaries (22). *U.Dev.*, Ger.

Schindewolfoceras MILLER, 1938 [**Gon. chemungensis* VANUXEM, 1842]. Like *Sanderbergoceras* but sutures with smaller ventral lobe and more auxiliaries (46). *U.Dev.*, N.Y.——FIG. 27*B*. **S. chemungensis* (VANUXEM); ×2 (107).

FIG. 28. *Sandbergeroceras tuberculosocostatum* (SANDBERGER & SANDBERGER), U.Dev., Ger.; ×1 (68).

Superfamily PHARCICERATACEAE Hyatt, 1900

[*nom. transl.* MILLER & FURNISH, herein (*ex* Pharciceratidae HYATT, 1900)]

Conch subdiscoidal to lenticular, umbilicus moderate to large, growth lines biconvex, no prominent sculpture. Sutures with large divided ventral lobe (22,46,68,100). *U.Dev.*

Family GEPHUROCERATIDAE Frech, 1901

[*nom. correct.* proposed MILLER & FURNISH, 1955 (*pro* Gephyroceratidae FRECH, 1901) ICZN pend.] [=Manticoceratidae WEDEKIND, 1918]

Sutures with large bifid ventral lobe and characteristically few or no auxiliaries (100). *U.Dev.*

Manticoceras HYATT, 1884 [**Gon. simulator* HALL, 1874] [=*Gephuroceras* HYATT, 1884 (*Gephyroceras* AUCTT.); *Crickites* WEDEKIND, 1913]. Conch subdiscoidal to lenticular, umbilicus moderate to large. Sutures form 6 lobes (46,100). *U. Dev.*, widespread in N.Am.-Eurasia-N.Afr.-W. Austral.——FIGS. 29; 30*C*. *M. sinuosum* (HALL),

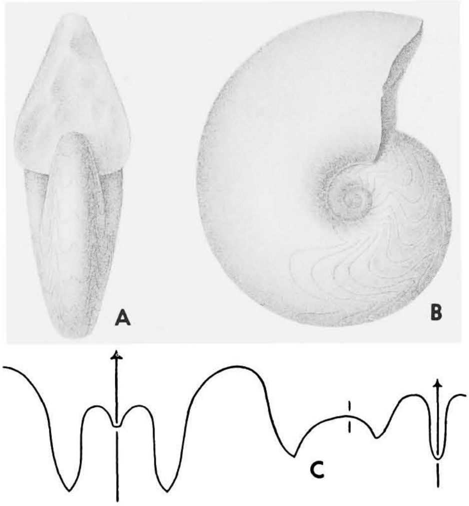

FIG. 29. *Manticoceras sinuosum* (HALL), U.Dev., N.Y.; *A,B*, ×0.5; *C*, enlarged (12).

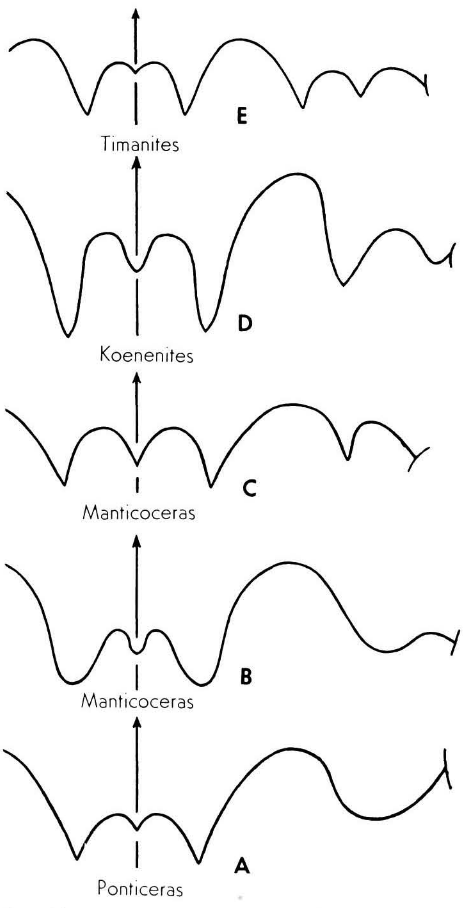

FIG. 30. Sutures of *Ponticeras (A), Manticoceras (B,C), Koenenites (D), and Timanites (E)* (110).

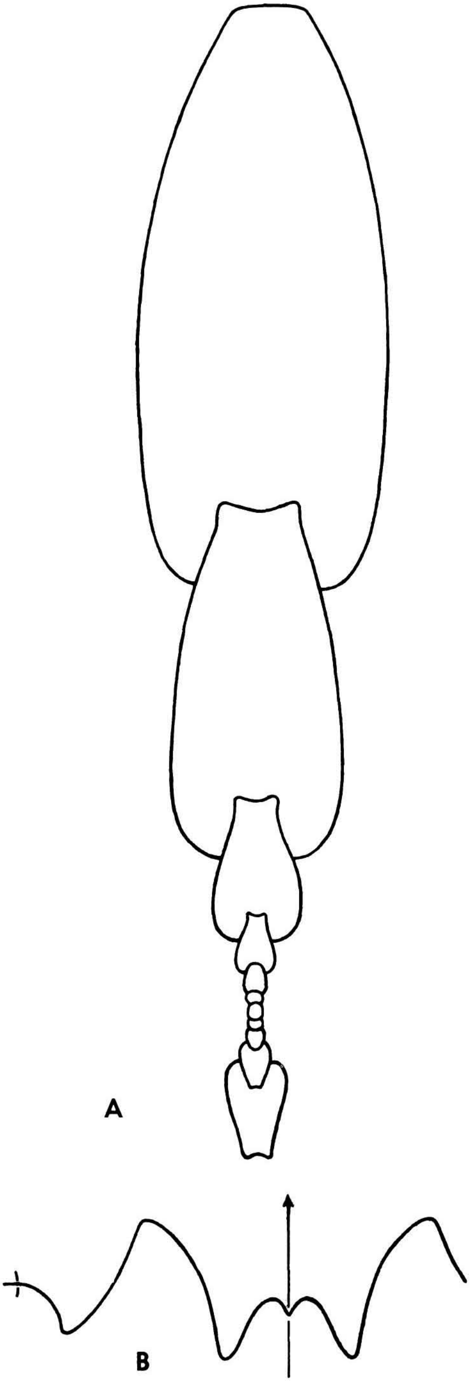

FIG. 31. *Probeloceras lutheri* (CLARKE), U.Dev., N.Y.; *A*, enlarged; *B*, ×5 (12).

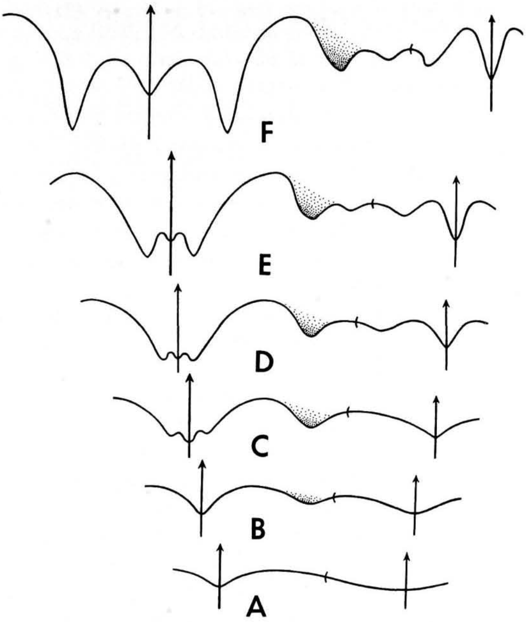

FIG. 32. Ontogeny of sutures in *Koenenites cooperi* MILLER, U.Dev., Mich.; *A-E*, enlarged; *F*, ×2 (46).

N.Y.; 29*A,B*, ×0.5 (12); 29*C*, enlarged (12); 30*C*, ×1 (107).——FIGS. 30*B*; 35*A*. **M. simulator* (HALL), N.Y.; both ×2 (107).

Ponticeras MATERN, 1929 [**Am. aequabilis* BEYRICH, 1837]. Like *Manticoceras* but with wider umbilici and more primitive sutures which form only 4 distinct lobes (46). *U.Dev.*, Eu.-N.Afr.-USA.——FIG. 30*A*. **P aequabilis* (BEYRICH), Ger.; ×2.5 (3).

Probeloceras CLARKE, 1899 [**Gon. lutheri* CLARKE, 1885]. Thinly discoidal conch with flattened venter and wide umbilici. Sutures form 4 lobes and subangular 1st lateral saddle (12,46). *U.Dev.*, E. USA.——FIG. 31. **P. lutheri* (CLARKE), N.Y.; *A*, enlarged; *B*, ×5 (12).

Koenenites WEDEKIND, 1913 [**Gon. lamellosus* SANDB.-S., 1851]. Like *Manticoceras* but sutures with additional lobe (on umbilical wall) (46,100). *U.Dev.*, Ger.-Fr.-N.Afr.-USA.——FIGS. 32; 33. *K. cooperi* MILLER, Mich.; 32*A-E*, enlarged; 32*F*, ×2; 33*A*, ×1.3; 33*B*, ×7 (all 46).——FIG. 30*D*. **K. lamellosus* (SANDB-S.), Ger.; ×2 (68).

Timanites MOJSISOVICS, 1882 [**T. keyserlingi* MILLER, 1937] [=*Hoeninghausia* GÜRICH, 1896]. Conch lenticular with angular venter and small umbilici. Sutures form 10 lobes (46). *U.Dev.*, Eu.-N.Afr.-W.Can.——FIGS. 30*E*; 34. **T. keyserlingi* MILLER, Timans; 30*E*, ×1; 34*A,B*, ×0.7 (all 35).

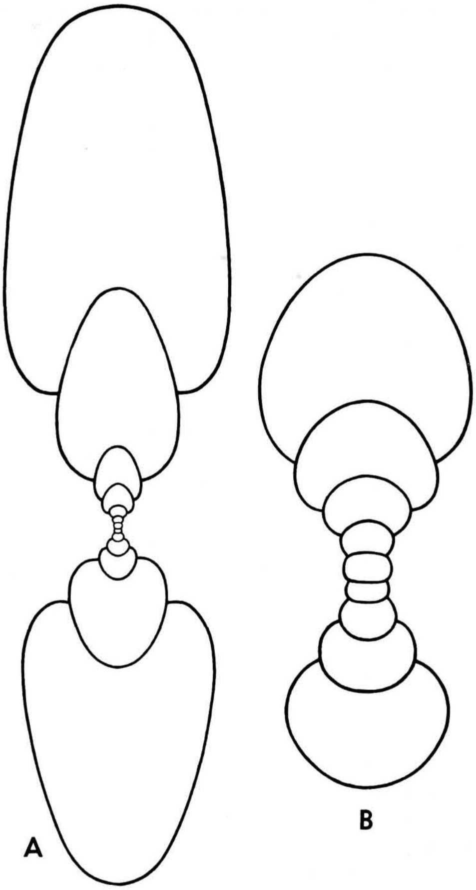

FIG. 33. Cross sections of *Koenenites cooperi* MILLER, U.Dev., Mich.; *A*, ×1.3; *B*, ×7 (46).

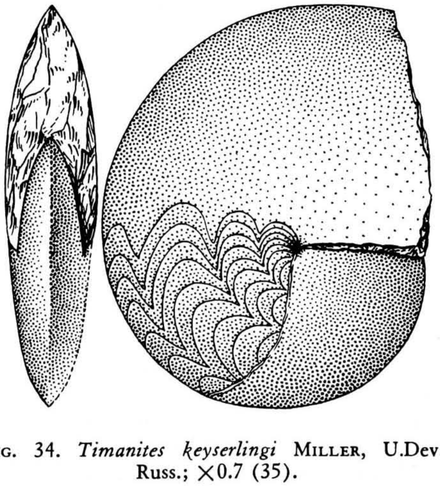

FIG. 34. *Timanites keyserlingi* MILLER, U.Dev., Russ.; ×0.7 (35).

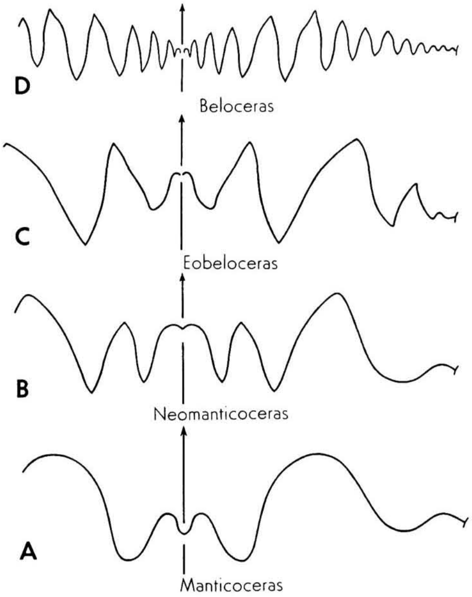

FIG. 35. Sutures of *Manticoceras (A)*, ×2; *Neomanticoceras (B)*, enlarged; *Eobeloceras (C)*, enlarged; and *Beloceras (D)*, ×1 (110).

Family PHARCICERATIDAE, Hyatt, 1900

[=Synpharciceratidae SCHINDEWOLF, 1936]

Conch globular to subdiscoidal; sutures with rounded lobes (100). *U.Dev.*

Pharciceras HYATT, 1884 [**Gon. tridens* SANDB.-S., 1850]. Conch thickly subdiscoidal; sutures with 3 to 6 pairs of lateral and auxiliary lobes (68,100). *U.Dev.*, Eurasia-N.Afr.

Synpharciceras SCHINDEWOLF, 1940 [**Gon. clavilobus* SANDB. S., 1850] [=*Neopharciceras* BOGOSLOVSKY, 1955]. Like *Pharciceras* but conch discoidal and with more sutural elements (68). *U.Dev.*, Eurasia-N.Afr.

Nordiceras BOGOSLOVSKY, 1955 [**Prolecanites timanicus* HOLZAPFEL, 1899]. Like *Pharciceras* but conch thinly discoidal (35). *U.Dev.*, Eurasia.

Sphaeropharciceras BOGOLOVSKY, 1955 [**S. sandbergerorum*]. Like *Pharciceras* but conch globular and suture simpler (68). *U.Dev.*, Eurasia-N.Afr.

Family BELOCERATIDAE Frech, 1902

[*nom. transl.* J.P.SMITH, 1903 (*ex* Beloceratinae FRECH, 1902)]

Conch subdiscoidal to lenticular, umbilicus small to moderate. Suture forms angular adventitious lobes within ventral lobe (68, 100). *U.Dev.*

Beloceras HYATT, 1884 [**Gon. sagittarius* SANDB.-S., 1851]. Conch lenticular, umbilicus moderately small. Suture forms series of adventitious lobes within ventral lobe and series of auxiliaries (21, 68,100). *U.Dev.*, Eurasia-N.Afr.-N.Y.——FIG. 35*D*. **B. sagittarium* (SANDB.-S.), Ger.; ×1 (68).

Neomanticoceras SCHINDEWOLF, 1936 [**Manticoceras paradoxum* MATERN, 1931] [=*Anabeloceras* CLARKE, 1897 *(nom. nud.)*]. Like *Manticoceras* but suture has pair of adventitious lobes within ventral lobe (46). *U.Dev.*, Ger.-N.Y.——FIGS. 35*B;* 36. *N. naplesense* (CLARKE), N.Y.; 35*B*, enlarged; 36, ×1 (12).

FIG. 36. *Neomanticoceras naplesense* (CLARKE), U. Dev., N.Y.; ×1 (12).

Eobeloceras SCHINDEWOLF, 1936 [**Am. multiseptatus* VON BUCH, 1832]. Like *Neomanticoceras* but suture has auxiliaries (11,46). *U.Dev.*, Ger.-N.Afr.-N.Y.——FIGS. 35*C;* 37. *E. iynx* (CLARKE), N.Y.; 35*C*, enlarged; 37, ×2 (12).

FIG. 37. *Eobeloceras iynx* (CLARKE), U.Dev., N.Y.; ×2 (12).

Suborder CLYMENIINA Hyatt, 1884

[*nom. correct.* MILLER & FURNISH, 1954 (*pro* Clymeninae HYATT, 1884)] [=Intrasiphonata ZITTEL, 1895; Clymeniacea WEDEKIND, 1914; Clymenoidea SCHINDEWOLF, 1923]

Primitive Ammonoidea with dorsally situated marginal siphuncle (Fig. 38,*1*). As reported in 2 genera (*Acanthoclymenia, Cymaclymenia*), the siphuncle primarily has a ventral position in the 1st few septa (Fig. 38,*2b*) and then migrates to its definite dorsal location during early adolescence. This seems to indicate derivation of the Clymeniina from goniatites with a ventrally placed siphuncle. Septal necks cylindrical, retrochoanitic, commonly very long, forming a continuous siphuncular tube (Fig. 38,*1*). Shell tightly coiled, without umbilical perforation, typically subdiscoidal and widely umbilicate, but some subglobular and deeply involute, smooth or strongly ribbed and spinose. Growth lines usually denote a lateral and a deep ventral hyponomic sinus. Protoconch (Fig. 38,*2a,b*) spheroidal or ellipsoidal, with latisellate prosuture (Fig. 38,*2c*) (in those few shells where it can be observed); following early adolescent sutures (Fig. 38,*2d*) invariably with ventral lobe, which in Gonioclymeniaceae persists throughout ontogenetic development, whereas in Clymeniaceae it is replaced by a very characteristic ventral saddle fused with the 2 1st lateral saddles (Fig. 38,*3a-c*). The dorsal lobe persists in these 2 groups, but in Parawocklumeriaceae it also, as well as the ventral lobe, is replaced by a secondary saddle during ontogeny (Fig. 38,*4*). Both evolutionary trends are unique among ammonoids. Lobes and saddles rounded or pointed, not denticulate. Septa concave in the median plane. Length of body chamber about one volution and more. Aptychi or anaptychi not observed. *U.Dev.*

The Clymeniina apparently represent a monophyletic group derived from *Archoceras* or some related form of Anarcestidae and confined to the Upper Devonian. The group is distributed mainly in Europe and northern Africa; it is more scarcely represented also in the other continents (with possible exception of Asia).

Superfamily GONIOCLYMENIACEAE Hyatt, 1884

[*nom. transl. et correct.* MILLER & FURNISH, 1954 (*ex* Gonioclymenidae HYATT, 1884)] [=Gonioclymeniacea SCHINDEWOLF, 1923; Gonioclymenida SCHIND., 1937]

Dorsal and ventral lobes retained throughout ontogenetic development, but latter may be secondarily divided by a median saddle. Septal necks usually very long, forming more or less continuous tube for siphuncle. Suture in primitive members consisting of ventral, lateral, and dorsal lobes only, in more advanced forms additionally with umbilical and adventitious lobes. Shell variable, in typical forms narrowly subdiscoidal and widely umbilicate, with compressed whorl section, in some offshoots broadly subdiscoidal or subglobular, with narrow or closed umbilicus and depressed whorl section. *U. Dev. (Manticoceras z.-Wocklumeria z.).*

The Gonioclymeniacea are considered to be the conservative group of Clymeniina and the root stock of Clymeniaceae and Parawocklumeriaceae.

Family HEXACLYMENIIDAE Lange, 1929

Shell small (few cm. in diameter), narrowly subdiscoidal, slightly involute, widely umbilicate, with depressed whorls, increasing slowly in height. Suture with ventral, lateral, and dorsal lobes only; ventral lobe moderately deep, broadly rounded. Septal necks originally short but in later forms long, forming a continuous siphuncular tube. Growth lines with lateral sinus, prominent ventrolateral salient, and deep hyponomic sinus. *U.Dev.(Platyclymenia z.-Wocklumeria z.).*

Hexaclymenia SCHINDEWOLF, 1923 [**Clymenia hexagona* WEDEKIND, 1908]. Whorl section subtriangular, with rounded whorl sides and carinate venter; keel flanked by pair of broad grooves on ventrolateral shoulders. Growth lines with deep lateral sinus and prominent ventrolateral salient, without marked ribs. Septal necks short. *U.Dev. (Platyclymenia z.),* Eu.——FIG. 39,*1*. **H. hexagona* (WDKD.), Ger.; *1a,b,* ×1; *1c,* suture at maturity (enlarged) (99).

Progonioclymenia SCHINDEWOLF, 1937 [**Clymenia acuticostata* BRAUN in MÜNSTER, 1842]. Whorl section rectangular, with flattened whorl sides and sulcate venter. Ribs strong, prorsiradiate, faintly sinuous, partly with ventrolateral spines. Septal necks long, forming continuous tube. *U.Dev. (Clymenia z.),* Eu.——FIG. 39,2. **P. acuticostata*

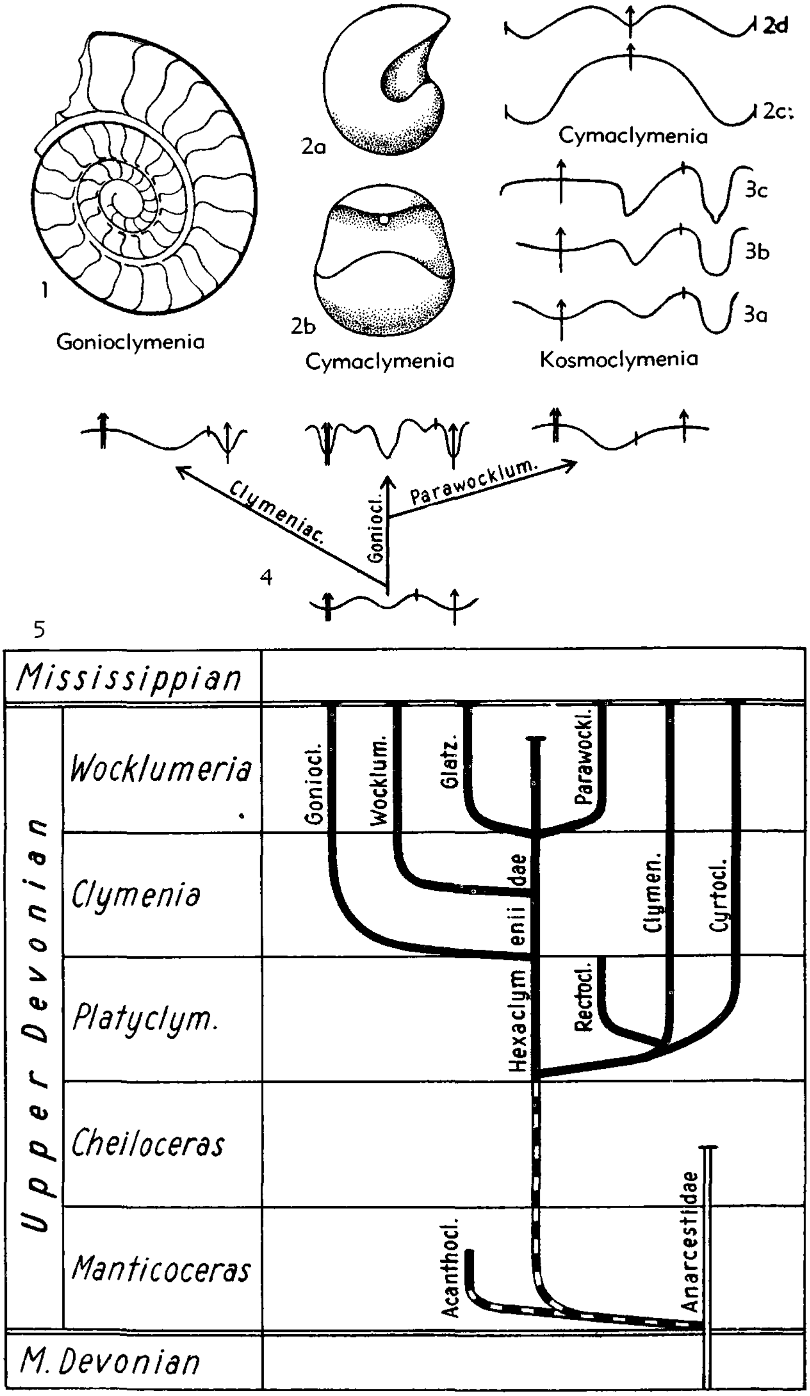

FIG. 38. General features of Clymeniina (113n).——*1, Gonioclymenia subcarinata* (MÜNSTER), U.Dev., *Clymenia* zone, Ger.; *median section* (X2).——*2, Cymaclymenia euryomphala* SCHINDEWOLF, U.Dev., *Wocklumeria* zone, Ger.;·*2a,b,* protoconch, side and front view (X40); *2c,* prosuture; *2d,* primary suture. ——*3, Kosmoclymenia undulata* (MÜNSTER), U.Dev., *Clymenia* zone, Ger.; *3a-c,* development of suture (enlarged).——*4,* Evolution of sutures in superfamilies of Clymeniina.——*5,* Supposed phylogenetic relationships of the families of Clymeniina.

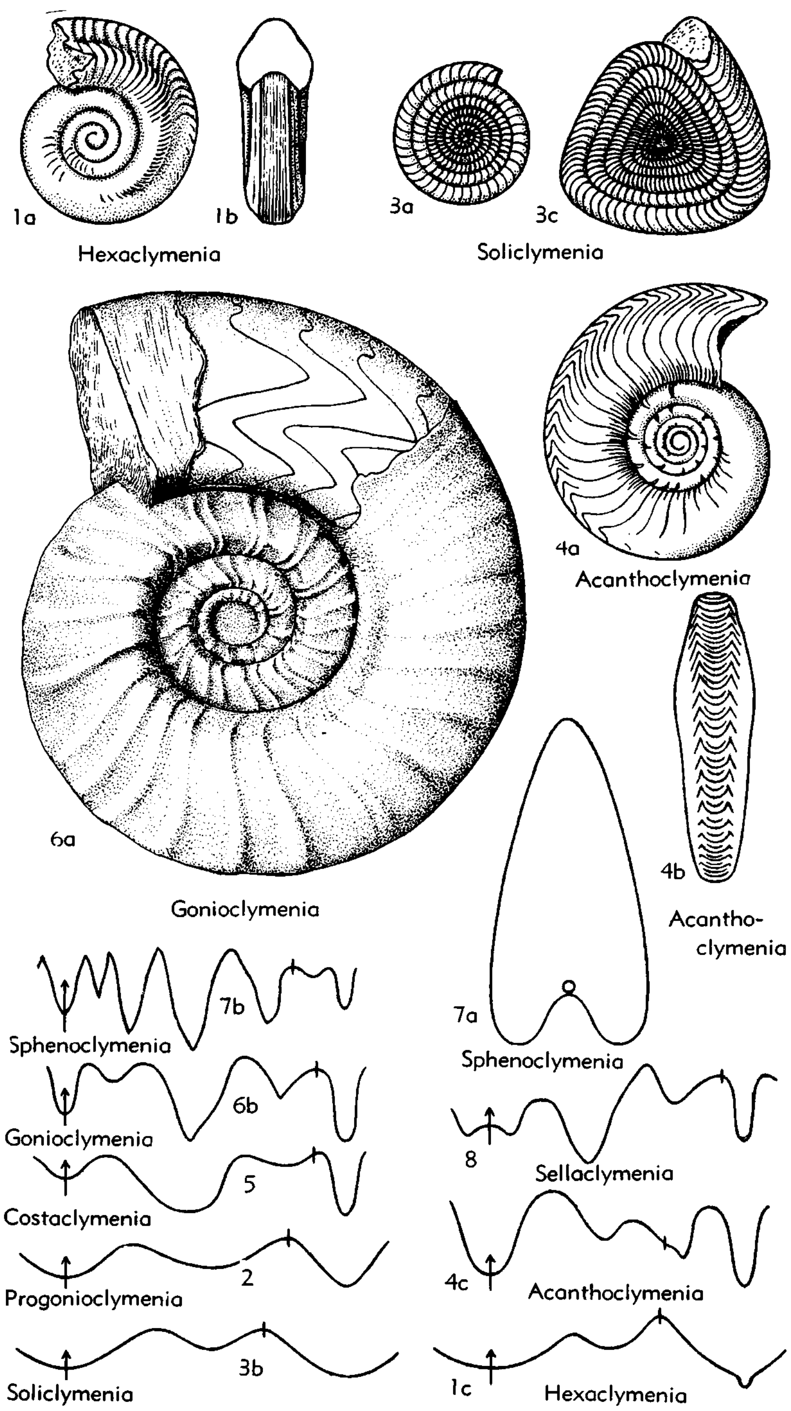

Fig. 39. Hexaclymeniidae, Acanthoclymeniidae, Gonioclymeniidae (p. L37-L40).

(BRAUN), Ger.; suture at maturity (enlarged) (114).

Soliclymenia SCHINDEWOLF, 1937 [**Goniatites solarioides* VON BUCH, 1840]. Whorl section broadly reniform, with rounded sides and venter. Ribs fine, densely crowded, deeply concave on the whorl sides, without spines. Shell in some forms with triangular coiling. *U.Dev.(Wocklumeria z.)*, Eu.——FIG. 39,*3a,b*. **S. solarioides* (BUCH), Ger.; *3a*, ×2; *3b*, suture at maturity (enlarged) (114). ——FIG. 39,*3c*. *P. paradoxa* (MÜNSTER), Ger.; ×2 (114).

Family ACANTHOCLYMENIIDAE Schindewolf, 1955

Shell small (few cm. in diameter), subdiscoidal, slightly involute, widely umbilicate, with compressed whorls. Suture with ventral, lateral, and dorsal lobes supplemented by pointed umbilical lobe situated inside the umbilical seam; ventral lobe deeply rounded. Growth lines with lateral sinus, prominent angular ventrolateral salient, and deep hyponomic sinus. *U.Dev. (Manticoceras z.)*.

The only genus so far known *(Acanthoclymenia)* was formerly included in the family Gonioclymeniidae, for its characters would not mean more than a generic difference from *Costaclymenia* of this family. But since *Acanthoclymenia* appears to be a very early isolate offshoot of Hexaclymeniidae, not in evolutionary continuity with the coherent group of Gonioclymeniidae, it seems advisable to place it in a family of its own.

Acanthoclymenia HYATT, 1900 [**Clymenia (Cyrtoclymenia) neapolitana* CLARKE, 1892]. Whorl section subtrapezoidal. Suture with lateral lobe shallow, rounded; dorsal lobe angular. *U.Dev. (Manticoceras z.)*, N.Am.——FIG. 39,*4*. **A. neapolitana* (CLARKE), N.Y.; *4a,b*, ×3; *4c*, suture at maturity (enlarged) (46).

Family GONIOCLYMENIIDAE Hyatt, 1884

[*nom. correct.* WEDEKIND, 1913 (*pro* Gonioclymenidae HYATT, 1884)]

Shell large (up to 25 cm. in diameter), narrowly subdiscoidal, slightly involute, widely umbilicate, with compressed whorls, increasing rapidly in height. Suture, in addition to ventral, lateral, and dorsal lobes, comprising one or more umbilical and adventitious lobes. Septal necks long, forming continuous siphuncular tube. Growth lines with shallow sinus near umbilical seam, a broad shallow ventrolateral salient, and deeply rounded hyponomic sinus. Usually with prominent ribs and spines. *U.Dev. (Clymenia z.-Wocklumeria z.)*.

Costaclymenia SCHINDEWOLF, 1920 [**Goniatites binodosus* MÜNSTER, 1832] [?=*Trochoclymenia* SCHIND., 1926]. Shell narrowly subdiscoidal, very widely umbilicate, with rectangular, compressed whorl section. Ribs faint or strong, nearly rectilinear, radiate, with or without ventrolateral and dorsolateral spines. Suture with shallow, rounded ventral lobe, broadly rounded lateral lobe, shallow, rounded umbilical lobe outside the umbilical seam, and deep, pointed dorsal lobe. *U.Dev.(Clymenia z.)*, Eu.——FIG. 39,*5*. **C. binodosa* (MÜNSTER), Ger.; suture at maturity (114).

Gonioclymenia HYATT, 1884 [**Goniatites speciosus* MÜNSTER, 1832] [=*Schizoclymenia* SCHINDEWOLF, 1920 (obj.)]. Shell as in *Costaclymenia* but with somewhat broader, subtrapezoidal whorl section and sulcate venter. Ribs faintly prorsiradiate, with broad shallow ventrolateral salient and ventrolateral spines. Suture with deep angular ventral lobe, pointed lateral and umbilical lobes, and an additional adventitious lobe. *U.Dev.(Clymenia z.)*, Eu.-N.Afr.——FIG. 39,*6a,b*. **G. speciosa* (MÜNSTER), Ger.; *6a*, ×1; *6b*, suture at maturity (114n).

Kalloclymenia WEDEKIND, 1914 [**Goniatites subarmatus* MÜNSTER, 1832; SD SCHINDEWOLF, herein]. Suture and sculpture as in *Gonioclymenia* but with lower rectangular whorl section and without ventral sulcus. *U.Dev.(Wocklumeria z.)*, Eu.-N. Afr.

K. (Kalloclymenia). Without distinct parabolic ribs and nodes. Occurrence as for genus.

K. (Otoclymenia) SCHINDEWOLF, 1923 [**Gonioclymenia uhligi* FRECH, 1902]. With marked parabolic ribs and nodes. Occurrence as for genus.

Sphenoclymenia SCHINDEWOLF, 1920 [**Goniatites maximus* MÜNSTER, 1832]. Shell narrowly subdiscoidal, with high fastigate or subrectangular whorl section, without marked ribs and spines. Suture highly differentiated with 2 umbilical and 2 adventitious lobes. *U.Dev.(Wocklumeria z.)*, Eu.-N.Afr..——FIG. 39,*7*. **S. maxima* (MÜNSTER), Ger.; *7a*, whorl sec., ×0.5; *7b*, suture at maturity, enlarged (28).

Sellaclymenia HYATT, 1884 [**Clymenia angulosa* MÜNSTER, 1843 (=**Goniatites planus* MÜNSTER, 1832)]. Shell narrowly subdiscoidal, with high subrectangular whorl section, smooth or with ventrolateral ribs and spines. Suture with same number of elements as in *Costaclymenia* but ventral lobe divided by a low, broad median saddle. *U.Dev.(Clymenia z.-Wocklumeria z.)*, Eu.——FIG. 39,*8*. **S. plana* (MÜNSTER), Ger.; suture at maturity, enlarged (114).

Family WOCKLUMERIIDAE Schindewolf, 1937

[*nom. correct.* SCHIND., 1949 (*ex* Wocklumeridae SCHIND., 1937] [=?Miroclymeniinae SCHIND., 1924; Biloclymeniidae BOGOSLOVSKY, 1955]

Shell of moderate size, broadly subdiscoidal or subglobular, strongly involute, more or less narrowly umbilicate, with triangular coiling in later representatives, without ventral keel. Suture with additional umbilical lobes; deep ventral lobe without median saddle (except in one uncertain genus). Septal necks long cylindrical, in some genera forming a continuous siphuncular tube. Growth lines nearly rectilinear; without prominent ribs. *U.Dev.(Clymenia z.-Wocklumeria z.).*

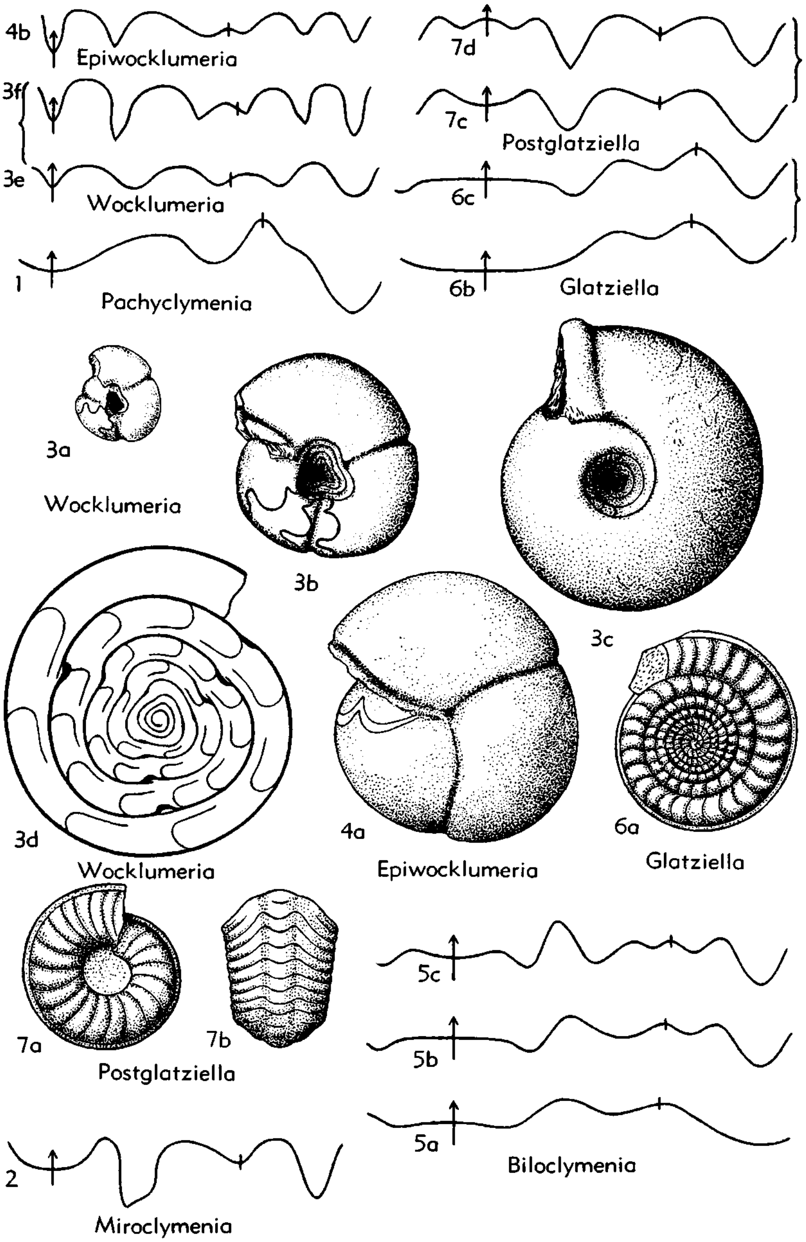

FIG. 40. Wocklumeriidae, Glatziellidae (p. L42).

The subfamily Miroclymeniinae was founded on the doubtful genus *Miroclymenia,* represented by a single specimen, which might be an immature stage of some other clymeniid. The type has been lost and no additional specimens have yet been discovered. It seems inadvisable to maintain this *genus inquirendum* as type genus of a subfamily and possibly of the family here called Wocklumeriidae.

Pachyclymenia SCHINDEWOLF, 1937 [**P. abeli*]. Shell broadly subdiscoidal, with moderately wide umbilicus, without constrictions and triangular coiling. Suture consisting of ventral, lateral, dorsal lobes, and an incipient umbilical lobe inside the umbilical seam; ventral lobe shallow, rounded. Growth lines with broad, shallow ventrolateral salient. *U.Dev.(Clymenia z.),* Eu.——FIG. 40,*1*. **P. abeli,* Ger.; suture at maturity, enlarged (114).

?**Miroclymenia** SCHINDEWOLF, 1923 [**M. interpres*]. Like *Pachyclymenia* but more narrowly umbilicate. Umbilical lobe well developed, divided by the umbilical seam; lateral lobe pointed. Genus very doubtful. *U.Dev.(Clymenia z.),* Eu.——FIG. 40,*2*. **M. interpres,* Ger.; suture at maturity, enlarged (114).

Wocklumeria WEDEKIND, 1918 [**W. denckmanni* (=**Goniatites sphaeroides* RH. RICHTER, 1848)]. Shell broadly subdiscoidal or subglobular, with moderately wide umbilicus and depressed whorl section; in youth with triangular coiling and deep, straight constrictions, at maturity spirally coiled, without constrictions. Suture with 3 umbilical lobes; ventral lobe deep and pointed, others likewise pointed. Growth lines practically rectilinear. *U.Dev.(Wocklumeria z.),* Eu.-N.Afr.——FIG. 40,*3*. **W. sphaeroides* (RICHTER), Ger.; *3a,d,* ×2; *3b,* ×1.5; *3c,* ×1; *3e-f,* development of suture, enlarged (all 114).

Epiwocklumeria SCHINDEWOLF, 1937 [**Wocklumeria paradoxa* var. *applanata* WEDEKIND, 1918]. Like *Wocklumeria* but narrowly subdiscoidal, with closed umbilicus and compressed whorl section. Shell at maturity also with subtriangular periphery and strong, adorally convex constrictions. Umbilical lobes rounded. *U.Dev.(Wocklumeria z.),* Eu. ——FIG. 40,*4*. **E. applanata* (WDKD.), Ger.; *4a,* ×1.3; *4b,* suture at maturity, enlarged (114).

Biloclymenia SCHINDEWOLF, 1923 [**Clymenia bilobata* MÜNSTER, 1839] [=Cymaclymeniae GÜMBEL, 1863 (*non Cymaclymenia* HYATT, 1884); *Kiaclymenia* BOGOSLOVSKY, 1955]. Spirally coiled like *Pachyclymenia* but with 2 umbilical lobes and median saddle in broad external lobe. Doubtful taxonomic position. *U.Dev.(Clymenia z.),* Eu.——FIG. 40,*5*. **B. bilobata* (MÜNSTER), Ger.; *5a-c,* development of suture, enlarged (114).

Family GLATZIELLIDAE Schindewolf, 1928

[*nom. transl.* SCHIND., 1939 (*ex* Glatziellinae SCHIND., 1928)]

Shell small, broadly subdiscoidal or subglobular, strongly involute, more or less narrowly umbilicate, without triangular coiling, venter carinate. Suture invariably with median saddle. Septal necks short to long cylindrical but not forming a continuous tube. Growth lines with deep lateral sinus and prominent ventrolateral salient. Mostly ribbed. *U.Dev.(Wocklumeria z.).*

Glatziella RENZ, 1913 [**G. helenae;* SD SCHINDEWOLF, herein]. Shell subdiscoidal, evolute, widely umbilicate or subglobular, involute, narrowly umbilicate. Suture with 3 lobes only; ventral lobe broad, divided by median saddle; lateral lobe shallow, rounded, situated near umbilical seams. *U. Dev.(Wocklumeria z.),* Eu.——FIG. 40,*6*. **G. helenae,* Ger.; *6a,* ×1 (RENZ); *6b,c,* development of suture, enlarged (114).

Postglatziella SCHINDEWOLF, 1937 [**P. carinata*]. Like *Glatziella* but subglobular and narrowly umbilicate. Suture with additional umbilical lobe; lateral lobe deep, pointed, situated on middle of whorl sides. *U.Dev.(Wocklumeria z.),* Eu.—— FIG. 40,*7*. **P. carinata,* Ger.; *7a,* ×2; *7c,d,* development of suture, enlarged (all 114).

Superfamily CLYMENIACEAE Edwards, 1849

[*nom. transl. et correct.* MILLER & FURNISH, 1954 (*ex* Clymenidae EDW., 1849)] [=Platyclymeniacea SCHINDEWOLF, 1923; Platyclymenida SCHIND., 1937]

Ventral lobe developed in earliest ontogenetic stages only, later replaced by ventral saddle; dorsal lobe persisting throughout ontogenetic development; suture mostly simple, undifferentiated. Septal necks usually short, not forming continuous tube for siphuncle. Shell variable, narrowly or more broadly subdiscoidal, with wide or narrow umbilicus. Growth lines with lateral and hyponomic sinus and more or less prominent ventrolateral salient. *U.Dev. (Platyclymenia z.-Wocklumeria z.).*

Family CLYMENIIDAE Edwards, 1849

[*nom. correct.* MILLER & FURNISH, 1954 (*pro* Clymenidae EDW., 1849)] [=Platyclymeniidae WEDEKIND, 1914]

Shell narrowly subdiscoidal, widely umbilicate, increasing slowly in height, with low whorl section, and rounded or flattened, rarely fastigate or carinate venter, smooth or ribbed. Growth lines with shallow, narrowly rounded ventrolateral salient. Suture simple, with lateral and dorsal lobes only, which may be supplemented by an adventitious lobe. *U.Dev.(Platyclymenia z.-Wocklumeria z.).*

Platyclymenia Hyatt, 1884 [**Goniatites annulatus* Münster, 1832] [=*Varioclymenia* Wedekind, 1908; *Annulites* Wdkd., 1914 (obj.); *Choneclymenia* Perna, 1914 *(nom. nud.)*; *Stenoclymenia* Lange, 1929]. Shell subdiscoidal, widely umbilicate, either ribbed or smooth. Growth lines and ribs with broad, shallow sinus on the whorl sides, without dorsolateral salient. Lateral lobe broadly rounded, no adventitious lobe. *U.Dev.(Platyclymenia z.),* Eu.-N.Afr.-N.Am.-?W. Austral.

P. (Platyclymenia). Whorl section rectangular,

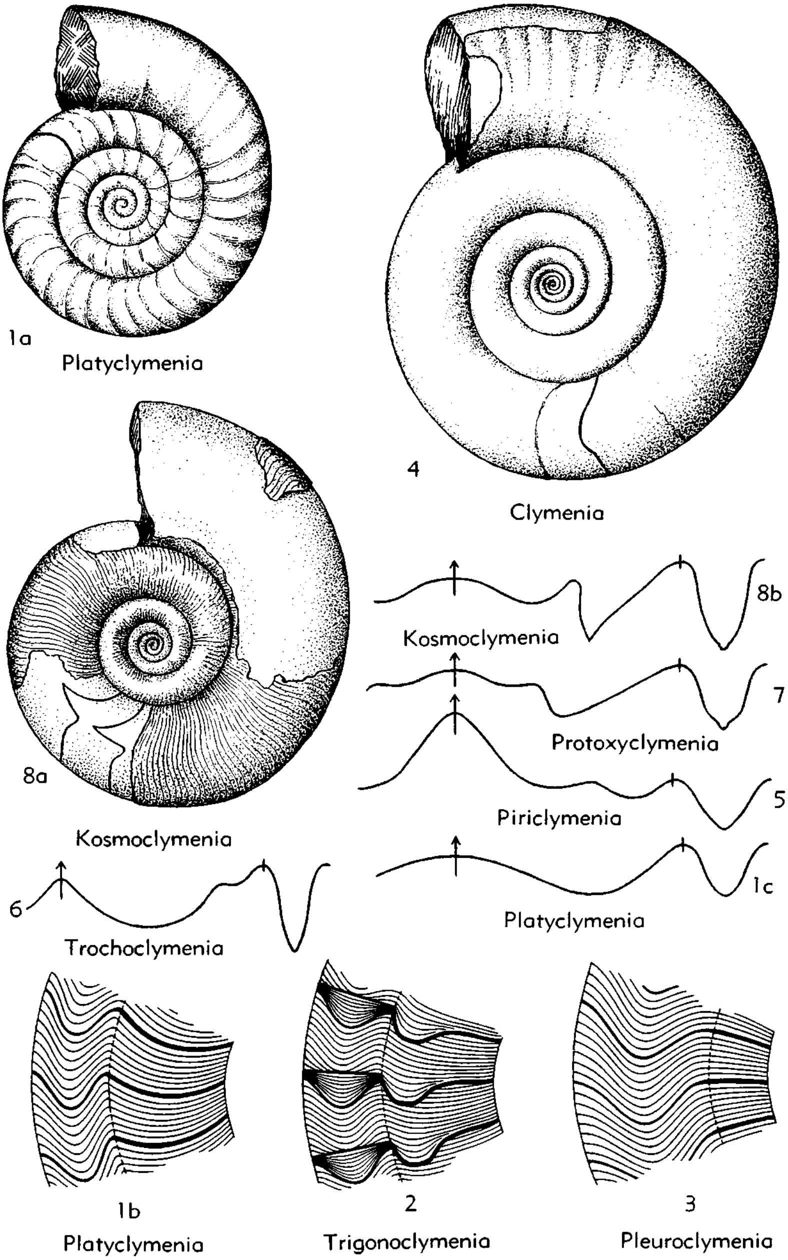

Fig. 41. Clymeniidae (p. L43-L44).

with flattened sides and relatively narrow venter. Ribs, if present, without parabolic ears and subtriangular structures on venter. Occurrence as for genus.——Fig. 41,*1*. **P. (P.) annulata* (Münster), Ger.; *1a*, ×1.5; *1b*, ×2.5; *1c*, suture at maturity, enlarged (all 113).

P. (Trigonoclymenia) Schindewolf, 1934 [**Clymenia spinosa* Münster, 1842]. Like *P. (Platyclymenia)* but with parabolic ears and subtriangular structures on venter. Occurrence as for genus.——Fig. 41,*2*. **P. (T.) spinosa* (Münster), Ger.; ×2.5 (114).

P. (Pleuroclymenia) Schindewolf, 1934 [**P. (Pl.) crassissima* Schind., 1955 (*nom. nov. pro Platyclymenia crassa* Schind., 1923, preoccupied)]. Whorl section broadly reniform with rounded sides and broad venter. Ribs without parabolic ears and subtriangular structures on venter. Occurrence as for genus.——Fig. 41,*3*. *P. (Pl.) americana* (Raymond), Mont.; ×2.5 (112).——Fig. 42. *P. (Pl.) polypleura* (Raymond), Mont.; *A-C*, ×0.5; *D*, enlarged (46).

Clymenia Münster, 1834 [*pro Planulites* Münster, 1832 (*non* Lamarck, 1801)] [**Planulites laevigatus* Münster, 1832; SD Frech, 1902] [=*Clymenites* Münster, 1835 *(nom. nud.)*; *Endosiphonites* Ansted, 1838 *(nom. nud.)*; *Oxyclymenia* Hyatt, 1884 (obj.); *Orthoclymenia* Wdkd., 1908 *(nom. nud.)*; *Laevigites* Wdkd., 1914 *(nom. nud.)*]. Like *Platyclymenia* but with very faint, approximately rectilinear growth lines, without marked ribs. Venter rounded or fastigate. *U.Dev.(Clymenia z.)*, Eu.-?W.Austral.——Fig. 41,*4*. **C. laevigata* (Münster), Ger.; ×0.75 (114n).

Piriclymenia Schindewolf, 1937 [**Platyclymenia piriformis* H. Schmidt, 1924]. Shell subdiscoidal, widely umbilicate, with subtriangular whorl section and fastigate venter, strongly ribbed. Suture with highly elevated ventral saddle, rounded lateral lobe situated near umbilical seam, and shallow, rounded adventitious lobe. *U.Dev.(Clymenia z.)*, Eu.——Fig. 41,*5*. **P. piriformis* (Schmidt), Ger.; suture at maturity, enlarged (114).

?Trochoclymenia Schindewolf, 1926 [**Clymenia wysogorskii* Frech, 1902]. Shell narrowly subdiscoidal, evolute, widely umbilicate. Suture as in *Clymenia* but with an additional small, shallow umbilical lobe. (Genus doubtful; founded on single specimen, which may be an abnormal representative of *Costaclymenia*). *U.Dev.(Wocklumeria z.)*, Eu.——Fig. 41,*6*. **T. wysogorskii* (Frech), Ger.; suture at maturity enlarged (114).

Protoxyclymenia Schindewolf, 1923 [**Clymenia dunkeri* Münster, 1839]. Like *Platyclymenia* but growth lines with dorsolateral salient, without marked ribs. Suture with shallow, incipient adventitious lobe. *U.Dev.(Platyclymenia z.-Clymenia z.)*, Eu.——Fig. 41,*7*. **P. dunkeri* (Münster), *Clymenia* z., Ger.; suture at maturity, enlarged (114).

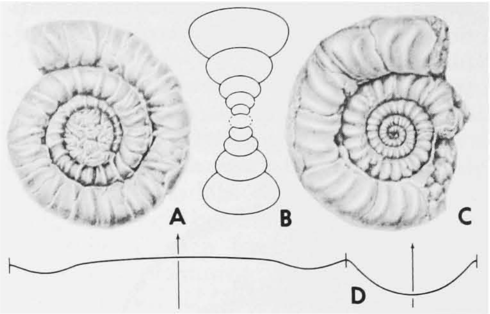

Fig. 42. *Platyclymenia (Pleuroclymenia) polypleura* (Raymond), Mont.; *A-C*, ×0.5; *D*, enlarged (46).

Kosmoclymenia Schindewolf, 1949 [**Planulites undulatus* Münster, 1832] [=Oxyclymeniae Gümbel, 1863 (*non Oxyclymenia* Hyatt, 1884)]. Like *Protoxyclymenia* but with deep, pointed lateral lobe and with distinct, moderately deep adventitious lobe. Venter rounded, flattened, fastigate or carinate. *U.Dev.(Clymenia z.-Wocklumeria z.)*, Eu.-N.Afr.——Fig. 41,*8*. **K. undulata* (Münster), *Clymenia z.*, Ger.; *8a*, ×1; *8b*, suture at maturity, enlarged (114n).

Family CYRTOCLYMENIIDAE Hyatt, 1884

[*nom. correct.* Schindewolf, 1949 (*pro* Cyrtoclymenidae Hyatt, 1884)] [=Cymaclymenidae Hyatt, 1884; Striatoclymenidae Miller, 1938]

Shell broadly subdiscoidal, narrowly umbilicate, increasing quickly in height, with low whorl section and rounded, rarely carinate venter. Growth lines with prominent, broad ventrolateral salient. Suture, in addition to lateral and dorsal lobes, may comprise an umbilical and an adventitious lobe. *U.Dev.(Platyclymenia z.-Wocklumeria z.)*.

Cyrtoclymenia Hyatt, 1884 [**Planulites angustiseptatus* Münster, 1832] [=*Protactoclymenia* Wedekind, 1908; *Lenticlymenia* H. Schmidt, 1924 *(nom. nud.)*]. Shell broadly subdiscoidal or subglobular, smooth or faintly ribbed. Suture with broadly rounded lateral lobe and dorsal lobe only. *U.Dev.(Platyclymenia z.-Wocklumeria z.)*, Eu.-N. Afr.-W.Austral.——Fig. 43,*1*. *C. frechi* (Tokarenko), *Platyclymenia z.*, Ger.; ×1.3 (113n).——Fig. 43,*2*. **C. angustiseptata* (Münster), *Clymenia* z., Ger.; suture at maturity, enlarged (114).

Genuclymenia Wedekind, 1908 [**G. frechi;* SD Schindewolf, herein]. Shell subdiscoidal with crowded ribs. Suture with rounded lateral lobe, shallow, rounded umbilical lobe, inside umbilical seam, and likewise shallow adventitious lobe. *U. Dev.(Platyclymenia z.)*, Eu.——Fig. 43,*3*. **G. frechi*, Ger.; *3a*, ×1; *3b*, suture at maturity, enlarged (99).

Cymaclymenia Hyatt, 1884 [*non* Cymaclymeniae

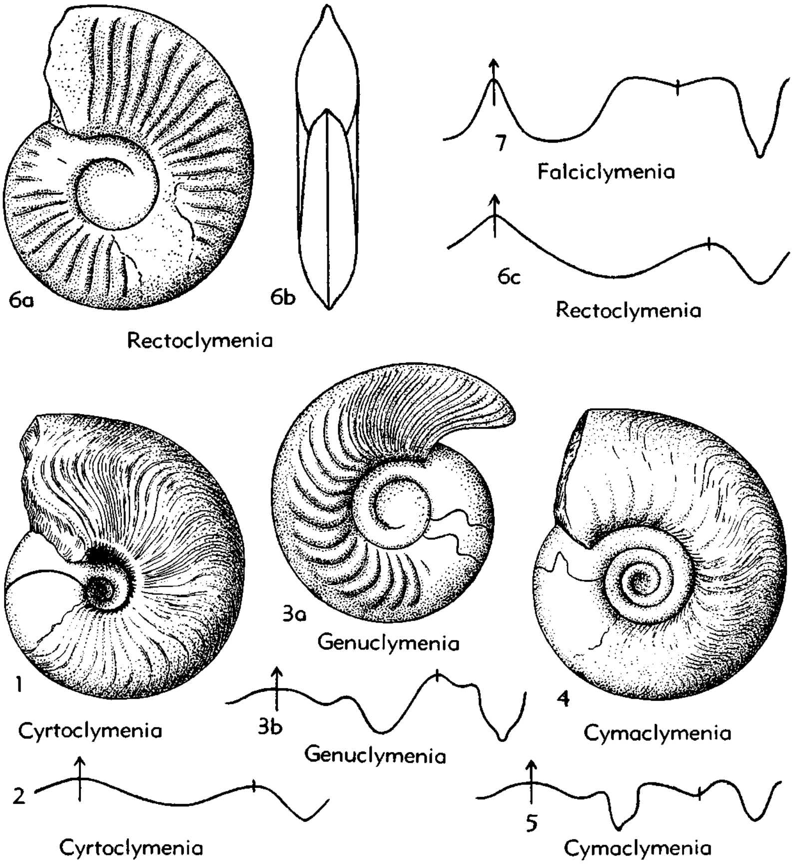

Fig. 43. Cyrtoclymeniidae, Rectoclymeniidae (p. L44-L45).

Gümbel, 1863] [**Planulites striatus* Münster, 1832] [=*Postclymenia* H. Schmidt, 1924; *Striatoclymenia* Matern, 1931 *(nom. nud.)*]. Like *Genuclymenia* but with pointed, asymmetrical lateral lobe and deep, pointed umbilical lobe, divided by umbilical seam. Smooth or ribbed. *U.Dev. (Platyclymenia z.-Wocklumeria z.),* Eu.-N.Afr.——Fig. 43,*4*. *C. camerata* Schindewolf, *Clymenia* z., Ger.; ×1.3 (113).——Fig. 43,*5*. **C. striata* (Münster), *Clymenia* z., Ger.; suture at maturity, enlarged (114).

Family RECTOCLYMENIIDAE Schindewolf, 1923

Shell thinly subdiscoidal, narrowly or rather widely umbilicate, increasing rapidly in height, with high whorl section and more or less fastigate venter. Growth lines with low dorsolateral and ventrolateral salients and shallow lateral sinus, approximately rectilinear. Ribs likewise nearly straight. Suture simple, with lateral and dorsal lobes only, which may be supplemented by an umbilical lobe. *U.Dev.(Platyclymenia z.).*

Rectoclymenia Wedekind, 1908 [**R. roemeri;* SD Wdkd., 1914]. Suture with a shallow, very broad lateral lobe and dorsal lobe only. *U.Dev.(Platyclymenia z.),* Eu.——Fig. 43,*6*. **R. roemeri,* Ger.; *6a,b,* ×1; *6c,* suture at maturity, enlarged (99).

Falciclymenia Schindewolf, 1923 [**Goniatites falcifer* Münster, 1840]. Suture with moderately deep lateral lobe, narrowed by newly added umbilical lobe. *U.Dev.(Platyclymenia z.),* Eu.-N.Am.——Fig. 43,*7*. **F. falcifera* (Münster), Ger.; suture at maturity, enlarged (114).——Fig. 44. *F. bowsheri,* N.Mex.; *A,B,* ×0.6; *C,* ×0.9 (Miller & Collinson).

Superfamily PARAWOCKLUMERIACEAE Schindewolf, 1937

[*nom. transl.* Schind., 1955 (*ex* Parawocklumeridae Schind., 1937)]

Ventral as well as dorsal lobe developed in early ontogenetic stages only, replaced

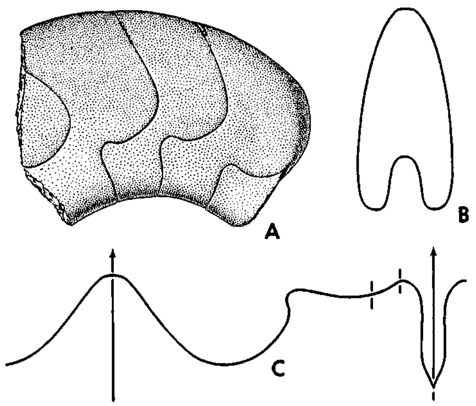

FIG. 44. ***Falciclymenia bowsheri*** MILLER & COLLINSON, U.Dev., USA(N.Mex.); *A,B,* ×1; *C,* enlarged.

by saddles during ontogeny. Septal necks originally long cylindrical, in more advanced forms short, not forming a continuous tube. Small but autonomous group, for the present involving one family only. *U.Dev. (Wocklumeria z.).*

Family PARAWOCKLUMERIIDAE Schindewolf, 1937

[*nom. correct.* SCHIND., 1949 (*pro* Parawocklumeridae SCHIND., 1937)]

Shell in earlier forms subdiscoidal, widely umbilicate, later subglobose, narrowly umbilicate with depressed whorls, invariably with triangular coiling. Growth lines originally with lateral and hyponomic sinus, in derived forms nearly rectilinear. Without marked ribs. *U.Dev.(Wocklumeria z.).*

Kamptoclymenia SCHINDEWOLF, 1937 [**K. endogona*]. Shell subdiscoidal, widely umbilicate, in youth coiled triangularly or quadrangularly, at maturity with normal spiral or triangular coiling. Ventral and dorsal lobe each divided by a rising saddle, no umbilical lobes. *U.Dev.(Wocklumeria z.),* Eu.——FIG. 45,*1*. **K. endogona,* Ger.; *1a,* reduced; *1b,c,* development of suture, enlarged (113).——FIG. 45,*2*. *K. trigona* SCHIND., Ger.; reduced (113).——FIG. 45,*3*. *K. trivaricata* SCHIND., Ger.; *3a,* reduced; *3b,* suture at maturity, enlarged (114).

Triaclymenia SCHINDEWOLF, 1937 [**T. triangularis*]. Shell with moderately wide umbilicus, triangularly coiled also in adult. Ventral and dorsal lobe each

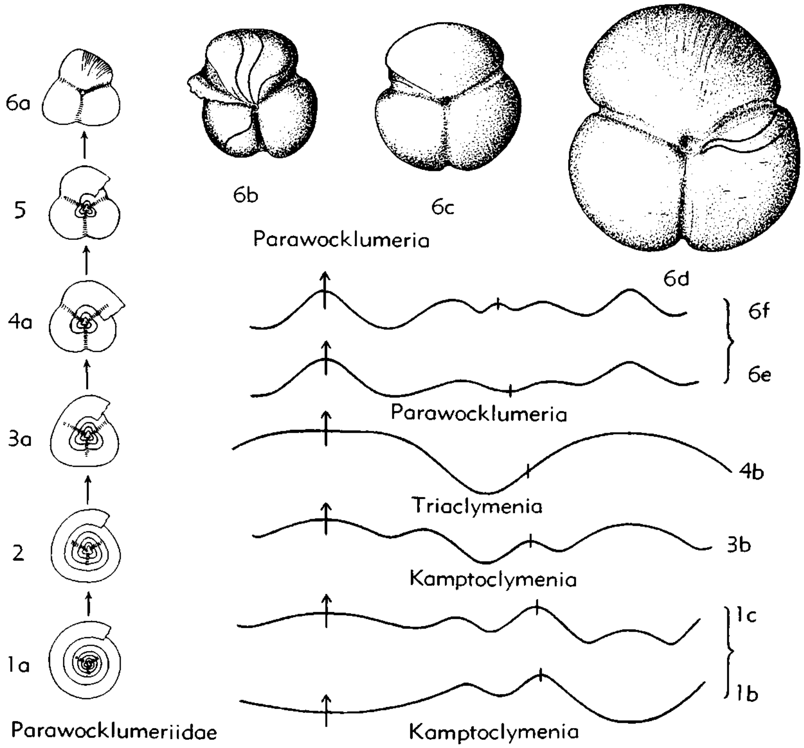

FIG. 45. Parawocklumeriidae (p. L46-L47).

definitely replaced by a broad saddle, no umbilical lobes. *U.Dev.(Wocklumeria z.),* Eu.——FIG. 45,*4.* **T. triangularis,* Ger.; *4a,* reduced; *4b,* suture at maturity, enlarged (114).

Parawocklumeria SCHINDEWOLF, 1926 [**Wocklumeria paradoxa* WEDEKIND, 1918]. Shell with moderately wide or narrow umbilicus, triangularly coiled also in adult and trilobate by deep constrictions. Suture with 3 umbilical lobes. *U.Dev. (Wocklumeria z.),* Eu.——FIG. 45,*5. P. distorta* (TIETZE), Ger.; reduced (113).——FIG. 45,*6.* **P. paradoxa* (WDKD.), Ger.; *6a,* reduced; *6b,c,* ×2; *6d,* ×1.3; *6e,f,* development of suture, enlarged (all 114).

Suborder GONIATITINA Hyatt, 1884

[*nom. correct.* DELEPINE, 1952 (*pro* Goniatitinae HYATT, 1884)]

Basic suture of 8 lobes but primitive forms have fewer and advanced forms have ammonitic sutures with auxiliaries; in all but primitive representatives, siphuncle prochoanitic (46,50,52,78,100). *M.Dev.-U.Perm.*

Superfamily CHEILOCERATACEAE Frech, 1897

[*nom. transl.* MILLER & FURNISH, 1954 (*ex* Cheiloceratidae FRECH, 1897)]

Sutures typically with 3 pairs of lobes of which the external lateral pair arises adventitiously (52,100). *M.Dev.-M.Perm.*

Family TORNOCERATIDAE Arthaber, 1911

[*nom. correct.* J.P.SMITH, 1913 (*ex* Tornoceratea ARTH., 1911)]

Conch subdiscoidal, growth lines biconvex. Sutures form 6 to 10 lobes, the ventral one undivided and those on lateral areas originating as subdivisions of external and internal lateral saddles (46,100). *M.Dev.-U.Dev.*

Tornoceras HYATT, 1884 [**Gon. uniangularis* CONRAD, 1842] [=*Parodiceras* HYATT, 1884 *(Parodoceras, auctt.); Epitornoceras* FRECH, 1902]. Sutures form 6 lobes, lateral ones rounded. Sculpture, umbilicus, and shape of sutures variable (46,100). *M.Dev.-U.Dev.*

T. (Tornoceras). Closed umbilicus and moderate sutural flexures. *M.Dev.-U.Dev.;* widespread N. Am.-Eurasia-N.Afr.-W.Austral.——FIG. 46; 47*B.* **T. (T.) uniangulare,* U.Dev., N.Y.; 46, ×1; 47*B,* ×2.5 (107).——FIG. 47*A. T. (T.) discoideum* (HALL), M.Dev., N.Y.; ×1.3 (12).——FIG. 48. *T. (T.) crebriseptum* RAYMOND, U.Dev., Mont.; *A-D,* enlarged (110).

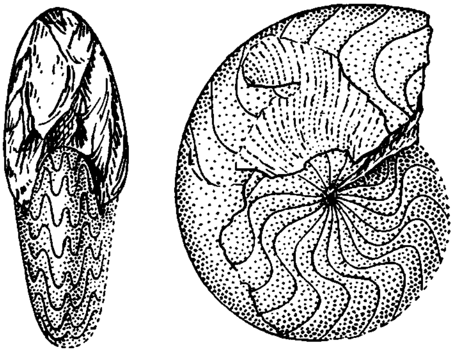

FIG. 46. *Tornoceras uniangulare* (CONRAD), U.Dev., N.Y.; ×1 (110).

T. (Aulatornoceras) SCHINDEWOLF, 1922 [**Gon. auris* QUENSTEDT, 1846]. Conch with ventrolateral grooves. *U.Dev.,* N.Am.-Eu.——FIG. 47*C.* **T. (A.) auris* (QUENST.), U.Dev., Ger.; ×5 (110).——FIGS. 49; 50. *T. (A.) bicostatum* (HALL), U.Dev., N.Y.; 49, enlarged; 50, ×3 (12).

T. (Protornoceras) DYBCZYŃSKI, 1913 [**P. polonicum*] [=*Pernoceras* SCHINDEWOLF, 1922]. Umbilicus open. Sutures with little relief. *M.Dev.-U.Dev.,* Eu.

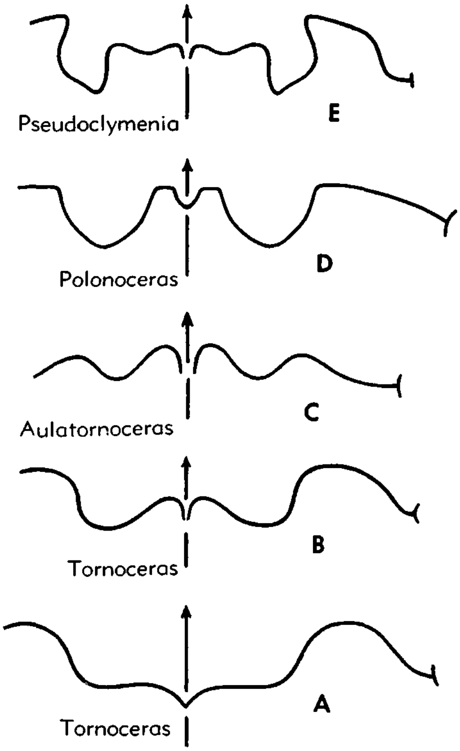

FIG. 47. Sutures of 3 subgenera of *Tornoceras* *(A-D),* and *Pseudoclymenia (E)* (110).

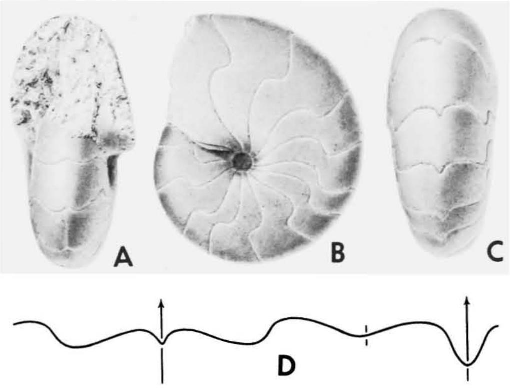

Fig. 48. *Tornoceras (Tornoceras) crebriseptum* Raymond, U.Dev., Mont.; *A-D*, enlarged (110).

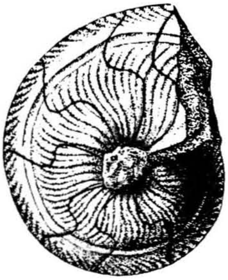

Fig. 49. *Tornoceras (Aulatornoceras) bicostatum* (Hall), U.Dev., N.Y., enlarged (12).

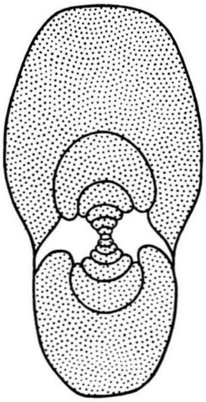

Fig. 50. Cross section of *Tornoceras (Aulatornoceras) bicostatum* (Hall), U.Dev., N.Y.; ×3 (12).

T. (Polonoceras) Dybczyński, 1913 [**P. planum*]. Conch angular ventrolaterally. Sutures form prominent ventrolateral saddles. *U.Dev.*, Eu.——Fig. 47*D*. **T. (P.) planum*, U.Dev., Pol.; ×2 (105).

Pseudoclymenia Frech, 1897 [**Gon. sandbergeri* Gümbel, 1862 (*non* Foord & Crick, 1897)]. Like *Tornoceras* but characteristically narrower conch and wider umbilicus (100). *U.Dev.*, Eu.-N.Afr.-W. Austral.——Fig. 47*E*. **P. sandbergeri* (Gümbel), Ger.; ×1.3.

Lobotornoceras Schindewolf, 1936 [**Gon. ausavensis* Steininger, 1855]. Like *Tornoceras* but internal sutures form additional pair of lobes (46). *U.Dev.*, Eu.

Posttornoceras Wedekind, 1910 [**P. balvei*]. Like *Sporadoceras* but biconvex growth lines (100). *U.Dev.*, Ger.-?Pol.

Family CHEILOCERATIDAE Frech, 1897

Sutures form 4 to 12 lobes, ventral one undivided and those of lateral areas originating as subdivisions of external and internal lateral saddles (70,100). *U.Dev.-M.Perm.*

Subfamily CHEILOCERATINAE Frech, 1897

[*ex* Cheiloceratidae]

Sutures consist of 6 to 10 lobes, of which 5 (including umbilical) are external. Growth lines convex, forming lateral salients. *U.Dev.*

Cheiloceras Frech, 1897 [**Gon. subpartitus* Münster, 1839] [=*Eucheiloceras* Schmidt, 1921; *Cheilocerotes* Strand, 1929]. Conch subglobular to thickly lenticular; umbilicus closed. Lateral and dorsal lobes of sutures variable (45,97,100). *U. Dev.*

C. (Cheiloceras). Suture with shallow lateral and flat undivided dorsal lobes (100). *U.Dev.*, Eurasia-N.Afr.-W.Austral.——Fig. 51. **C. (C.) subpartitum* (Münster), U.Dev., Ger.; ×1 (100).——Fig. 25*C*. *C. (C.)* sp., U.Dev., Ger.; enlarged (73).

Fig. 51. *Cheiloceras subpartitum* (Münster), U. Dev., Ger.; ×1 (100).

C. (Torleyoceras) Wedekind, 1918 [**Gon. retrorsus curvispina* Sandb.-S., 1851] [=*Centroceras* Wdkd., 1908 (*non* Hyatt, 1884); *Staffites* Wdkd., 1918; *Centroceratos* Strand, 1929]. Sutures with deep lateral lobes and more or less trifid dorsal lobe (100). *U.Dev.*, Eu.

C. (Dyscheiloceras) Schmidt, 1921 [**C. (D.) biesenbergense*]. Conch subdiscoidal; dorsal lobe of sutures bifid (45). *U.Dev.*, Ger.

Dimeroceras Hyatt, 1884 [**Gon. mamillifer* Sandb.-S., 1850]. Like *Cheiloceras* but suture has large lateral lobe and umbilical lobe outside umbilicus (100). *U.Dev.*, Eurasia-N.Afr.-W.Austral.

Heminautilinus Hyatt, 1884 [**Gon. hybridus* Münster, 1832]. Poorly known. May be senior synonym of *Cheiloceras* (46,73). *U.Dev.*, Ger.

Subfamily RAYMONDICERATINAE Miller & Furnish, nov.

Sutures have 4 distinct lobes; growth lines convex. *U.Dev.*

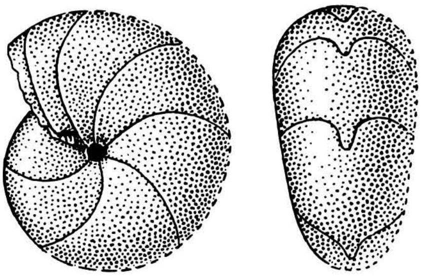

FIG. 52. *Raymondiceras simplex* (Raymond), U. Dev., Mont.; ×2 (112).

Raymondiceras Schindewolf, 1934 [**Prolobites simplex* Raymond, 1909]. Conch subglobular with small closed umbilici. Sutures have incipient lobe in broad 1st lateral saddle (46). *U.Dev.,* Mont. ——Fig. 25*B;* 52. **R. simplex* (Raymond); 25*B,* enlarged; 52, ×2 (112).

Subfamily SPORADOCERATINAE Miller & Furnish, nov.

Sutures with 10 to 12 lobes, of which 3 (excluding umbilical) are internal (70,100). *U.Dev.*

Sporadoceras Hyatt, 1884[**Am. muensteri* von Buch, 1832] [=*Cryptoclymenia, Maeneceras* Hyatt, 1884]. Conch subglobular to discoidal, umbilicus small, closed. Sutures with lobes next to ventral lobe formed adventitiously in 1st lateral saddles (46,70,100). *U.Dev.,* Eurasia-N.Afr.-W. Austral.-E.USA.——Fig. 53. **S. muensteri* (Buch), Ger.; ×1 (68).——Fig. 26*A. S. biferum* (Phillips), Ger.; ×1 (68).——Fig. 54. *S. milleri* (Flower & Caster), Pa.; ×1.5 (110).

Discoclymenia Hyatt, 1884 [**Gon. cucullatus* von Buch, 1839] [=*Wedekindoceras* Schindewolf, 1923]. Like *Sporadoceras* but suture with additional adventitious lobes in 1st lateral saddles (70). *U.Dev.,* Eu.-N.Afr.

Praeglyphioceras Wedekind, 1908 [**Sporadoceras pseudosphaericum* Frech, 1902]. Like *Sporadoceras* but lobes of sutures next to ventral lobe develop by that lobe becoming trifid. Affinities uncertain (22). *U.Dev.,* Ger.

Subfamily IMITOCERATINAE Ruzhencev, 1950

[*nom. transl.* Miller & Furnish, herein (*ex* Imitoceratidae Ruzhencev, 1950)]

Sutures with 8 distinct lobes. *U.Dev.-M. Perm.*

Imitoceras Schindewolf, 1923 [**Am. rotatorius* de Koninck, 1844] [=*Brancoceras* Hyatt, 1884 (*non* Steinmann, 1881); *Balvia* Lange, 1929; *Neoaganides* Plummer & Scott, 1937; *Irinoceras* Ruzhencev, 1947; *non Aganides* de Montfort, 1808]. Conch globular to discoidal, with closed umbilici (48,70). *U.Dev.-M.Perm.;* widespread in Eurasia-N.Afr.-USA.——Fig. 55. **I. rotatorium* (Kon.), L.Miss., Ind.; *A-C,* ×0.9; *D,* ×1.75.——Fig. 56. *I. grahamense* (Plummer-S.), U.Penn., Kans.; ×2 (110).

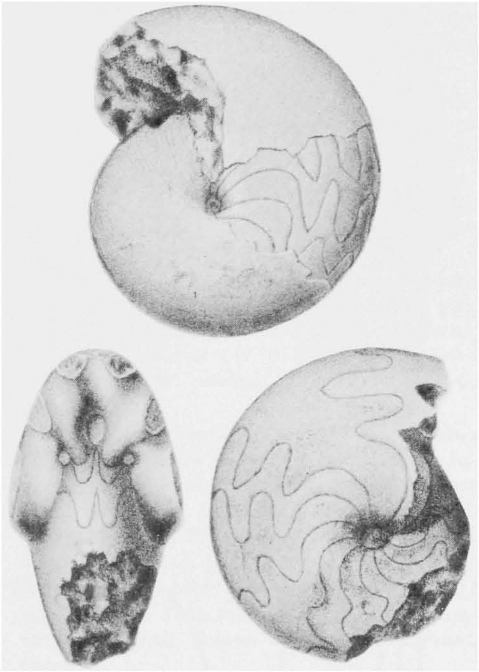

FIG. 53. *Sporadoceras muensteri* (von Buch), U. Dev., Ger.; ×1 (68).

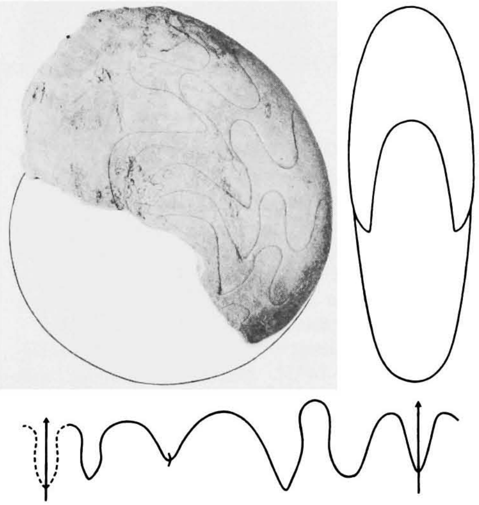

FIG. 54. *Sporadoceras milleri* (Flower & Caster), U.Dev., Pa.; ×1.5 (110).

Prionoceras Hyatt, 1884 (*non* Buckman, 1920) [**Gon. divisus* Münster, 1843] [=?*Postprolobites*

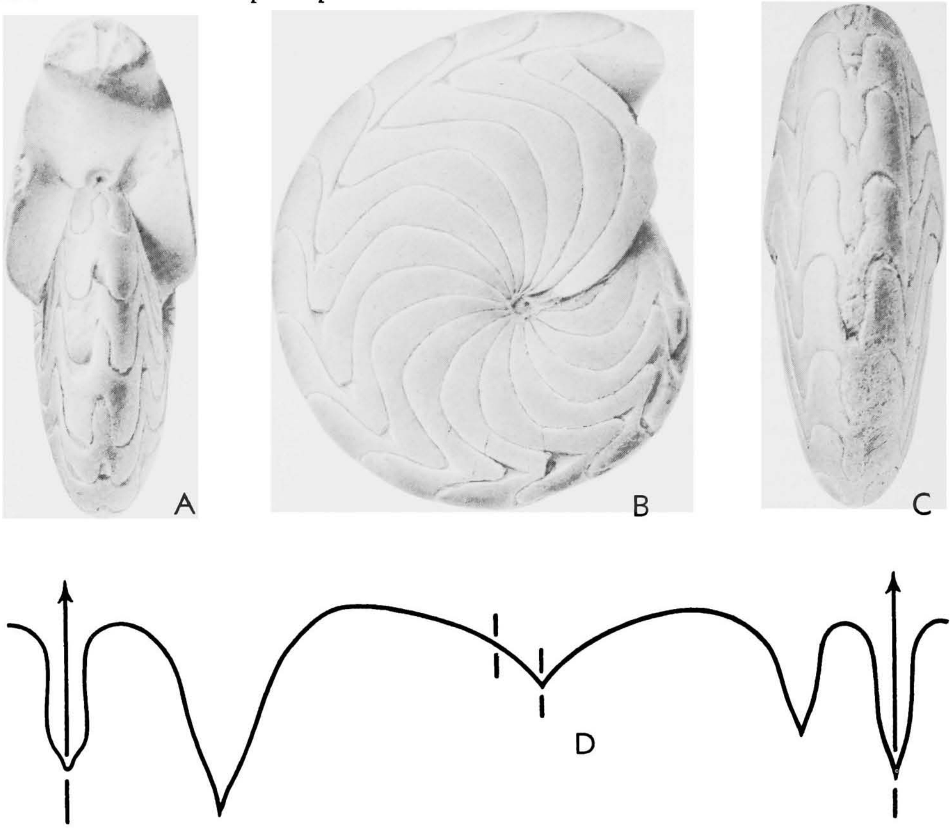

FIG. 55. *Imitoceras rotatorium* (DE KONINCK), L.Miss., Ind.; *A-C,* ×0.9; *D,* ×1.75 (110).

WEDEKIND, 1913]. Subglobular conch with constrictions that form lateral salient. Sutures poorly known. May be senior synonym of *Imitoceras* (48, 70). *U.Dev.-L.Carb.,* Ger.

Hunanites CHAO, 1940 [**H. hsiehi*]. Globular conch with transverse ribs and closed umbilici. Sutures as in *Imitoceras* but ventral and lateral lobes serrate. *Perm.,* Arabia-China(Hunan).

Gattendorfia SCHINDEWOLF, 1920 [**Gon. subinvolutus* MÜNSTER, 1843]. Like *Imitoceras* but with open umbilici; umbilical lobe centers outside umbilical seam (44,48,70). *U.Dev.-L.Carb.(Miss.),* widespread in Eurasia-N.Afr.-USA.

Paralytoceras FRECH, 1902 [**Cly. crispa* TIETZE, 1870]. Subdiscoidal conch with moderately large umbilicus. Sutures poorly known. May be senior synonym of *Gattendorfia* (22). *U.Dev.,* Ger.

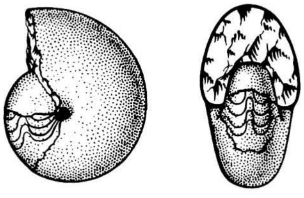

FIG. 56. *Imitoceras grahamense* (PLUMMER & SCOTT), U.Penn., Kans.; ×2 (60).

Kazakhstania LIBROVITCH, 1940 [**Gattendorfia (K.) karagandaensis*]. Like *Gattendorfia* but with large umbilici (44,53). *L.Carb.(Miss.),* Kazakhstan-Mich.

Superfamily AGATHICERATACEAE Arthaber, 1911

[*nom. transl.* MILLER & FURNISH, 1954 (*ex* Agathiceratidae ARTHABER, 1911)]

Subdiscoidal to globular conchs with variable umbilici and sutures that are goniatitic to ammonitic. In primitive representatives sutures have trifid lateral lobe, which gives rise to 3 (or 4) independent lobes in advanced forms. *L.Penn.-M.Perm.*

Family AGATHICERATIDAE Arthaber, 1911

Conch subdiscoidal to globular, umbilicus small, test prominently longitudinally lirate. Sutures goniatitic (30,50). *L.Penn.-M.Perm.*

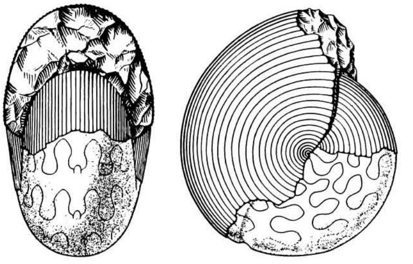

FIG. 57. *Agathiceras suessi* Gemmellaro, M.Perm., Sicily; ×2 (24).

Agathiceras Gemmellaro, 1887 [*A. suessi] [=*Gaetanoceras* Ruzhencev, 1938; *Paragathiceras* Ruzh., 1950]. Suture forms 3 subequal lateral lobes but a single dorsolateral lobe; external lobes spatulate, internal ones V-shaped. Siphuncle retrochoanitic with long septal necks (54,65). *L.Penn.-M.Perm.*, widespread, locally very abundant.——FIG. 57. *A. suessi, M.Perm., Sicily; ×2 (110).——FIG. 11*A-E*. *A. uralicum* Karpinsky, M.Perm., Urals; enlarged.——FIG. 58. *A. frechi* Böse, U. Penn., Tex.; ×2 (110).

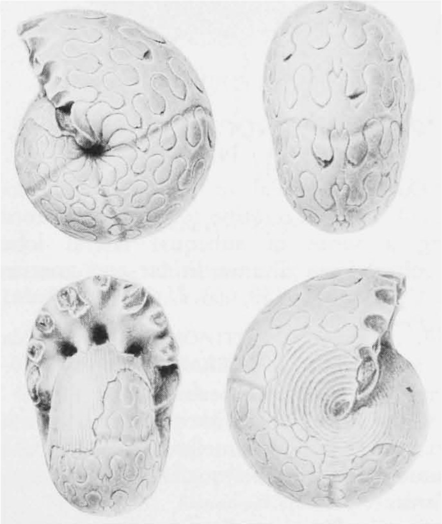

FIG. 58. *Agathiceras frechi* Böse, U.Penn., Tex.; ×2 (54).

Proshumardites Rauser, 1928 [*P. karpinskii]. Like *Agathiceras* but sutures more primitive (15,65). *U.Carb.*, M.Asia-Urals-Sp.-N.Afr.

Family SHUMARDITIDAE Plummer & Scott, 1937

Conch subglobular to globular, with moderately small to large umbilicus and generally advanced goniatitic sutures in which external and internal lateral lobes and dorsal lobe are trifid. Gradational with and ancestral to Popanoceratidae and Perrinitidae (49,60,65). *U.Penn.(U.Carb.).*

Shumardites Smith, 1903 [*S. simondsi]. Umbilicus moderately large. Divisions of external lateral lobe of suture subequal, umbilical lobe relatively simple, dorsolateral lobe asymmetrical (49,65). *U.Carb. (U.Penn.)*, Tex. - N.Mex. - Urals.——FIG. 59*F*. *S. simondsi, U.Penn., Tex.; ×2. [*Shumardites*=*Postaktubites* Ruzhencev, 1955.]

Vidrioceras Böse, 1919 [*V. uddeni]. Like *Shumardites* but with smaller umbilicus. Sutures with broad trifid umbilical lobe and divisions of dorsolateral lobe subequal (49,50). *U.Penn.*, Tex.——FIG. 59*A-D*. *V. uddeni, U.Penn., Tex.; *A-C*, ×1.25; *D*, ×2.

Subshumardites Schindewolf, 1939 [*Shumardites fornicatus Plummer & Scott, 1937] [=*Parashumardites* Ruzhencev, 1939]. Like *Shumardites* but suture with broad trifid umbilical lobe (65). *U. Carb.(U.Penn.)*, Tex.-Okla.-USSR.——FIG. 59*E*. *S. eurinus* (Ruzh.), U. Carb., Urals; ×2 (65).

Pericleites Renz, 1910 [*Paralegoceras (Pericleites) atticum]. Like *Shumardites* but with smaller umbilicus; internal sutures unknown. *?U.Penn.*, Greece.

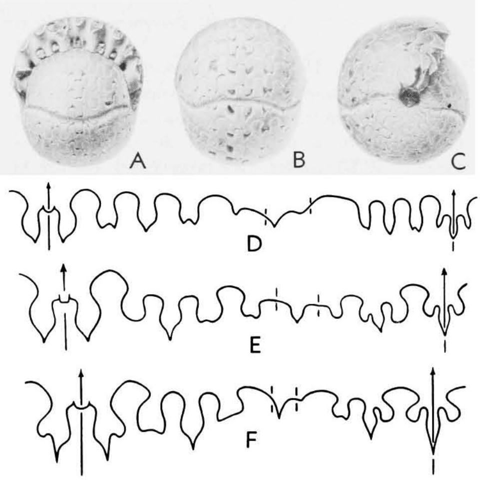

FIG. 59. *Vidrioceras (A-D)*, *Subshumardites (E)*, and *Shumardites (F)*, U.Penn. (110, 65).

Family PERRINITIDAE Miller & Furnish, 1940

Conch thickly subdiscoidal to subglobular and involute, umbilicus small. Sutures ammonitic with distinctly V-shaped lateral lobes of which there are 5 pairs both externally and internally. Evolved directly from Shumarditidae (50). *L.Perm.-M.Perm.*

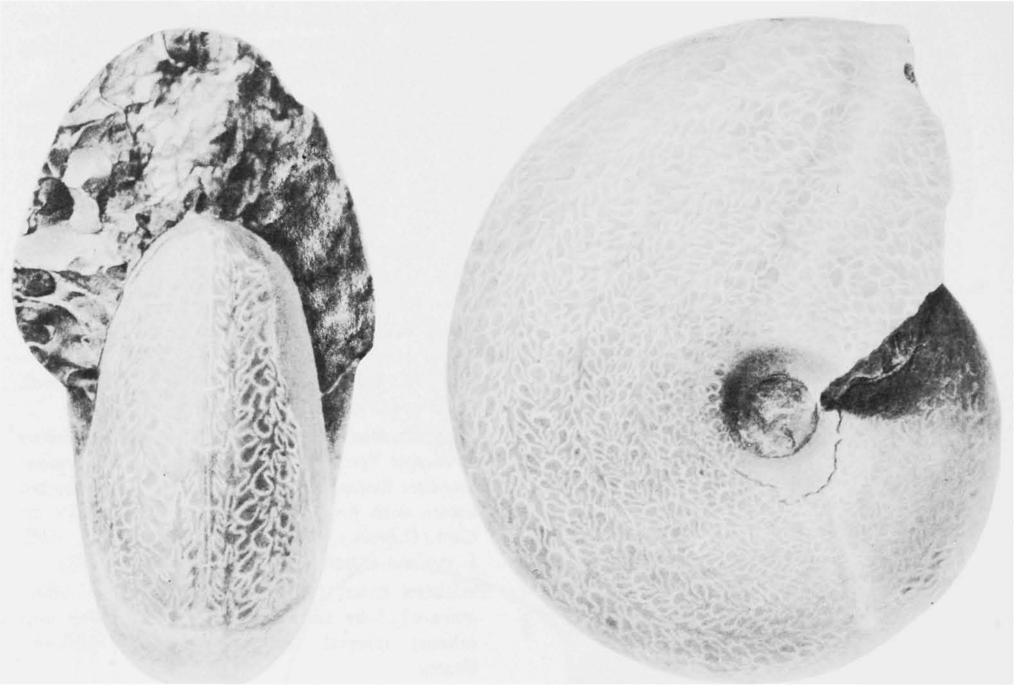

FIG. 60. *Perrinites hilli* (SMITH), M.Perm., Tex.; ×1.8 (110).

Perrinites BÖSE, 1919 [**Waagenoceras hilli* SMITH, 1903] [=*Paraperrinites* TOUMANSKY, 1939]. External and internal sutures prominently digitate. Conch attains a diameter of 30 cm. (50). *M. Perm.,* W.USA.-Mex.-Colombia-Timor-Crimea-M. Asia.——FIGS. 7*C;* 8*A-F;* 60; 61*B.* **P. hilli* (SMITH), M.Perm., Tex.; 7*C,* ×1.3; 8*A-F,* enlarged; 60, ×1.8; 61*B,* ×2.

Properrinites ELIAS, 1938 [**Perrinites boesei* PLUMMER & SCOTT, 1937]. Like *Perrinites* but sutures less strongly digitate. Gradational with and intermediate between *Shumardites* and *Perrinites. L. Perm.,* SW.USA.-M.Asia-Timor.——FIG. 61*A.* **P. boesei* (PLUMMER-S.), L.Perm., Tex.; ×10. [*Properrinites*=*Metaperrinites* RUZHENCEV, 1955.]

Superfamily CYCLOLOBACEAE Zittel, 1895

[*nom. transl.* MILLER & FURNISH, 1954 (*ex* Cyclolobidae ZITTEL, 1895)]

Thickly discoidal to globular conchs, typically with small umbilici and ceratitic sutures that possess auxiliary lobes. Primitive representatives have few auxiliary lobes, but advanced forms have many and have ammonitic sutures. *U.Carb.(M.Penn.)-U. Perm.*

Family POPANOCERATIDAE Hyatt, 1900

Conch discoidal to globular, umbilicus small. Sutures ceratitic to ammonitic, forming a series of subequal lateral lobes. Evolved from Shumarditidae and ancestral to Cyclolobidae (50, 66). *U.Carb.(M.Penn.)-U.Perm.*

Subfamily POPANOCERATINAE Hyatt, 1900

[*nom. transl.* (*ex* Popanoceratidae HYATT, 1900)]

Conch discoidal, with prominent sinuous transverse growth lamellae. Lateral lobes of sutures tend to be quadrifid. *L.Perm.-M. Perm.*

Popanoceras HYATT, 1884 [**Gon. sobolewskyanus* DE VERNEUIL, 1845] [=*Gemmellaroceras* TOUMANSKY, 1937 (*non* HYATT, 1900); *Tauroceras* TOUM., 1938; *Neopopanoceras* SCHINDEWOLF, 1939]. Lateral areas of conch bear series of depressions during adolescence. Prongs of ventral lobe of sutures large and multidigitate (50). *M.Perm.,* Urals-N. Zem.-Crimea-Alps-Sicily-Tunisia-M. Asia - Timor-Tex.——FIG. 62. *P. bowmani* (BÖSE), Tex.; *A-C,* ×1.5; *D,* ×4.——FIG. 2,8*a,b. P. scrobiculatum* GEMMELLARO, Sicily, ×1 (24).

Propopanoceras TOUMANSKY, 1938 [**Popanoceras lahuseni* KARPINSKY, 1889] [=*Protopopanoceras* RUZHENCEV, 1938]. Like *Popanoceras* but prongs

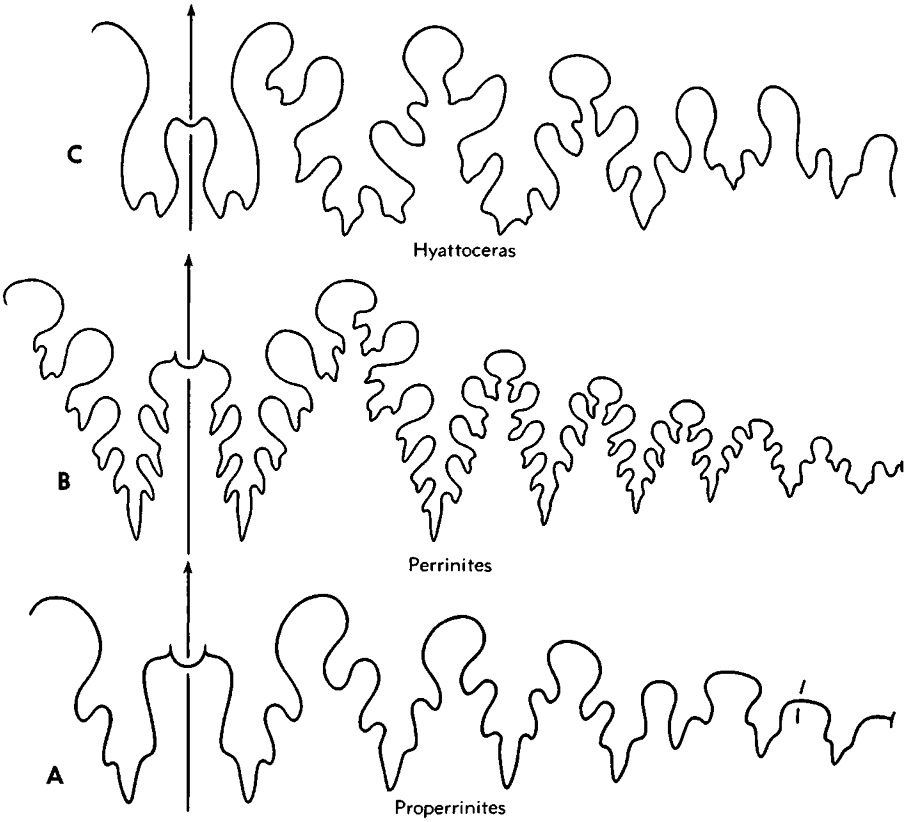

Fig. 61. Sutures of *Properrinites (A), Perrinites (B),* and *Hyattoceras (C),* Perm. (110).

of ventral lobe of sutures small and bifid (66). *L.Perm.-M.Perm.,* Urals.

Subfamily MARATHONITINAE Ruzhencev, 1938

[*ex* Marathonitidae]

Conch subglobular to globular. Lateral lobes of sutures tend to be trifid. *U.Carb. (M.Penn.)-U.Perm.*

Peritrochia Girty, 1908 [**P. erebus*] [=*Marathonites* Böse, 1919; *Pseudovidrioceras* Ruzhencev, 1936; *Prostacheoceras* Ruzh., 1937; *Kargalites* Ruzh., 1938; *Policeras* Toumansky, 1939; *Almites* Toum., 1941; *Martites* Toum., 1949; *Subkargalites, Neomarathonites* Ruzh., 1950; *Tabantalites* Ruzh., 1952]. Both external and internal sutures form 3 to 5 pairs of lateral lobes. Gradational with *Shumardites* and *Stacheoceras* (30,50,65). *U.Carb.-(M.Penn.)-M.Perm.,* W.USA-Chiapas-Sicily-Crimea-Urals-M.Asia-Timor.——Fig. 64. *P. ganti* (Smith), U.Penn., Tex.; ×1.

Stacheoceras Gemmellaro, 1887 [**S. mediterraneum*] [=*Waagenia* Krotow, 1885 (*non* Kriechbaumer, 1874, *et auctt.*); *Waagenina* Krotow, 1888, *Neostacheoceras* Schindewolf, 1931; *Martoceras, Pamirites* Toumansky, 1938]. Like *Peritrochia* but both external and internal sutures form 5 to 10 pairs of lateral lobes (50). *M.Perm.-U.Perm.,* Sicily-Croatia-Tunisia-Crimea-Urals-Pamirs-Armenia-Salt R.-Himal.-Timor - Japan - SW.USA-Coah.——Fig. 7*B;* 64. *S. toumanskyae* Miller & Furnish, M.Perm., Coah.; 7*B,* ×3; 64, ×1.

Subfamily HYATTOCERATINAE Miller & Furnish, nov.

Umbilicus closed; sutures ammonitic. *M. Perm.*

Hyattoceras Gemmellaro, 1887 [**H. geinitzi*] [=*Abichia* Gemm., 1887; *Prohyattoceras* Oyens, 1938 (*nom. nud.*)]. Superficially resembles perrinitids, but subdivisions of ventral lobe of sutures small and bifid (24). *M.Perm.,* Sicily-Timor.——Fig. 2,7*a,b;* 61*C.* **H. geinitzi,* Sicily; 2,7*a,b,* ×1.25; 61*C,* enlarged (24).——Fig. 2,2*a-c. H. abichi* Gemm., Sicily; ×1.25 (24). [*Hyattoceras*= *Demarezites* Ruzhencev, 1955.]

Family CYCLOLOBIDAE Zittel, 1895

Conch thickly subdiscoidal to subglobular,

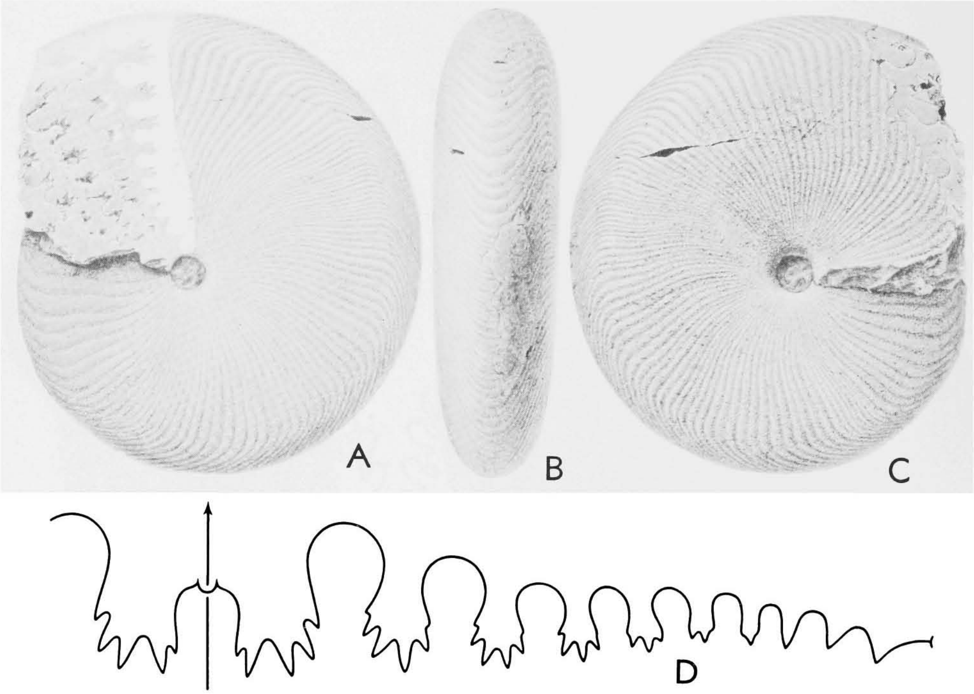

FIG. 62. *Popanoceras bowmani* (BÖSE), M.Perm., Tex.; *A-C*, ×1.5; *D*, ×4 (110).

umbilicus open but small. Sutures ammonitic, with numerous lobes that have subparallel flanks. Evolved from Marathonitinae (50). *M.Perm.-U.Perm.*

Cyclolobus WAAGEN, 1879 [**C. oldhami*] [=*Krafftoceras* DIENER, 1903; *Godthaabites* FREBOLD, 1932]. Conch thickly subdiscoidal. Both external and internal suture arcuate, with 10 to 15 pairs of lateral lobes and 1st lateral saddle divided (93,95). *U.Perm.*, SaltR.-Himal.-S.China-Madag.-Greenl.——FIG. 65. **C. oldhami*, SaltR.; *A,B*, ×0.9; *C*, ×1.7 (95).

Timorites HANIEL, 1915 [**T. curvicostatus*] [=*Hanieloceras* MILLER, 1933; *Wanneroceras* TOUMANSKY, 1937 *(nom. nud.)*]. Like *Cyclolobus* but sutures form only 8 to 10 pairs of lateral lobes and conch bears relatively prominent ribs (47, 50). *M.Perm.*, Timor-Japan-E.Sib.-Tex.-Coah.——FIG. 66. **T. curvicostatus*, Timor; *A,B*, ×0.5; *C*, ×1 (96).

Waagenoceras GEMMELLARO, 1887 [**W. mojsisovicsi*]. Conch subglobular. Both external and internal sutures more or less arcuate and form 4 to 8 pairs of lateral lobes (47,50). *M.Perm.*, Sicily-Tex.-Coah.-Timor.-E.China.——FIGS. 2,*1a,b;* 67*A,B*. *W. guadalupense* GIRTY, Tex.; all ×1.——FIG. 67*C,D*. *W. dieneri* BÖSE, Tex.; ×1.7. [*Waagenoceras*=*Mexicoceras* RUZHENCEV, 1955.]

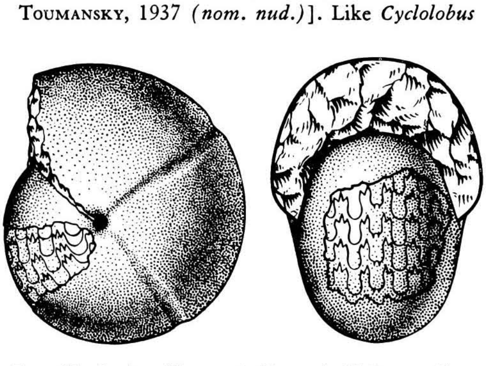

FIG. 63. *Peritrochia ganti* (SMITH), U.Penn., Tex.; ×1 (110).

FIG. 64. *Stacheoceras toumanskyae* MILLER & FURNISH, M.Perm., Coah.; ×1 (110).

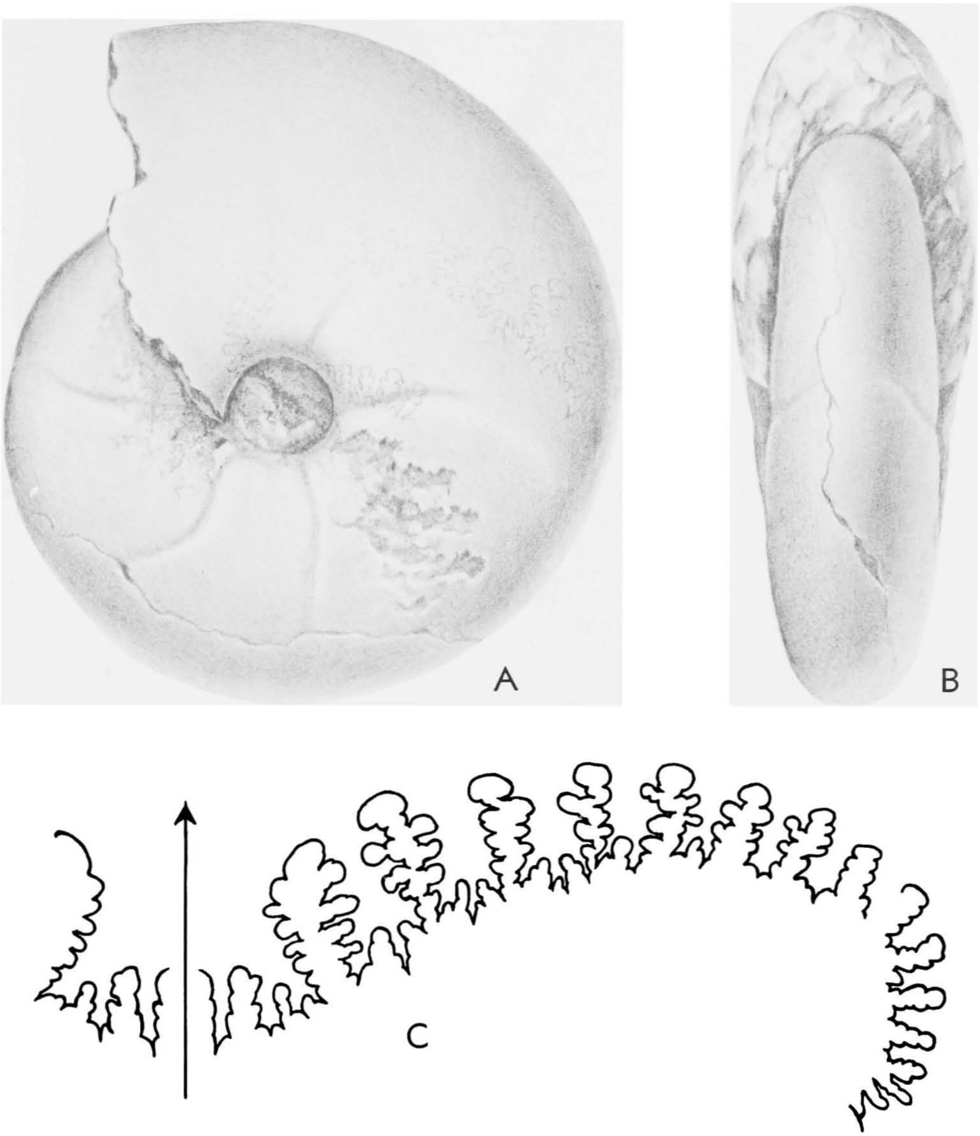

Fig. 65. *Cyclolobus oldhami* Waagen, U.Perm., SaltR.; *A,B,* ×0.9; *C,* ×1.7 (95).

Superfamily GONIATITACEAE de Haan, 1825

[*nom. transl.* Miller & Furnish, 1954 (*ex* Goniatitea de Haan, 1825)]

Thinly discoidal or lenticular to globular conchs with variable umbilici and sculpture. Sutures goniatitic, with ventral lobe prominently bifid and lateral lobe undivided. *L. Carb.(L.Miss.)-U.Perm.*

Family GONIATITIDAE de Haan, 1825

[*pro* Goniatitea]

Characteristically without prominent sculpture. Sutures form 8 lobes (4,22,44,55, 60,78). *L.Carb.(L.Miss.)-L.Perm.*

Subfamily GONIATITINAE de Haan, 1825

[*ex* Goniatitea]

Typical goniatites with small to moderate umbilici. Suture with narrow ventral lobe. *L.Carb.(L.Miss.)-M.Penn.*

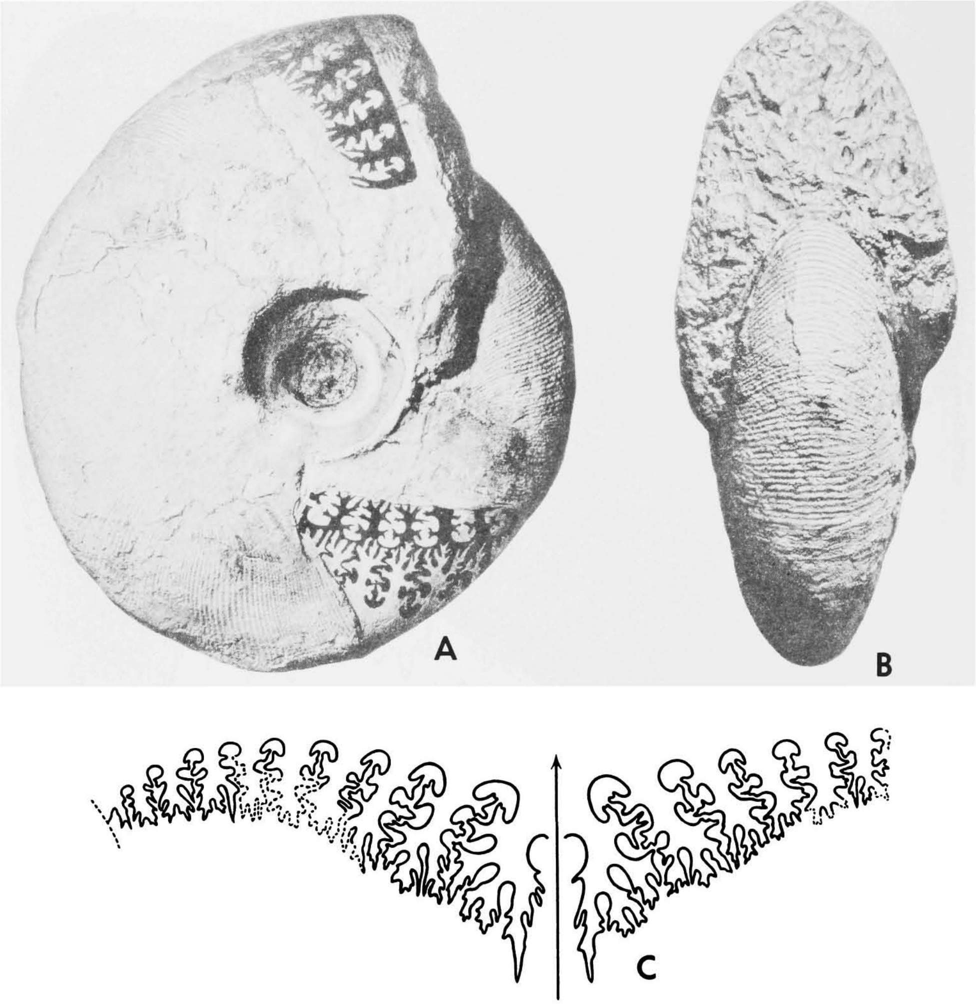

Fig. 66. *Timorites curvicostatus* Haniel, M.Perm., Timor; *A,B,* ×0.5; *C,* ×1 (96).

Goniatites de Haan, 1825 [**Conchyliolithus Nautilites sphaericus* Martin, 1809] [=*Glyphioceras* Hyatt, 1884; *Sphenoceras* Foord, 1903; *Paraglyphioceras* Brüning, 1923]. Conch globular, umbilicus small. First lateral saddle of suture subangular to angular (4,20,21). *L.Carb.(U.Miss.),* widespread in Eurasia-N.Afr.-N.Am.——Fig. 68. *Gon. choctawensis* Shumard, Tex.; *A-C,* ×2; *D,* ×4.

Nautellipsites Parkinson, 1822 [**Ellipsolites ovatus* Sowerby, 1813]. Poorly known. May be senior synonym of *Goniatites* or *Beyrichoceras* (4,16,21). *L.Carb.,* Ire.

Cravenoceras Bisat, 1928 [**Homoceras malhamense* Bisat, 1924]. Like *Goniatites* but 1st lateral saddles of sutures rounded (55,60). *L.Carb.(U.Miss.)-U.Carb.(L.Penn.),* locally abundant in Eurasia-N. Afr.-N.Am.——Fig. 69. *S. hesperium* Miller & Furnish, U.Miss., Nev.; ×2 (102). [*Cravenoceras* =*Richardsonites* Elias, 1956.]

Homoceras Hyatt, 1884 [**Gon. calyx* Phillips]. Poorly known; type immature (4). *L.Carb.,* Eng.

Homoceratoides Bisat, 1924 [**H. prereticulatum*]. Conch discoidal, with small umbilici and biconvex growth lines. Sutures of type species unknown (4). *L.Carb.,* Eurasia.

Reticuloceras Bisat, 1924 [**Gon. reticulatus* Phillips, 1836] [=*Verneuilites* Librovitch, 1939]. Conch subdiscoidal to lenticular with small umbilici and biconvex growth lines. Suture with small ventral lobe (4). *L.Carb.,* Eurasia.

Anthracoceras Frech, 1899 [**Nomismoceras (Anthracoceras) discus*]. Like *Reticuloceras* but suture with wider ventral lobe. Type poorly known. *L.Carb.(U.Miss.)-U.Carb.(M.Penn.),* Eurasia-?N.Afr.-?N.Am.-?S.Am.

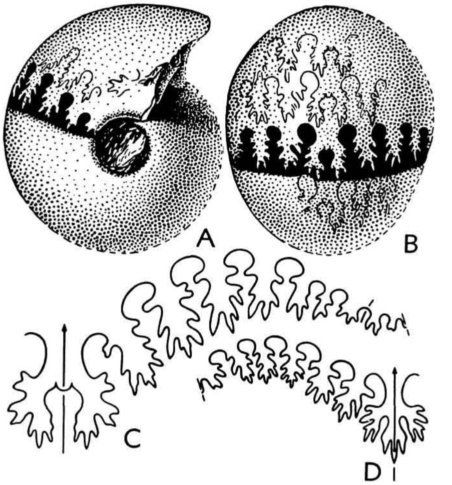

FIG. 67. *Waagenoceras,* M.Perm., Tex.; *A,B, W. guadalupense* GIRTY, ×1; *C,D, W. dieneri* BÖSE, ×1.7 (110).

Beyrichoceras FOORD, 1903 [**Gon. obtusus* PHILLIPS, 1836] [=*Cravenites* BISAT, 1950; *Cowdaleoceras* BISAT, 1952]. Conch thickly subdiscoidal with small umbilici. Ventral lobe of suture constricted distally (4,20,53). *L.Carb.(Miss.),* Eu.-N.Afr.-N.Am.——FIG. 70. *B. hornerae* MILLER, L.Miss., Mo.; *A-C,* ×0.4; *D,* ×1.

Muensteroceras HYATT, 1884 [**Gon. oweni parallela* HALL, 1860] [=*Eoglyphioceras* BRÜNING, 1923; *Beyrichoceratoides* BISAT, 1924; *Karakoramoceras* MILLER, 1931; *Bollandites, Bollandoceras* BISAT, 1952]. Conch discoidal to globular, with small to moderate umbilici. Ventral lobe of suture narrow and with parallel sides (6,15,44,48,53). *L. Carb.(Miss.),* N.Am.-Eurasia-N.Afr.-Austral.——FIG. 71. **M. parallelum* (HALL), L.Miss., Ind.; *A-C,* ×1.8; *D,* ×3.4.

Subfamily NEOGLYPHIOCERATINAE Plummer & Scott, 1937

[*ex* Neoglyphioceratidae]

Conch subdiscoidal, umbilicus small to

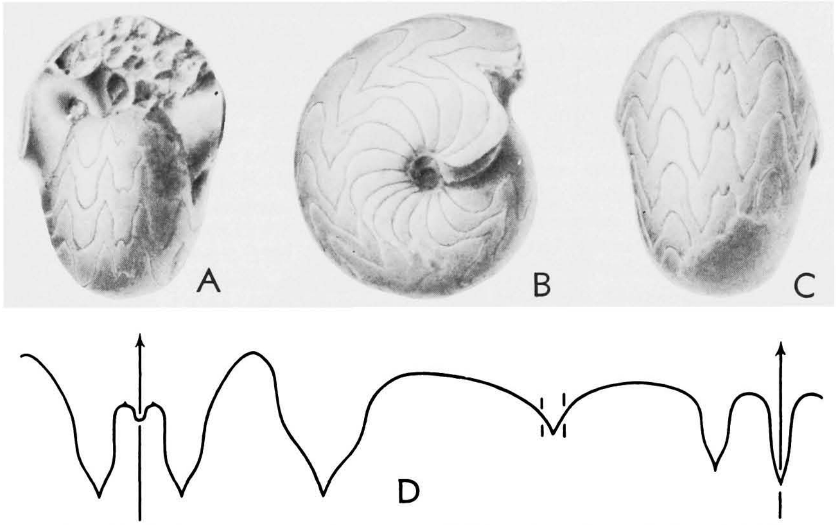

FIG. 68. *Goniatites choctawensis* SHUMARD, U.Miss., Tex.; *A-C,* ×2; *D,* ×4 (110).

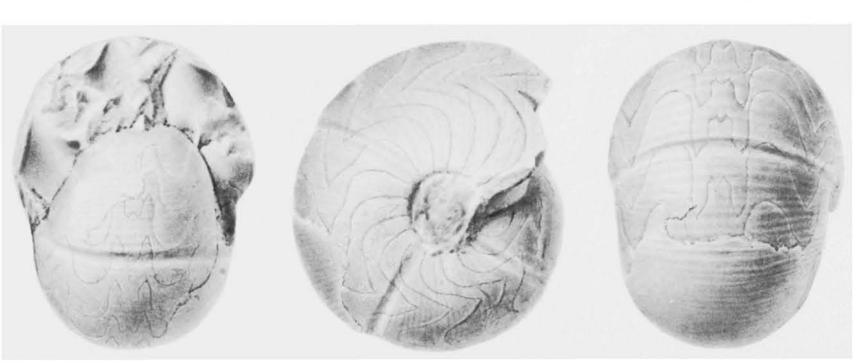

FIG. 69. *Cravenoceras hesperium* MILLER & FURNISH, U.Miss., Nev.; ×2 (102).

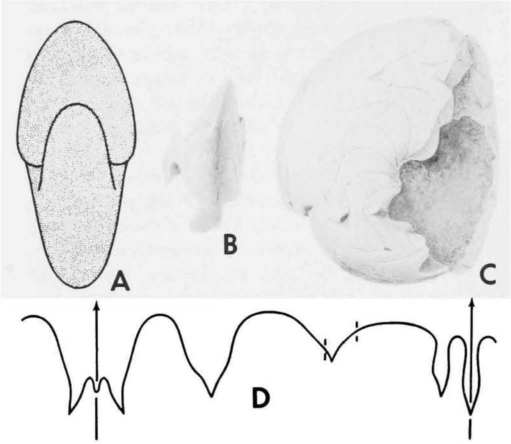

FIG. 70. *Beyrichoceras hornerae* MILLER, L.Miss., Mo.; *A-C*, ×0.4; *D*, ×1 (110).

FIG. 72. *Lyrogoniatites newsomi georgiensis* MILLER & FURNISH, U.Miss., Ga.; ×1 (110).

moderately large, prominent longitudinal sculpture. Ventral lobe of suture broad (51). *L.Carb.(U.Miss.)*.

Lyrogoniatites MILLER & FURNISH, 1940 [**L. newsomi georgiensis*] [=*Entogonoceras* PLUMMER & SCOTT, 1937 *(nom. nud.)*]. Umbilicus moderately large (51,60). *L.Carb.(U.Miss.)*, USA-Eng.-N.Afr. ——FIG. 72. **L. newsomi georgiensis*, Ga.; ×1.

Neoglyphioceras BRÜNING, 1923 [**Gon. spiralis* PHILLIPS, 1841] [=*Lusitanoceras* PEREIRA DE SOUSA, 1924; *Paragoniatites* LIBROVITCH, 1938]. Umbilicus small (51). *L.Carb.(U.Miss.)*, N.Am.-Eurasia-N.Afr.——FIG. 73. *N. subcirculare* (MILLER), Ky.; *A,B*, ×2; *C*, enlarged.

Subfamily PERICYCLINAE Miller & Furnish, nov.

Conch subdiscoidal to globular; umbilicus moderate to large; prominent transverse sculpture; narrow ventral lobe (21,76). *L. Carb.(Miss.)*.

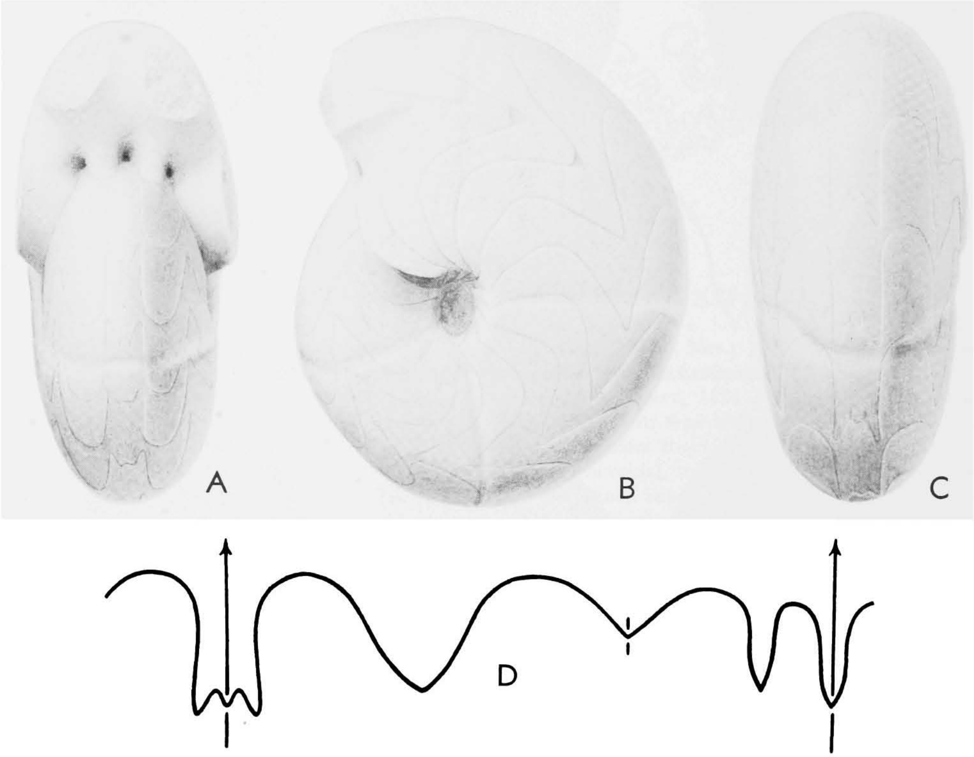

FIG. 71. *Muensteroceras parallelum* (HALL), L.Miss., Ind.; *A-C*, ×1.8; *D*, ×3.4 (110).

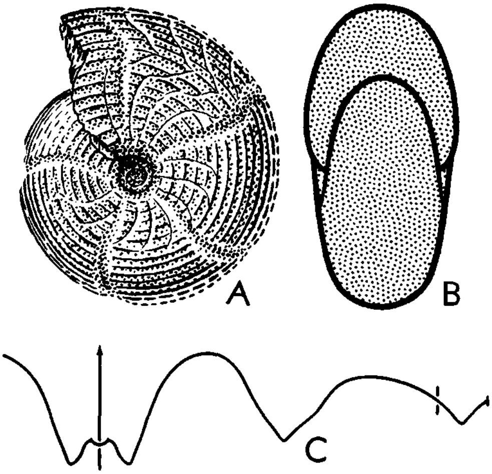

FIG. 73. *Neoglyphioceras subcirculare* (Miller), U. Miss., Ky.; *A,B,* ×2; *C,* enlarged (110).

Pericyclus Mojsisovics, 1882 [**Gon. princeps* de Koninck, 1842]. May be junior synonym of *Ammonellipsites* (14,20,42,44,76). *L.Carb.(Miss.).*

P. (Pericyclus). Conch thickly subdiscoidal with wide umbilicus and prominent undivided ribs parallel to constrictions (14). *L.Carb.(L.Miss.),* locally abundant in Eurasia-N.Afr., rare in USA.——Fig. 74. **P. (P.) princeps* (Kon.), L. Carb., Belg.; *A,B,* ×1; *C,* ×1.25 (14).

P. (Caenocyclus) Schindewolf, 1922 [**P. (C.) perisphinctoides*]. Conch discoidal, ribs divided; sutures unknown (76). *L.Carb.,* Ger.

P. (Fascipericyclus) Turner, 1948 [**Gon. fasciculatus* M'Coy, 1844] [=*Schizocyclus* Schindewolf, 1951]. Sutures with subangular first lateral saddles and low saddle dividing ventral lobe (76). *L.Carb.,* Eurasia.

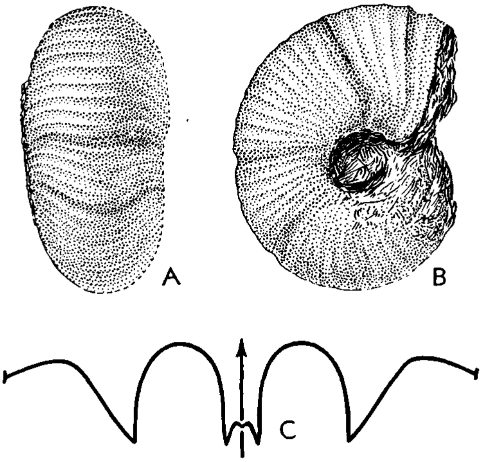

FIG. 74. *Pericyclus princeps* (De Koninck), L.Carb., Belg.; *A,B,* ×1; *C,* ×1.25 (14).

P. (Rotopericyclus) Turner, 1948 [**P. rotuliformis* Crick, 1899] [=*Hammatocyclus* Schindewolf, 1951]. Wide umbilicus with nodose margins (76). *L.Carb.,* Eu.

P. (Trapezocyclus) Turner, 1948 [**P. trapezoidalis* Crick, 1899]. Conch with fine longitudinal lirae (20). *L.Carb.,* Ire.

P. (Helicocyclus) Schindewolf, 1951 [**P. (H.) gracillimus*]. Conch discoidal, umbilicus very wide (76). *L.Carb.,* Eurasia.

P. (Stenocyclus) Schindewolf, 1951 [**P. (P.) carinatus* Schind., 1926]. Conch with ventral carina, narrow umbilicus, divided ribs. *L.Carb.,* Ger.

Ammonellipsites Parkinson, 1822 [**A. funatus*] [=*Discus* King, 1884 (*non* Fitzinger, 1833); *Trematodiscus* Meek & Worthen, 1861 (*non* Haeckel, 1860); *Trematoceras* Hyatt, 1884 (*non* Eichwald, 1851); *Coelonautilus* Foord, 1889; *Streptodiscus* Miller, 1892; *Kaypericyclus* Turner, 1948; *Eurycyclus* Schindewolf, 1951]. Poorly known. May be senior synonym of *Pericyclus* (21, 76). *L.Carb.,* Ire.-?W.Eu.

Subfamily GIRTYOCERATINAE Wedekind, 1918

Conch discoidal to lenticular; umbilicus variable. Ventral lobe of sutures broad (51, 55). *L.Carb.(U.Miss.).*

Eumorphoceras Girty, 1909 [**E. bisulcatum*]. Conch thickly discoidal, venter flattened, umbilicus moderate, sculpture prominent, sinuous ribs and ventrolateral sulcus (55). *L.Carb.(U.Miss.),* W.USA-W.Eu.-?Morocco.——Fig. 75. **E. bisulcatum,* Tex.; *A-C,* ×3.5; *D,* ×7. [*Eumorphoceras*= *Edmooroceras* Elias, 1956.]

Girtyoceras Wedekind, 1918 [**Adelphoceras meslerianum* Girty, 1909] [=*Adelphoceras* Girty, 1909 (*non* Barrande, 1874); *Sagittoceras* Hind, 1918; *Dryochoceras* Morgan, 1924; ?*Sudeticeras* Patteisky, 1929; ?*Karagandoceras* Librovitch, 1940; *Hudsonoceras* Moore, 1946]. Conch lenticular, venter angular at maturity. Gradational with

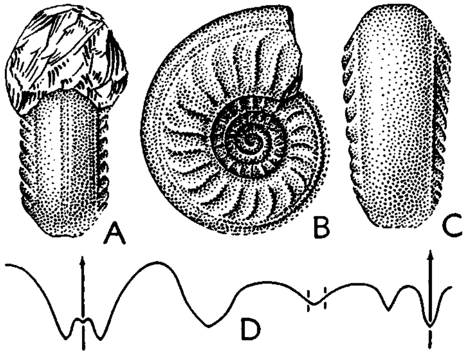

FIG. 75. *Eumorphoceras bisulcatum* Girty, U.Miss., Tex.; *A-C,* ×3.5; *D,* ×7 (110).

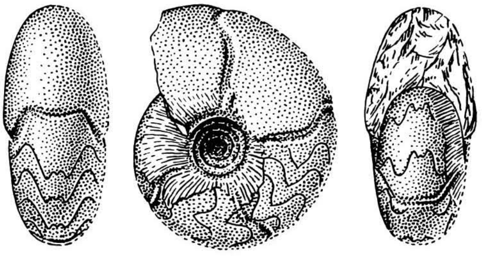

FIG. 76. *Girtyoceras meslerianum* (GIRTY), U.Miss., Okla.; ×2.5 (110).

FIG. 77. *Girtyoceras meslerianum* (GIRTY), U.Miss., Tex.; ×0.8 (110).

Eumorphoceras and superficially similar to *Gonioloboceras* (51). *L.Carb.(U.Miss.),* N.Am.-Eurasia-N.Afr.——FIG. 76,77. **G. meslerianum* (GIRTY); 76, Okla., ×2.5; 77, Tex., ×0.8 (110).

Nomismoceras HYATT, 1884 [**Gon. spirorbis* PHILLIPS]. Conch discoidal; umbilicus large. Syntypes of type species small and probably immature. *L. Carb.,* Eng.

Entogonites KITTL, 1904 [**Tetragonites grimmeri* KITTL, 1904] [=*Tetragonites* KITTL, 1904 (*non* KOSSMAT, 1895); *Kittliella* FRECH, 1906]. Conch thinly discoidal, with large umbilicus; prominent ribbed sculpture with ventrolateral salient and sulcus; inner whorls coiled quadrangularly. Sutures may have extra pair of lobes (78). *L.Carb.(L. Miss.),* Ger.-Yugo.-Alaska.

Subfamily BISATOCERATINAE Miller & Furnish, nov.

Conch thickly subdiscoidal to globular, umbilicus small and characteristcally closed. Ventral lobe of suture broad and bifid with rounded or linear-lanceolate prongs (4). *L. Carb.(U.Miss.)-U.Carb.(U.Penn.).*

Bisatoceras MILLER & OWEN, 1937 [**B. primum*] [=*Schartymites* LIBROVITCH, 1939; *Pseudobisatoceras* MAXIMOVA, 1940]. Conch thickly subdiscoidal, umbilicus closed. Ventral lobe of sutures with prominent linear-lanceolate prongs. *L.Penn.-M.Penn.;* C.USA-SW.USA.——FIG. 78. **B. primum,* M.Penn., Okla.; ×1.

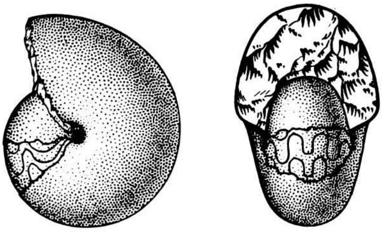

FIG. 78. *Bisatoceras primum* MILLER & OWEN, M. Penn., Okla.; ×1 (110).

Pennoceras MILLER & UNKLESBAY, 1942 [**P. seamani*]. Conch subglobular, umbilicus closed, prominent transverse sculpture. Ventral lobe of sutures with small rounded prongs. *U.Penn.,* Ohio-Pa.

Nuculoceras BISAT, 1924 [**N. nuculum*]. Conch globular, umbilicus small, transverse sculpture. Ventral lobe of sutures with small rounded prongs (4). *L.Carb.,* Eng.

Subfamily GONIOLOBOCERATINAE Spath, 1934

[*ex* Gonioloboceratidae]

Conch sublenticular, umbilicus small. Sutural inflections prominent and ventral lobe broad (60). *M.Penn.-L.Perm.*

Gonioloboceras HYATT, 1900 [**Gon. goniolobus* MEEK, 1877] [=*Milleroceras* HYATT, 1900; *Gurleyoceras* MILLER, 1932]. Venter narrowly rounded. First lateral saddle of sutures angular (49). *M. Penn.-L.Perm.,* C.USA-SW.USA.——FIG. 79. **G. goniolobum* (MEEK), U.Penn., Kans.; ×1.

Gonioglyphioceras PLUMMER & SCOTT, 1937 [**Gonioloboceras welleri gracile* GIRTY, 1911] [=*Eudissoceras* MILLER & OWEN, 1937]. Like

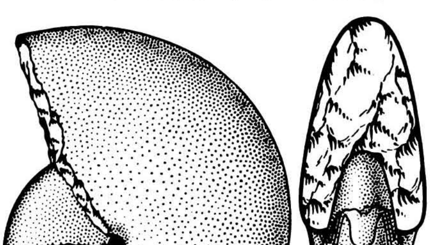

FIG. 79. *Gonioloboceras goniolobum* (MEEK), U. Penn., Kans.; ×1 (110).

Gonioloboceras but with retuse venter and sutures with rounded lateral lobe (60). *M.Penn.*, Okla.-Ill.-Ohio.

Wiedeyoceras MILLER, 1932 [**Eumorphoceras sanctijohanis* WIEDEY, 1929]. Like *Gonioloboceras* but 1st lateral saddle of suture rounded. *M.Penn.*, Iowa.

Family NEOICOCERATIDAE Hyatt, 1900

[=Gastriocerata ARTHABER, 1911]

Conch variable in shape and characteristically with prominent sculpture, umbilicus moderately small to large. Sutures form 8 lobes (24,50,60,65,78). *L.Carb.(L.Penn.)-U.Perm.*

Gastrioceras HYATT, 1884 [**Conchyliolithus Nautilithes Ammonites (Listeri)* MARTIN, 1809] [=*Neoicoceras* HYATT, 1900; *Branneroceras* PLUMMER & SCOTT, 1937]. Conch subdiscoidal to globular, umbilicus moderate to large, with nodose or ribbed margins. Suture with prongs of ventral lobe relatively narrow (4,60,78). *U.Carb.(Penn.)*, widespread.——FIG. 80. **G. listeri* (MARTIN), L. Penn., Eng.; *A,B*, ×1.——FIG. 81*A,B*. *G. reticulatum* YIN, U.Carb., China; ×0.5 (101).——FIG. 81*C*. *G. branneri* SMITH, L.Penn., Ark., ×1.5. [*Gastrioceras*=*Tschungkuoceras* GERTH, 1950.]

Eoasianites RUZHENCEV, 1933 [**E. subhanieli*] [=*Prometalegoceras, Glaphyrites* RUZH., 1936; *Trochilioceras, Preshumardites* PLUMMER & SCOTT, 1937; *Syngastrioceras* LIBROVITCH, 1938; *Ambiguites* SMITH, 1938; *Neoglaphyrites, Somoholites* RUZH., 1938]. Conch subglobular to globular, umbilicus moderate in size, with margins not prominently nodose or ribbed (50,65,66). *L.Carb.-L.Perm.*, widespread, locally abundant.——FIG. 82. *E. angulatus* (GIRTY), M.Penn., Okla.; ×0.7. [*Eoasianites*=*Pronoceras* PLUMMER-S., 1950 *(nom. nud.)*.]

Neoshumardites RUZHENCEV, 1936 [**N. triceps*]. Like *Eoasianites* but with lateral lobe of suture distinctly trifid (49,65). *M.Penn.-M.Perm.*, Tex.-Okla.-Ohio-Urals.——FIG. 83. *N.* sp., U.Penn., Okla.; ×1.——FIG. 84. *N. cuyleri* (PLUMMER & SCOTT), U.Penn., Tex.; ×1.6. [*Neoshumardites*=*Aktubites* RUZHENCEV, 1955.]

Pseudoparalegoceras MILLER, 1934 [**Gastrioceras russiense* TZWETAEV, 1888] [=*Strawnoceras*

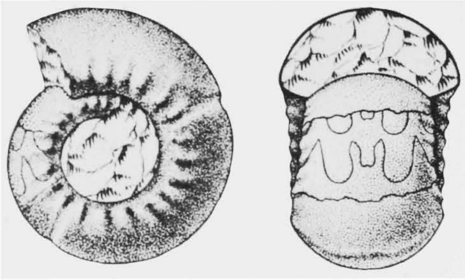

FIG. 80. *Gastrioceras listeri* (MARTIN), U.Carb., Eng.; ×1 (110).

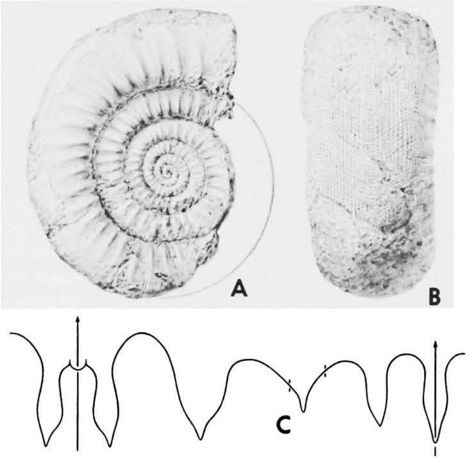

FIG. 81. *Gastrioceras. A,B, G. reticulatum* YIN, L. Penn., China; ×0.5 (101). *C, G. branneri* SMITH, L.Penn., Ark.; ×1.5 (110).

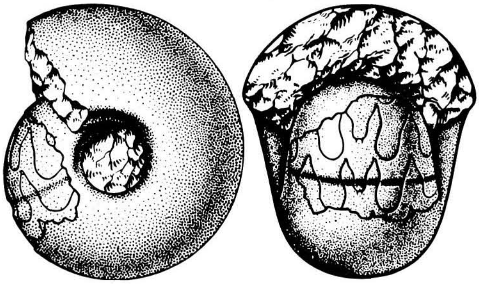

FIG. 82. *Eoasianites angulatus* (GIRTY), M.Penn., Okla.; ×0.7 (110).

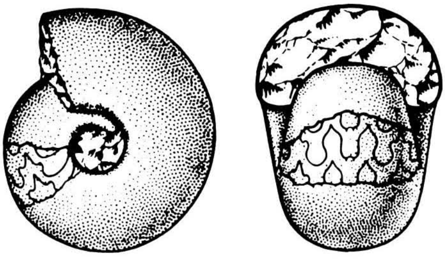

FIG. 83. *Neoshumardites* sp., U.Penn., Okla.; ×1 (110).

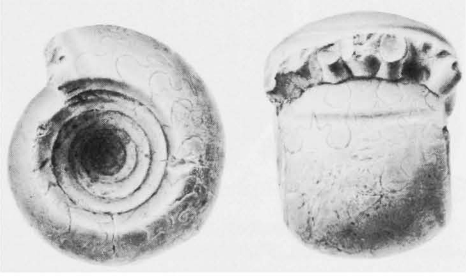

FIG. 84. *Neoshumardites cuyleri* (PLUMMER & SCOTT), U.Penn., Tex.; ×1.6 (110).

FIG. 85. *Pseudoparalegoceras williamsi* Miller & Downs, L.Penn., Ark.; ×0.6 (110).

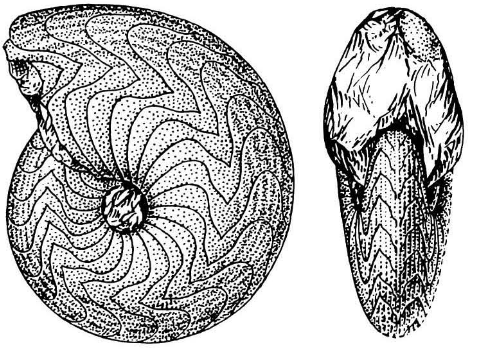

FIG. 88. *Pseudogastrioceras abichianum* (Möller), U.Perm., Armenia; ×0.8 (103).

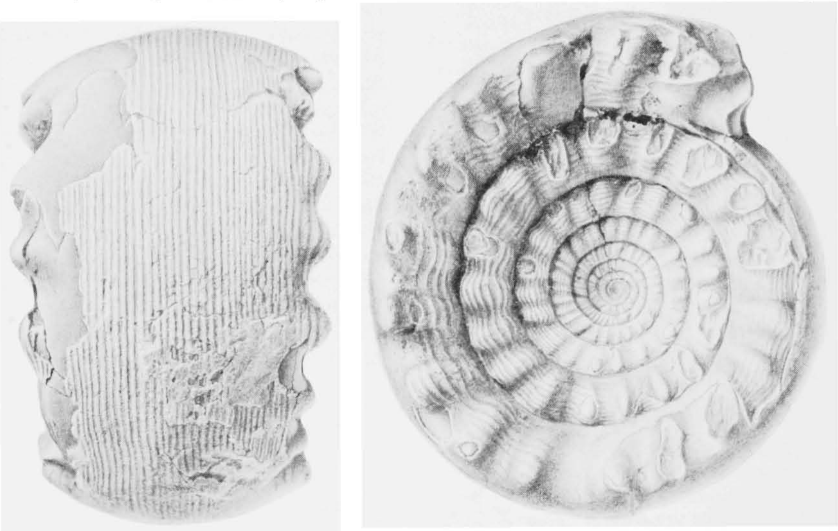

FIG. 86. *Paragastrioceras jossae* (de Verneuil), M.Perm., Urals; ×1.5 (110).

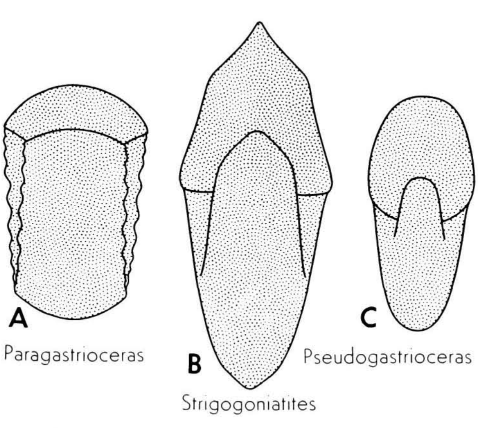

FIG. 87. *Paragastrioceras (A)*, ×1.5; *Strigogoniatites (B)*, ×0.5; *Pseudogastrioceras (C)*, ×0.5 (110).

Plummer & Scott, 1935 *(nom. nud.)*; *Phaneroceras* Plummer-S., 1937; *Eoparalegoceras* Delépine, 1939]. Like *Eoasianites* but conch thickly subdiscoidal and with umbilical lobe of suture on umbilical margin or adventral to it (51). *U.Carb. (Penn.)*, SW.USA - Peru - N.Afr. - Russ.(Moscow).——Fig. 85. *P. williamsi* Miller & Downs, L. Penn., Ark.; ×0.6——Fig. 94*A*. *P. bellilineatum* Miller & Furnish, L.Penn., Tex.; ×1.5.

Owenoceras Miller & Furnish, 1940 [**Neoglyphioceras bellilineatum* Miller & Owen, 1939]. Like *Eoasianites* but longitudinally lirate (51). *M.Penn.*, Mo.-Okla.

Paragastrioceras Tchernow, 1907 [**Gon. jossae* de Verneuil, 1845] [=*Girtyites* Wedekind, 1918]. Conch thickly subdiscoidal, with broad low whorls and large umbilicus with prominently nodose margin; test longitudinally lirate (50). *M.Perm.*, Urals.——Figs. 86; 87*A*. **P. jossae* (Verneuil), M. Perm., Urals; 86, ×1.5 (110); 87*A*, ×1.5 (110).

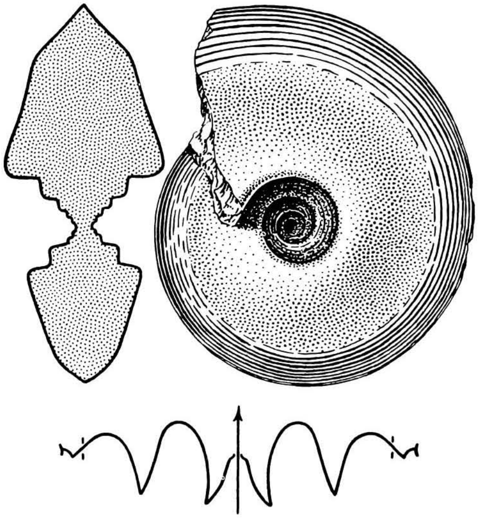

FIG. 89. *Strigogoniatites angulatus* (HANIEL), M.Perm., Timor; ×0.5 (110).

Pseudogastrioceras SPATH, 1930 [**Gon. abichianus* MÖLLER, 1879] [=*Uraloceras* RUZHENCEV, 1936; *Altudoceras* RUZH., 1940]. Like *Paragastrioceras* but with characteristically narrower whorls, smaller umbilicus with marginal ribs rather than nodes, and coarser longitudinal sculpture (50,66). *L. Perm.-U.Perm.*, widespread.——FIGS. 87*C;* 88. **P. abichianum* (MÖLLER), U.Perm., Armenia; 87*C*, ×0.5; 88, ×0.8 (103).

Synuraloceras RUZHENCEV, 1952 [**S. carinatum*]. Like *Eoasianites* but discoidal conch with angular venter (67). *L.Perm.*, Urals.

Strigogoniatites SPATH, 1934 [**Glyphioceras angulatum* HANIEL, 1915]. Like *Pseudogastrioceras* but with angular venter (50). *M.Perm.*, Timor-?China-Sicily-Tex.-Coah.——FIGS. 87*B;* 89. **S. angulatus* (HAN.), Timor; 87*B*, ×0.5; 89, ×0.5 (30). [*Strigogoniatites*=?*Grabauites* SUN, 1939.]

Atsabites HANIEL, 1915 [**A. weberi*]. Like *Pseudogastrioceras* but discoidal, with whorls slightly impressed dorsally (50). *M.Perm.*, Timor-Tex.

FIG. 90. *Metalegoceras schucherti* MILLER & FURNISH, M.Perm., Tex.; ×1.3 (110).

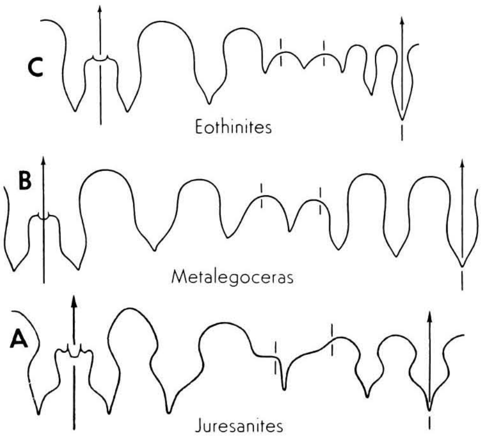

FIG. 91. Sutures of *Juresanites (A)*, ×1.7; *Metalegoceras (B)*, ×1.3; *Eothinites (C)*, enlarged (110).

Eupleuroceras MILLER & CLINE, 1934 [**E. bellulum*]. Like *Atsabites* but keeled ventrally, not longitudinally lirate, and sutures more primitive. Only immature stages known (60). *U.Penn.*, Okla.-Tex.

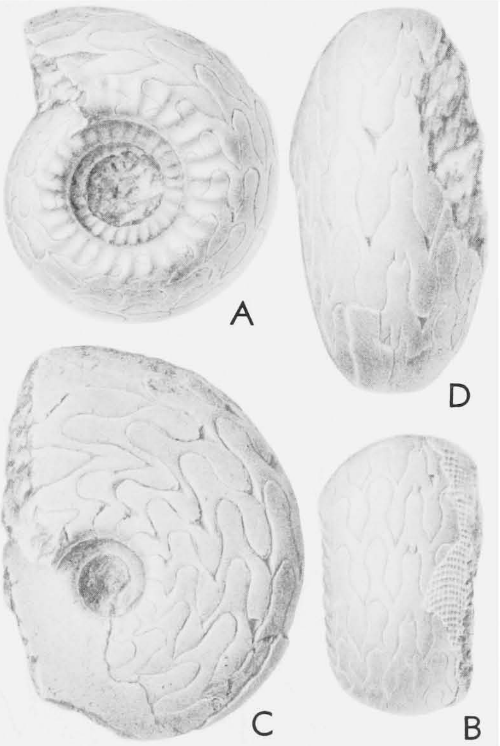

FIG. 92. *Schistoceras. A,B, S. hildrethi* (MORTON), U.Penn., Mo.; ×1.5 (110). *C,D, S. missouriense* (MILLER & FABER), U.Penn., Mo.; ×1.5 (110).

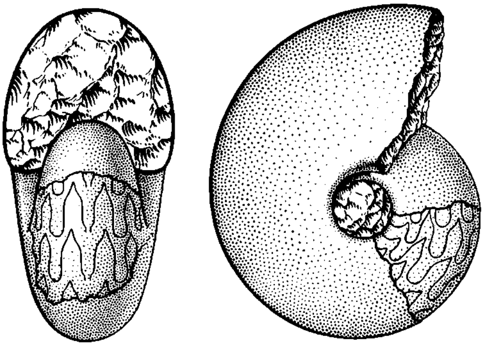

FIG. 93. *Schistoceras missouriense* (MILLER & FABER), U. Penn., Tex.; ×0.9 (110).

Epiglyphioceras SPATH, 1930 [**Glyphioceras meneghinii* GEMMELLARO, 1887]. Thinly discoidal conch with wide umbilicus and slightly involute whorls, prominent sinuous growth lines (24). *M.Perm.;* Sicily.

Family METALEGOCERATIDAE Plummer & Scott, 1937

Conch discoidal to subglobular with moderate to large umbilicus. Sutures goniatitic, forming 12 to 14 lobes (50,66). *L.Perm.-M.Perm.*

Metalegoceras SCHINDEWOLF, 1931 [**Paralegoceras sundaicum evoluta* HANIEL, 1915] [=*Epilegoceras* TCHERNOW, 1907 *(nom. nud.); Asianites* RUZHEN-

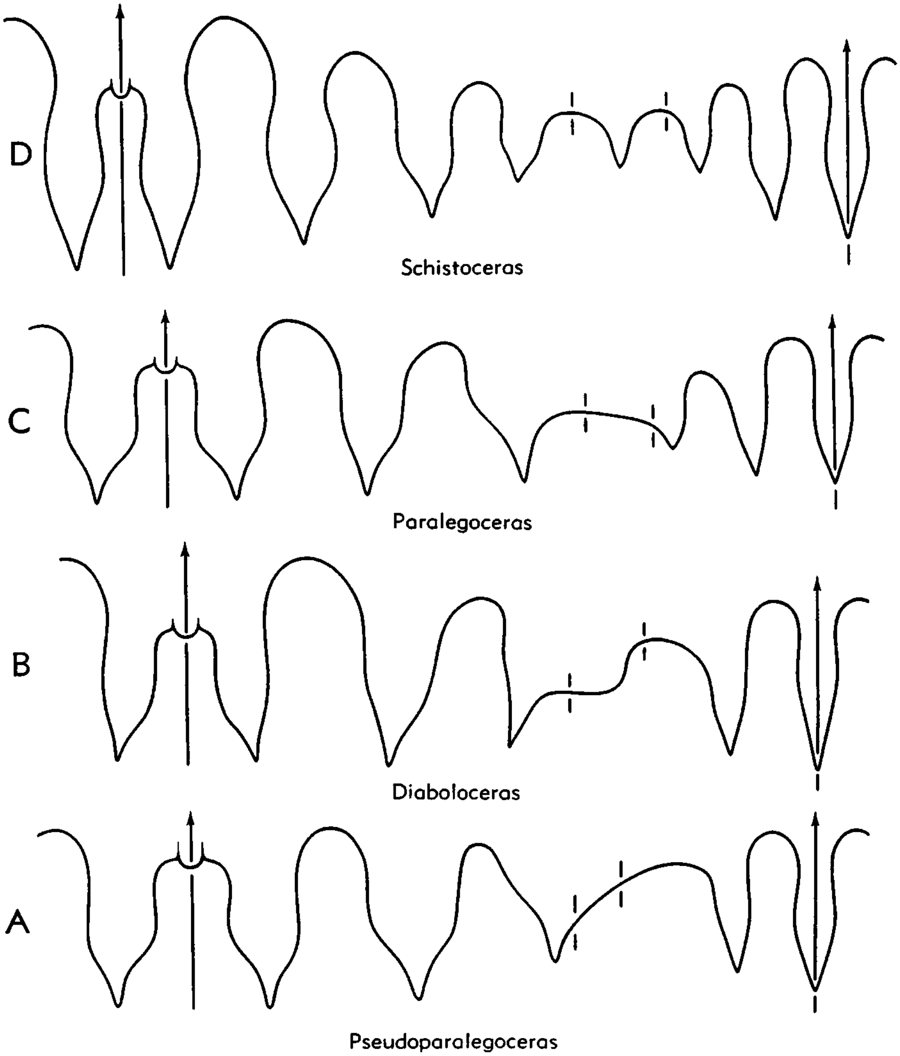

FIG. 94. Sutures of *Pseudoparalegoceras (A)*, ×1.5; *Diaboloceras (B)*, ×2.5; *Paralegoceras (C)*, ×1.5; *Schistoceras (D)*, ×2 (110).

CEV, 1933; *Dodecalegoceras* VOINOVA, 1934; *Bransonoceras* MILLER & PARIZEK, 1948]. Conch thickly subdiscoidal to subglobular. Sutures forming 12 lobes (30, 50, 66, 67). *L.Perm.-M.Perm.*, Tex.-N.Mex.-Urals-Arabia-Timor-W.Austral.——FIG. 90. *M. schucherti* MILLER & FURNISH, M.Perm., Tex.; ×1.3.——FIG. 91*B*. **M. evolutum* (HAN.), M. Perm., Timor; ×1.3 (30).

Eothinites RUZHENCEV, 1933 [**E. ḳargalensis*] [=*Uralites* TCHERNOW, 1907 *(nom. nud.), non* VOINOVA, 1934 *(nom. nud.); Rhiphaeites* RUZH., 1933]. Like *Metalegoceras* but with narrower conch (50). *M.Perm.*, Urals-Timor-Tex.——FIG. 91*C*. *E. uralensis* (RUZH.), Urals; enlarged (113).

Juresanites MAXIMOVA, 1940 [**J. primitivus*]. Like *Metalegoceras* but with more primitive sutures (66). *L.Perm.*, Urals.——FIG. 91*A*. **J. primitivus;* ×1.6 (66).

Pseudoschistoceras TEICHERT, 1944 [**P. simile*]. Like *Metalegoceras* but sutures form an additional lobe in umbilical region. *?L.Perm.*, W.Austral.

Family SCHISTOCERATIDAE Schmidt, 1929

Conch discoidal to subdiscoidal with moderate to large umbilicus, reticulate surface, and goniatitic sutures forming 10 to 16 lanceolate lobes (51,65). *U.Carb.(L.Penn.)-L.Perm.*

Subfamily SCHISTOCERATINAE Schmidt, 1929

[*ex* Schistoceratidae]

Conch thickly subdiscoidal. Sutures forming gradational series of 10 to 14 lobes. *U. Carb.(L.Penn.).*

Schistoceras HYATT, 1884 [**Gon. missouriensis* MILLER & FABER, 1892] [=*Paraschistoceras, Metaschistoceras* PLUMMER & SCOTT, 1937]. Moderate to large umbilicus with more or less nodose borders. Sutures form 14 lobes (51,60). *M.Penn.-L.Perm.*, USA-Urals.——FIG. 92*A,B*. *S. hildrethi* (MORTON), U.Penn., Mo.; ×1.5.——FIGS. 92*C,D;* 93; 94*D*. **S. missouriense* (MILLER & FABER), U.Penn., USA; 92*C,D*, ×1.5 (Mo.); 93, ×0.9 (Tex.); 94*D*, ×2 (Tex.).

Pintoceras PLUMMER & SCOTT, 1937 [**P. postvenatum*] [=*Eoschistoceras* RUZHENCEV, 1952]. Like *Schistoceras* but with depressed conch, large umbilicus, triangularly coiled inner whorls, and more primitive sutures. *U.Carb.(M.Penn.)*, Tex.-Okla.-Turkistan.

Paralegoceras HYATT, 1884 [**Gon. iowensis* MEEK & WORTHEN, 1860] [=*Bendoceras* PLUMMER & SCOTT, 1937]. Like *Pintoceras* but sutures form 10 lobes (51). *L.Penn.*, Iowa-Ark.-Okla.-Tex.——FIGS. 94*C;* 95*D;* 96. **P. iowense* (MEEK-W.), Iowa-Tex.; 94*C*, ×1.5; 95*D*, ×0.5; 96, ×0.75.——FIG. 95*A-C*. *P. texanum* (SHUMARD), Okla.; *A,B*, ×1.3; *C*, ×0.7.

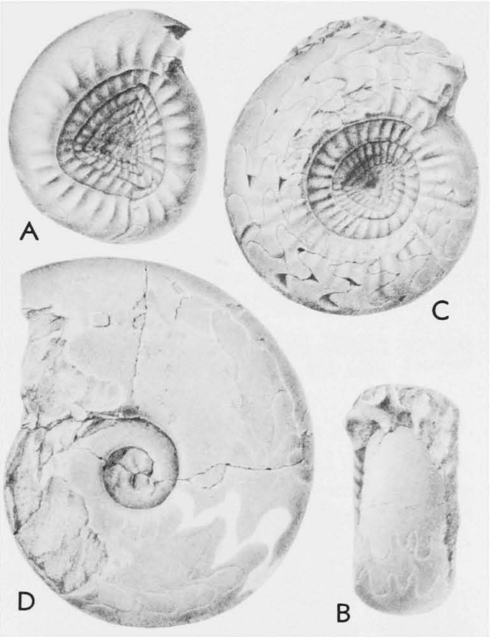

FIG. 95. *Paralegoceras. A-C, P. texanum* (SHUMARD), L.Penn., Okla.; *A,B*, ×1.3; *C*, ×0.7 (110). *D, P. iowense* (MEEK & WORTHEN), L.Penn., Iowa; ×0.5 (110).

Diaboloceras MILLER & FURNISH, 1940 [**D. varicostatum*]. Like *Paralegoceras* but with more primitive sutures (51). *L.Penn.*, Tex.-Okla.——FIGS. 94*B;* 97. **D. varicostatum*, Tex.; 94*B*, ×2.5; 97, ×1.5.

Winslowoceras MILLER & DOWNS, 1948 [**W. henbesti*]. Like *Paralegoceras* and *Diaboloceras* but with discoidal conch and flattened venter. *L.Penn.*, Ark.-Okla.——FIG. 98. **W. henbesti*, Ark.; *A,B*, ×0.7; *C*, ×1.3.

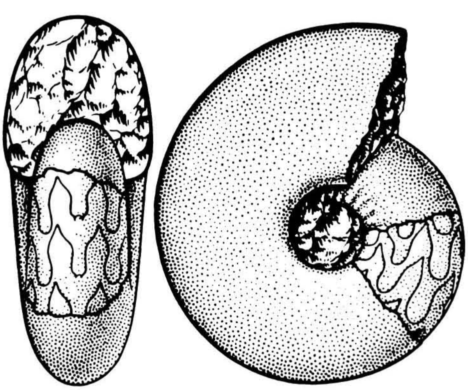

FIG. 96. *Paralegoceras iowense* (MEEK & WORTHEN), L.Penn., Tex.; ×0.75 (110).

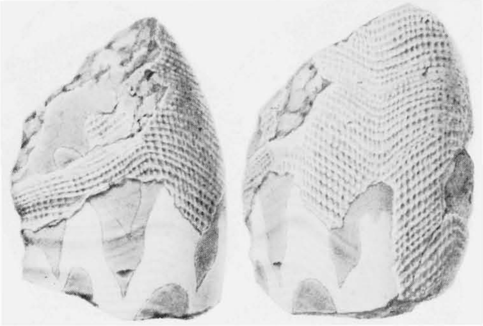

FIG. 97. *Diaboloceras varicostatum* MILLER & FURNISH, L.Penn., Tex.; ×1.5 (110).

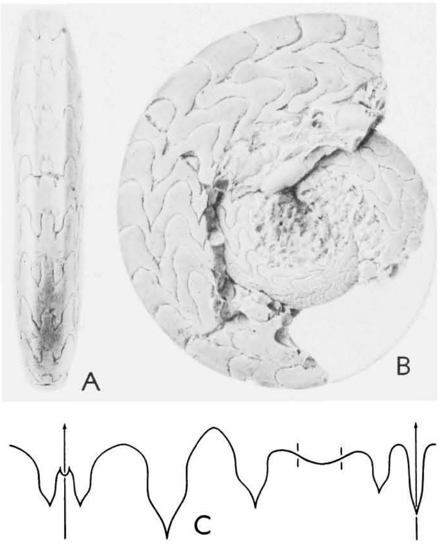

FIG. 98. *Winslowoceras henbesti* MILLER & DOWNS, L.Penn., Ark.; *A,B,* ×0.7; *C,* ×1.3 (110).

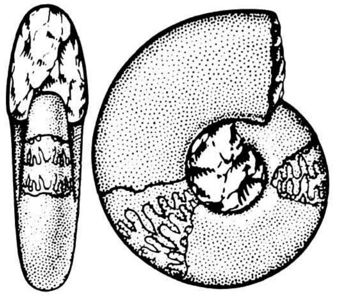

FIG. 99. *Wellerites mohri* PLUMMER & SCOTT, M. Penn., Tex., ×0.5 (110).

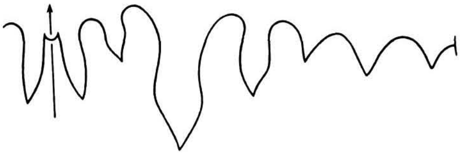

FIG. 100. Suture of *Wellerites mohri* PLUMMER & SCOTT, M.Penn., Tex.; ×4 (110).

Subfamily WELLERITINAE Plummer & Scott, 1937

[*ex* Welleritidae]

Conch discoidal. Sutures forming 16 lobes of which ventrolateral 2 are adventitious. *M.Penn.*

Wellerites PLUMMER & SCOTT, 1937 [**W. mohri*] [=*Walkerites* SMITH, 1938]. Probably evolved from "*Paralegoceras*" *moorei* (PLUMMER-S.) (60). *U.Carb.(M.Penn.)*, Tex.-Okla.-Ohio-Urals.——FIG. 99; 100. **W. mohri,* Tex.; 99, ×0.5; 100, ×4 (60).

Superfamily ADRIANITACEAE Schindewolf, 1931

[*ex* Adrianitidae]

Discoidal to globular conchs with variable umbilici. Goniatitic suture with 10 to 30 lobes which tend to be subequal (24,30,50). *U.Carb.(M.Penn.)-M.Perm.*

Family ADRIANITIDAE Schindewolf, 1931

Characters of superfamily. *U.Carb.(M. Penn.)-M.Perm.*

Subfamily ADRIANITINAE Schindewolf, 1931

[*ex* Adrianitidae]

Typical more advanced adrianitids, with sutures forming 14 to 30 lobes. *L.Perm.-M. Perm.*

Adrianites GEMMELLARO, 1887 [**A. elegans*] [=*Epadrianites* SCHINDEWOLF, 1931; *Palermites* TOUMANSKY, 1937; *Neocrimites* RUZHENCEV, 1940; *Aricoceras, Basleoceras, Metacrimites, Metaricoceras, Neoaricoceras, Sosiocrimites* RUZH., 1950]. Subglobular to globular conchs with small umbilici, generally longitudinally lirate test. Sutures with 20 to 30 lobes (24,30,50,65). *M.Perm.,* widespread. ——FIG. 101. **A. elegans,* Sicily; ×2.——FIG. 7*A*. *A. defordi,* MILLER & FURNISH, Tex.; ×1.3.——FIG. 11*A'-E'*. *A. dunbari* MILLER-F., Coah.; enlarged.——FIG. 2,3*a,b*. *A. kingi* GEMM., M.Perm., Sicily; ×1.25 (24).——FIG. 2,4. *A. ensifer* GEMM., M.Perm., Sicily; ×1.25 (24).——FIG. 2,5*a,b*. *A. distefanoi* GEMM., Sicily; ×1.25 (24).

Hoffmannia GEMMELLARO, 1887 [**Adrianites (H.) hoffmanni*]. Like *Adrianites* but discoidal conchs with large umbilici, prominent growth lines, and sutures forming about 20 lobes (24). *M.Perm.,* Sicily-?Tex.

Doryceras GEMMELLARO, 1887 [**D. fimbriatum*]

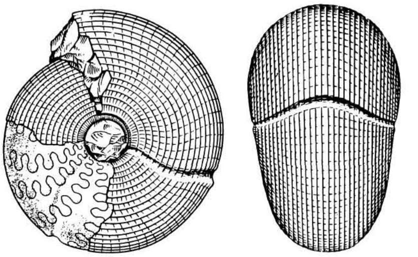

FIG. 101. *Adrianites elegans* GEMMELLARO, M.Perm., Sicily; ×2 (110).

[=?*Pseudagathiceras* SCHINDEWOLF, 1931; *Sizilites* TOUMANSKY, 1937]. Like *Adrianites* but subdiscoidal to subglobular conch with large umbilici and sutures forming 14 to 18 lobes (24,47,65). *M. Perm.*, Sicily-Timor-Coah.——FIG. 2,6. *D. spinosum* (MILLER), M.Perm., Coah.; ×2 (110).

Crimites TOUMANSKY, 1937 [**C. pamiricus*]. Like *Adrianites* but a globular conch with sutures forming about 14 lobes (65). *L.Perm.-M.Perm.*, Pamirs-Urals-Timor.

Texoceras MILLER & FURNISH, 1937 [**Agathoceras texanum* GIRTY, 1908]. Like *Adrianites* but subglobular conch with reticulate surface and sutures forming 14 rounded lobes (50). *M.Perm.*, Tex. ——FIG. 102. **T. texanum* (GIRTY); *A,B*, ×1.3; *C*, ×2; *D*, ×3.

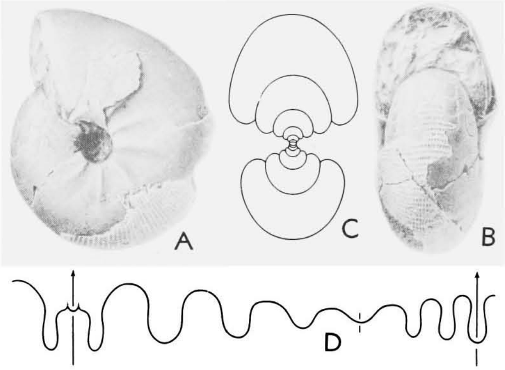

FIG. 102. *Texoceras texanum* (GIRTY), M.Perm., Tex.; *A,B*, ×1.3; *C*, ×2; *D*, ×3 (110).

Subfamily DUNBARITINAE Miller & Furnish, nov.

Primitive adrianitids with sutures forming 10 lobes. *M.Penn.-U.Penn.*

Dunbarites MILLER & FURNISH, 1940 [**Paralegoceras rectilaterale* MILLER, 1930]. Thickly discoidal conch with flattened venter (51). *M.Penn.-U.Penn.*, Tex.-Okla.

Emilites RUZHENCEV, 1938 [**Paralegoceras incertum* BÖSE, 1919] [=*Plummerites* MILLER & FURNISH, 1940]. Like *Dunbarites* but globular conch with sutures denticulate in umbilical regions (50,65). *U.Penn.*, Tex.-Urals.——FIG. 103. **E. incertus* (BÖSE), Tex.; ×3.

FIG. 103. *Emilites incertus* (BÖSE), U.Penn., Tex.; ×3 (110).

Subfamily CLINOLOBINAE Miller & Furnish, nov.

Conch thinly discoidal and keeled ventrally, with large umbilicus, prominent transverse sculpture, and sutures forming ?14 lobes; general course of external sutures V-shaped (24). *M.Perm.*

Clinolobus GEMMELLARO, 1887 [**C. telleri*]. Unique; known from few small specimens. *M. Perm.*, Sicily.—FIG. 104. **C. telleri*; ×4 (24).

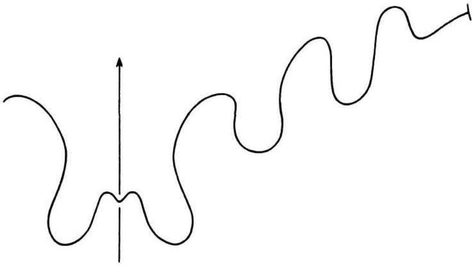

FIG. 104. Suture of *Clinolobus telleri* GEMMELLARO, M.Perm., Sicily; ×4 (24).

Superfamily DIMORPHOCERATACEAE Hyatt, 1884

[*ex* Dimorphocerae]

Subdiscoidal to lenticular conch with inconspicuous closed umbilici. Sutures goniatitic with large prominently bifid ventral lobe and external lobes more or less subdivided. *L.Carb.(U.Miss.)-M.Perm.*

Family DIMORPHOCERATIDAE Hyatt, 1884

[*pro* Dimorphocerae]

External lateral lobes and prongs of ventral lobe of sutures tend to be bifid (49,65). *L.Carb.(U.Miss.)-U.Carb.(U.Penn.), ?L. Perm.*

Dimorphoceras HYATT, 1884 [**Gon. gilbertsoni*

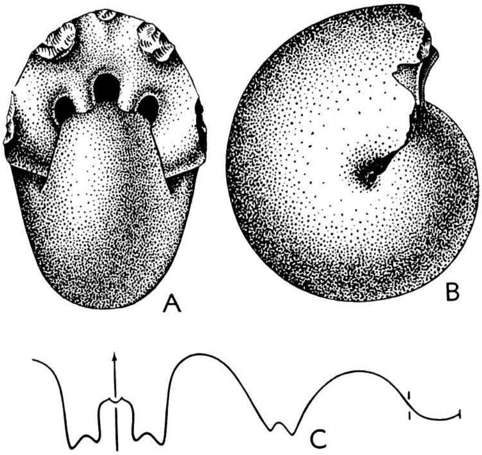

FIG. 105. *Dimorphoceras edwini* MILLER & FURNISH, U.Miss., Ky.; *A,B,* ×5; *C,* ×7 (110).

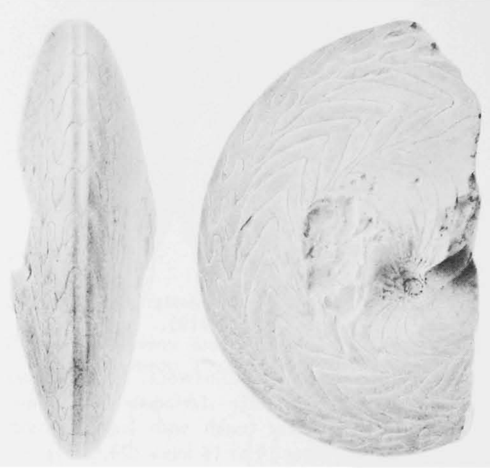

FIG. 106. *Neodimorphoceras texanum* (SMITH), U. Penn., Tex.; ×0.8 (110).

PHILLIPS, 1836] [=*Trizonoceras* GIRTY, 1909; *Politoceras* LIBROVITCH, 1946; *Paradimorphoceras* RUZHENCEV, 1949]. Venter rounded; external lobes of sutures variably serrate (4,15,21,51,65). *L.Carb. (U.Miss.)-U.Carb.(M.Penn.),* Eurasia-N.Afr.-N. Am.——FIG. 105. *D. edwini* MILLER & FURNISH, U.Miss., Ky.; *A,B,* ×5; C, ×7.

Neodimorphoceras SCHMIDT, 1925 [**Dimorphoceras texanum* SMITH, 1903] [=*Texites* SMITH, 1927; *Berkhoceras* LIBROVITCH, 1938; *Kazakhoceras* RUZHENCEV, 1947]. Conch lenticular; venter subacute or retuse. Sutures with prongs of ventral lobe prominently bifid and 1st lateral saddle subangular (49). *L.Carb.(U.Miss.)-U.Carb.(U.Penn.),* Tex. - Okla. - Eng. -Menorca-Urals-N.Zem.——FIGS. 106; 107; 108. **N. texanum* (SMITH), U.Penn., Tex.; 106, ×0.8; 107, ×10; 108*A-C,* ×15; 108*D,* ×4.5.

Shuichengoceras YIN, 1935 [**S. yohi*] [=*Pinoceras* RUZHENCEV, 1941]. Like *Neodimorphoceras* but venter rounded (101). *U.Carb.(U.Penn.), ?L. Perm.,* Kweichow-Urals-SW.USA.

Family THALASSOCERATIDAE Hyatt, 1900

Lobes of external sutures serrate to digitate (50,65). *L.Carb.(U.Miss.)-M.Perm.*

Thalassoceras GEMMELLARO, 1887 [**T. phillipsi*] [=*Prothalassoceras* BÖSE, 1919]. Lobes of external sutures digitate (24,50,65). *L.Perm.-M.Perm.,* widespread in Eurasia-Austral.-N.Am. —— FIG. 109,*B. T. welleri* (BÖSE), L.Perm., Tex.; ×2.5.

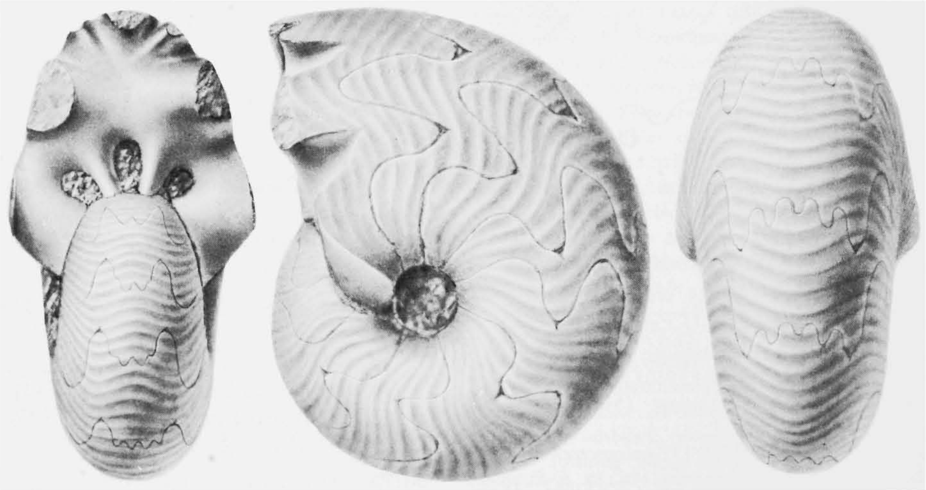

FIG. 107. *Neodimorphoceras texanum* (SMITH), U.Penn., Tex.; ×10 (110).

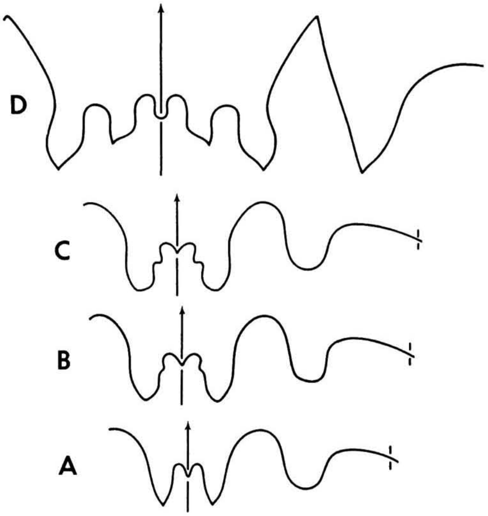

Fig. 108. Ontogeny of sutures in *Neodimorphoceras texanum* (Smith), U.Penn., Tex.; *A-C,* ×15; *D,* ×4.5 (110).

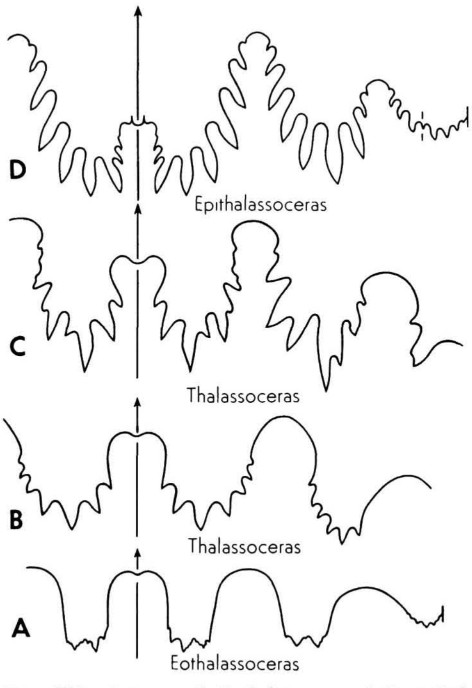

Fig. 109. Sutures of *Eothalassoceras (A),* ×2.5; *Thalassoceras (B,C),* ×2.5, enlarged; *Epithalassoceras (D),* ×3 (110).

——Fig. 109*C*. **T. phillipsi,* M.Perm., Sicily; enlarged (24).

Eothalassoceras Miller & Furnish, 1940 [**Prothalassoceras inexpectans* Miller & Owen, 1937] [=*Uralites* Voinova, 1934 *(nom. nud.), non* Tchernow, 1907 *(nom. nud.); Aristoceras* Ruzhencev, 1940]. Lobes of external sutures irregularly serrate (49,50,65). *U.Carb.(L.Penn.)-L. Perm.,* W.USA-Urals-N.Afr.——Fig. 109*A*. **E. inexpectans* (Miller-O.), M.Penn., Okla.; ×2.5. ——Fig. 110. *E. caddoense* (Plummer & Scott), U.Penn., Okla.; ×1.

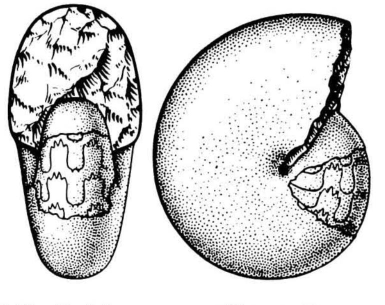

Fig. 110. *Eothalassoceras caddoense* Plummer & Scott, U.Penn., Okla.; ×1 (110).

Delepinoceras Miller & Furnish, 1954 [**Dimorphoceras thalassoide* Delépine, 1937]. Like *Thalassoceras* but lobes of sutures somewhat trifid (52). *L.Carb.,* Pyrenees-N.Afr.

Gleboceras Ruzhencev, 1950 [**G. mirandum*]. Like *Eothalassoceras* but sutures with prongs of ventral lobe not subdivided (65). *U.Carb.,* Urals.

Epithalassoceras Miller & Furnish, 1940 [**E. ruzencevi*]. Like *Thalassoceras* but sutures more advanced, with internal lateral lobes bifid (47,50). *M.Perm.,* Coah.——Fig. 109*D*. **E. ruzencevi;* ×3.

Suborder PROLECANITINA Miller & Furnish, 1954

Discoidal to thinly lenticular conchs with goniatitic to ceratitic sutures characteristically forming auxiliary lobes; simple retrochoanitic siphuncles (50,52,54). *U.Dev.-U. Trias.*

Superfamily PROLECANITACEAE Hyatt, 1884

[*ex* Prolecanitidae]

Conch characteristically with large umbilici; no prominent sculpture. Sutures goniatitic to ceratitic (50,52). *U.Dev.-M. Perm.*

Family PROLECANITIDAE Hyatt, 1884

Conch discoidal to lenticular with moderate to large umbilicus. Sutures goniatitic, characteristically forming a series of subequal lobes and saddles with undivided ventral lobe (16,53,71,78). *U.Dev.-L.Carb.(U. Miss.).*

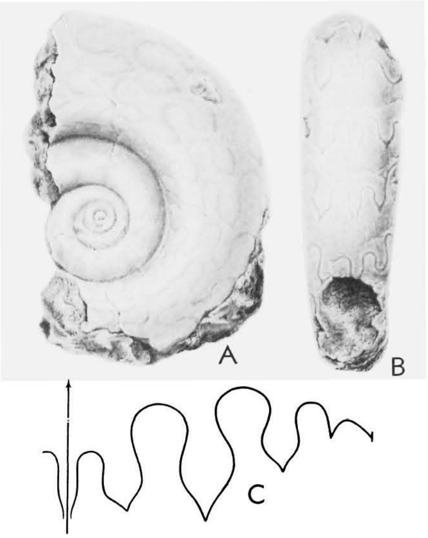

FIG. 111. *Prolecanites americanus* MILLER & GARNER, U.Miss., Ind.; *A,B,* ×1; *C,* ×2 (110).

Prolecanites MOJSISOVICS, 1882 [**P. mojsisovicsi* MILLER, 1938] [=*Paraprolecanites* KARPINSKY, 1889; *Metacanites* SCHINDEWOLF, 1922; *Dombarocanites, Rhipaeocanites* RUZHENCEV, 1949]. Discoidal conch with large umbilici. Sutures form 12 lobes (68,78). *L.Carb.(U.Miss.),* Ger.-Eng.-Yugo.-?Sp.-Urals-?Kazak-USA (Ind.)-Can. (Alba.).——FIG. 111. *P. americanus* MILLER & GARNER, Ind.; *A,B,* ×1; *C,* ×2.——FIG. 9*A*. *P. hesteri* MOORE, Eng.; ×7.

Protocanites SCHMIDT, 1922 [**Gon. lyoni* MEEK & WORTHEN, 1860]. Like *Prolecanites* but sutures form 8 lobes (48). *L.Carb.(L.Miss.),* USA-Eurasia-N.Afr.-SE.Austral.——FIG. 112. **P. lyoni* (MEEK-W.), Mo.; *A,B,* ×1; *C,* ×2.

Cycloclymenia HYATT, 1884 [**Cly. planorbiformis* MÜNSTER] [=*Phenacoceras* FRECH, 1902; *Balvites* WEDEKIND, 1914]. Like *Protocanites* but depressed whorls and prominent growth increments (41,70). *U.Dev.,* Ger.

Merocanites SCHINDEWOLF, 1922 [**Ellipsolites compressus* SOWERBY, 1813]. Like *Prolecanites* but sutures form 10 lobes (53). *L.Carb.(L.Miss.),* Eurasia-C.USA.

Acrocanites SCHINDEWOLF, 1922 [**A. multilobatus*]. Like *Prolecanites* but angular venter, moderate umbilici, and suture with numerous auxiliary lobes (14,71). *L.Carb.,* Ger.-Belg.-N.Afr.

Family PRODROMITIDAE Arthaber, 1911

Conch thinly lenticular with keeled venter and small umbilicus. Sutures ceratitic, with broad trifid ventral lobe and numerous auxiliaries (48). *L.Miss.*

Prodromites SMITH & WELLER, 1901 [**Gon. gorbyi* MILLER, 1891]. Known from single species. *L. Miss.,* Mo.-Iowa-Ill.-Ind.——FIGS. 113; 114. **P. gorbyi* (MILLER), Mo.; 113, ×1; 114*A-F,* enlarged (48).

Family DARAELITIDAE Tchernow, 1907

[*ex* Daraelitinae]

Conch discoidal with no prominent sculpture, umbilicus moderately large. Sutures goniatitic to ceratitic, with trifid ventral lobe and few auxiliary lobes. Evolved from prolecanitids (50,51,65). *L.Carb.(U.Miss.)-M. Perm.*

Daraelites GEMMELLARO, 1887 [**D. meeki*] [=*Prodaraelites* TCHERNOW, 1907]. Ceratitic sutures with broad ventral lobe (24,50). *L.Perm.-M.Perm.,* Sicily-Urals-M.Asia-Timor-Tex.——FIG. 9*E*. **D. meeki,* M.Perm., Sicily; ×4 (24).

Boesites MILLER & FURNISH, 1940 [**Daraelites texanus* BÖSE] [=*Metadaraelites* RUZHENCEV, 1940]. Like *Daraelites* but suture with narrower ventral lobe and broader 1st lateral lobe, serration largely confined to 1st lateral lobe. Ancestral to and gradational with *Daraelites* (51,65). *L.Penn.-L.Perm.,* Tex.-Okla.-Urals.——FIGS. 9*D;* 115. **B. texanus* (BÖSE), U.Penn., Tex.; 9*D,* ×7; 115, ×1.5.

Epicanites SCHINDEWOLF, 1926 [**Paraprolecanites sandbergeri* SCHMIDT, 1925] [=*Praedaraelites* SCHIND., 1934]. Like *Boesites* but with more primtive sutures (51). *L.Carb.(U.Miss.),* Alg.-Menorca-Pyrenees-Eng.-Ger.-Indochina-Okla. —— FIG. 9*B*. **E. sandbergeri* (SCHMIDT), Alg.; enlarged (106).——FIG. 9*C*. *E. culmiensis* (KOBOLD), Ger.; ×4 (109).——FIG. 116. *E. loeblichi* MILLER & FURNISH, Okla.; *A,B,* ×5; *C,* ×15.

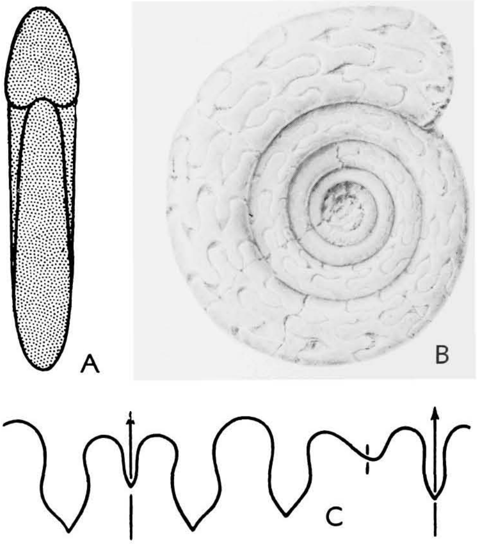

FIG. 112. *Protocanites lyoni* (MEEK & WORTHEN), L.Miss., Mo.; *A,B,* ×1; *C,* ×2 (110).

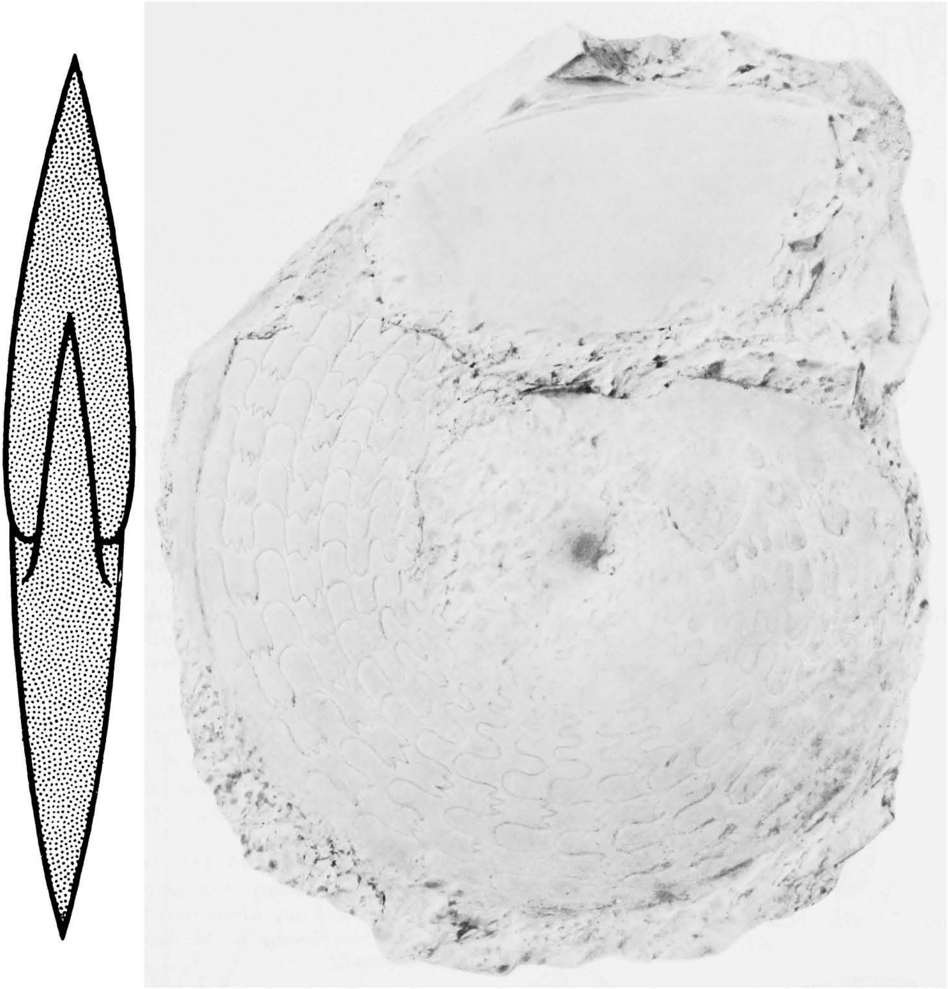

FIG. 113. *Prodromites gorbyi* (MILLER), L.Miss., Mo.; ×1 (110).

Superfamily MEDLICOTTIACEAE Karpinsky, 1889

[*nom. transl. et correct.* MILLER & FURNISH, 1954 (*ex* Medlicottinae KARP., 1889)] [=Pronoritacea HYATT & SMITH, 1905; Pronoritaceae BASSE, 1952]

Discoidal to thinly lenticular conchs with flattened or retuse venter, small umbilici, and commonly ventrolateral nodes or ribs. Sutures have modified 1st lateral lobe or saddle or both and form a series of undivided or bifid auxiliary lobes (50,64,65, 66, 83a). *L.Carb.(U.Miss.)-U.Trias.*

Family PRONORITIDAE Frech, 1901

[*ex* Pronoritinae]

Conch discoidal with no prominent sculpture. Sutures with trifid ventral lobe, large bifid 1st lateral lobe, and characteristically unmodified 1st lateral saddle (50,65). *L. Carb.(U.Miss.)-M.Perm.*

Pronorites MOJSISOVICS, 1882 [**Gon. cyclolobus* PHILLIPS, 1836] [=*Ibergiceras* KARPINSKY, 1889; *Subpronorites* TCHERNOW, 1907; *Megapronorites* RUZHENCEV, 1949]. Sutures with prongs of 1st lateral lobe not subdivided (21,78). *L.Carb.(U. Miss.)-U.Carb.(Penn.),* Eurasia-N.Afr.-N.Am.-S. Am.——FIGS. 10*A*; 117. *P. arkansasensis* SMITH, L.Penn., Okla.; 10*A*, ×1; 117, ×0.9.

Stenopronorites SCHINDEWOLF, 1934 [**Pronorites cyclolobus uralensis* KARPINSKY, 1889]. Like *Pronorites* but has ventral ribs (50). *U.Carb.(U. Penn.),* Urals-Kans.

Tridentites RUZHENCEV, 1936 [**Pronorites tridens* SCHMIDT, 1925]. Like *Pronorites* but suture with dorsal prong of 1st lateral lobe bifid. *L.Carb.,* Belg.

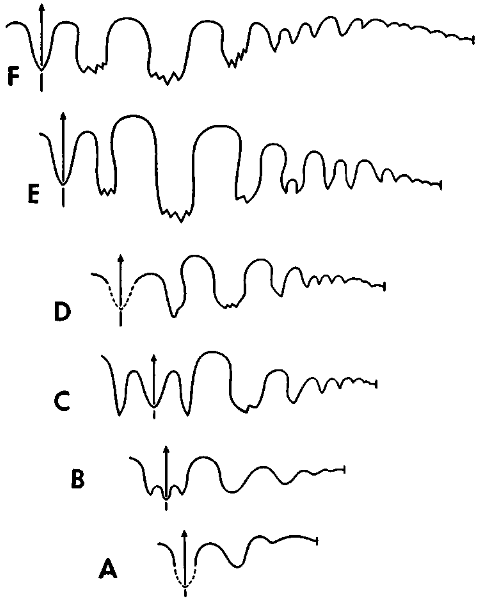

Fig. 114. Ontogeny of sutures in *Prodromites gorbyi* (Miller), L.Miss., Mo.; enlarged (48).

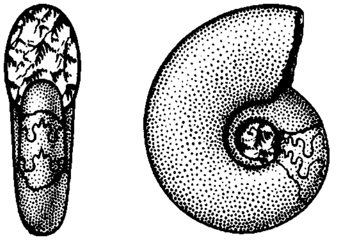

Fig. 115. *Boesites texanus* (Böse), U.Penn., Tex.; ×1.5 (110).

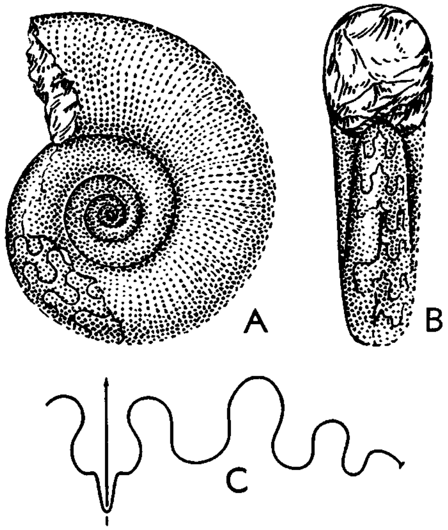

Fig. 116. *Epicanites loeblichi* Miller & Furnish, U. Miss., Okla.; *A,B*, ×5; *C*, ×15 (110).

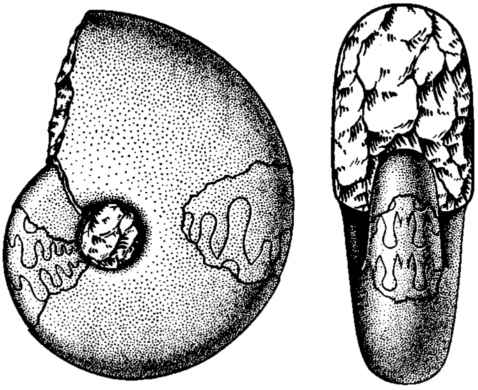

Fig. 117. *Pronorites arkansasensis* Smith, L.Penn., Okla.; ×0.9 (110).

Neopronorites Ruzhencev, 1936 [**Parapronorites permicus* Tchernow, 1907] [=*Sakmarites* Ruzh., 1936; *Epipronorites* Maximova, 1938; *Shikanites* Ruzh., 1938; *Metapronorites* Librovitch, 1938]. Like *Pronorites* but suture with prongs of 1st lateral lobe and adjacent lateral lobes serrate (50,65, 66). *U.Penn.-M.Perm.*, Urals-Bukhara-Timor-W. Tex.——Fig. 118*A*. **N. permicus* (Tchernow), M.Perm., Urals; ×10 (85).——Fig. 118*B*. *N. bakeri* Miller & Furnish, L.Perm., Tex.; ×8.

Parapronorites Gemmellaro, 1887 [**P. konincki*]. Like *Pronorites* but suture with prongs of 1st lateral lobe and several adjacent lobes bifid (24). *M. Perm.*, Sicily-Timor.——Fig. 118*C*. **P. konincki*, Sicily; enlarged (24).

Sundaites Haniel, 1915 [**S. levis*]. Like *Parapronorites* but suture with prongs of 1st lateral lobe undivided and adventitious lobe in 1st lateral saddle. May belong in Medlicottiinae (30). *M. Perm.*, Timor.

Family MEDLICOTTIIDAE Karpinsky, 1889

[*ex* Medlicottinae]

Conch discoidal to thinly lenticular and with flattened or retuse venter. Sutures with narrow ventral lobe and modified 1st lateral saddle (50). *U.Carb.(L.Penn.)-L.Trias.*

Subfamily UDDENITINAE Miller & Furnish, 1940

Discoidal conch. Sutures with auxiliary lobes undivided. Transitional between pronoritids and typical medlicottiids (50,51,65). *U.Carb.(Penn.).*

Uddenites Böse, 1919 [**U. schucherti*]. Venter retuse. Sutures with ventral portion of 1st lateral lobe intermediate in depth (50,65). *U.Carb.(U. Penn.)*, Tex.-Urals.——Fig. 10*C*. **U. schucherti*, Tex.; ×5.

Prouddenites Miller, 1930 [**P. primus*] [=*Daix-*

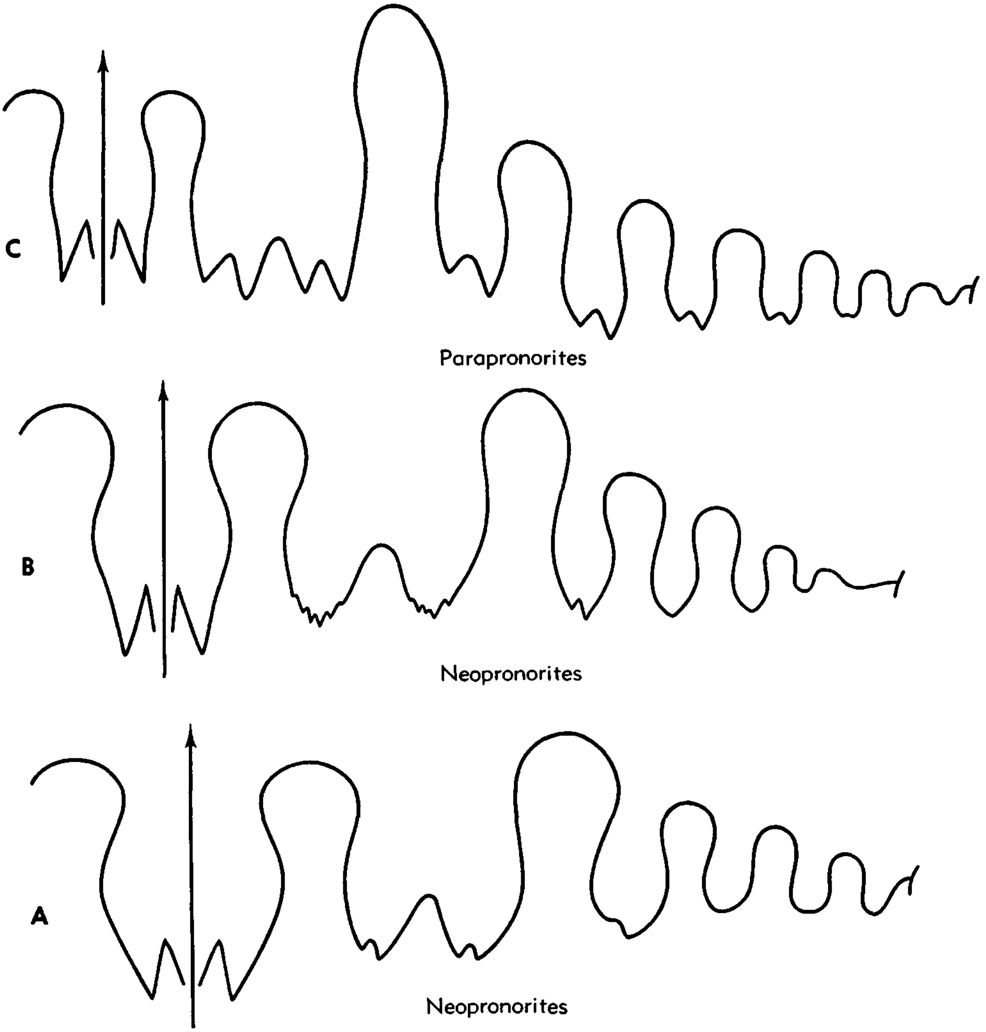

FIG. 118. Sutures of *Neopronorites (A,B),* ×10, ×8 (85); *Parapronorites (C),* enlarged (24).

ites RUZHENCEV, 1941; *Uralopronorites* LIBROVITCH, 1947]. Venter flattened. Sutures with 1st lateral lobe unequally trifid. Intermediate between *Pronorites* and *Uddenites* (51,65). *L.Penn.-U.Penn.,* Tex.-Okla.-Kans.-Mo.-Urals.——FIGS. 10*B;* 119. **P. primus,* U.Penn.; 10*B,* ×4 (Tex.); 119, ×1.5 (Okla.).

Uddenoceras MILLER & FURNISH, 1954 [**Uddenites oweni* MILLER-F., 1940]. Like *Uddenites* but ventrolateral portion of suture forms broad saddle (50,65). *U.Penn.,* Tex.-Urals.——FIGS. 10*A'-C',D;* 120. **U. oweni* MILLER-F., Tex.; 10*A'-C',* ×10; 10*D,* ×5; 120*A,B,* ×2; 120*C,* ×3.

Subfamily MEDLICOTTIINAE Karpinsky, 1889

[*pro* Medlicottinae]

Discoidal to thinly lenticular conch with

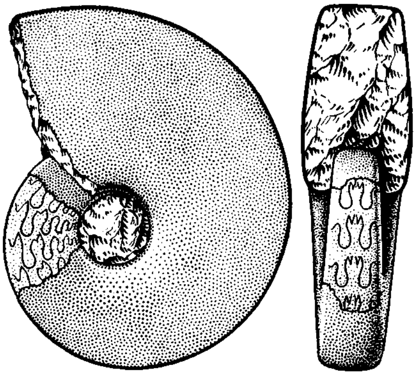

FIG. 119. *Prouddenites primus* MILLER, U.Penn., Okla.; ×1.5 (110).

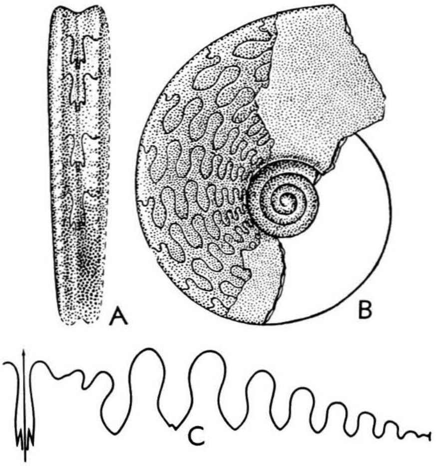

FIG. 120. *Uddenoceras oweni* Miller & Furnish, U.Penn., Tex.; *A,B,* ×2; *C,* ×3 (110).

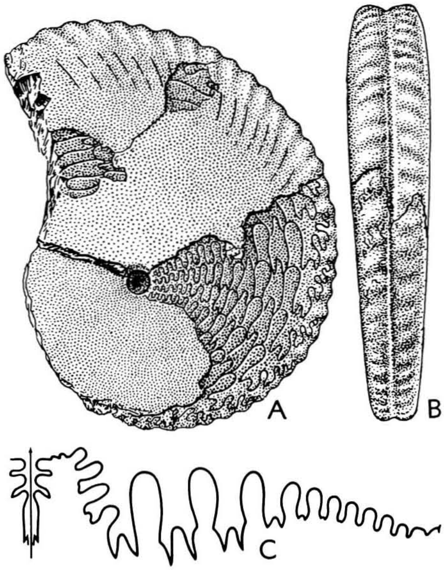

FIG. 122. *Artinsḳia falx* (Eichwald), M.Perm., Urals; *A,B,* ×1; *C,* ×2 (110).

retuse venter. Sutures with bifid auxiliary lobes (24,30,50,64). *U.Carb.(U.Penn.)-L.Trias.*

Medlicottia Waagen, 1880 [**Gon. orbignyanus* de Verneuil] [=*Eumedlicottia* Spath, 1934; *Neogeoceras* Ruzhencev, 1947]. Thinly lenticular conch, characteristically without prominent ventrolateral sculpture. Sutures with 1st lateral saddle high and digitate (50,64). *L.Perm.-U.Perm.,* widespread.——Fig. 121. *M. whitneyi* Böse, M.Perm., Tex.; ×1.3.

Artinskia Karpinsky, 1926 [**Gon. falx* Eichwald, 1857] [=*Prosicanites* Tchernow, 1907 *(nom. nud.); Prosicanites* Toumansky & Borneman, 1937; *Synartinsḳia* Ruzhencev, 1939; *Aḳmilleria* Ruzh., 1940; *Aḳtubinsḳia* Ruzh., 1947]. Discoidal conch with ventrolateral nodes. Sutures as in *Medlicottia* but more primitive (50,64,66). *U.Penn.-M.Perm.,* widespread in Eurasia-SW.USA.——Fig. 122. **A. falx* (Eichw.), M.Perm., Urals; *A,B,* ×1; *C,* ×2.

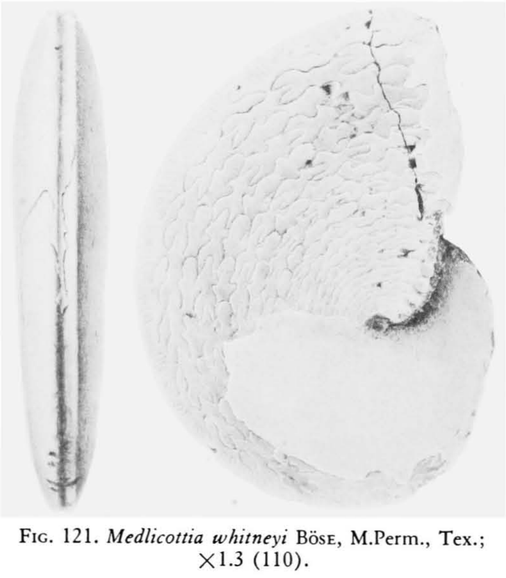

FIG. 121. *Medlicottia whitneyi* Böse, M.Perm., Tex.; ×1.3 (110).

Propinacoceras Gemmellaro, 1887 [**P. beyrichi*] [=*Artioceras* Ruzhencev, 1947]. Like *Artinsḳia* but sutures with 1st lateral saddles lower, broader, and lacking subdivisions on ventral flank (24,50). *M.Perm.,* widespread in Eurasia-N.Am.

Episageceras Noetling, 1904 [**Sageceras (Medlicottia) wynnei* Waagen, 1887]. Like *Medlicottia* but broader conch and sutures with smaller 2nd lateral lobe (93; Spath, 1934). *U.Perm.-L.Trias.,* SaltR.-Himal.-?Japan-Timor-Madag.

Sicanites Gemmellaro, 1887 [**Medlicottia schopeni* (=*S. mojsisovicsi*) Gemm., 1887]. Like *Medlicottia* but sutures with enlarged adventitious lobe in 1st lateral saddle (24,50). *M.Perm.,* Sicily-?Croatia-Timor.

Family SAGECERATIDAE Hyatt, 1900

Conch thinly lenticular or discoidal. Sutures ceratitic, with series of adventitious lobes in 1st lateral saddle (83a). *L.Trias.-U.Trias.*

Sageceras Mojsisovics, 1873 [**Gon. haidingeri* Hauer, 1847]. Lenticular conchs with flattened bicarinate venter and small umbilici. Sutures form numerous subequal auxiliary and adventitious lobes (Spath, 1934). *M.Trias.-U.Trias.,* S.Eu.-Tur-

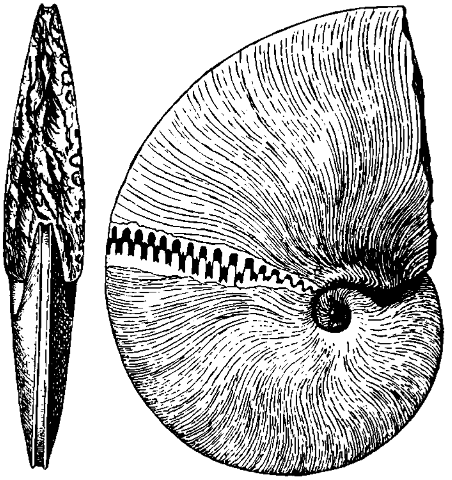

FIG. 123. *Sageceras haidingeri* (HAUER), U.Trias., Aus.; ×1 (115).

key-Timor.-W.USA.——FIG. 123. **S. haidingeri* (HAUER), U.Trias., Aus.; ×1 (115).

Pseudosageceras DIENER, 1895 [**P. multilobatum* NOETLING, 1905] [=*Frechiceras* KRAFFT, 1902; *Metasageceras* RENZ & RENZ, 1948]. Like *Sageceras* but has narrow angular or retuse venter and closed umbilicus (83a). *L.Trias.,* E.Sib.-S.China-Timor-Himal.-SaltR.-Balkans-Spitz.-W.USA.

Cordillerites HYATT & SMITH, 1905 [**C. angulatus*]. Like *Sageceras* but umbilicus closed and sutures with lobes not subequal (HYATT & SMITH, 1905). *L.Trias.,* W.USA-Greece.

Parasageceras WELTER, 1915 [**P. discoidale*]. Like *Sageceras* but discoidal conch with rounded venter and closed umbilicus (WELTER, 1915). *M.Trias.,* Timor.

UNRECOGNIZED GENERIC NAMES APPLIED TO PALEOZOIC AMMONOIDEA

Aganides DE MONTFORT, 1808. Type, which was not named specifically, is of uncertain derivation and affinities. The nautiloid generic name *Aturia* BRONN, 1838, may be a junior synonym.

Prehoffmannia PLUMMER & SCOTT, 1937 [**P. milleri*]. Sutures unknown; type small and probably immature. *U.Penn.,* Tex.

Pseudonomismoceras FRECH, 1899 [**P. silesiacum*]. Type specimen small, evolute. Sutures unknown (78). *L.Carb.,* Ger.

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SOURCES OF ILLUSTRATIONS

Many of the illustrations were prepared by or under the direct supervision of the authors over a period of years. Originals of the others were printed in publications cited in the reference list and indicated by index numbers in parentheses at the close of the generic diagnoses. The only exceptions appeared in reports by the following authors:

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(115) **Zittel, K. A. von**

MESOZOIC AMMONOIDEA

By W. J. ARKELL, BERNHARD KUMMEL, and C. W. WRIGHT

CONTENTS

INTRODUCTION TO MESOZOIC AMMONOIDEA

By W. J. ARKELL

Although the Ammonoidea appeared in the Early Devonian and did not become extinct until the end of the Cretaceous, our knowledge of them is confined almost entirely to the hard parts, the shells and (more rarely) opercula. The soft parts are completely unknown, except for such inferences as can be drawn from the living chambers of the shells they inhabited (which very rarely retain vague muscle scars) and from distribution of the shells in time and space and their ecological associations (Fig. 124). Not even any tracks are definitely attributable to the animals. It follows that classification of the ammonoids, and even their position in the Tetrabranchiata, is to a large extent conjectural and tentative. Nevertheless, their extreme abundance, world-wide distribution, multiplicity of forms, and rapidity of evolution, make them almost ideal zonal fossils and justify the great amount of attention they have received.

MORPHOLOGY

GENERAL FEATURES OF SHELL

The shell is univalve, coiled, normally in a plane spiral but also in a variety of other ways or nearly straight, and is generally assumed to have been external, though arguments have been put forward for supposing that certain types were internal. It forms an elongated cone, divisible into 3 main sections: the **protoconch** or initial chamber; a long camerate portion or **phragmocone;** and a single large terminal **body chamber,** which in at least many genera is known to have been closed by a separate, simple or compound operculum, the **aptychus** (Fig. 124). In size the adult shells vary from about a centimeter to extremes of up to nearly 3 meters in diameter. The phragmocone and body chamber together constitute the **conch,** as opposed to the small initial chamber, the protoconch.

The whole of the shell substance, or **test,** with minor exceptions mentioned below, is calcareous. By analogy with *Nautilus* shell, and from the fact that fossil ammonite shells have frequently been removed by solution while incrusting oysters and serpulids, which are known to be of calcite, remain intact, it is inferred that ammonoid shells were of aragonite. Commonly the aragonite has been replaced by secondary calcite, but studies of some shells based on refraction (39a, p. 323) and x-rays (375a) have demonstrated the persistence of primary aragonite. The **siphuncle** tube (see below), however, is phosphatic, and many aptychi are carbonaceous, probably in life being at least partly chitinous ("horny"), though basically composed of calcite. The test is generally made up of 2 shelly layers, of which the outer is lamellar and the inner is prismatic and much thinner (39a). The total thickness of the test varies widely and seems to be of

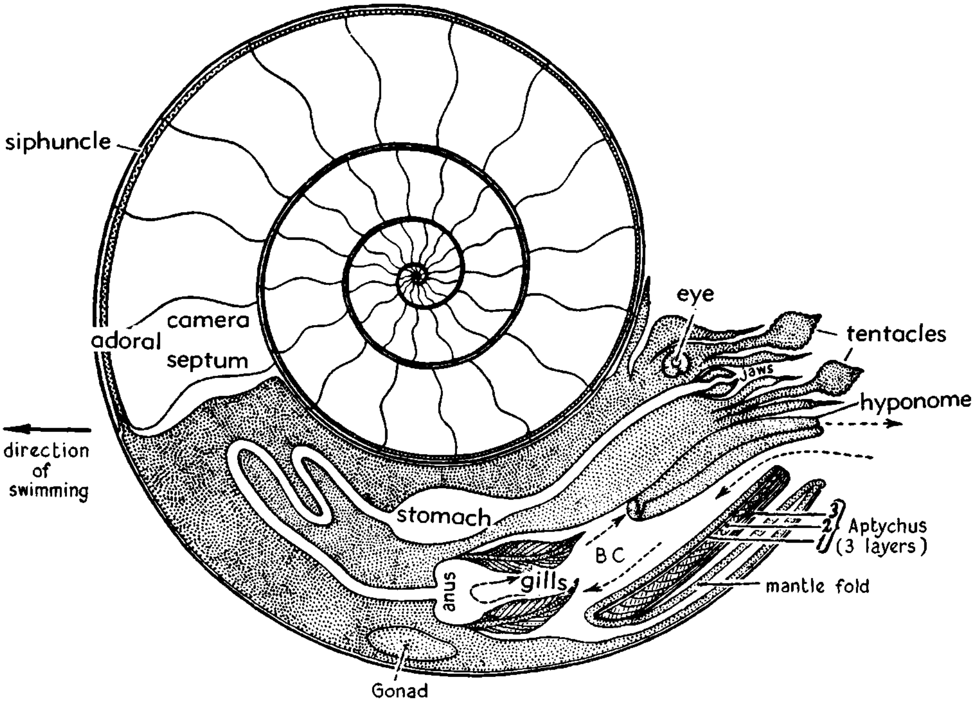

Fig. 124. Median section of ammonite shell in the plane of coiling, showing the septate phragmocone with siphuncle, and the body chamber, the whole in the supposed position in life. In the body chamber is a hypothetical "reconstruction" of the animal, based on analogy with living *Nautilus,* as envisaged by M. Schmidt and F. Trauth, with a cross section of the aptychus in its inferred retracted position on the ventral side of the body chamber. The arrows show water circulation to the gills and out through the hyponome. *BC,* bronchial chamber of mantle cavity (509).

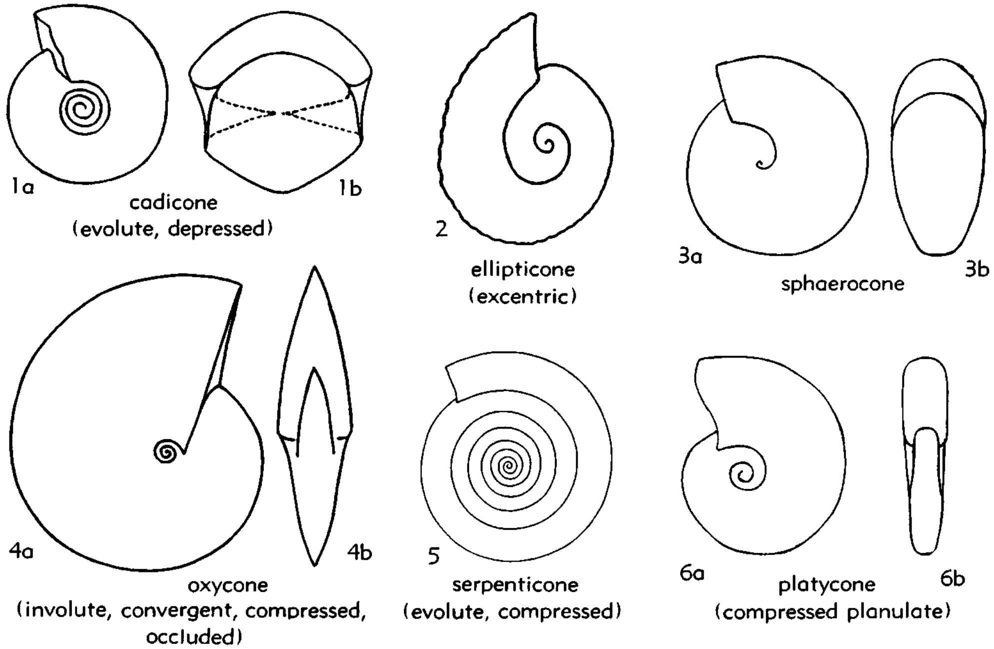

FIG. 125. Types of coiling in ammonoid conchs; planispiral forms (583, 650).

little systematic importance. As a rule, it is very thin in the suborders Phylloceratina and Lytoceratina, but in some species of *Lytoceras* it is as thick as in most other ammonites. In parts of some large forms of Ammonitina the thickness may reach 1 cm. During solution of the test, recrystallization sometimes results in leaving small crystals of calcite or, more rarely, nests or groups of minute calcite pyramids, called **conellae,** attached to the natural internal mold. Conellae occur chiefly under hollow keels and tubercles, where they result from diagenetic chemical change of a late-formed shell layer secreted after withdrawal of the mantle from parts of the primary test (195,196) (Fig. 136).

The typical ammonoid is tightly coiled in a plane spiral about the protoconch. Each coil or volution is called a **whorl.** The concave surface on each side enclosed by the last whorl is called the **umbilicus,** and the coiling is said to be **evolute** or **involute** according to whether the umbilicus is wide or narrow. These terms are vague and relative, varying with the style of coiling normal for different famiiles or genera. Another way of assessing them is by the degree to which the whorls overlap one another. A typically coiled ammonoid shell, neither evolute nor involute, neither compressed nor inflated, is called **planulate.** More inflated forms are **sphaerocones** or **cadicones;** more compressed forms are **platycones** or **oxycones** (see glossary and Fig. 125).

Some forms develop elliptic coiling in the last whorl **(ellipticones).** Some are not tightly coiled at the center, where there is an umbilical perforation; others begin to uncoil with the last whorl. These and other more aberrant forms are known as **heteromorphs** (Fig. 126). Definitions of the principal forms will be found in the glossary under **cyrtocone, gyrocone, helicoid,** and **torticone** (Figs. 125, 126). As in gastropods, the great majority of ammonoids are coiled in the same direction, which is assumed to be dextral, but a few are sinistrally coiled.

In describing features of the conch, those which are nearer to the apex or protoconch are called **adapical,** those which are nearer the aperture are called **adoral.** These terms are also used in a directional sense: for instance, "the whole cone enlarges adorally, from the first or adapical chamber." For the walls of the conch and for directional indi-

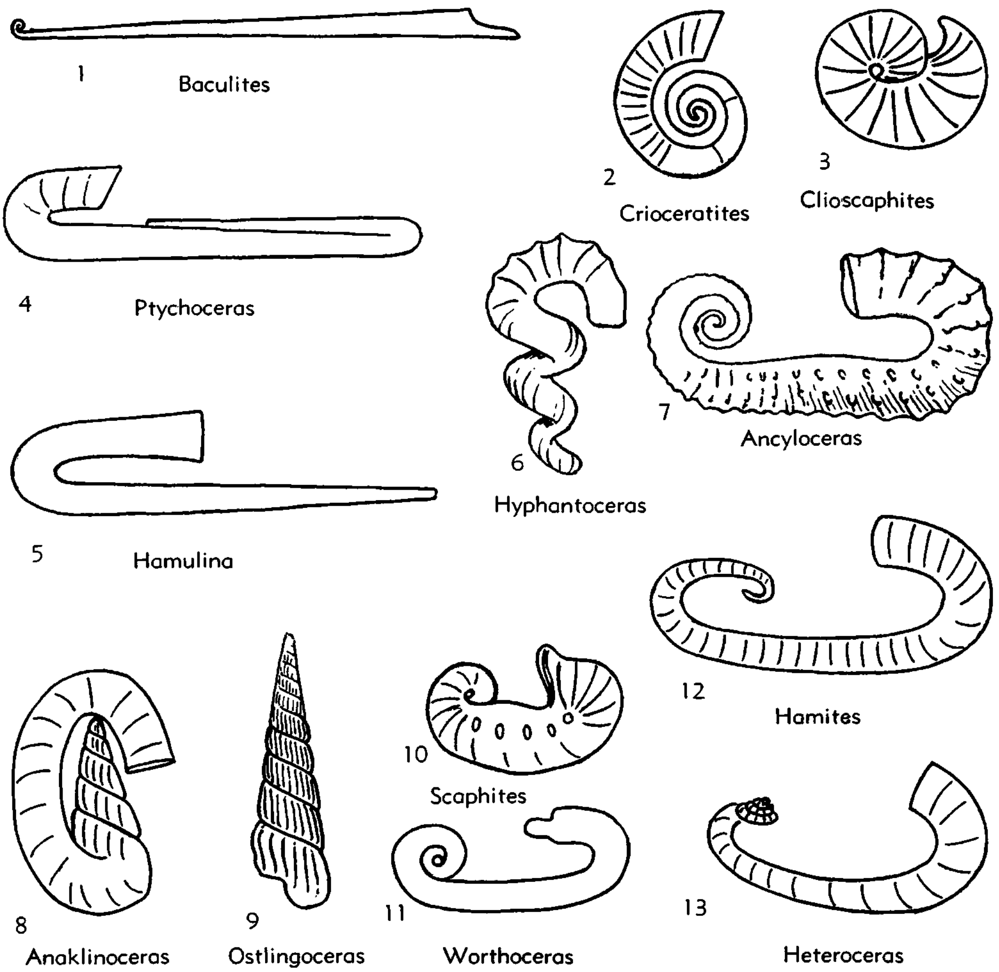

FIG. 126. Types of coiling in ammonoid conchs; heteromorphs (735).

cations at right angles to the long axis, the conventional terms **ventral** and **dorsal** and left and right whorl sides are used, based on the assumption that in normally coiled forms the animal was orientated as in living *Nautilus,* with the dorsum towards the center of the coil and venter outwards (Fig. 124). Thus, the periphery of the ammonite is the **venter** and the opposite side is the **dorsum** (Fig. 127). There is evidence to show that in life, as with living *Nautilus,* the **aperture** must normally have lain at the underside, though facing horizontally or upward (523). The dimensions usually measured are the same for Mesozoic as for Paleozoic ammonoids and have been explained in the first part of this volume (Fig. 124).

PROTOCONCH

All ammonoid shells begin with a globular or barrel-shaped embryonic chamber, the **protoconch,** which forms the apex of the cone and is different in character from all subsequent chambers (Fig. 128). Its longer axis is normal to the plane of coiling, and generally it is wider than the initial (1st postembryonic) chamber of the conch. It is separated adorally from the conch by the **prosiphon** and 2 **prosepta,** which appear to be continuous with the shell wall instead of cemented to it as are the true septa (Fig. 129). The shell wall ends in a blind projection, the **flange** ("internal ridge" of GRANDJEAN, 1910).

PHRAGMOCONE

The **phragmocone** (Figs. 124,130) comprises the bulk of the ammonoid shell and gives it the characteristic chambered appearance. The chambers, or **camerae,** are divided by a series of more or less regularly spaced walls, or **septa.** These were laid down presumably by the mantle of the animal, which moved forward periodically as the shell grew. The septa become gradually more widely spaced (absolutely, not relatively) until maturity, after which they tend to become crowded, or **approximated.** This fact affords a method of recognizing a mature shell.

The septal edges, where they join the inside of the walls of the whorl, are on the whole simple in primitive ammonoids and in the earliest growth stage of all ammonoids, and they become more complex and frilled in the adult of more advanced types. Some late types, however, show reversionary simplification. The pattern formed by the septal edges, or **sutures,** is an important systematic character and has been much studied: the septal sutures, therefore, are dealt with in a separate section.

All the septa of the phragmocone are pierced by a hollow tube, the **siphuncle,** which runs through all the camerae and opens into the body chamber (Figs. 124, 130). It consists of a phosphatic tube or sheath which enclosed a membranous organ not preserved in the fossil state except sometimes as a structureless, carbonaceous mass (?conchiolin). The siphuncle begins with a bulblike sac, the **caecum,** which occupies most of the initial chambers (Fig. 129). In the earliest whorls, the position of the siphuncle is unstable and it may wander from central or dorsal to ventral (SPATH, 1933, 1950), but in general it settles down to a dorsal position in the clymenias and to a ventral position in all other ammonoids (Figs. 124, 130). As growth proceeds it enlarges relatively little and soon occupies a very much smaller proportion of the whorl. Mineralization of the sheath appears to have lagged behind general shell growth, for in both young and old ammonoids the phosphatic tube is absent in the last-formed camerae, although the septa are pierced. The number of camerae without the tube increases with age of the individual and may reach from a half to a whole whorl (TRUEMAN, 1920).

At the opening in each septum **(septal foramen)** where the siphuncle passes through, the edges of the foramen are produced in a ringlike extension called the **septal neck** or **septal funnel,** which surrounds and clasps the siphuncle. In primitive ammonoids, as in nautiloids, the septal necks project adapically and are called **retrochoanitic;** in more advanced forms the septal necks begin from early adolescence to be projected adorally **(prochoanitic).**

BODY CHAMBER

The **body chamber,** or living chamber, is distinguished from the rest of the conch by being nonseptate (Fig. 124). It varies greatly

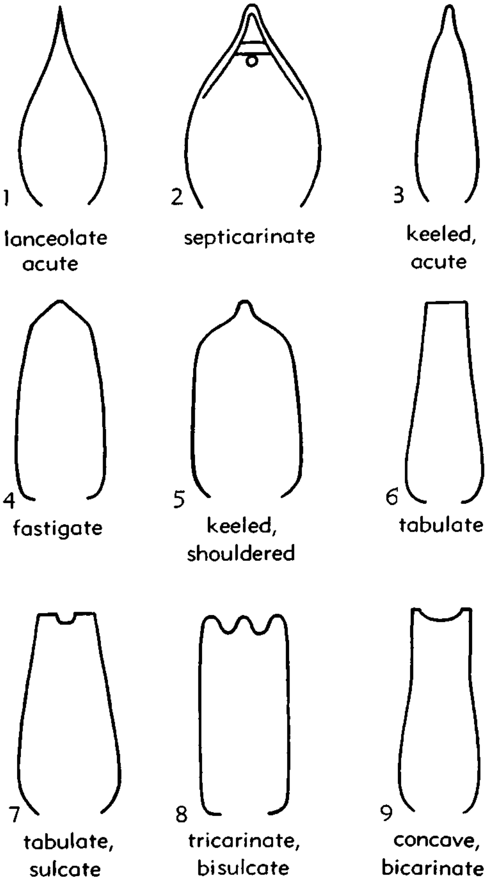

FIG. 127. Types of whorl sections and venters of ammonoid conchs (583,650).

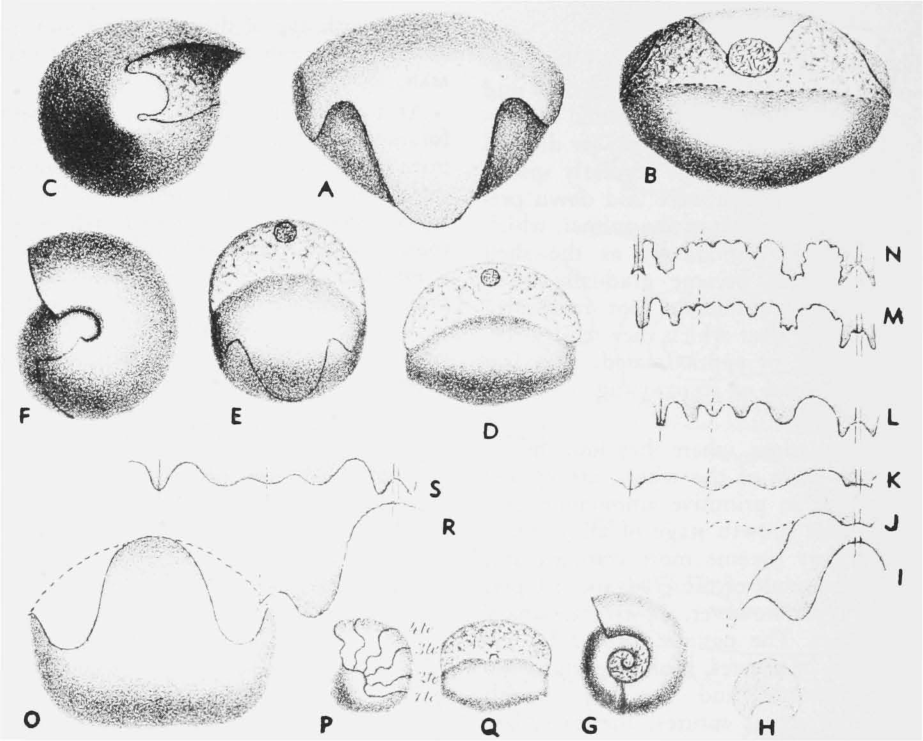

FIG. 128. Protoconchs and early sutures of Jurassic and Cretaceous ammonoids (47).——*A-N, Oxynoticeras,* L.Jur.(Sinem.); *A-C,* protoconch from above, front, and side; *D,* appearance at diameter of 0.6 mm.; *E,F,* at diameter of 0.8 mm.; *G,* conch with 1st constriction; *H,* whorl section at diameter of 4 mm.; *I-K,* 1st 3 sutures; *L-N,* sutures at diameter of 2.5 mm., 5 mm., and 11 mm.——*O-S, Hysteroceras,* L.Cret.(Alb.); *O,* protoconch from above; *P,Q,* appearance at 6th suture; *R,* 1st suture; *S,* 3rd suture. (Much enlarged.)

in length in different groups, from less than half a whorl to more than a whorl and a half, but in most ammonites the length is between half a whorl and one whorl. In some forms it tends to decrease in length with growth, but in others its length relative to whorl length remains constant, as does its volume relative to that of the phragmocone. As a rule there is an inverse relation between length of body chamber and area of whorl section, the longest body chambers being usually found in many-whorled, evolute planulates. Owing to the fact that there were no septa to obstruct the passage of mud into the body chamber after decay of the animal, it often happens that the body chamber alone is preserved in its original form, whereas the phragmocone, with its hollow camerae or partial filling of secondary calcite crystals, was crushed; in other circumstances, however, especially in shales, phragmocones are pyritized and intact but body chambers crushed and destroyed.

Very rarely, natural internal molds of the body chamber show more or less obscure muscle scars (90,227,545).

Commonly, but not invariably, the adult body chamber undergoes modifications of form. The commonest is contraction of the whorl section, which generally begins at the dorsum. Consequently, it is common for the ventral (outer) surface to continue in the normal spiral while the inner edge of the last whorl **(umbilical seam)** departs from the spiral and runs out tangentially, either gradually or abruptly. The venter also may develop a hump or knee bend. Such excentric coiling of the last whorl or last half or quarter whorl may take many forms (Figs. 125, 126). All are evidence of a mature shell. The contraction is often seen to be accompanied by modification or disappearance of ornament.

APERTURE AND PERISTOME

Many ammonites have a simple apertural

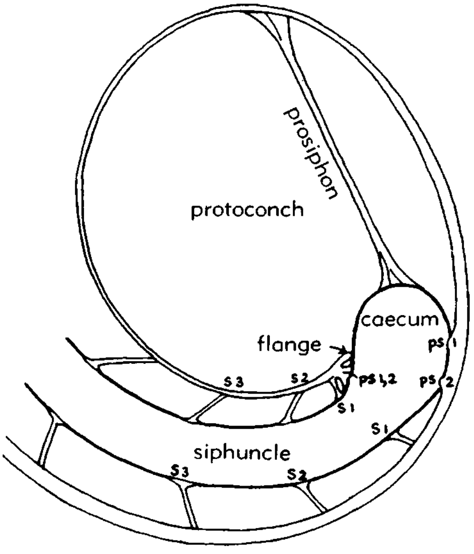

FIG. 129. Median section at apex of *Sphaeroceras,* M. Jur., in plane of coiling, much enlarged (*ps1,* 1st proseptum; *ps2,* 2nd proseptum; *s1, s2, s3,* 1st 3 septa) (178).

margin, or **peristome,** at all growth stages. In these forms the body chamber simply ends like a severed tube, or else the end is marked by a simple contraction, or by a contraction and raised band or collar, and in some shells, with a narrow liplike extension of the ventral area. Many other forms, however, identical with the simple forms in almost every particular, have a greatly modified or elaborated peristome (Fig. 131). The commonest adjunct to the aperture is a pair of **lappets,** one on each side. These are flaplike, or elongate, digitate, or necked (spatulate) extensions of the shell. In some forms they are nearly a quarter whorl in length, and they may be directed outward and dorsally so as to embrace the sides of the preceding whorl, or inward so as to touch at the extremities and divide the aperture into 2 parts. With or without these, a ventral extension of the lip may form a **ventral lappet;** or the ventral extension may be developed as a long, tapering **rostrum,** which can be straight or recurved like a horn, or even recoiled. Such apertures contrast strongly with those of many Paleozoic goniatites and clymenias, which have a hyponomic sinus on the venter, as in nautiloids. In some extreme forms of Jurassic age (*Oecoptychius,* Callov.), long spatulate lappets are accompanied by a modified rostrum which ends in a hooded structure shaped like a tea cozy. In such forms the aperture is divided into 3 parts, and the movement of the animal must have been much restricted. In some others (*Ebrayiceras,* Bath.), 2 digitate ventral lappets join projections of the greatly extended lateral lappets and between them almost completely close the aperture, leaving 5 small holes (130).

DIMORPHISM

It is a remarkable fact that all ammonites with lappets (but not necessarily those with rostra) are smaller than those with simple aperture which most closely resemble them in other respects. In the Mesozoic, especially in the Middle and Upper Jurassic, there is repeated dimorphism in nearly all families: large forms with simple or merely contracted apertures are found side by side with small forms bearing lappets. The size ratio is commonly 1:1.5 or 1:2, but it may be even more. This fact early led to the suggestion (529) that lappets were a feature of

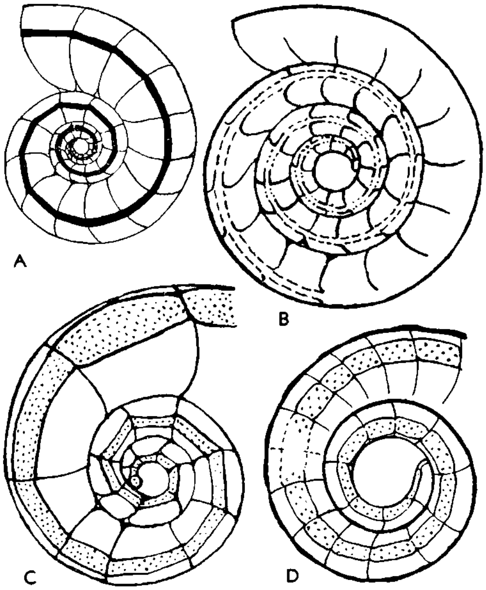

FIG. 130. Median sections through inner whorls of ammonoid conchs which show wandering in position of the siphuncle in early ontogeny (713). *A, Lissoceras,* ×20; *B, Leiophyllites,* ×28; *C, Strigoceras,* ×28; *D, Tropites,* ×40. In *B,* the siphuncle is external in the 1st 3 camerae but in others its initial position is internal, later wandering about until it settles into an external position.

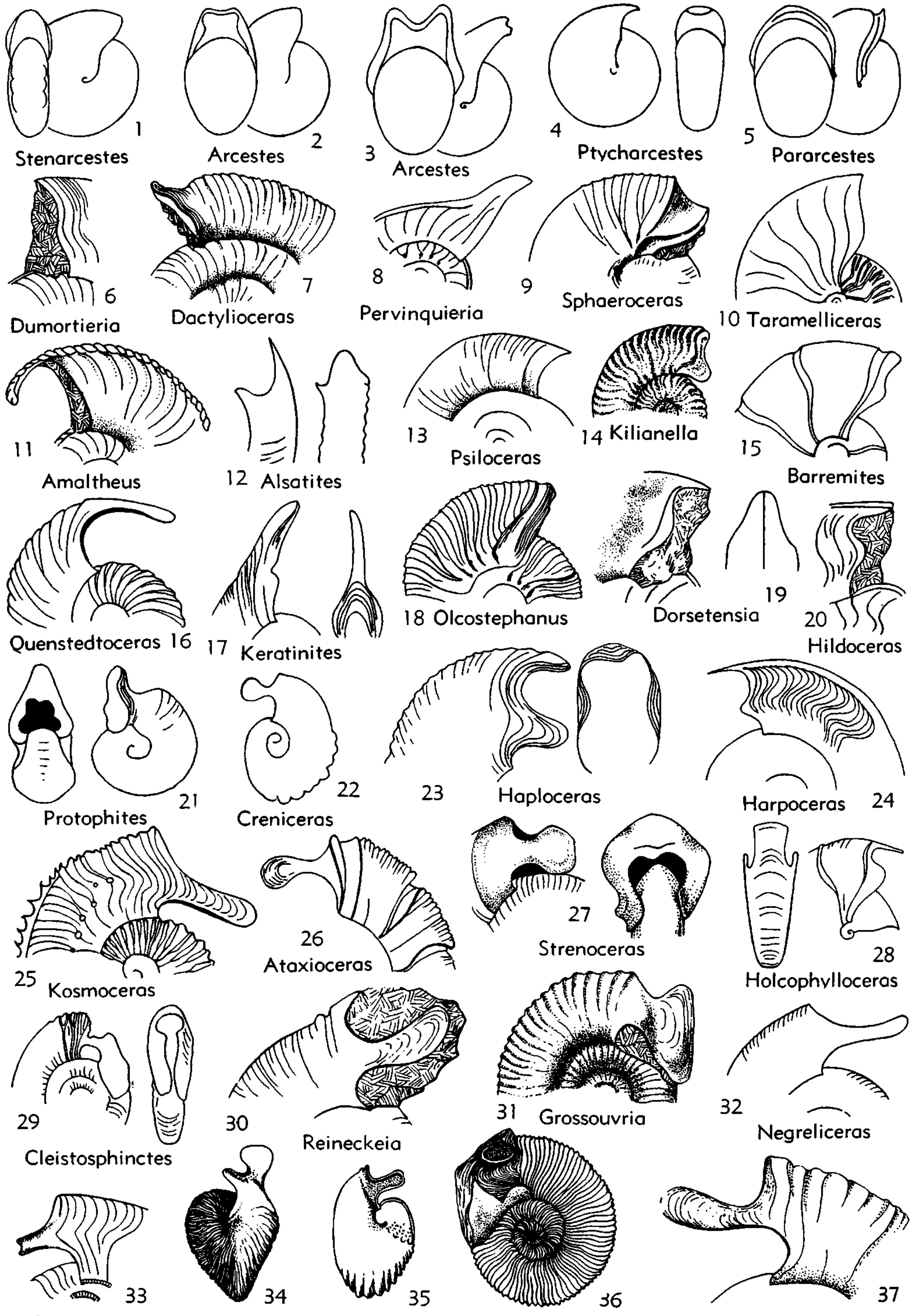

Fig. 131. Types of apertures in ammonoid conchs (650).

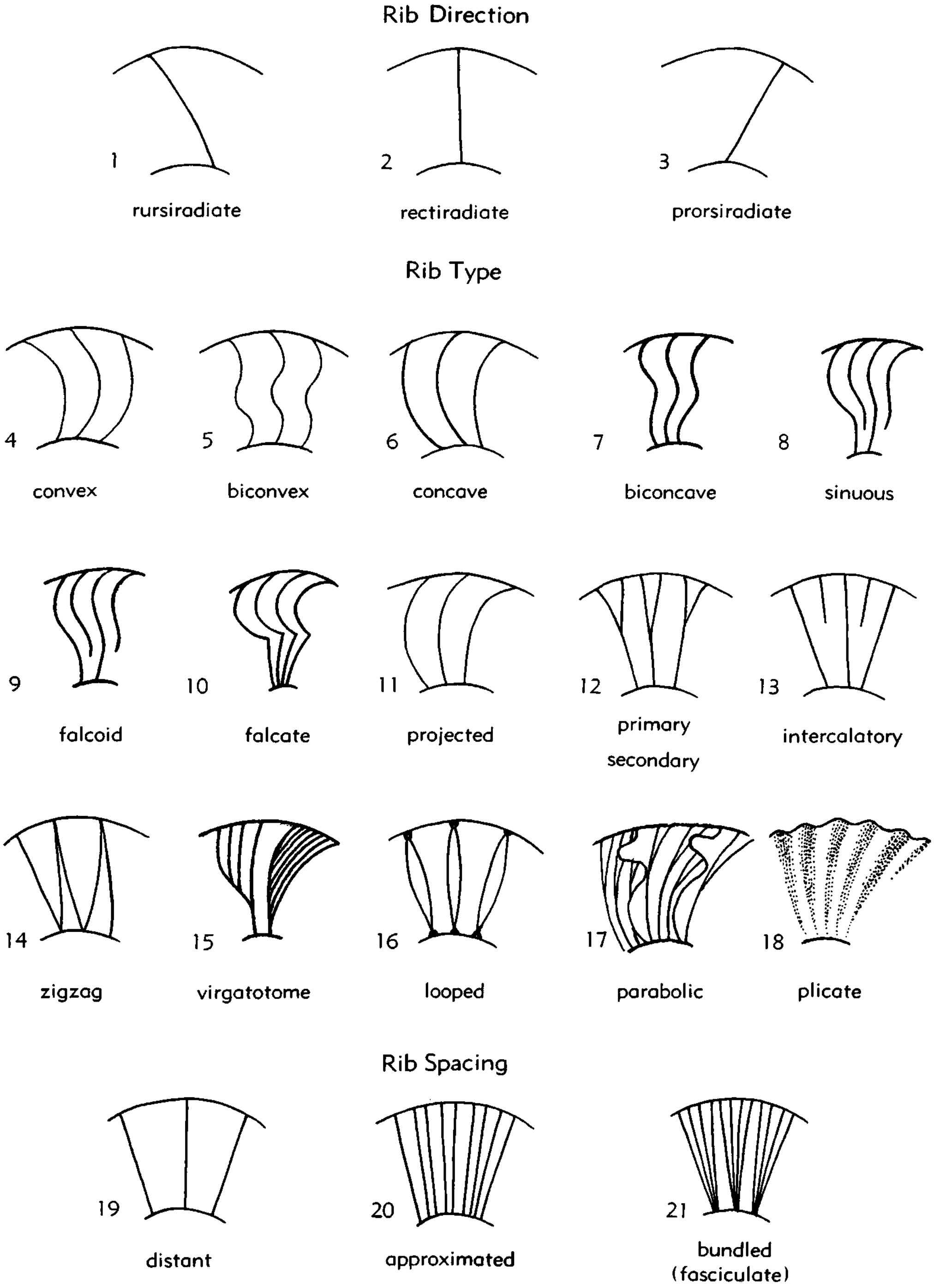

FIG. 132. Types of ribbing on ammonoid conchs (650).

the young. But one of the difficulties of this hypothesis is the necessity of assuming that these large structures were repeatedly cast off or resorbed to allow shell growth to proceed. Moreover, all the other indications generally show that the shells with lappets were adult. An exhaustive treatment of the problem by POMPECKJ (347) showed that lappets (and elaborated rostra) are features only of maturity. In many species the growth lines and ornament are clearly seen to bend forward on the whorl sides in gradually increasing degree to conform to the shape of the lappet, providing unmistakable evidence for the gradual growth and differentiation of the lappet in maturity.

In the late 19th and early 20th centuries this dimorphism was generally assumed to be sexual. The theory was propounded by MUNIER CHALMAS (305) and was accepted by most of the principal authorities (e.g., GLANGEAUD, 176; HAUG, ROLLIER, and others). According to the theory, the small forms with lappets were males and the large forms with simple peristome were females, which required a larger body chamber to accommodate their ova. BUCKMAN & BATHER (67), however, were sceptical and preferred to regard the lappets and other elaborations of the peristome as features of either gerontism or phylogerontism. One of the objections mentioned by them has since been confirmed; namely, that in living *Nautilus* the male shell is slightly broader and more commodious than the female. It may be objected further that the resemblance of lappets to male claspers of insects is misleading, since the lappets were of rigid shell and some of them met in the middle of the aperture. Their only conceivable function seems to be protective, and it is more likely to have been the female than the male that had delicate organs or ova or young brood in need of protection. It is attractive to seek an analogy in the shell grown by the female argonaut specially to serve as a brood pouch.

There are some families in strata as high as the Middle and Upper Jurassic in which no lappets have been reported (e.g., Macrocephalitidae), and the theory of sexual dimorphism can only be shelved as unproved, until new evidence is forthcoming. Meanwhile lappets are regarded as of at least subgeneric rank in the present classification; an open verdict must be passed for the time being on their function, if any.

ORNAMENT

RIBBING

The surface of even the smoothest ammonites is covered with **growth lines,** each one of which represents a former peristome.

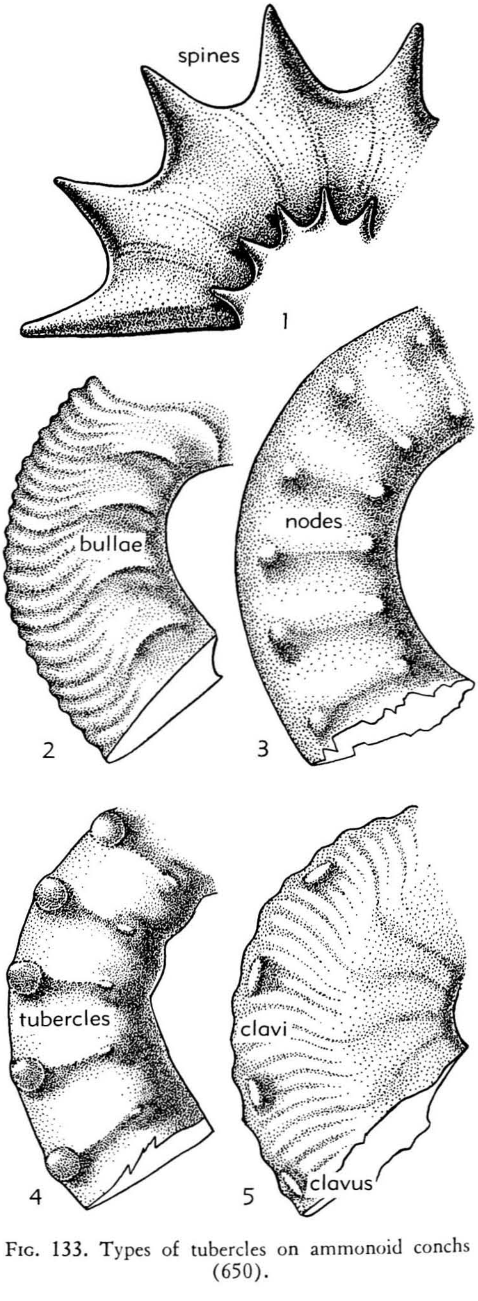

FIG. 133. Types of tubercles on ammonoid conchs (650).

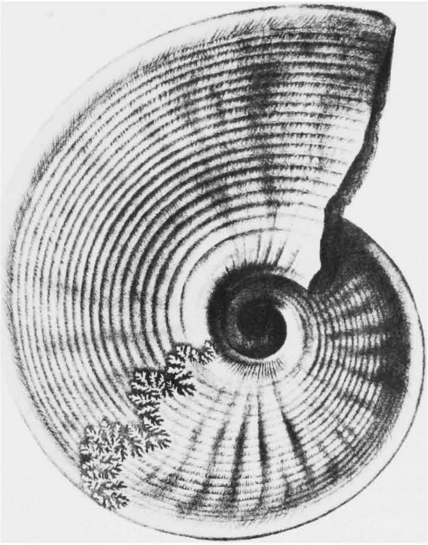

FIG. 134. Strigation as shown on the conch of *Amaltheus pseudamaltheus,* L.Jur.(Pliensb.), Eng. (737).

In many shells the growth lines are accentuated or raised as lamellae, which may be crinkled, or they appear as fine radial lines **(lirae)** or are accompanied by them. Usually the surface is also more or less covered by raised radial **ribs.** Generally these are folds in the test which consequently show almost as strongly on the internal mold, although less sharply. Ribs are not necessarily parallel to the growth lines, and commonly they are quite independent of them. Ribs (Fig. 132) may be simple or branched (**biplicate, triplicate,** etc.), or bundled (**fasciculate**), either close together **(dense)** or far apart **(distant),** straight, curved, flexuous **(sigmoid),** sickle-shaped **(falcate),** or curved forward only at the periphery **(projected);** and their general direction may be radial **(rectiradiate)** or inclined forward **(prorsiradiate)** or backward **(rursiradiate).** The main stem of a branched rib is called the **primary** and the branches the **secondaries.** A loose secondary (usually, however, joined to a primary on the other side) is an **intercalatory.** Some ribs are flared.

Either on the ribs or independent of them almost any number of rows of **tubercles** may occur (Fig. 133). Tubercles on the internal mold commonly represent spines on the test, and large spines may be hollow. Tubercles or nodes elongated radially are termed **bullae,** those elongated in the direction of coiling are **clavi.** Clavi are commonly found on the venter or ventrolateral edge **(shoulder),** and ribs may be looped to them.

In addition, many ammonites bear spiral systems of ornament: i.e., linear ornament running in the direction of coiling. The umbilicus may have a raised rim; the middle of the whorl sides or the venter may bear a groove or a raised flattened band **(fillet);** or the whole or part of the whorls may be covered with longitudinal lines **(lirae)** or corded or knotted ridges **(strigation)** (Fig. 134).

KEELS

The venter may have one or more raised longitudinal ridges **(keels).** The common form of keel is central and single, but it may be bounded by **furrows,** beyond which a pair of **false keels** may occur, one on each

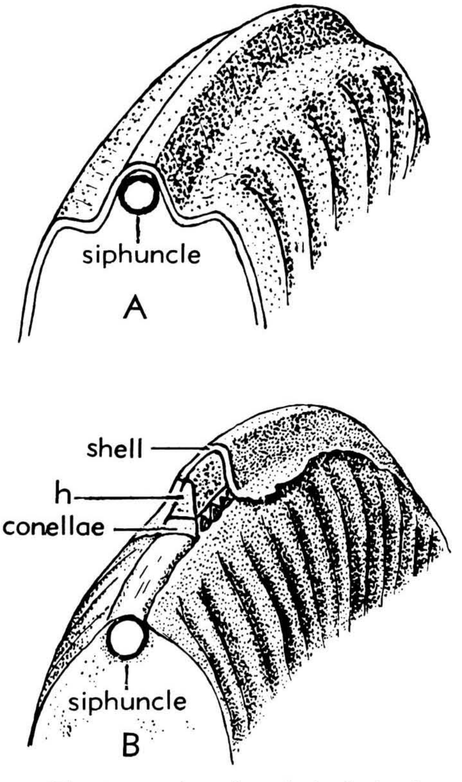

FIG. 135. Cross sections through the keels of ammonoid conchs showing *(A)* open type and *(B)* hollow floored type, in both indicating structure and position of the siphuncle (*h,* hollow keel filled with matrix, conellae appearing in the keel floor) (196).

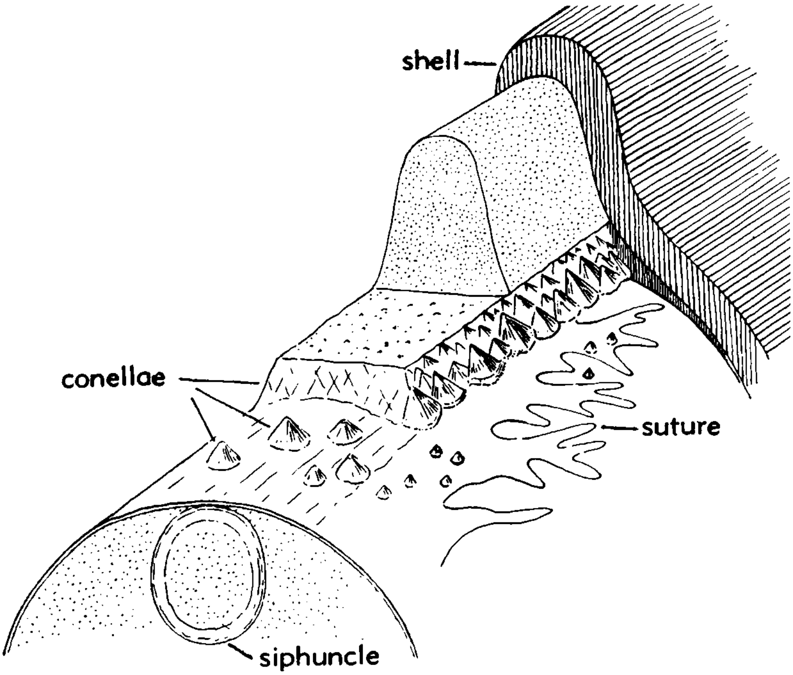

Fig. 136. Diagrammatic dissection of hollow floored keel showing keel floor in various stages of diagenetic dissolution, being converted into conellae, those scattered toward the flank denoting an original lateral extension of the keel floor substance (corresponds to vertically ruled area) (196).

ventrolateral edge. Such a venter is said to be **tricarinate-bisulcate.** The true keel covers the siphuncle and may have protected it. The keel may be solid, or a hollow extension of the shell cavity, or hollow and floored, being separated from the camerae by a shell floor (195, 196) (Figs. 135, 136). The hollow floored keel in some genera is a transient feature in the growth of individuals; it may pass from unfloored to floored and back again before maturity is reached, but in none does the floor continue far over the body chamber. In some forms a keel on early and middle whorls fades and then gives place to a ventral groove on the last whorl (*Semiformiceras,* Tithon.); in others a groove on early whorls gradually fills up and is followed by a tall keel on the last whorl (*Styracoceras,* Callov.). Also, a persistent keel on the test may be represented by a groove on parts of the internal mold (*Schistophylloceras,* Sinem.), such a ventral groove on a mold being deceptively simulated, however, by falling away of the siphuncle. Keels may be **entire** (smooth) or **serrate** or **clavate,** or they may be represented only by a median ventral row of serrations or clavi.

FEATHER STRUCTURE

A rarer kind of ornament that is seldom seen because it is apparently confined to the structure of the inner shell layers occurs on all or the outer half of the whorl sides, chiefly in oxycones; this consists of a band of delicate, forwardly directed chevrons, standing in scarcely perceptible relief and thus generally visible only by low-angle lighting (Fig. 137). It has been figured in some Cretaceous pseudoceratites (*Placenticeras,* Hyatt, 1903, p. 222, pl. 47) and in Bathonian and Oxfordian oppeliids (Waagen, 1869, pl. 18, fig. 5; Petitclerc, 1918) and has been observed by Arkell in a Bajocian *Protoecotraustes* and by Wright an Albian *Beudanticeras* and *Brewericeras.*[1] The explanation is unknown.

COLOR

Traces of color patterns are confined to the outer shell layer and seem to require special preservation—usually in a clay—to

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[1] Since this was written, feather structure has been figured in *Taramelliceras* (Kimm.) (197).

survive (Fig. 138). They take the form of longitudinal brown stripes on a white ground in *Amaltheus, Androgynoceras,* and *Tragophylloceras* (all Pliensb.) (475), and of one or more lateral longitudinal white stripes on brown in *Leioceras* (Baj.) and *Asteroceras* (Sinem.) (GREPPIN, 1898, p. 22). Radial stripes have been noticed in *Pleuroceras* (Pliensb.) (411). Other and bolder patterns occur in Paleozoic straight and curved nautiloids (395).

CONSTRICTIONS AND PARABOLAE

In many ammonites, especially from Jurassic rocks, the phragmocone is periodically constricted. Some shells carry 8 or more **constrictions** on each whorl (Fig. 139). They vary in kind and direction in different families, being definable as **rectiradiate, prorsiradiate, sigmoid,** or **angular**. In phylloceratids they may exhibit a backward knee bend on the whorl sides and a marked sinus, convex forward, on the venter. Some are conspicuous on both test and internal mold; some are prominent on the internal mold but invisible on the test; others correspond to a ridge on the test.

Rather commonly constrictions are accompanied on one or both sides by an oblique simple rib, or a flared or merely oblique simple rib may replace the constriction. Such constrictions or ribs or both commonly cut more or less obliquely across the ordinary ribbing, being more prorsiradiate than the previously formed ribs which they truncate, but parallel to the next-formed ribs. Extreme examples are *Morphoceras* (Baj.-Bath.) and *Spitidiscus* (Neocom.). Such special oblique ribs are distinguished as **parabolic ribs;** with any accompanying irregularities and associated features they are known collectively as **parabolae.**

In many perisphinctids the segment of whorl following a constriction starts larger than the preceding segment **(segmental growth).** From this fact and the new phase of ribbing laid down in a more prorsiradiate direction which starts after each constriction, it is clear that the parabolae represent growth halts. They are not, however, the same as the peristomes of the adult shell, for often no such constrictions or other features may be found at the end of the adult body chamber.

In other perisphinctids (especially *Grossouvria,* Callov.) the parabolae, which are numerous, have no constriction but consist of a parabolic line, barely visible by any difference of relief, but perceptible by the fact that it and succeeding growth lines cut across the previously formed set. Such parabolae swing gently forward on the whorl sides and back on the shoulders and have a more marked and even angular flaplike forward projection or lip on the venter; and between, on the shoulders, a small parabolic node occurs on each side. The nodes are placed on small backward extensions of the new segment. They overrun the growth lines of the previously formed segment and their edge is parallel to the subsequently formed growth lines (Fig. 140). They belong, therefore, to the next-formed segment of whorl, perhaps infillings of notches in the former peristome (290, 499, 502). In some

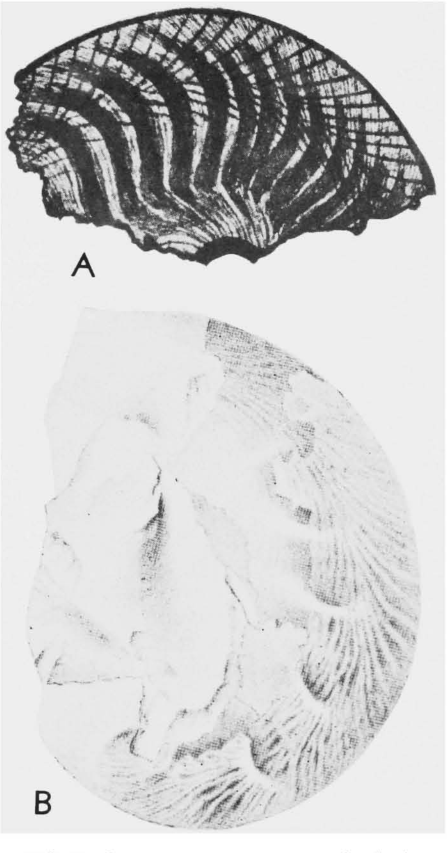

FIG. 137. Feather ornament or structure in the inner or middle layer of the test of an Oxfordian *Oppelia* (*A*) and an Upper Cretaceous *Placenticeras* (*B*) (*A*, 680; *B*, 202).

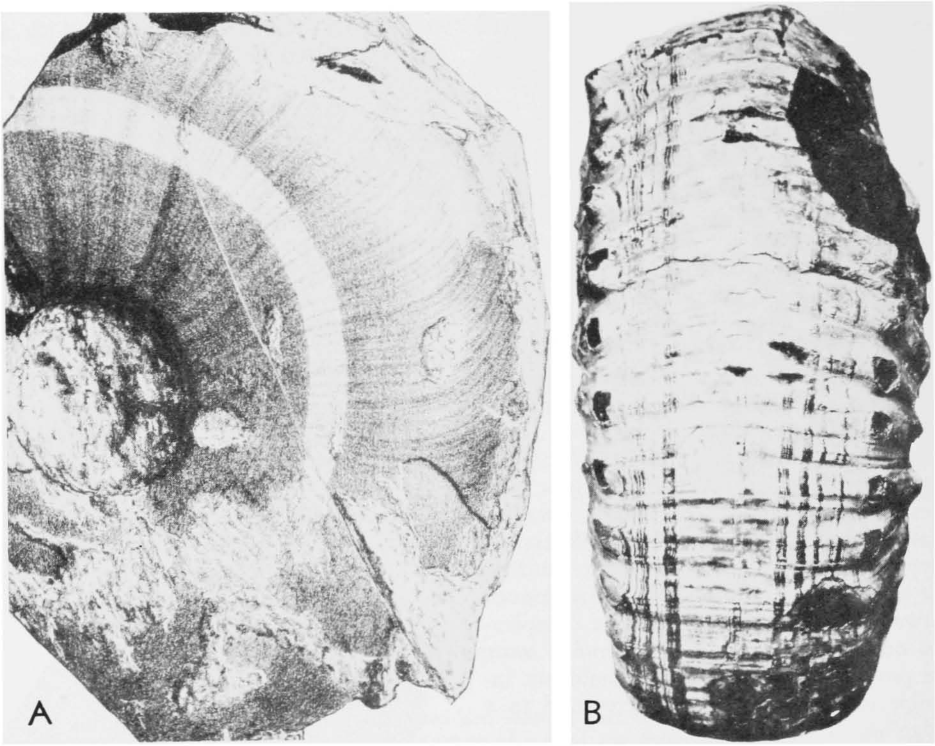

FIG. 138. Color banding on the side of a *Leioceras (A)*, M.Jur.(Baj.), Schleifenberg, near Basel, Switz., and on the venter of an *Androgynoceras (B)* L.Jur.(Pliensb.), Napton, Eng.; both ×1 (*A*, 629a; *B*, 475).

perisphinctids, parabolae are so numerous that they almost completely overwhelm the normal ribbing (see *Paraboliceras*, in systematic section).

SUTURES

Sutures are the lines or patterns traced on the surface of the internal mold of the phragmocone by the septal edges. They represent the junction of septum with shell wall. Each departure from a simple annular line represents a corresponding fold in the septum; and since all such folds die out towards the center of the septum, the more worn an internal mold, the simpler will be the sutures displayed. All sutures rightly should be studied as part of the septa as a whole, but it is only by great labor and destruction of material or chance favorable preservation that complete septa are visible. Outstanding studies of such material, to which the student is referred, are those by BRANCO (47), PFAFF (343), and SWINNERTON & TRUEMAN (501). Moreover, it is normally only the external suture, that is, the part traced upon the externally exposed parts of the whorl (whorl sides and venter), that is visible (Fig. 141). In perfect material of normally involute shells, an operation is necessary to expose the internal suture (part pertaining to the impressed area). Nevertheless, features of the internal suture may have great systematic value and cannot safely be ignored.

All major backward (adapical) inflections of the suture are known as **lobes** and forward (adoral) inflections as **saddles.** In more highly differentiated sutures, which may trace an extremely complex pattern, the minor frills upon the lobes are called **lobules** and those (commonly leaf-shaped) upon the saddles are called **folioles.**

In the earliest ammonites, the 1st-formed suture tends to be a simple annulus or ring, but in later forms it shows a prominent external saddle (Fig. 128). The 2nd suture, which is close to the 1st, always has a ventral lobe, but it is slight in the earliest ammonites and becomes more accentuated in later forms. The subsequent sutures become

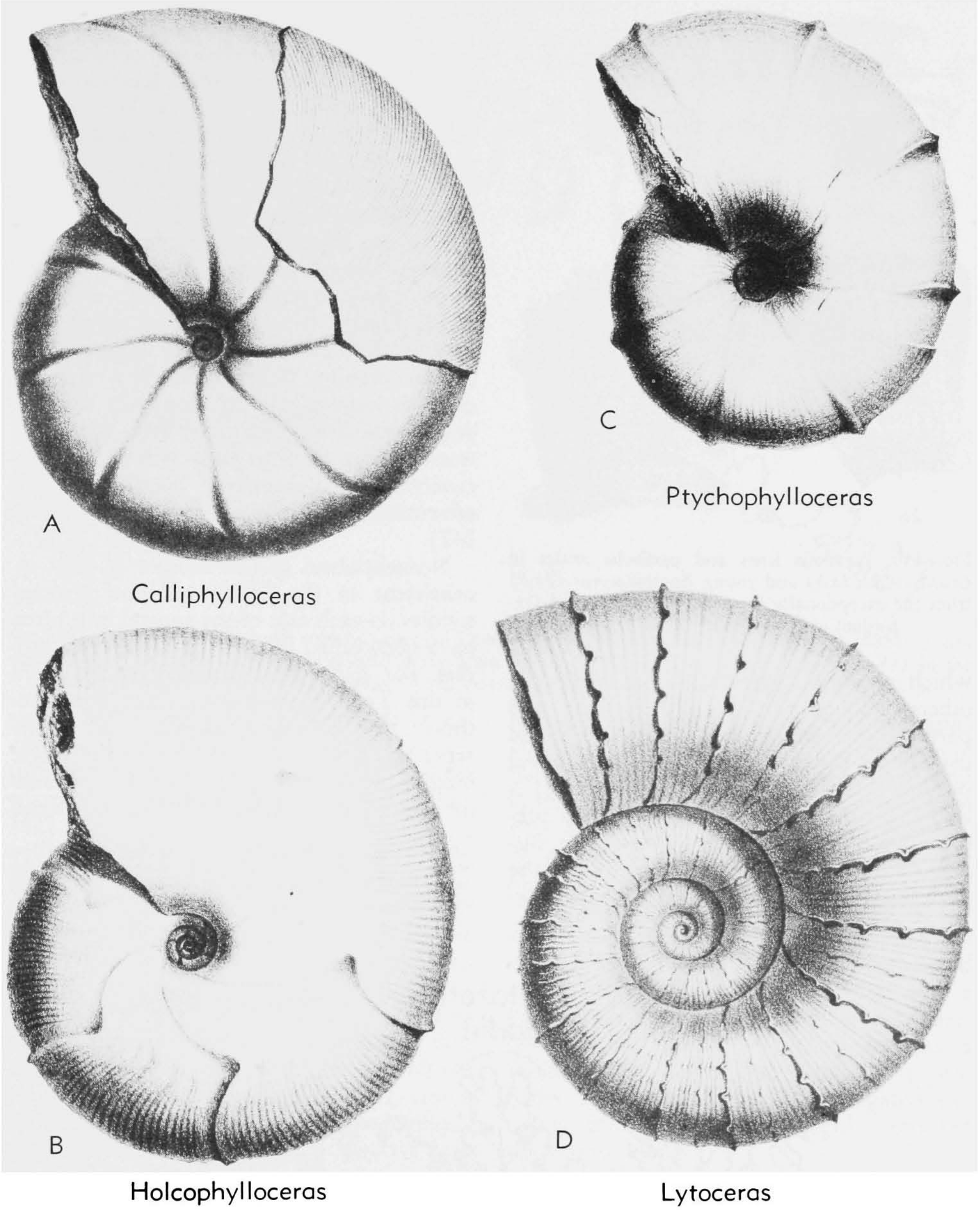

FIG. 139. Constrictions and flares are illustrated by the fundamental stocks Phylloceratina and Lytoceratina (330).——*A, Calliphylloceras,* constrictions on internal cast, not on test.——*B, Holcophylloceras,* constrictions on cast and test, and with median lateral knee bend and ventral labial ridge.——*C, Ptychophylloceras,* riblike flares or labial ridges.——*D, Lytoceras,* crinkled flares on test only.

progressively more differentiated in all ammonites, though the extent to which differentiation is carried differs greatly.

The 1st primary lobes, formed at an early stage of development, are the **ventral lobe** (sometimes called external or siphonal), **dorsal lobe** (sometimes called internal or antisiphonal), **lateral lobe** ("first lateral"), and **umbilical lobe.**[1] The umbilical lobe,

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[1] Various systems of symbols have been devised for representing these lobes and their relative lengths but are not used in this section of the *Treatise*.

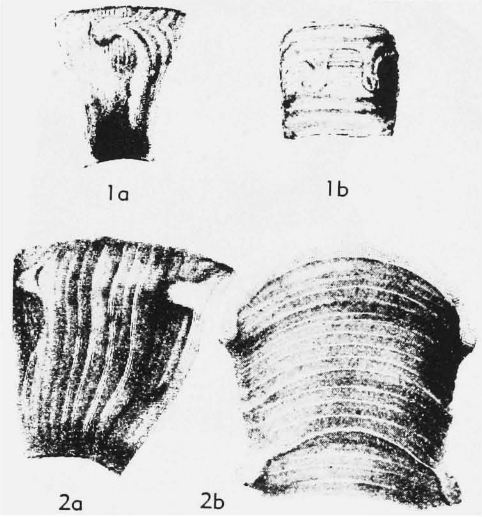

FIG. 140. Parabolic lines and parabolic nodes in *Grossouvria (1a,b)* and young *Euaspidoceras (2a,b)* from the exceptionally preserved Callovian and Oxfordian of Poland and Russia (290).

which appears somewhat later than the others, belongs partly to the external and partly to the internal suture, being centered usually on the umbilical seam. Its external portion (which alone is visible normally) is known as the **suspensive lobe,** and its subdivisions are the **auxiliary lobes.** The suspensive lobe may run straight toward the umbilical seam or be curved steeply backward (adapically) when it is said to be **retracted.** It has been shown that ontogenetically the so-called 2nd lateral lobe of many ammonites is really a development from the primary umbilical lobe; in other words, the 2nd lateral of some forms is homologous with the 1st auxiliary of others.

As differentiation proceeds, in the later ammonites, minor accessory lobes are formed between the primaries. Such lobes may acquire special importance between the ventral and lateral lobes, originating either from near the base of these primary lobes or from the intervening saddle, and they may become as large as the primary lobes and impossible to distinguish from them except by tracing them back to early whorls and discovering their ontogeny. Such are called **adventitious lobes** (or adventive lobes) (Fig. 142).

Nomenclature of the saddles is very inconsistent in the literature. The primary saddles on each side of the ventral lobe often have been called the ventral or external saddles, but it has been decided to call them in this *Treatise* (following some other authors) the 1st lateral saddles, and to reserve the term ventral saddle for the single median secondary saddle formed by subdivision of the ventral lobe.[2] The 2nd lateral

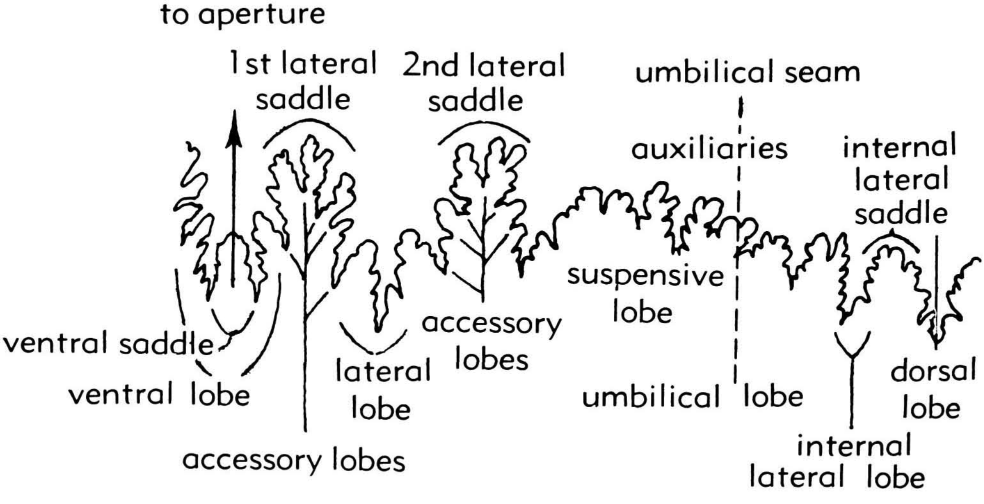

FIG. 141. Terminology of suture line. The arrowed black line on left represents the median line of the venter, the parallel unbroken line on right the median line of the dorsum. The broken parallel line (umbilical seam) separates the external and internal parts of the suture (583).

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[2] The initial "ventral saddle" of the first suture, from which both the ventral lobe and resulting first lateral saddles are formed, may be distinguished as the initial external saddle.

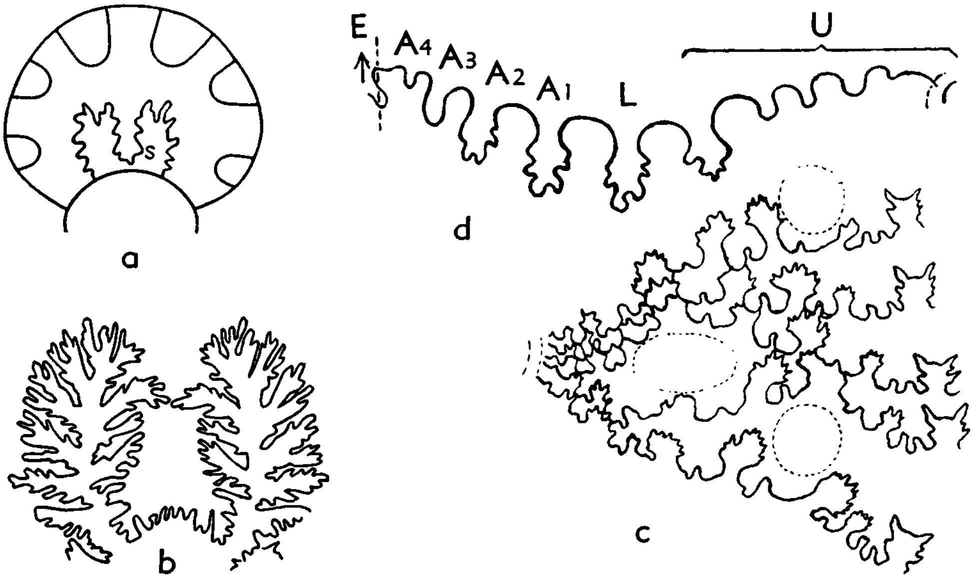

FIG. 142. Special types of septal sutures from the Cretaceous; *a,b,* septal lobe in a lytoceratid (585); *c,* unstable sutures in *Knemiceras* sp., a pseudoceratite from Persia (713); *d,* adventitious lobes *(A1-A4)* in the suture of *Engonoceras* sp., from Texas.——*E,* external lobe, *L,* lateral lobe, *U,* umbilical lobe (713).

saddle is thus the saddle between the lateral and the umbilical lobes. On the internal suture the term dorsolateral is used for the corresponding lateral lobes and saddles (Fig. 141).

On the basis of their general plan, ammonoid sutures are classed in 3 main categories: goniatitic, ceratitic, and ammonitic. **Goniatitic sutures** have all or most of the lobes and saddles plain, without frilling (entire, not denticulate), though the ventral lobe alone may be denticulate; **ceratitic sutures** have the saddles entire but the lobes denticulate; **ammonitic sutures** have all the elements denticulate. (Abundant figures of all 3 types will be found in the systematic parts of this volume.) In a general way these categories represent phylogenetic grades; the names, indeed, are taken from the 3 ancient "genera," *Goniatites* (characteristic of the Paleozoic), *Ceratites* (characteristic of the Triassic), and *Ammonites* (characteristic of the whole Mesozoic). But highly complex, typically ammonitic sutures are found in some families of the Early Permian; ceratitic sutures appear in some families of the Early Mississippian; goniatitic sutures occur in some Triassic and Cretaceous ammonites unrelated to the true goniatites; and more or less ceratitic sutures reappear in both the Jurassic and Cretaceous in numerous families totally unrelated to the Triassic ceratites. The Jurassic and Cretaceous forms are known as pseudoceratites, and they are explained as reversionary, or atavistic, modifications of normal ammonites (Figs. 142-144).

The general direction and course of the suture line is to a large extent linked to whorl shape. Thus, a highly compressed whorl shape is commonly associated with a straight or arcuate suture line with numerous relatively short elements, whereas a round or depressed whorl section is generally linked with few and elongated elements and, commonly, a highly retracted suspensive lobe.

The width of the spaces between the sutures (and septa) may vary greatly on a single ammonite and still more between similar individuals. Apart from this, like the ribs, they tend to become approximated toward the adult body chamber, and thus afford another means of recognizing a mature ammonite. In approximated sutures the lobes and saddles become shorter. Where highly differentiated sutures are close together it may often be observed that the extremities of some lobes impinge against the saddle of the preceding suture and a con-

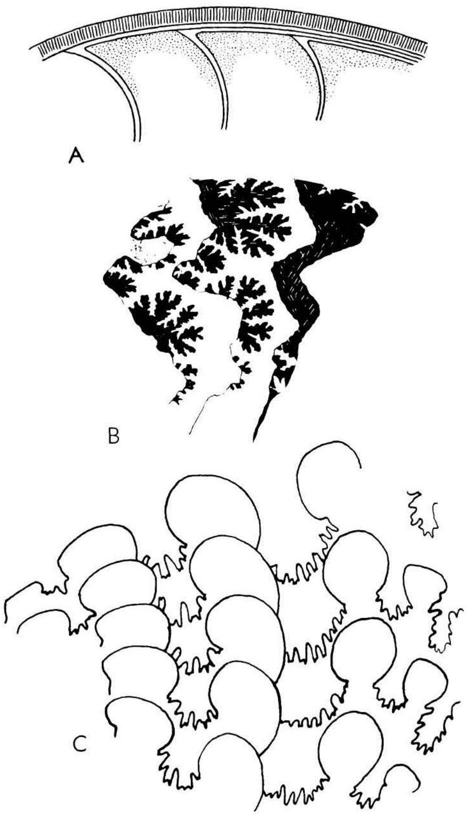

FIG. 143. Overlapping septal sutures.——*A*, diagrammatic longitudinal section (196).——*B*, Overlapping septal layers in a *Sonninia* from Goslar, Ger., with some lobules showing through (196).——*C*, Truncated lobe-endings in *Tissotia* sp., a pseudoceratite from the Peruvian Andes (233).

siderable part of such lobes may appear to be missing. In reality, however, they are continued underneath the preceding septal edge and concealed by matrix filling the preceding camera (Fig. 143). This results from the fact that toward the end of ontogeny the mantle begins to form a new septum without moving forward a full camera length in the whorl, so that the frills of the new septum are built on the inside of the old, instead of against the shell wall (195). In some Lytoceratina a form of this process is normal and becomes a character of systematic value. In these ammonites a bifid extension of the internal lobe climbs halfway up the face of the preceding septum, forming a **septal lobe** (Fig. 142).

A great deal of variation in sutural details must be allowed for within species—much more than has been admitted by some systematic workers who limited their field of study. The degree of variation and its nature differs from family to family, however, and must be assessed with discrimination. Variation is greatest among regressive types in which the suture is undergoing secondary simplification; it reaches extremes in some Jurassic and Cretaceous pseudoceratites (Figs. 142, 144). It should be borne in mind, moreover, that figures of sutures in the literature, even if they show the internal as well as external suture (which is rare), commonly are more or less distorted from the

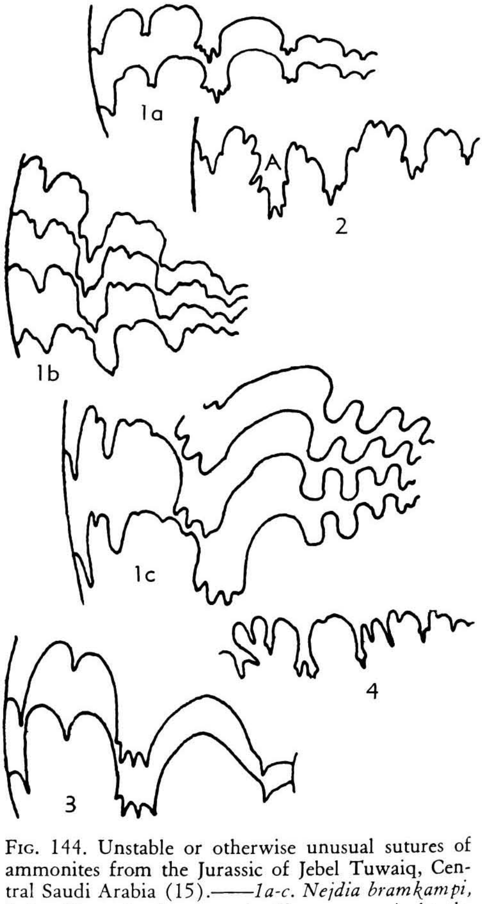

FIG. 144. Unstable or otherwise unusual sutures of ammonites from the Jurassic of Jebel Tuwaiq, Central Saudi Arabia (15).——*1a-c. Nejdia bramkampi*, L.Jur.(Toarc.); *1a*, normal; *1b,c*, progressively abnormal lobes, the auxiliary lobes and saddles in *1c* becoming pseudoceratitic and subequal.——*2. Nejdia furnishi*, L.Jur.(Toarc.), with adventitious lobe (*A*).——*3. Bouleiceras* sp., L.Jur.(Toarc), pseudoceratitic suture.——*4. Bramkampia steinekei* M.Jur. (Bath.) with degenerated digitate suture reminiscent of Cretaceous patterns.

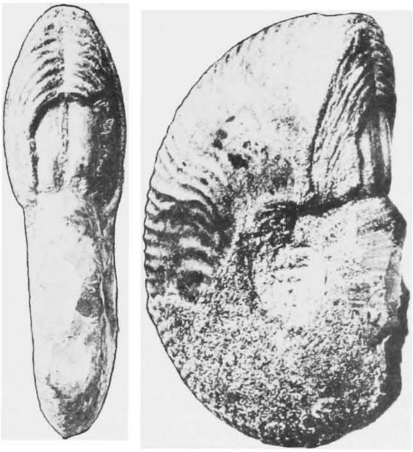

FIG. 145. Aptychus (Lamellaptychus) in position, closing aperture of an *Oppelia,* M.Jur.(Baj.), Dundry, Eng.; the inner or dorsal part of both valves is broken away, showing natural internal mold. (509).

necessity of delineating a cone on a plane surface, and in any case portray only one-half of a complete suture, whereas it is well known that the same suture may show considerable differences on opposite sides of the whorl. In some heteromorphs such bilateral asymmetry reaches extreme lengths and becomes standardized.

Sometimes an ammonite is found with the last septum incomplete, death having cut short its growth. In such specimens it is invariably the umbilical part of the suture that is present, showing that this was the first part to be formed (501, p. 35).

APTYCHI

The calcareous or horny plates called **aptychi** are generally agreed to have been ammonoid opercula. For the most part they are found separately, but enough have been discovered in place, either closing the aperture of ammonites or in various positions (usually ventral) within the body chamber, to leave no doubt of their nature.

The commonest forms, the true aptychi *sensu stricto,* consist of a pair of subtriangular calcareous plates joined along a hinge-like straight edge and gently convex, with a superficial resemblance to an open pair of pelecypod valves. When found united in an ammonite, the combined outline of the plates almost exactly fits the aperture. The concave smooth surface faces inward; the convex ornamented surface faces outward (Fig. 145). Another type, the **anaptychus,** consists of a single plate and is chitinous, or "horny," instead of calcareous and may only partly close the aperture with considerable misfit (Fig. 146). Anaptychi occur from the Lower Devonian to the Cretaceous, but bivalved aptychi (which are much commoner) so far as known are confined to the Mesozoic. In the Upper Cretaceous a 3rd type appears, the **synaptychus,** a calcareous operculum formed by fusion of bivalved aptychus plates.

Many finds of all sorts of aptychi suggest that when not serving as an operculum the aptychus was withdrawn into the ventral

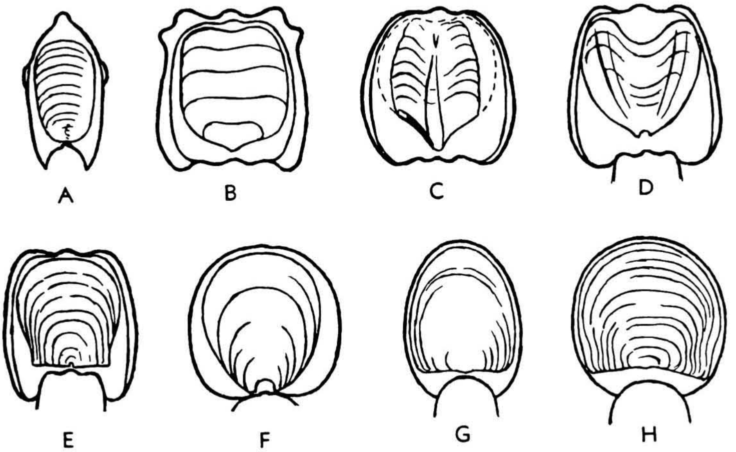

FIG. 146. Anaptychi of the Lias, drawn in closed position in the aperture of ammonite genera with which they have been found associated (425). *A, Amaltheus; B, Pleuroceras; C, Metophioceras; D, Arietites; E, Euasteroceras; F, Alsatites; G, Psiloceras; H, Lytoceras* (425).

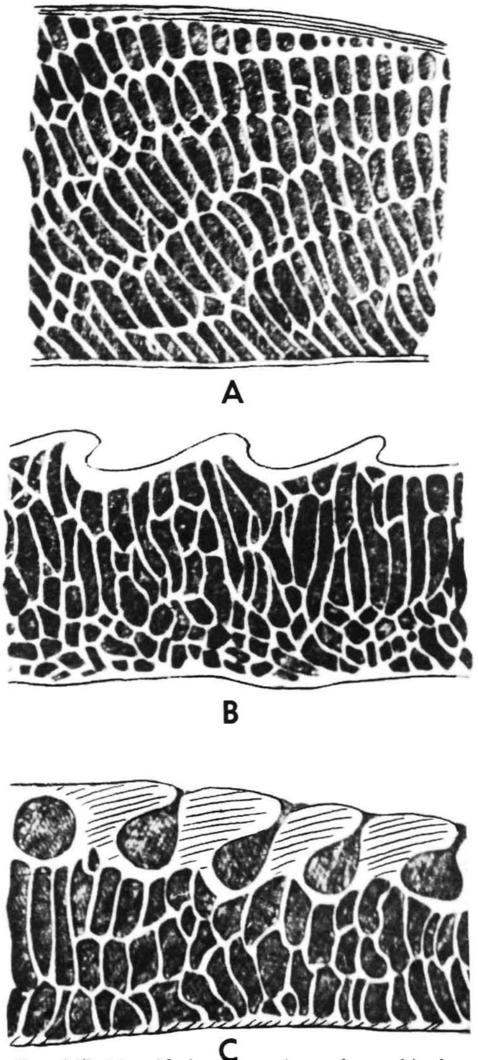

FIG. 147. Magnified cross sections of aptychi, showing internal structure of the shell (661). *A*, Laevaptychus; *B*, Lamellaptychus; *C*, Punctaptychus.

side of the body chamber with the dorsal end directed adorally (Fig. 124).

Aptychi consist of 3 layers: 2 thin lamellar layers enclosing a thicker middle layer with a cellular or tubular structure (Fig. 147). The surface of the outer layer is commonly punctate, granulated, or ribbed and furrowed, while the inner layer, adjacent to the mantle of the animal, is smooth but for growth lines. Current classification is mainly based on the ornamentation of the outer, convex surface, and to a smaller extent on shape and thickness. The technical descriptive terms used for bivalved aptychi, and a list of the "form genera," will be found at the end of the systematic part of this volume (Figs. 556-558). In the body of the systematic part, brief descriptions of aptychi are inserted whenever these have been found inside body chambers of species of the ammonoid families or subfamilies treated. There are many genera and families, however, and even suborders, containing no species with which aptychi have ever been found intimately associated, while in other groups, no more abundant in species or individuals, such an association is not uncommon (e.g., Aspidoceratidae, Oppeliidae). The taxa with which no aptychi have been found associated are so numerous (for instance, the whole of the Clymeniina and Phylloceratina) that there is a strong presumption that they never possessed aptychi capable of preservation.

Aptychi are especially common in bituminous shales of the Toarcian and Lower Kimmeridgian and in Tithonian limestones in many parts of the world. They may form so-called aptychus beds, where they abound to the exclusion of ammonites. Various explanations of this have been put forward and more than one may be correct in different circumstances. In limestone formations, abundance of aptychi most likely may be due to vagaries of current-sorting; on decay of the animal the aptychi might have fallen to the bottom while the chambered shells were carried elsewhere by currents. In bituminous shales, however, it is possible that differences of chemical composition played a leading part; the aptychi, being calcitic or chitinous, may have resisted chemical and physical changes which destroyed the aragonite shells of the ammonites.

ONTOGENY

It is generally assumed that the larva of the ammonoid, inhabiting the protoconch, was free-swimming or drifting (meroplanktonic). This hypothesis explains well the world-wide distribution of so many ammonite genera and even of species, and their sudden (cryptogenic) appearance in regions where no likely ancestors can be found, but the assumption is only a hypothesis. In any case, the protoconch represents a separate episode in the life history of the animal, totally different from all that followed.

The development of the conch, by contrast, was a reasonably continuous process, in which the shell enlarged as an expanding cone, typically coiling in a logarithmic spiral.[1] When examined in detail, the process of enlargement is found to be not so continuous as it appears superficially, but to have proceeded in stages of 2 orders. In the first place, the body of the animal did not move forward continuously in the shell but periodically rested while a septum was secreted. At every forward move the previously formed camera (but not the siphuncle) was vacated entirely by the animal—a process which has been likened to the molting (ecdysis) of arthropods and arthropod larvae, except that the abandoned parts were not discarded (as in some orthocone nautiloids) but were retained as a hydrostatic apparatus (28).

Superimposed on this periodicity there was a longer-term periodicity in the growth of the shell as a whole. In all Jurassic genera dissected by Currie (94), a change of growth ratios at the 2nd-3rd half whorl was observed and this was interpreted to define the end of the 1st postlarval growth stage (?nepionic stage of Hyatt, 1889, p. 18).[2] Similar changes take place at varying intervals throughout the phragmocone. In many shells they are marked by parabolae, as previously described. In some families a sudden increase in size and change in direction of ribbing follows each constriction. This has been described as "segmental growth" and attributed to periodical slowing down of activity to allow enlargement of the soft parts (315, p. 94; 445).

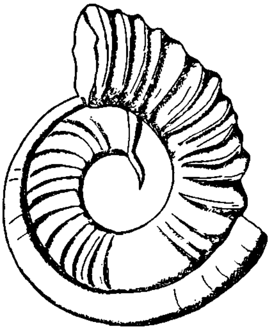

Fig. 148. *Serpula* growing on the venter of an ammonite *(Schlotheimia)* and partly covered by growth of the ammonite whorl (415).

Other changes, progressive or sudden, are illustrated by many of the morphological shell features described above; for instance, the conversion of a ventral groove into a keel or vice versa, the development or disappearance of tubercles and spines, the change of narrow dense ribs into enormous swollen wedges (this last being a major change in the accommodation of the animal, since the ribs are folds in the shell, not superficial features). The greatest changes of all took place in many individuals at the beginning of the adult stage, involving more or less profound alterations of volume and shape of the body chamber and specialization of the aperture.

All these ontogenetic changes have to be borne in mind and are serious obstacles to the application of statistical and graphical methods for identification and classification of ammonites. No set of measurements can be plotted directly against another for the comparison of 2 individual shells, for the various changes took place at different diameters according to the ultimate size of the individual, or to whether its growth was precocious or retarded at any stage (549). The philosophical soundness of elaborate use of statistical methods for selected features of complex organisms (such as those attempted for ammonites, for instance, by Brinkmann, 1929, and Fradin, 1950) is questionable in any case (58).

In the final (?gerontic) growth stage, secretion of carbonate of lime seems to have gone on at undiminished rate after enlargement of the soft parts slackened off. This is the only possible interpretation of the crowding of septa and ribs toward the end of the mature conch; or the enlargement of ribs where there was no crowding. The same surplus of capacity for secretion of shell substance may also have played a part in the production of lappets, rostra, and other features of so many adult peristomes.

It is impossible to put any absolute value on the rate of growth of the ammonite shell,

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[1] The mathematics of the spiral has been studied by Rollier (1924), Currie (1942, 1943, 1944), D'Arcy Thompson (1942, p. 748-822), Vecchia (1945), and others.

[2] Currie's description of this as the "post-embryonic" stage seems open to objection.

but an estimate has been made by SCHINDEWOLF (415). He found that certain Lower Lias ammonites are completely encircled by a single large *Serpula* tube, which must have grown in some sort of symbiotic association with the ammonites (Fig. 148). From a number of the most closely related living serpulids he estimated that the rate of growth of the ammonites was of the order of one whorl in 4 months to 3 years. On the assumption that growth stages were seasonal, CURRIE (94, p. 198) estimated for certain genera development of about 6 whorls in 4 years.

PHYLOGENY, CLASSIFICATION, EVOLUTION

To the idealistically minded taxonomist it is a maxim that classification must be based on phylogeny. To some of his more practically minded colleagues it is a truism that phylogeny can only be deduced from an accurate morphological classification. It is certain that attempts to pursue either classification or phylogeny separately lead to progression in circles. Both depend entirely on accurate knowledge of the morphology of all the forms that lived (and this includes their ontogeny), and on their stratigraphical order. The principal aim of this *Treatise* is to present a synoptic picture of the facts so far known, not to give directives or guidance on the evaluation and interpretation of the facts. The present subsection therefore attempts only a brief explanation and justification of the arrangement that has been adopted in the systematic sections.

ORIGIN OF MESOZOIC AMMONOIDEA

The oldest undoubted ammonoids are the Anarcestaceae, which occur in the Lower Devonian. From them the Palaeozoic ammonoids diverged in 3 main streams. One was the Clymeniina, with dorsal siphuncle, which became extinct at the end of the Devonian. The 2nd was the Goniatitina, which comprised the great majority of Upper Paleozoic ammonoids and became extinct in the Permian. The 3rd (which appeared already in the Late Devonian) was the Prolecanitina, which carried on over the Paleozoic-Mesozoic boundary and gave rise to all Mesozoic ammonoids.

The primary distinction between the Prolecanitina and the Goniatitina rests, according to SCHINDEWOLF (419), on the ontogeny of the suture line. In the Prolecanitina, the lateral lobe arises near the umbilical seam and in the course of development shifts ventrally until it occupies a normal position, midway between the umbilical seam and the mid-line of the venter, while at the same time a new umbilical lobe arises in the vicinity of the umbilical seam. This is the normal course of development for all Mesozoic ammonoids and indicates their ancestry in the Prolecanitina. In the Goniatitina, on the other hand, the lateral lobe remains small and close to the umbilical seam throughout development, while a false lateral lobe gradually forms in the middle of the lateral saddle. Thus, the lateral lobe of adult goniatites is not homologous with that of later ammonites but is really an adventitious lobe.

COURSE OF EVOLUTION OF MESOZOIC AMMONOIDEA

In the Early Triassic a great burst of evolutionary radiation sprang from the xenodiscids, a stock derived from the Prolecanitina. Most of these are grouped by KUMMEL (1952) in 8 superfamilies, together comprising the suborder Ceratitina (Fig. 149). All of them became extinct before the end of the Triassic. But one entirely new stock, which arose already in the Early Triassic, survived the general extinction in the Rhaetian and carried on into the Jurassic. This was the Phylloceratina, which must have been the rootstock of all the Jurassic and Cretaceous ammonoids (Figs. 150, 151).

With the beginning of the Jurassic a new phenomenon appears. This is the side-by-side existence of a persistent stock (the same superfamily Phyllocerataceae which began in the Early Triassic and continued with little change to the end of the Cretaceous) and a number of new radiations from it consisting of superfamilies and families, each of which itself radiated repeatedly so as to form a complicated tangle of lineages. At the beginning of the Jurassic, one of these branches, the Lytoceratina, which presumably arose from the Phylloceratina some-where during the passage from Trias to Lias but soon became completely differentiated, itself became a persistent stock and gave off more radiations than arose directly from the parent Phylloceratina (Figs. 150, 151).

PRACTICAL DIFFICULTIES OF CLASSIFICATION

The key to unravelling the resulting tangle of Jurassic and Cretaceous ammonites on sound phylogenetic lines has long been sought but not yet found. A phylogenetic classification here breaks down. There are so many ammonites (at least in the Jurassic) which cannot reliably be traced back to their parent stock that it is still a practical necessity to retain a polyphyletic suborder Ammonitina for all those ammonites (the vast majority) that do not bear a definitely recognizable affinity to either the stable Phylloceratina or the stable Lytoceratina. It is probable that the rootstock of most of those that appeared after the Sinemurian and before the Valanginian was the Lytoceratina, but accessions from the Phylloceratina also may have recurred, especially to the superfamily Haplocerataceae (Fig. 150).

Attempts in the past to construct phylogenetic trees as a basis for a classification have relied upon a variety of characters and have been influenced by principles or "laws" fashionable in different periods and countries, which may without cynicism be described as the current prejudices with which successive workers have evaluated morphological characters and chosen those on which they laid emphasis.

The 19th century pioneers, from von Buch and Quenstedt onwards, based their classification upon shell form: all oxycones were grouped together, regardless of age, and so on for all the main form types. This "forthright morphological" school has had its adherents down to recent times; for instance, Rollier (384) and Steinmann (494, 496) did not flinch at including in the same genus similar forms from any part of the Triassic, Jurassic, or Cretaceous. Theirs was "vertical" classification *par excellence.* This simple principle was attacked by many workers, such as Pompeckj (352), Hyatt, Buckman, and others, and substitutes were sought.

ITERATIVE EVOLUTION

This hypothesis was first propounded by Salfeld (396, 400-402) and elaborated by Frebold (150), Spath, and others. It postulates that the conservative Phylloceratina and Lytoceratina repeatedly gave off waves of fresh derivatives which at different times and places rang fresh changes on all the well-tried shell forms. Salfeld announced in 1922: "So it is certain that of all the families erected for the Jurassic and Cretaceous ammonites nothing remains." All new studies of faunas have added to the crowd of known examples of heterochronous homeomorphy. As a specially interesting example one may cite *Cymbites,* a series of small, globular, rather featureless ammonites found at successive horizons in the lower Lias. Buckman (62) regarded these as the "radical of all the ammonites" which was derived from a similar Triassic form, perhaps *Nannites.* Spath considered them degenerate "end forms" and distributed them among 3 separate Liassic families according to their stratigraphical horizon, and they are so retained here. *Lissoceras* and *Haploceras,* however, other small smooth ammonite genera of the Middle and Upper Jurassic, which Buckman regarded as degenerate end forms, were believed by Spath to be iterative passage forms from Phylloceratina to Oppeliidae. The present writer believes Buckman more likely to have been right (Fig. 150). These examples serve to illustrate what has happened throughout the classification.

The possibilities of variation in all characters of the ammonite shell are limited, and so are the possible combinations of environmental factors to which the ammonites had to adapt themselves. Accordingly, similar adaptations must have recurred repeatedly throughout Mesozoic time. The logical conclusion to which acceptance of this hypothesis leads is an increasingly "horizontal" classification that depends absolutely on accurate stratigraphical information. The complexity of the modern classification, seen in the systematic parts of this *Treatise,* results mainly from acceptance in large measure of the theory of iterative evolution, although there are comparatively few proved examples of its occurrence. We often feel sure that it has occurred and that we should be deceived if we accepted similarities at their face value

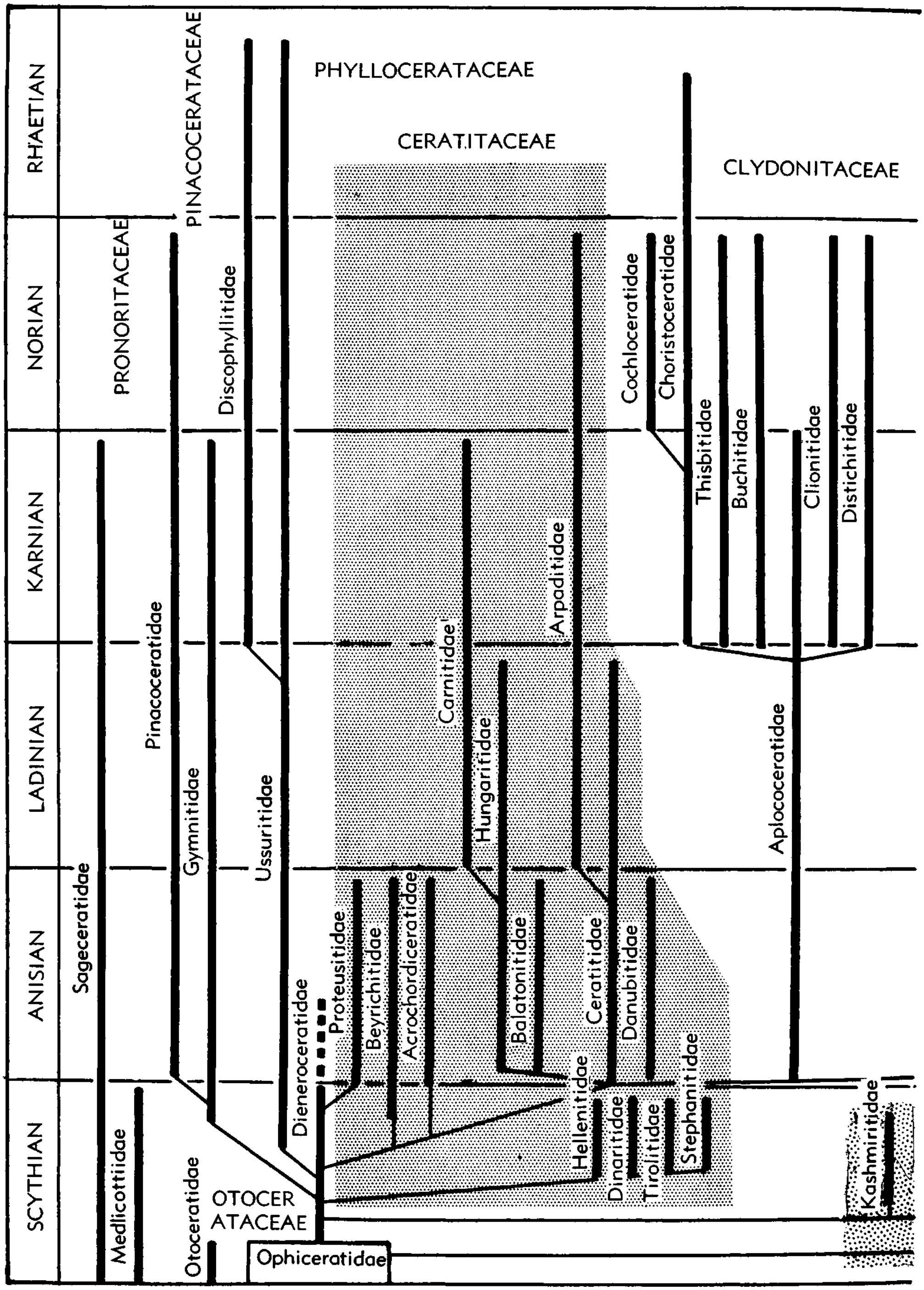

Fig. 149. Chart showing diagrammatically the phylogeny and range of the Triassic ammonoid families and superfamilies (650).

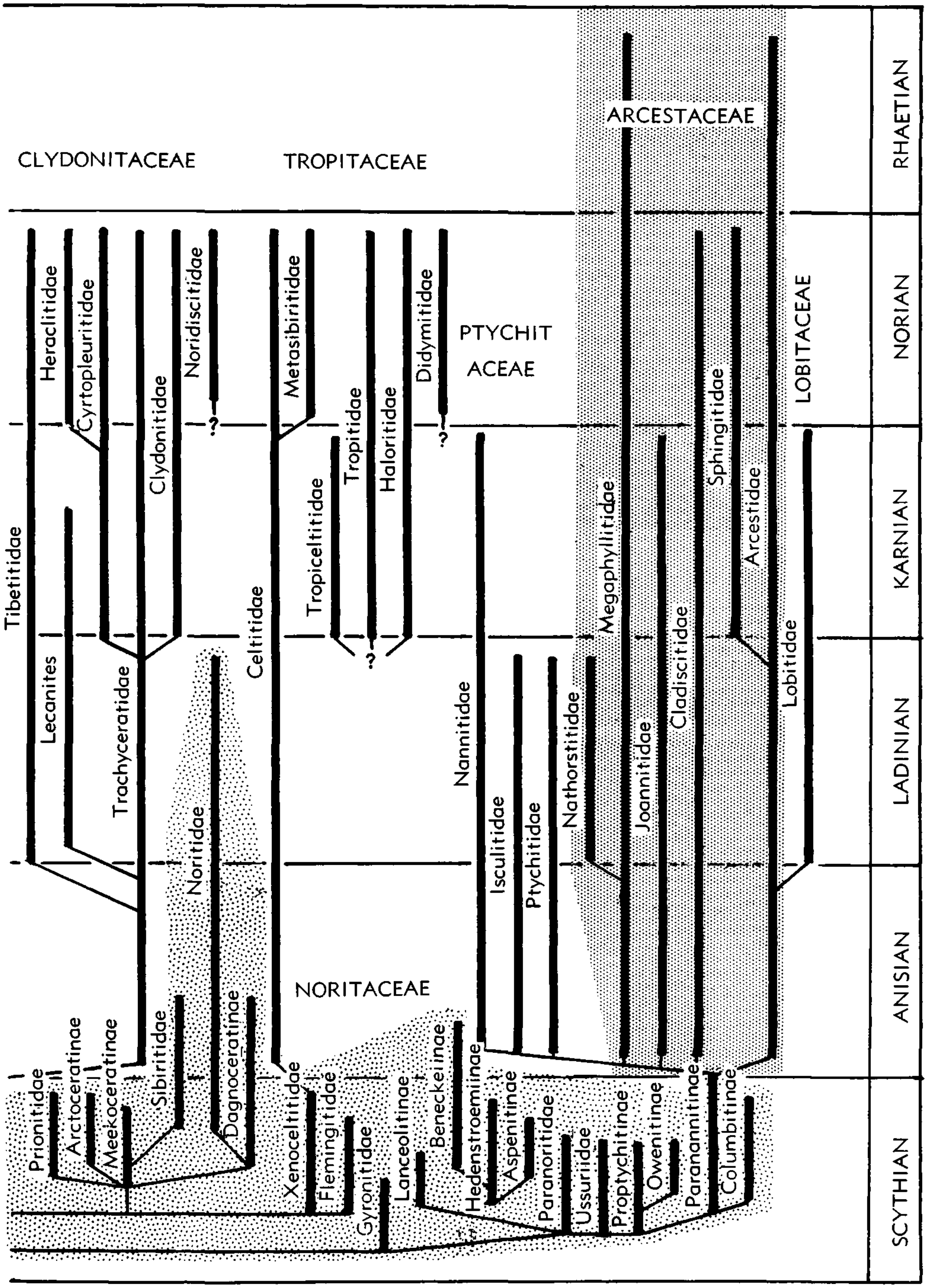

FIG. 149. *(continued from facing page).*

(Haas, 1942, has brought together a few outstanding examples), but we can seldom demonstrate just what the "iterative" relationships are. The most baffling families are still those with relatively little ornament; they may always be just those critical transitions from the smooth "liostraca" (Phylloceratina) to ornamented "trachyostraca," or they may be secondarily simplified "regressions." The long-ranged, smooth Haploceratidae and Desmoceratidae have long been debated and are still a bone of contention. H. Douvillé as long ago as 1916 held that the Desmoceratidae descended directly from

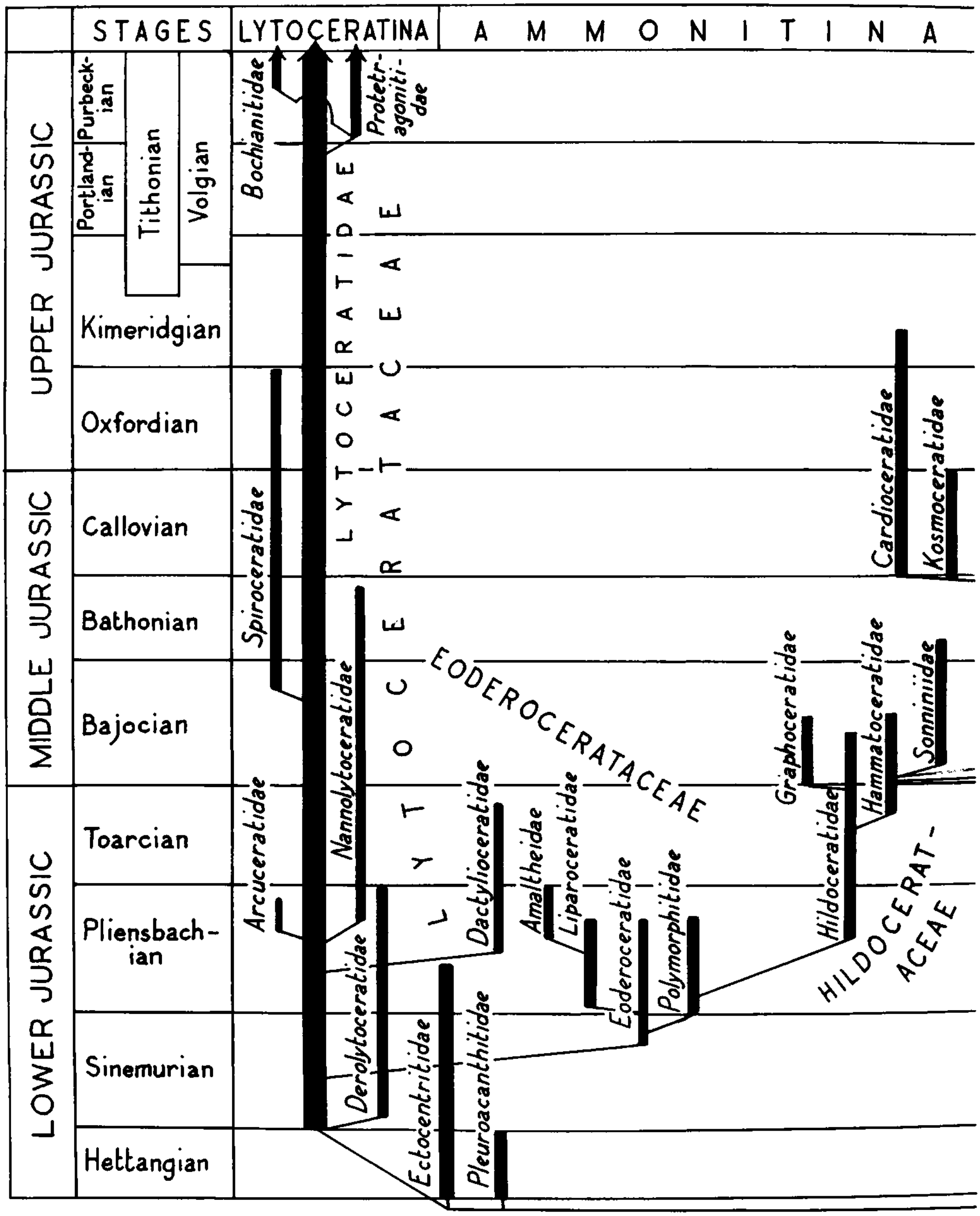

Fig. 150. Chart showing diagrammatically the phylogeny and range of the Jurassic ammonoids down to the family level (583).

the Phylloceratidae *(Sowerbyceras)* and this view is accepted here.

RECAPITULATION

For about half a century (roughly 1880-1930) these difficulties daunted few. In those happy years specialists thought they had the key in the theory of recapitulation ("palingenesis," "morphogenesis"). According to this theory, the ontogeny of the individual is a recapitulation of the phylogeny of the race, so that it was only necessary to study the ontogeny of an ammonite to discover the nature of its ancestors and therefore its posi-

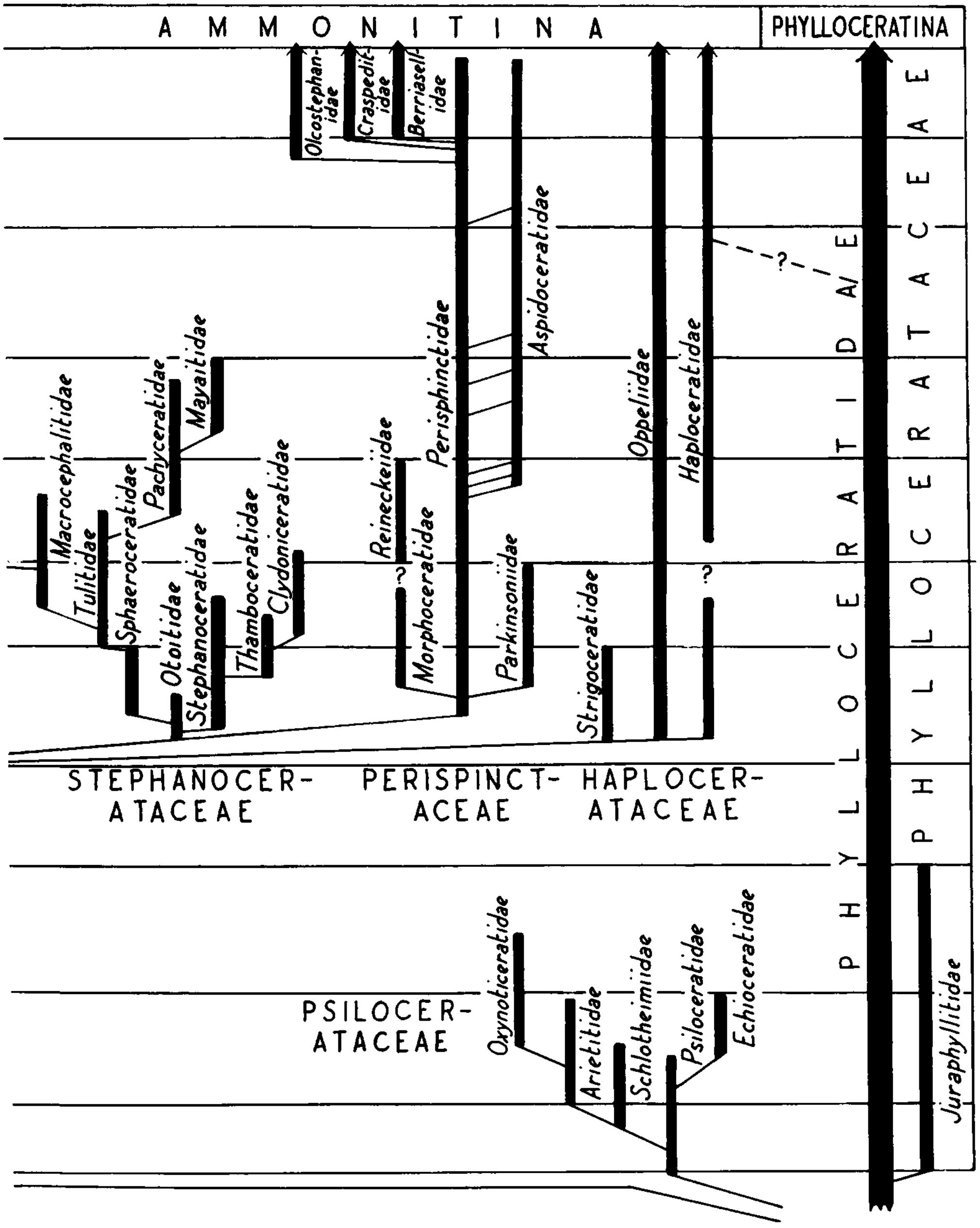

Fig. 150 *(continued from facing page).*

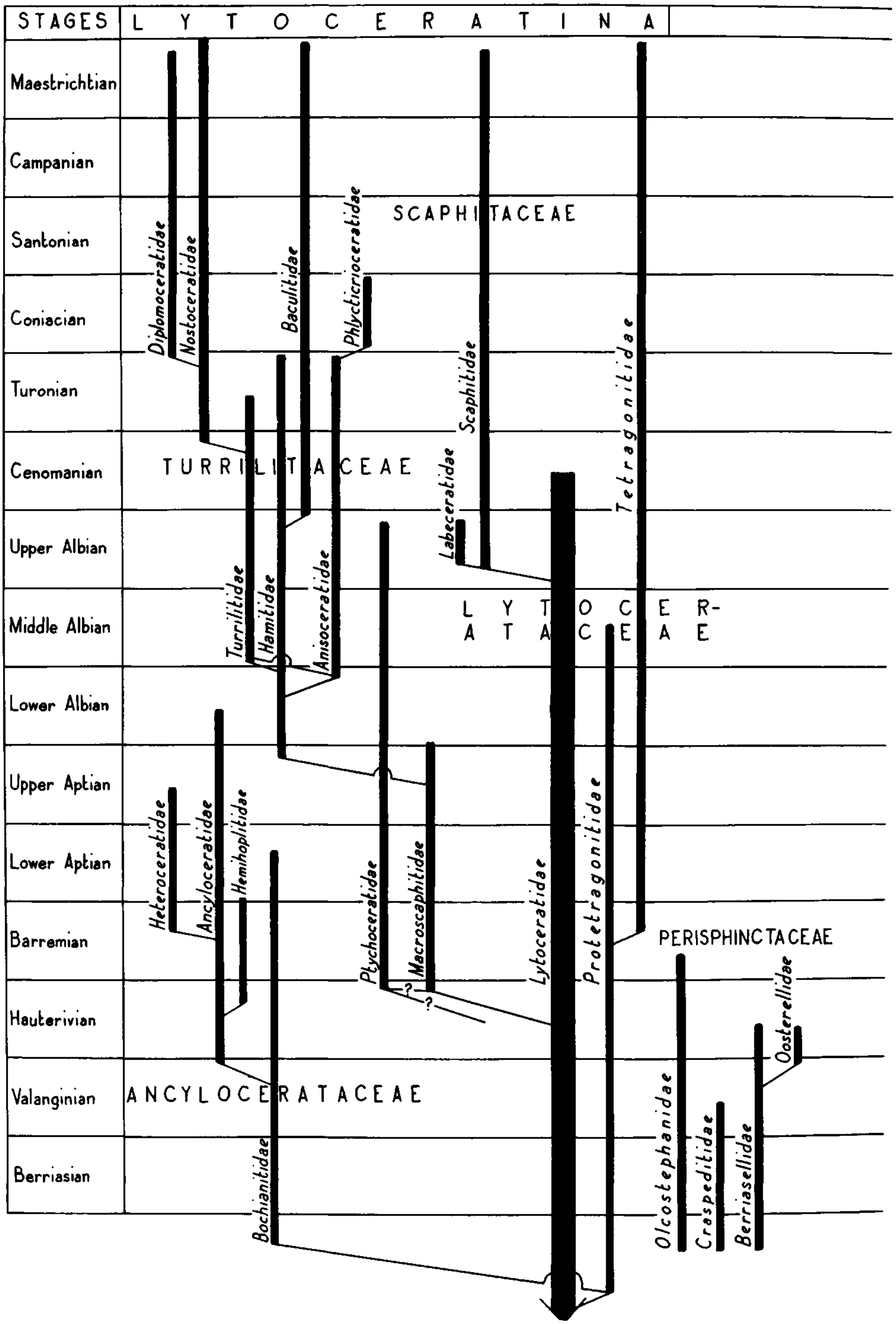

FIG. 151. Chart showing diagrammatically the phylogeny and range of the Cretaceous ammonoids down to family level (735).

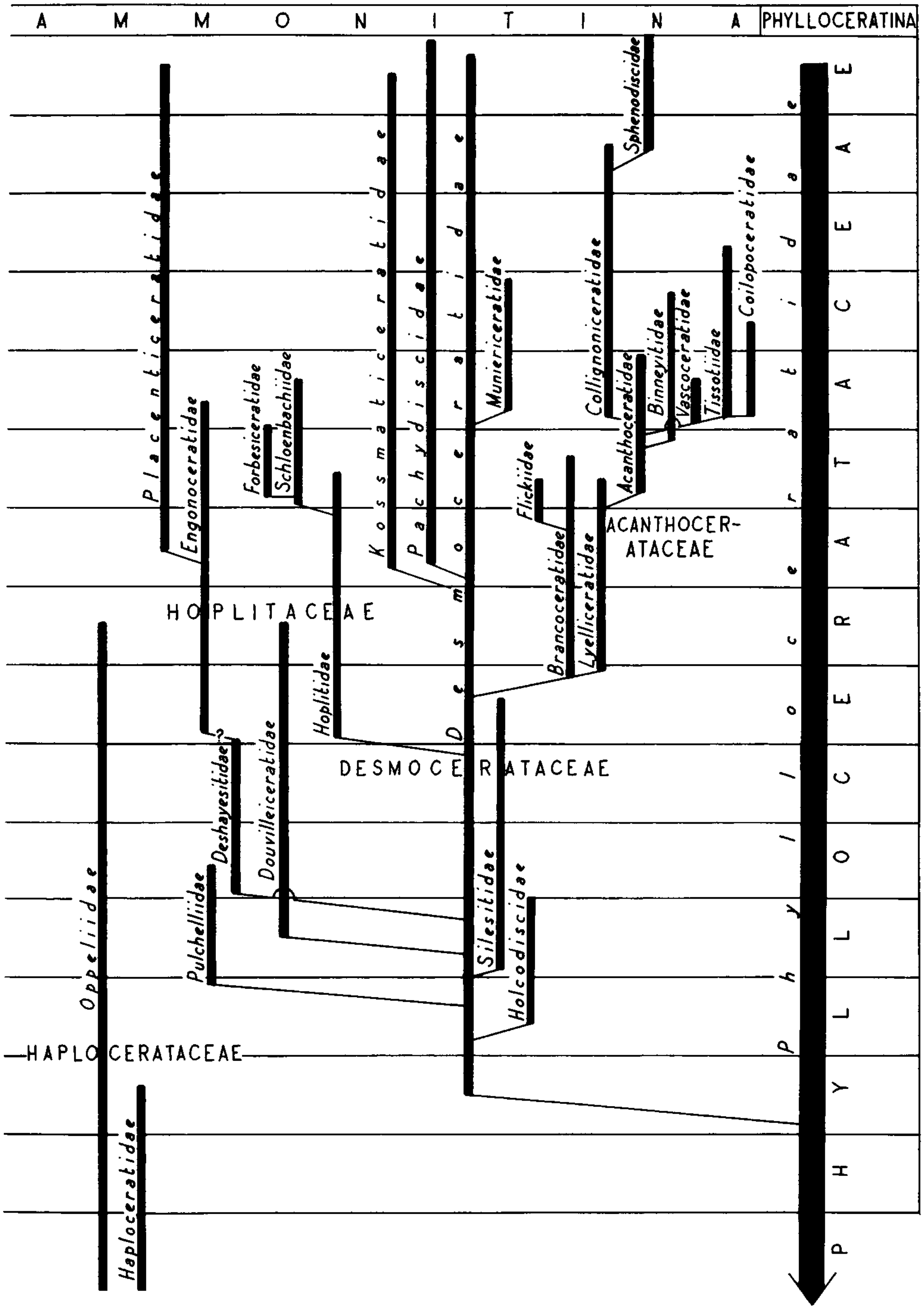

FIG. 151 *(continued from facing page).*

tion on the family tree. The imposing works of Hyatt (especially 1889) were the principal source of this doctrine, which was accepted wholesale by Buckman and most other workers. The papers of the 2nd and 3rd decades of the 20th century, written in the recapitulationist faith, make strange reading now. If, as was often found, all the expected stages were not present in ontogeny, they must have been skipped; then the "fact" that a stage had been skipped became itself of great significance, and forms were classed together because of characters which none of them possessed! All this was, of course, wrapped up in a scientific jargon: "tachygenesis," "bradygenesis," "palingenesis," "lipopalingenesis," and other terms. Buckman was enabled to pronounce with comfortable certainty and *ex cathedra* authority on the phylogeny and relationships of all the ammonites with which he dealt.

Whenever early stages of ammonites (nuclei) are well preserved in large numbers, however, they are found to show a greater range of variation in form and ornament than the adults. The young, in fact, are more "plastic." A classification based on them generally would be very different from that based on the middle and outer whorls. Large ammonites from the same horizon, otherwise identical, may possess surprisingly different nuclei. Thus, the painstaking quest after the early stages, the unraveling and destruction of many ammonites by time-consuming techniques, would lead to the conclusion that all groups are polyphyletic, if the recapitulation theory were invariably correct.

Nevertheless, studies of ontogeny undertaken in this period, especially those on the development of sutures, were a substantial contribution to knowledge (456, 519-521) which brought to light still more cases of homeomorphy. For instance, George (1930) showed that the Sinemurian oxycones united under the genus *Oxynoticeras* had various distinct types of sutural development and probably therefore sprang from different genera or subfamilies of the Arietitidae, although he could not indicate the likely ancestors of each. Like conclusions have been reached on the basis of ornament and shell form for the similar, much later oxycones classed as Cardioceratidae, with their component genera, and many other Jurassic and Cretaceous families.

CENOGENESIS AND PROTEROGENESIS

The recapitulation theory was fatally shaken in 1901, when Pavlow published the observation that in a number of Jurassic genera it is the young ammonites, in the neanic stage of Hyatt's scheme, that first show new characters of ribbing and whorl shape, which only at higher stratigraphical horizons spread on to the adults. He called this process "phylogenic acceleration" or "precession of characters," and because the inner whorls foretell the characters of their racial descendants he called them also the "prophetic phase." Pavlow pointed to similar phenomena among the belemnites, gastropods, and vertebrates, concluding: "It is to be hoped that, under the influence of the facts, the limitations of the recapitulation hypothesis will soon be realized and that outside those limits the field will be left free for other interpretations." But it was not until more than 20 years later that Pavlow's observations were independently repeated in the west, by Lewinski (1923), Spath (1924), and Schindewolf (1925, 1929, 1936) and gradually came to be taken into account in teaching. The early appearance of a new character is known to biologists as **cenogenesis;** and this term seems suitable for the process described by Pavlow, except that in the paleontological concept the subsequent incorporation of the character in descendent adults, as a firm character of the stock, is the most important element. Schindewolf coined for the process the term **proterogenesis.**

DOLLO'S LAW

Another "law" much relied on in early decades of the 20th century as the basis for phylogenetic pronouncements concerning ammonites was Dollo's (1922) "law of irreversibility of evolution." According to this "law," all evolutionary departures from the normal ammonite (usually conceived as a regularly coiled planulate) were dead ends. Thus, not only could heteromorphs not produce normally coiled descendants, but also oxycones and sphaerocones invariably must be at the end of their line of evolution, doomed productions destined for extinction.

Like most such hypotheses, this contains much truth and applies in numerous cases, but it led to error when accepted as a law. Most heteromorphs, oxycones, and sphaerocones do seem to have been dead ends, "specialized end forms." But the ammonites, as usual, produced exceptions which served to test the rule. For instance, while pronouncing on numerous cases in which Dollo's "law" seems to apply, authors persistently disregarded the oxycone genus *Amaltheus* which gave rise to the planulate genus *Pleuroceras,* and the oxycone *Cardioceras* which evolved into the planulate *Amoeboceras* and its subgenera. In both these examples, it is typical, normal planulates which are the end forms of lineages and indeed, of whole families. Moreover, the Cretaceous heteromorphs are by no means all "end forms" headed for early extinction. On the contrary, many of them persisted almost as long as the unmodified parent stock of the lytoceratids from which they arose.

EVALUATION OF CHARACTERS

Nearly all parts of the shell have been used at some time by some author as the basis for classification: protoconch and proseptum; body chamber (whether large or small); shape of the aperture (simple, constricted, or with lappets); presence or absence of a keel, nature of the keel (whether solid, hollow and open, or hollow and floored); ribbing and other ornament, its nature and direction (the "radial line"); and sutures. All have proved unreliable and no more worthy of singling out as of special importance than any other characters. Keels of all sorts, and grooves and other ventral features, come and go in any stock and may appear suddenly in the most unexpected context in an otherwise unkeeled or ungrooved family; Salfeld (1921) rightly declared that "ventral keels and furrows are secondary characters of subordinate systematic value." Body chambers of all types (113) and apertures of any kind appear in almost all stocks which otherwise agree in a great majority of characters, as already shown above. Ribbing and tubercles of 3 or 4 different types may follow each other in the life cycle of a single individual, and this may happen in almost any order (see examples cited by Deecke, 1913, p. 250 ff.). Too close attention to the radial line led Buckman into such elaborate subdivision of the Graphoceratidae that his monograph is practically unusable; this feature can hardly have even varietal significance in many groups where he assigned it generic rank. Sutures may be widely different on opposite sides of the same specimen and so different on otherwise identical shells that on the basis of sutures alone any number of genera might be made out of one species (for example, Fig. 144). Nor is there any reason to ascribe greater infallibility to details of the internal suture (402) than to those of the external suture. It is unsound to judge that the more difficult any character is to observe the greater is its importance.

It is against this background of scepticism learned by hard experience in the 1st half of the 20th century that one must evaluate attempts to find the thread that will enable phylogeny to be recognized and classification reorganized on a sound basis. A praiseworthy attempt has been made, using details of the early ontogeny of sutures, in a series of interesting papers by Schindewolf (410, 413, 417, 418). In a sample of genera examined, he finds that in the early suture lines certain details of the umbilical lobe develop in a different order in different genera (Fig. 152). In one group ("heterochrons," typically represented by the Stephanoceratidae) the 1st branch of the umbilical lobe is delayed in appearance for 2 or more sutures after the appearance of the 2nd and 3rd branches, while in the other group ("orthochrons," represented by the Perisphinctidae) the 1st branch appears from the start. On this basis Schindewolf would reclassify the Stephanocerataceae and Perisphinctaceae of the Middle and Upper Jurassic, involving many drastic rearrangements and separating some genera from all apparently related, contemporaneous forms which agree with them in most other characters. He considers that although this sutural peculiarity may appear trivial because it occurs only in the earliest stages of ontogeny, for that reason it is all the more significant, because independent of changing shell form and mode of life. However, it seems to the present writer unacceptable to separate, for instance, *Bigotites* and *Parkinsonia* from the other perisphinctids, and

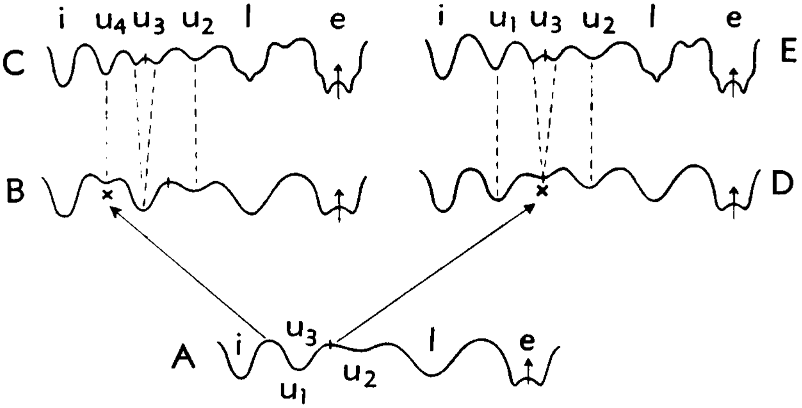

FIG. 152. Early ontogenetic development of the umbilical lobe in Stephanoceratidae *(B,C)* and "orthochrons" *(D,E)*; for further explanation see text (internal lobe, *i;* umbilical lobes u^1, u^2, u^3, u^4; lateral lobe, *l;* external lobe, *e*) (418).

Pseudoperisphinctes from the almost identical *Grossouvria,* on the grounds that they are "heterochrons," when among SCHINDEWOLF's list of "orthochrons" are found such completely unrelated Cretaceous genera as *Desmoceras, Puzosia, Leopoldia, Parahoplites, Schloenbachia,* and *Metaplacenticeras* (418, p. 127). On the inadvisability of reorganizing the entire classification on such a basis in the *Treatise,* all 3 authors of the Mesozoic ammonoid sections are agreed. We regard these differences in details of the earliest sutures as one more example of the vagaries of the "plastic young."

MACROEVOLUTION, MICROEVOLUTION, AND TRENDS

The most striking feature that emerges from study of the Mesozoic ammonites from the evolutionary point of view is the frequency with which history repeats itself during the approximately 125 million years of the era. The repetitions are of course never exact, but sufficiently close to be striking and to impose a rough pattern on the whole course of evolution of the order. It seems desirable to present a brief statement here, in order that the contribution which ammonites can make to the theory of evolution may be better known; for when they are mentioned in treatises on evolution their contribution is still commonly represented by out-of-date quotations from recapitulationist days.

Evolution is above all very uneven. Certain periods were outstandingly productive of new and virile forms, which often seem to have sprung into existence from nowhere (the so-called "cryptogenic" types of NEUMAYR, 1878) and to have become dominant almost simultaneously over a large part of the world. These are the periods of **paedomorphosis, macroevolution, saltative evolution, explosive radiation,** or evolutionary deployment, according to the terminology of various biologists and geneticists. How such sudden multiple creations were brought about is a task for the future to determine; but whether the process was one of adaptation to subtle nongeographical niches, or due to genetic drift and preadaptation, or to some mysterious manifestation of an *élan vital,* it must in any case go on record that they occurred. It would occupy too much space to give adequate examples; one of the earliest known (in the clymeniids) has been well illustrated by SCHINDEWOLF (416, p. 42, fig. 25).

Two other features of the phenomenon are common: the major innovations occurred cenogenetically (the new forms are different from the start of their postlarval ontogeny, and either incorporated the new features immediately in the whole of the ontogeny or progressively in succeeding generations, proterogenetically); and the new forms then proceeded to evolve more gradually on divergent or more or less parallel lines, going through one or more of a series of standard changes, which were repeated after each explosive phase.

This 2nd phase of slower, less spectacular, stereotyped evolution is, in biological terms, the phase of microevolution or gerontomorphosis. In it the new genera became specialized in a number of well-tried directions, such as running to sphaerocones or oxycones, or giant size, developing a keel (if the initial forms had none) or a groove or smooth band on the venter, and simplifying (smoothing out) the ribbing and sutures. This is the phenomenon of trends, which so strongly suggests an orthogenetic cause but must not necessarily be explained by orthogenesis. Moreover, some outstanding exceptions, such as the explosive evolution of the oxycone amaltheids from a planulate *Oistoceras* and their gradual evolution into planulate *Pleuroceras,* weigh heavily against a blind orthogenetic explanation of trends. It was parallel evolution of lineages on similar trends that repeatedly produced homeomorphs by leveling down and elimination of distinctive features or by repetition of stock characters; and they can be either isochronous or heterochronous. Extreme cases may appear to be atavistic because the simplification inevitably produces more primitive-looking types.

EXAMPLES OF AMMONOID EVOLUTION

WAAGEN (1869) in a pioneer work attempted to demonstrate **lineages,** or lines of descent, in the Oppeliidae from the Middle Bajocian to the Upper Callovian. His work contains an excellent discussion of the principles and difficulties, which should be read by all students of ammonites. The chief obstacle to such studies is that a lineage is an oversimplified concept; it is impossible to pick out a stratified succession of individuals which can with certainty be said to be genetically connected in the strict ancestor-descendant relationship. While we aim at deciphering such a lineage (*Formenreihe* of WAAGEN; *série genétique* of PAVLOW), what we actually deal with is a series of populations which may be made up of indefinite numbers of lineages, either evolving parallel in one stream (a **plexus**), or radiating in a variety of directions (*rameau genétique* of PAVLOW, 1901, p. 59) which may not be apparent because often not fulfilled, owing to premature extinction or merely preservation failure or collection failure. From these populations we have presented to us through the vagaries of (1) random preservation and (2) chance rock exposures, minute samples, from which in turn we pick individuals which we deem to be typical. Even then, in default of statistical analysis of the whole available population for a large number of characters, it is difficult to be sure that our choice of individuals is not guided by preconceptions of what we are looking for. These warnings must always be borne in mind, for disregard of them has led to erection of hypothetical family trees which further stratigraphical collecting showed to be impossible, as were *a fortiori* the phylogenetic "laws" deduced from them.

Nevertheless, detailed collecting in a circumscribed area, especially from cliff exposures, from geological sequences of reasonable lithological continuity, has produced examples of evolutionary lineages and radiations which may be accepted with some confidence. It is noteworthy that these examples invariably disprove one or more of the previously accepted "laws" discussed above (morphogenesis, irreversibility, etc.).

LIPAROCERATIDAE AND AMALTHEIDAE

The best and most detailed example that can be quoted probably is the phylogeny of the families Liparoceratidae and Amaltheidae, spanning the whole Pliensbachian stage. The Liparoceratidae of the lower Pliensbachian have been collected in great detail from the cliffs of the Dorset coast by W. D. LANG and monographed by L. F. SPATH (1938), and the Amaltheidae of the upper Pliensbachian (Domerian) have been similarly collected from all the British exposures by M. K. HOWARTH, who is preparing a monograph and has kindly contributed his results and Fig. 153.

The ancestral liparoceratid is an evolute, finely ribbed, bituberculate form which still shows much resemblance to the evolute Eoderoceratidae from which the stock sprang. At the same horizon (lower *jamesoni* zone) there are similarly ribbed and bituberculate forms which differ by being more involute (Fig. 153,*1a,b*) and therefore more like later typical *Liparoceras.* These latter gave rise at a slightly higher horizon in the *jamesoni* zone to still more involute sphaerocones, with coarsened and lengthened primary ribs and recessive inner and accentuated outer tubercles (Fig. 153,*2a,b*). From this in turn diverged 2 streams, one *(Liparoceras, Becheiceras)* becoming extreme sphaerocone and mainly fine-ribbed, the other *(Androgynoceras)* producing coarse and simple ribs in the inner whorls (Fig. 153,*3a,b, 4*). In this remarkable lineage the inner whorls are capricorn, and when separated would hardly be supposed to be congeneric with the sphaerocone ancestors and collaterals, or even with the hemisphaerocone and finely ribbed outer whorls of the same individuals. In successive species, however, the capricorn stage gradually spread (by proterogenesis) on to the middle and eventually the outer whorls, producing finally in the middle *davoei* zone complete capricorns (Fig. 153,*5a,b*).

At and near the top of the *davoei* zone the capricorn *Androgynoceras* is replaced by the capricorn *Oistoceras,* which is indistinguishable in side view but differs by significant developments of the venter. Instead of passing straight over the venter and remaining simple, the ribbing of *Oistoceras* (Fig. 153, *6a,b*) is projected forward, forming ventral chevrons; and in some morphologically advanced species the chevron ribs tend to bifurcate and the venter rises to an embryonic keel. These are the earliest manifestations of the essential characters of the succeeding family Amaltheidae. Exposures of the passage beds from lower to upper Pliensbachian, in which these changes occur, are adequate, and intensive collecting by HOWARTH and his predecessors has failed to reveal any other ammonites from which the amaltheids could have sprung.

The earliest forms in which a proto-keel has been found are nuclei from the topmost subzone of the *davoei* zone (SPATH, 1938, pl. 26, fig. 16). In the lowest subzone of the next-higher *margaritatus* zone there are passage forms (Fig. 153,*7*) from *Oistoceras* to fully differentiated *Amaltheus* (Fig. 153, *8a,b*). The transformation was rapid, and it is not at present possible to affirm that it was either proterogenetic or palingenetic. Although the first modifications of the venter took place apparently on the inner whorls, the further rise and crenulation of the keel and compression of the whorls to form the first oxycones *(Amaltheus stokesi)* occurred on the middle or outer whorls, while the nuclei remained stout and *Oistoceras*-like.

Amaltheus stokesi formed the rootstock for all the amaltheids, which are celebrated for their polymorphism. Attainment of the oxycone shape, far from being lethal, coincided with the beginning of repeated radiations. *Amaltheus margaritatus,* the zonal index fossil which typifies the genus for most of us, was not on the direct line of descent but on a divergent branch in which oxycone shape was pressed back to earlier whorls than in the direct line, and it ended in the extreme oxycone *Pseudoamaltheus.* Another side line ended in the completely smooth dwarf *Amauroceras.*

Meanwhile the main stream retained its stout inner whorls (in some species tuberculate and coronate) and relatively evolute coiling and gave rise, by way of passage forms (such as Fig. 153,*9a,b, 10a,b*) to the evolute, planulate, tuberculate genus *Pleuroceras* of the *spinatum* zone at the top of the Pliensbachian. *Pleuroceras* also seems to have arisen from a single ancestral stock and radiated into a number of species characterized by different styles of ribbing and tuberculation. The family then became extinct, leaving no successors in the Toarcian faunas.

This history illustrates the evolution of planulates into sphaerocones, dimorphs, and capricorns; of capricorns into keeled and

FIG. 153. Evolution of the Liparoceratidae (713) and Amaltheidae (637a).——*1a,b. Tetraspidoceras reynesi* SPATH, ancestral form, basal *jamesoni* zone.——*2a,b. Liparoceras (Parinodiceras) parinodus* (QUENST.), early sphaerocone, *jamesoni* zone.——*3a,b. Androgynoceras sparsicosta* (TRUEMAN), dimorph sphaerocone, with capricorn ribbing on the inner whorls, *centaurus* subzone.——*4. Androgynoceras henleyi* (J.SOWERBY), more evolute dimorph, with prolonged capricorn stage, *lataecosta* subzone.——*5a,b. Androgynoceras lataecosta* (J.DEC.SOWERBY), capricorn with normal venter, *lataecosta* subzone.——*6a,b. Oistoceras figulinum* (SIMPSON), capricorn with chevron ribs on venter, *figuli* subzone.——*7.* an early *Amaltheus* sp., oxycone, basal *stokesi* subzone.——*8a,b. Amaltheus stokesi* (J.SOWERBY), *stokesi* subzone.——*9a,b. Amaltheus subnodosus* (YOUNG & BIRD), *subnodosus* subzone.——*10a,b.* an early *Pleuroceras* sp., transitional from *Amaltheus,* basal *apyrenum* subzone.——*11a,b. Pleuroceras spinatum* (BRUGUIÈRE), a tuberculate planulate, *hawskerense* subzone. Figs. 1-11 are in stratigraphical order and show evolution of the stock through the whole Pliensbachian stage (198a).

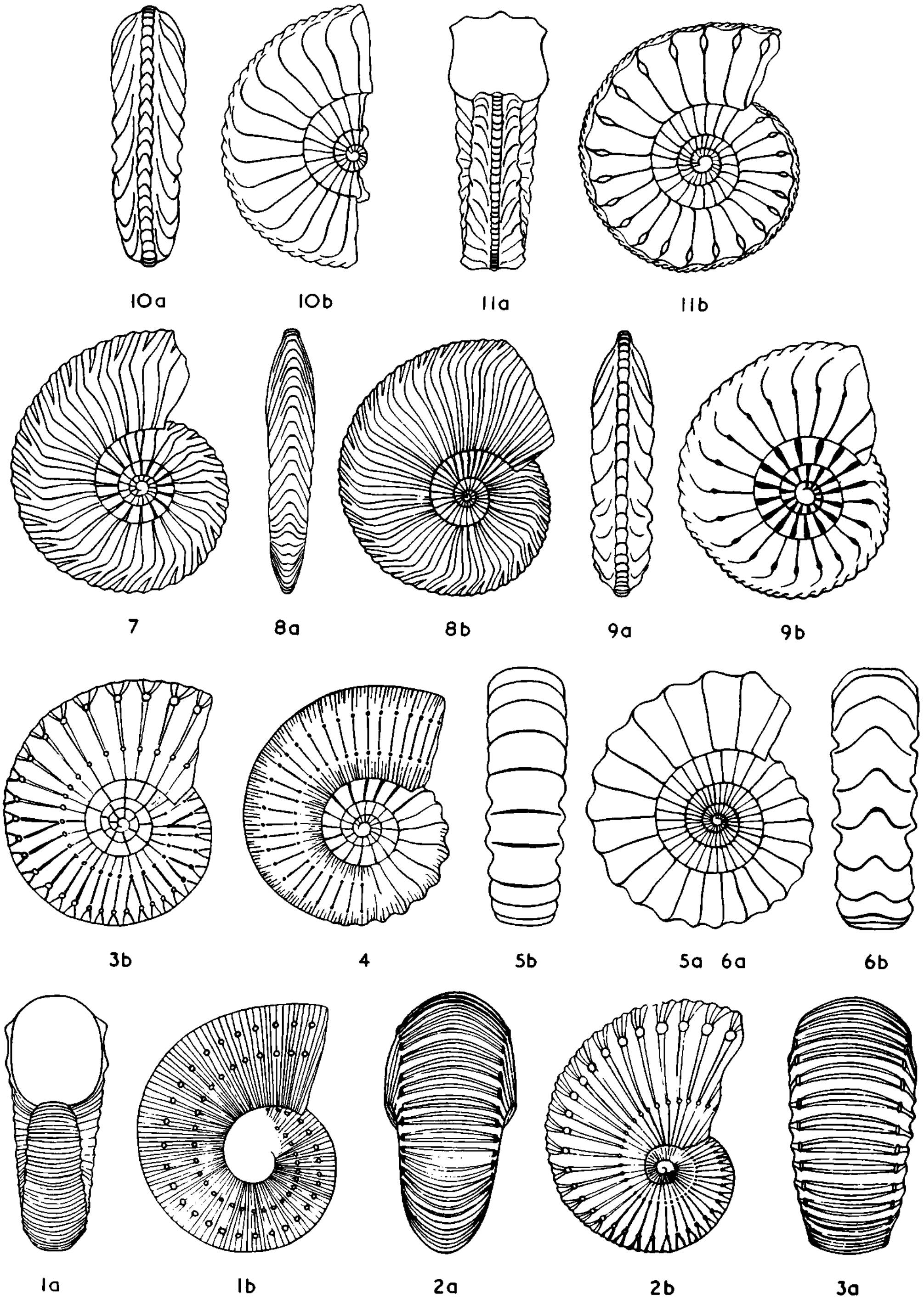

FIG. 153. *(Explanation on facing page).*

ribbed oxycones; and of these in turn back to planulates.

MACROCEPHALITIDAE AND CARDIOCERATIDAE

The whole story was repeated by the Macrocephalitidae and Cardioceratidae of the Middle and Upper Jurassic. There the sphaerocones *Macrocephalites* and *Tulites,* derived from the essentially planulate *Stephanoceras* stock of the Bajocian-Bathonian, are usually supposed to have produced the cadicone *Cadoceras* and oxycone *Quenstedtoceras* and *Cardioceras,* which reverted to planulate *Amoeboceras* and, before extinction in the Lower Kimmeridgian, finally produced various aberrant end forms, including smooth almost keel-less dwarfs *(Nannocardoceras)* analogous with *Amauroceras.*[1] There is an extraordinary resemblance between various successive stages in the 2 lineages and some of their offshoots (Arkell, 1950, p. 356), for example, (1) *Oistoceras* —>*Amaltheus*—>*Pleuroceras* and (2) *Quenstedtoceras (s.s.)*—>*Cardioceras (s.s.)* —>*Amoeboceras(s.s.)* and *Amoebites.*

The course of evolution of the Amaltheidae, as described above from M. K. Howarth's data, differs in an important respect from that inferred for the Cardioceratidae (Arkell, 1948, pp. 380-382, and in Arkell & Moy-Thomas, 1940). In the Cardioceratidae it seems that a number of different lineages evolved more or less parallel, each passing through comparable grades in respect of the main characters, whorl shape, ribbing style, keel development, etc., and also developing repeated lateral offshoots; and the morphologically defined genera *Cadoceras, Quenstedtoceras, Cardioceras,* and *Amoeboceras* are therefore polyphyletic grades—namely, cross sections of a plexus and its side branches. Taxa are of more stratigraphic value and less hypothetical if so defined than if the names were applied to lineages and defined vertically. Where possible, subgeneric names are used for the lineages and the old generic names are retained for the horizontal groupings of parallel grades.

DISCOHOPLITES AND HYPHOPLITES

It is highly probably that analysis of many supposed lineages would reveal a similar complexity and at least micropolyphyletic (if not macropolyphyletic) constitution of generic, subgeneric, and even family taxa. Some instances at family level are apparent in the phylogenetic charts (Figs. 149-151). A good example at generic or subgeneric level has been demonstrated for *Discohoplites* and *Hyphoplites* of the upper Albian and lower Cenomanian (Wright & Wright, 1949). Two species of *Discohoplites* are believed to have given rise by parallel evolution to 2 groups of *Hyphoplites.* The characters which arose in both lineages and transformed them from *Discohoplites* into *Hyphoplites* were regular peripheral tuberculation, at least on the early part of the adult body chamber, with consequent angular whorl section, and increased definition of the primary part of the falcate ribs. The 2 genera are thus polyphyletic grades in related parallel lineages.

CADOCERAS, MACROCEPHALITES, KOSMOCERAS, AND ASSOCIATED FORMS

The transformation of *Cadoceras* into *Quenstedtoceras* and the presumed origin of *Cadoceras* in a macrocephalitid illustrates proterogenetic acquisition of the oxycone form (Fig. 154). Another branch from *Macrocephalites* is supposed to have produced *Kepplerites* and *Kosmoceras* by proterogenetic acquisition of a tabulate venter. This last was one of the first instances of proterogenesis ever pointed out (Pavlow, 1901, p. 62) (see footnote, p. L116) (Fig. 154).

The genus *Kosmoceras* has been subjected to detailed and elaborate statistical analysis by Brinkmann (1929) on the basis of crushed shells collected at centimeter levels in the Oxford Clay brickpits at Peterborough, England.[2] On the strength of this analysis he distinguished 5 subgenera: *Kosmoceras s.s., Gulielmiceras, Gulielmites, Zugoḳosmoḳeras,* and *Spiniḳosmoḳeras,* which evolved side by side and are characterized by differences in whorl shape, habits of ribbing and tuberculation, and

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[1] *Macrocephalites,* however, is of Tethyan origin, while *Cadoceras* and the Cardioceratidae probably originated in the Boreal Sea from some contemporary collateral such as *Arctocephalites.*

[2] For *Zugokosmoceras* Brinkmann *(partim)* read *Gulielmites* Buckman, and for *Anaḳosmoceras* Brinkmann read *Gulielmiceras* Buckman; Brinkmann's usage does not accord with the Rules of Nomenclature.

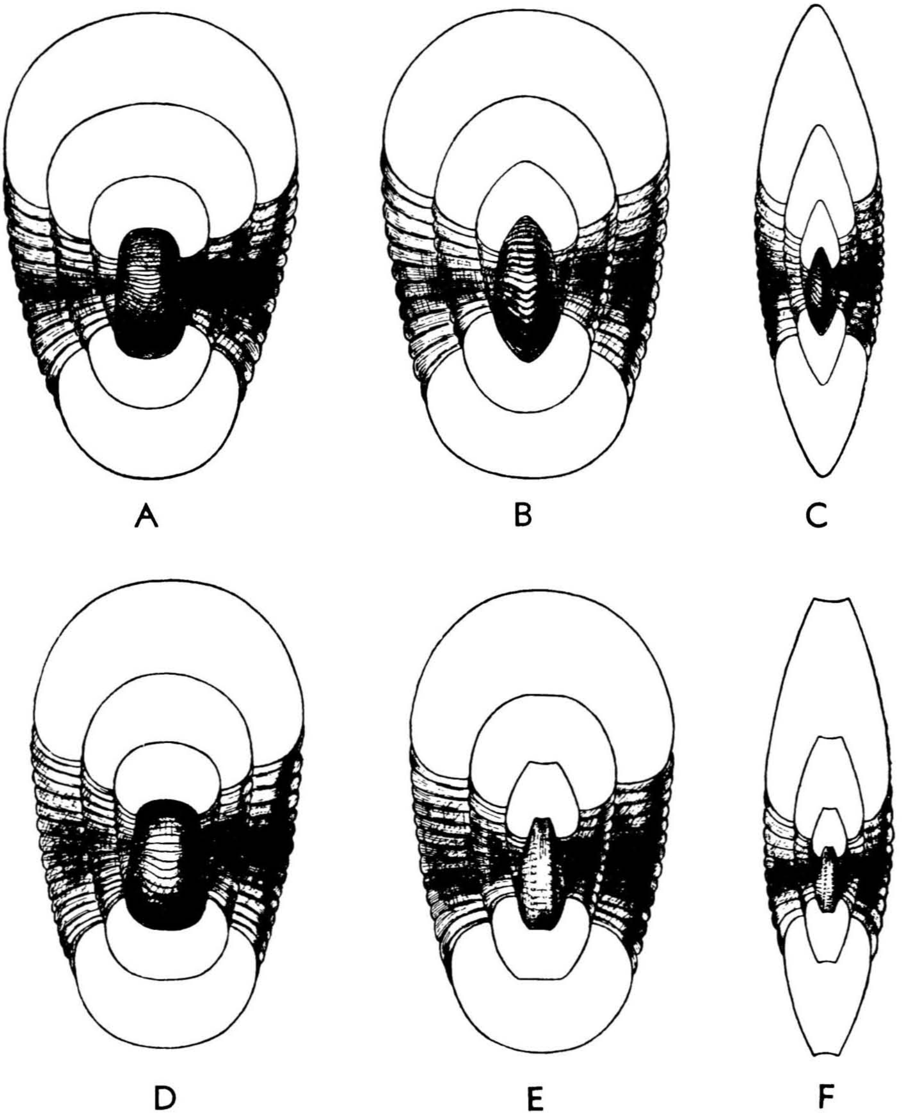

FIG. 154. Two examples of proterogenesis from the Callovian (416). *A,D,* the ancestral *Macrocephalites,* with rounded venter throughout. *B, Cadoceras. C, Quenstedtoceras,* showing sharpening of the venter beginning on early whorls. *E, Kepplerites, F, Kosmoceras,* showing tabulate venter beginning on early whorls.

structure of aperture (presence or absence of lappets) (Fig. 155).

CALLIZONICERAS AND LEYMERIELLIDAE

Another interesting phylogenetic series was made out by BRINKMANN in 50 m. of lower Albian clays exposed in a canal between Hanover and Peine, Germany, and neighboring brick pits. This series shows the evolution of *Callizoniceras (Wollemanniceras)*[1] *keilhacki* into Leymeriellidae (Fig. 156). At the start of the series the whorls have many plain constrictions with flat interspaces, on which at higher horizons simple ribs develop. Then a median ventral groove sets in and is further developed with differing depth and width in 2 parallel branches of the stock.

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[1] Called *Desmoceras* in BRINKMANN (57).

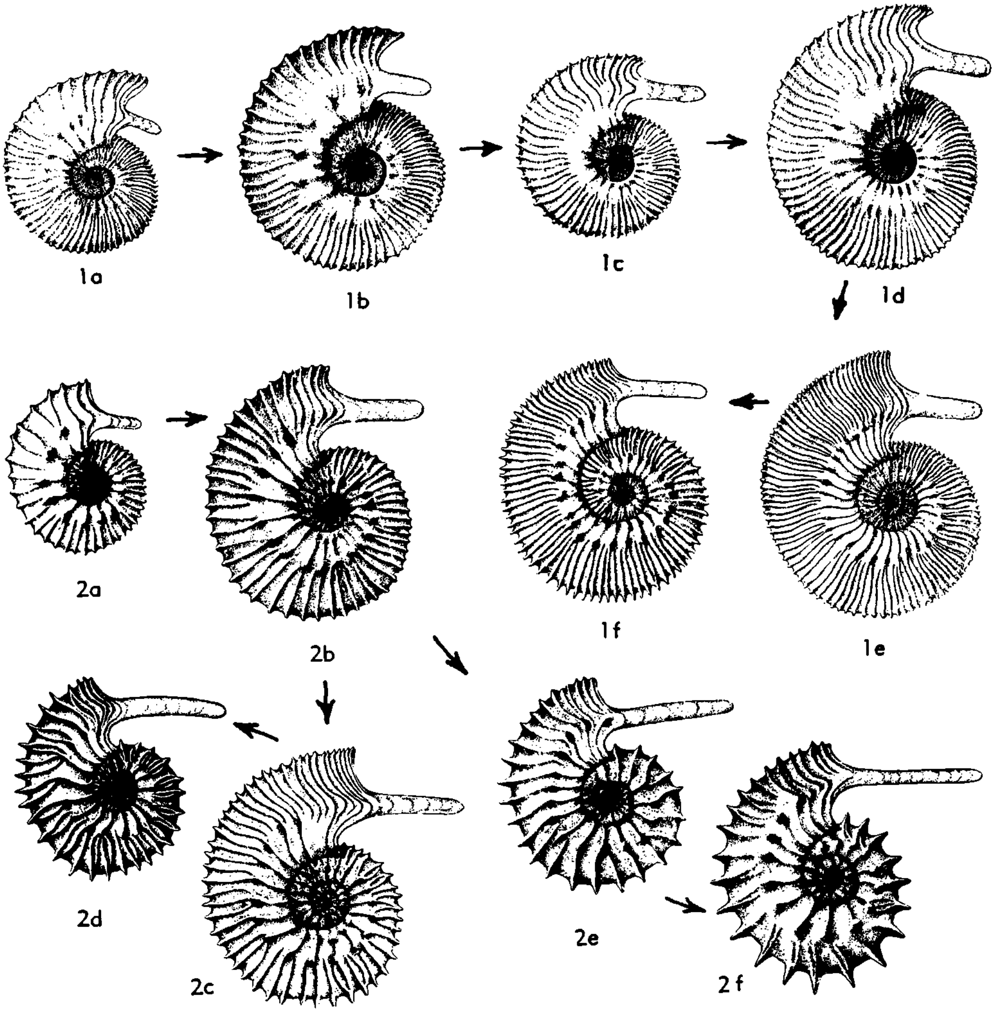

FIG. 155. Evolution of ornament and lappets in two lineages (subgenera) of *Kosmoceras,* M.Jur.(M. Callov.), Peterborough, Eng. (55).——*1a-f. Gulielmiceras.*——*2a-f. Spiniḳosmoḳeras.*

Decipherment of these sequences is favored by unusual continuity of lithology and therefore probably near-continuity of evolving faunas, prerequisites for any safe deductions as to descent. Where the stratigraphy is unfavorable, marked by wide changes in lithology, frequent absence of ammonites due to unfavorable environments, condensed faunas, etc., the decipherable history may be so fragmentary that classification is perforce horizontal and the taxa are bound to be more or less polyphyletic.

PALEOECOLOGY

So great is their variety in size, shape, style of coiling, thickness of test, external ornament, and internal complexity of sutures, that the Ammonoidea seem to comprise adaptations to a wide range of marine niches. There is a noticeable absence of ammonites (or they occur as rarities, usually worn or broken) from coral reef rocks and from rapidly deposited false-bedded sands and oölites (ARKELL, 1933, pp. 562-567, gives analysis of the distribution of ammonites in relation to these rocks in the British

Jurassic). In such environments the ammonites found may have been floated in, either unwillingly in life or posthumously. Practically all other types of sediment may be expected to yield ammonites in abundance, though commonly they are unaccountably barren.

RELATION OF SHELL FORM TO SEDIMENTARY ENVIRONMENT

Various attempts have been made, on lines also suggested by VAUGHAN (1940), to relate different types of shell to particular lithologies (for instance, MILLER & FURNISH, 1937; SCOTT, 1940). SCOTT's attempt contains many interesting and stimulating observations and suggestions, but most of his conclusions apply only to the area and formations studied and one is immediately confronted by contradictions on trying to apply his methods to other areas and other formations.

One repeatedly made observation is that the sharp-edged discoidal shell form with smooth surface appears to be ideally adapted to rapid swimming, and attention has been drawn to a number of occurrences where such forms are associated with clays and marls, whereas more or less contemporary tumid and highly ornamented forms are associated with a shallower, calcareous and detrital shelly facies. Examples of this in the Bajocian have been cited by WESTERMANN (1954, pp. 35-37). Others readily come to mind: for instance, dominance of the discoidal genus *Amaltheus* throughout Europe in the dominantly clayey lower Domerian and its replacement by the planulate, spinous *Pleuroceras* in the upper Domerian, this change coinciding in most areas with a change of lithology to limestones and ironstones; or the dominance of the discoidal *Oxycerites* in the Bathonian clays (Fuller's Earth facies); or the abundance of flat *Kosmoceras* and *Hecticoceras* in the Oxford Clay; and so on. But there are many obstacles to the acceptance of any generalization. For instance, the abundance of *Oxynoticeras* in lower Lias clays ("Oxynoticeratan") was a temporary phenomenon, for the similar, much thicker clays (also lower Lias) formed earlier and later contain all manner of other ammonites but no oxycones. Again, oxycone *Oxycerites* is most abundant of all in the limestone-ironstone facies of the Bathonian in Germany, although rare in that facies in England; the oxycone *Clydoniceras* is abundant in Bathonian shelly limestones wherever it occurs; and in the middle of the Oxford Clay over large tracts of the world is a zone characterized by and named after one of the stoutest of the stephanoceratacean types of shell, *Erymnoceras coronatum* and its allies, and by the stout and spinous *Reineckeia anceps* and its allies. Moreover, it is just the oxycones which most

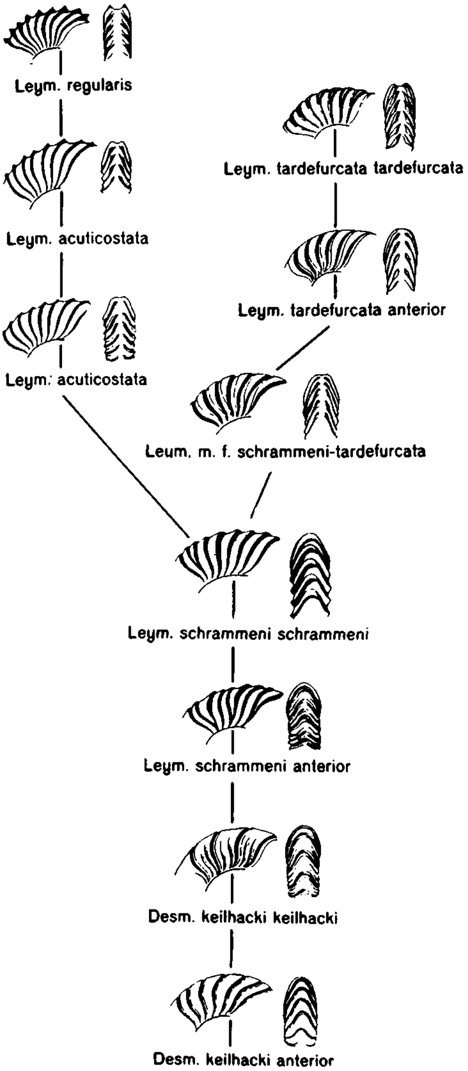

FIG. 156. Diagram illustrating the evolution of *Callizoniceras keilhacki* ("*Desmoceras*") into 2 lineages of *Leymeriella*, L.Cret.(L.Alb.), Ger. (57).

commonly display simplified, regressive, even pseudoceratitic types of suture, which have been explained as a sign of sluggishness and bottom-dwelling (454, 455).

RELATION OF SIZE TO ENVIRONMENT

Attempts have also been made to relate size of shell to sedimentary facies (REUTER, 1908), the conclusion being advanced that dwarf assemblages probably indicate some kind of unfavorable environment, deficient in aeration or salinity or warmth (246). On the other hand, large size (gigantism) has been claimed as an evolutionary trend independent of environment (314), for certainly it seems to occur in any stock at any time and irrespective of lithology, although perhaps the majority of giant ammonites are found in limestones. To ascribe size differences in ammonites to any particular environment is impossible, since small and large forms too often thrived together. (The total range of size in adult ammonites is from about 1 cm. to 3 m., or a ratio of 1:300, but the vast majority are intermediate about 10 to 30 cm.)

MODE OF LIFE

The mode of life of ammonites has been endlessly debated. The reader is referred especially to papers by WALTHER (1897), SOLGER (1901, 1902), JAEKEL (1902), BENECKE (1905, p. 544), JOHN (1909), ROTHPLETZ (1909), DIENER (1912), DOLLO (1912), SCUPIN (1912), FRECH (1915), PRELL (1921), STIELER (1923), H. SCHMIDT (1925, 1930), BERRY (1928), BEURLEN (1928), TRUEMAN (1941), and ARKELL (1949). At least 90 per cent of these fascinating discussions amount to conjecture. The total absence of tracks attributable to ammonites, with one possible exception (525) suggests that the majority of them were not habitually crawlers. Many could, however, have lived in mud on kinds of bottom in which no tracks would be preserved—for instance, among seaweed or sea grass. STIELER (1922) believes that the possession of a recurved rostrum can only be explained as an adaptation to such a bottom life, its advantage being that it would raise the aperture above the mud. BERRY (1928) attributed the coiling of the shell itself to the same cause, the straight ancestor having abandoned a nektonic for a benthonic mode of life. Asymmetry of sutures or siphuncle in some genera also suggests a life on the bottom, on one side, but other explanations are possible.

A number of the deductions made in these and other discussions by different authors are startlingly contradictory. For instance, BEURLEN (1928) asserted that the ammonite shell was not protective as in gastropods but served essentially as a hydrostatic apparatus, whereas BERRY (1928) asserted that the shell was essentially protective and the idea of a hydrostatic apparatus a myth. The weight of evidence seems to be on the side of BEURLEN and the similar views of DIENER (1912, 1922), who wrote with great experience and much persuasion. It is difficult to imagine that such a structure as the ammonite phragmocone evolved as a by-product, for only the body chamber at each stage of growth could have played any part in protecting the animal (Fig. 124). If the phragmocone functioned as a hydrostatic apparatus, it must have been possible for gas of some sort to pass through the siphuncle to and from the camerae; and this could only have occurred if in at least the larger, later formed camerae, the siphuncle tube did not become solid during life. Possibly the lag in phosphatization, previously mentioned, has a bearing on this problem. In any case, it appears that the camerae in living *Nautilus* and *Spirula* do contain gas (mainly nitrogen). If the purpose of this gas is merely "to render the shell buoyant once for all," as has been suggested, ammonites cannot have lived at great depths or their shells would have been crushed. The pressure exerted by sea water amounts to about a ton to the square inch at 1,000 fathoms. Therefore, if ammonites descended to more than about half this depth their shells (judging by some experiments with the much smaller and therefore much stronger *Spirula*) would be crushed unless the internal gas pressure could be raised to equalize the external water pressure. Provided that gas could pass through non-hardened parts of the siphuncle, this could be brought about simply by passive generation of gas, which would be sucked into the camerae by the partial vacuum. The shell would also be strengthened by its ribbing.

On moving suddenly upward, toward the surface, the shell would have a tendency to burst. The most efficient means imaginable to counteract this bursting tendency would be a series of septa, each having the maximum possible attachment to the inside of the shell and tied into the fabric of the shell walls just as the septal edges are found to be (Arkell, 1949, p. 409). If these deductions are sound, elaboration of sutures would denote adaptation to active swimming habits in deep water, and simplification of sutures would imply change of habitat to shallower waters, or sluggishness.

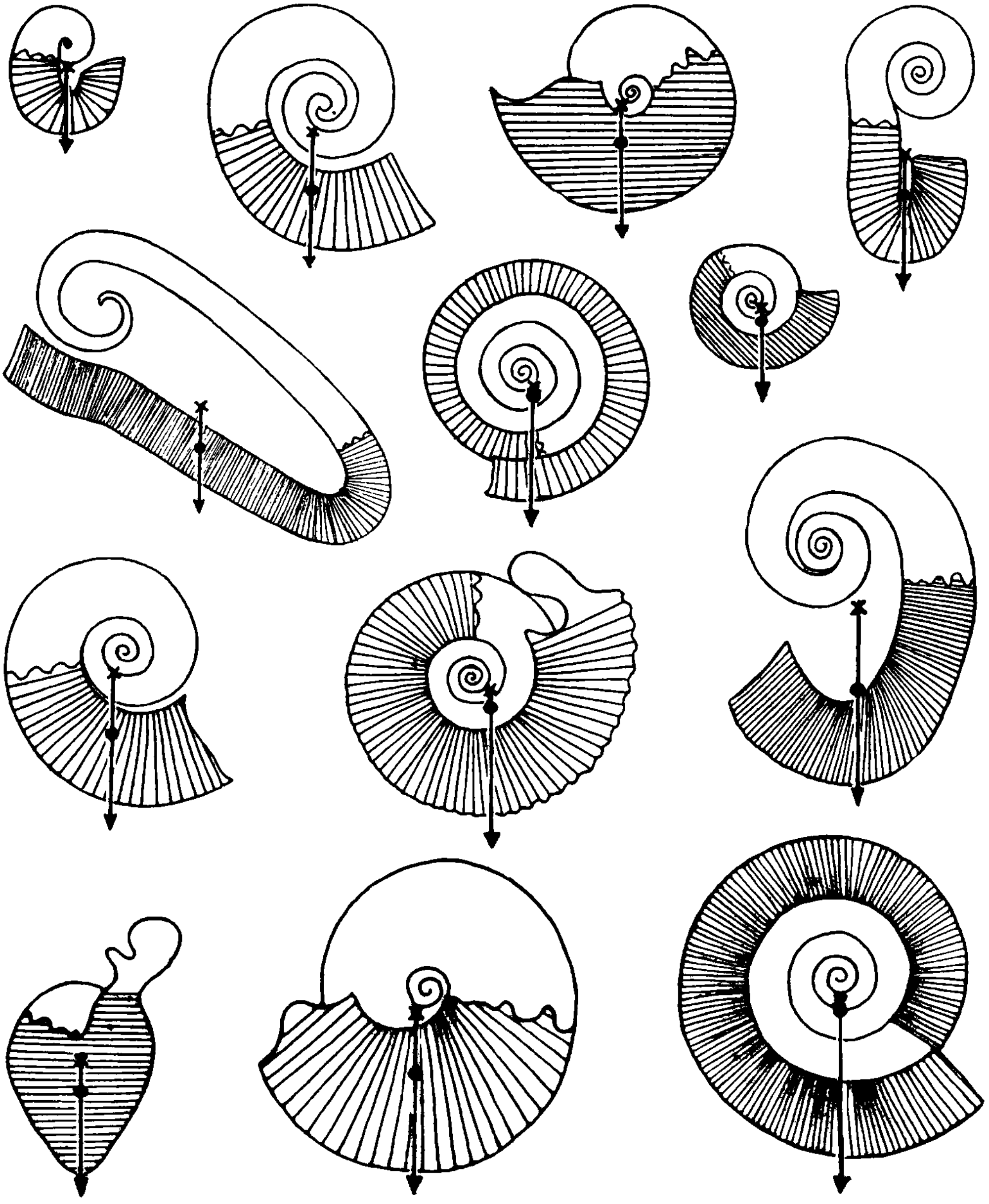

Fig. 157. Positions inferred for various ammonoids when floating or at rest, approximate position of center of buoyancy being shown by a cross and approximate position of center of gravity by a heavy dot (523).

This agrees with the fact that some of the most elaborate sutures are those of all the phylloceratids and lytoceratids, for which a free-swimming life in the open seas has always been postulated on general grounds.

New light on the normal attitude of the shells during life was thrown by TRUEMAN (1941), who calculated the positions of the center of gravity and center of buoyancy in a number of genera. He found that in evolute many-whorled shells the centers of gravity and buoyancy are so close together that the animal could easily have changed its position considerably, though the normal position of rest would be with the aperture facing half upward (Figs. 157, 158). The involute forms, however, must have been much more stable, and in them the aperture faced almost completely upward, as it does in the living *Nautilus*. The conclusion is that most ammonites probably did not habitually crawl, that some could do so fairly easily, and that others could crawl only by holding on to the bottom. In the uncoiled forms, such as scaphitids, the buoyant effect of the camerae would have made crawling almost impossible. If such heteromorphs lived on the bottom, theirs could only have been a stationary existence amongst mud and weeds. Most probably the majority of ammonites hovered and soared through the water not far above the bottom, resting near it without touching it, as does *Nautilus*. Spines could have served as balancers or stabilizers, or as protection against enemies.

TRUEMAN's calculations are confirmed by impressions of perisphinctids on the Solnhofen Slates. ROTHPLETZ (1909) showed that some of the perisphinctids which lie on the bedding planes at Solnhofen have beside them an impression of part of the venter (Fig. 158). He pointed out that the only possible interpretation of these is that the ammonite floated in shallow water, presumably on a receding tide, with its spiral plane vertical, that it first touched the bottom with its venter, and as the water continued to shallow the shell fell over on its side and was eventually left high and dry. In every specimen, the impression of part of the venter is just where it should be according to TRUEMAN's figures. The impression on the mud is so clear that if any of the animal had protruded from the shell it too must have left impressions. The inference is that the animals were completely retracted within their shells, perhaps dead.

FIG. 158. A perisphinctid with impression of its venter beside it, marking where it first "touched down" on the mud; U.Jur.(Kimm.), Solnhofen, Eu.; ×1 (110).

BREEDING HABITS

Light was also thrown by TRUEMAN (1941) on the breeding habits of ammonites. On measuring large numbers of shells massed together in the Marston Marble of the English lower Lias, he found that the material fell into 5 size groups. He interpreted these as showing that all the ammonites were killed at once and that 5 successive broods are represented. Whether the broods were seasonal or more frequent is unknown. Here successive broods of larvae grew into ammonites on the spot, but it is likely that the world-wide distribution of so many forms of ammonites is due chiefly to the larvae being carried away by ocean currents; this cause is likely to have been far more potent than *post mortem* drifting of shells.

FOOD

Direct evidence of the food eaten by ammonites is very meager. A mass of broken miniature aptychi and segments of siphuncles found in the body chamber of an *Oppelia steraspsis* from Solnhofen was originally thought to be remains of an unborn brood, but has been reinterpreted as the masticated remains of young oppeliids eaten cannibalistically (Gürich, 1924; Schwarzbach, 1936).

ENEMIES, INJURIES

Indications of the enemies that preyed on ammonites are little less rare. *Amaltheus* and belemnites have been found in the stomach of a saurian (Frentzen, 1936), and many belemnites have been discovered in the stomach of a fish, *Hybodus*. In the Upper Jurassic of southern Germany, many haploceratids and oppeliids have tongue-shaped pieces taken out of them, generally in the hinder part of the body chamber, as if they had been bitten. Decapod crustaceans are thought to have been the most likely causes of these mortalities (Roll, 1935).

Injuries to the body chamber during life were numerous and often produced monstrosities. When they were inflicted before maturity, subsequent parts of the shell may bear to the end various kinds of distortion in shape, ornament, and suture, commonly with displacement of siphuncle and keel and marked asymmetry. These distortions take various well-known forms and can usually be recognized with experience. A number have been figured and discussed in papers by Fraas (1863), Boone (1926), Destombes (1938), Spath (1945), Maubeuge (1949), Droutchtchine (1954), and Popov (1954). The abnormalities may continue to the end of the mature shell or, in less severe ones, disappear suddenly, with complete return to normal. When injured early, the whole shell may have quite different characters on opposite sides, producing divergences which, if found separated, would be taken for 2 different species or even genera. Perhaps the most remarkable example on record is that of a *Hysteroceras* in which the last 5 suture lines are completely reversed, the lobes pointing forward and the saddles backward, without any appreciable disfigurement of their elements or details (Haas, 1941). All such injuries were clearly inflicted on parts of the shell that were body chamber at the time. Contrary to some statements, no valid evidence is known indicating that injuries to camerae could be repaired.

GEOGRAPHIC DISTRIBUTION

The earliest ammonoids, found in Lower Devonian rocks, are known so far only in central Europe, but knowledge is still too incomplete to allow one safely to regard this as the cradle of all ammonoids. Most of the Paleozoic and Mesozoic forms are largely cosmopolitan. Their distribution seems to have been little influenced by latitude and therefore by any climatic zones. Nevertheless, some assemblages are much more widespread than others, and in all faunas there are genera, subfamilies, or even families, which are restricted in their distribution to certain parts of the world.

For the Jurassic, knowledge has now advanced to the point where maps can be drawn with some confidence showing distribution of faunas (Arkell, 1956). It emerges that in the Early Jurassic the ammonite faunas were world-wide at generic and often specific level. In the Bajocian they retreated from the Arctic Ocean border seas. In the Bathonian this retreat reached a climax and ammonites became greatly restricted. With the Callovian a general readvance began, but successive advances from the south and north can be traced over Europe. In the late Late Jurassic 2 distinct realms – Boreal and Tethyan-Pacific – became differentiated and correlation between them is extremely difficult. For some periods a subdivision of the latter into Tethyan and Pacific realms is possible, and at times various provinces developed marked characteristics. For instance, in the Toarcian, Callovian, and Oxfordian, certain special families mark out an Indian-Ethiopian province of the Tethyan realm, although stragglers from the province have lately been found in the western Tethys.

In the 19th century literature the "liostracous" suborders Phylloceratina and Lytoceratina were always portrayed as characteristic of the Tethys and of peculiar, deeper-water deposits, and the beds that produce them were put in opposition to the shallow-water deposits in which the trachyostracous families lived. It is true that the 2 liostracous suborders are usually far more abundant in the Tethys than farther north, but in southern Europe, including the middle of the Mediterranean and North Africa, and in the Caucasus and East Africa, there is a complete mixture at various horizons; Phylloceratina and Lytoceratina are as common as anywhere and the same shallow-water trachyostraca abound as well. Isolated occurrences of Phylloceratina and Lytoceratina, moreover, are now known in both Jurassic and Cretaceous deposits inside the Arctic Circle, in northern Siberia and Greenland.

The Mesozoic ammonoid faunas of the Arctic regions, and the rich Upper Cretaceous fauna of the Antarctic continent, prove that there can have been no ice caps in Mesozoic times—at least none anywhere near their present positions. The only positions in which cold poles could have been situated without affecting the evidence are in the North Pacific and a corresponding position in the South Atlantic (Arkell, 1956. This agrees with the long-known occurrence of very similar Jurassic temperate floras in Graham Land and east Greenland. The evidence is so unequivocal that it should be more widely realized and reckoned with by paleometeorologists and astronomers.

STRATIGRAPHIC DISTRIBUTION

The pre-eminence of ammonites as zonal marker fossils for local and world-wide correlations is undisputed. No other organisms enable the Upper Paleozoic and Mesozoic systems to be classified and correlated in anything like such detail. This usefulness is due to their rapidity of evolution, with wealth of forms changing rapidly up the stratal column, their wide distribution and comparative indifference to facies, and usually their ease of recognition, even in the field, without use of the microscope or laborious techniques.

Next after these qualities, the most remarkable fact about the stratigraphic distribution of the order is their 3 lean periods, at end of the Permian, end of the Triassic, and end of the Cretaceous (Figs. 159, 160). The first 2 crises were survived in each case by a single family, which then blossomed anew by explosive radiation to repopulate all the seas of the world, but the 3rd brought sudden extinction to the whole order. The last ammonites of the Late Cretaceous, in the Maastrichtian, show no special signs of degeneration. Their sutures are elaborately frilled and they differ in no perceptible way from the generations that preceded them and perpetuated their kind. Nor do the solitary families that managed to survive the 2 previous crises reveal in what characters they were superior to all the other families that went under at those times. It is, however, probably no coincidence that it was the Phylloceratina that came through from the Triassic to the Jurassic, for this was the most

Table 1. *Standard Stages and Ammonite Zones of the Triassic* (Bernhard Kummel)

Stages	Zones
Rhaetian	*Choristoceras marshi*
Norian	*Sirenites argonauta*
	Pinacoceras metternichi
	Cyrtopleurites bicrenatus
	Cladiscites ruber
	Sagenites giebeli
	Discophyllites patens
Carnian	*Tropites subbullatus*
	Carnites floridus
	Trachyceras aonoides
	Trachyceras aon
Ladinian	*Protrachyceras archelaus*
	Protrachyceras reitzi
Anisian	*Paraceratites trinodosus*
	Paraceratites binodosus
	Nicomedites osmani
	Neopopanoceras haugi
Scythian	*Prohungarites similis*
	Columbites parisianus
	Tirolites cassianus
	Anasibirites multiformis
	Meekoceras gracilitatis
	Flemingites flemingianus
	Koninckites volutus
	Xenodiscoides fallax
	Prionolobus rotundatus
	Proptychites rosenkrantzi
	Vishnuites decipiens
	Ophiceras commune
	Otoceras woodwardi

TABLE 2. *Standard Stages and Ammonite Zones of the Jurassic of Northwest Europe* (W. J. ARKELL)

	Stages	Zones
UPPER JURASSIC	Purbeckian	[No ammonites]
	Portlandian	*Titanites giganteus* *Glaucolithites gorei* *Zaraiskites albani*
	Kimmeridgian	*Pavlovia pallasioides* *Pavlovia rotunda* *Pectinatites pectinatus* *Subplanites wheatleyensis* *Subplanites* spp. *Gravesia gigas* *Gravesia gravesiana* *Aulacostephanus pseudomutabilis* *Rasenia mutabilis* *Rasenia cymodoce* *Pictonia baylei*
	Oxfordian	*Ringsteadia pseudocordata* *Decipia decipiens* *Perisphinctes cautisnigrae* *Perisphinctes plicatilis* *Cardioceras cordatum* *Quenstedtoceras mariae*
MIDDLE JURASSIC	Callovian	*Quenstedtoceras lamberti* *Peltoceras athleta* *Erymnoceras coronatum* *Kosmoceras jason* *Sigaloceras calloviense* *Proplanulites koenigi* *Macrocephalites macrocephalus*
	Bathonian	*Clydoniceras discus* *Oppelia aspidoides* *Tulites subcontractus* *Gracilisphinctes progracilis* *Zigzagiceras zigzag*
	Bajocian	*Parkinsonia parkinsoni* *Garantiana garantiana* *Strenoceras subfurcatum* *Stephanoceras humphriesianum* *Otoites sauzei* *Sonninia sowerbyi* *Ludwigia murchisonae* *Tmetoceras scissum* *Leioceras opalinum*
LOWER JURASSIC	Toarcian	*Lytoceras jurense* *Hildoceras bifrons* *Harpoceras falcifer* *Dactylioceras tenuicostatum*
	Pliensbachian	*Pleuroceras spinatum* *Amaltheus margaritatus* *Prodactylioceras davoei* *Tragophylloceras ibex* *Uptonia jamesoni*
	Sinemurian	*Echioceras raricostatum* *Oxynoticeras oxynotum* *Asteroceras obtusum* *Euasteroceras turneri* *Arnioceras semicostatum* *Arietites bucklandi*
	Hettangian	*Schlotheimia angulata* *Psiloceras planorbis*

TABLE 3. *Upper Jurassic Ammonite Zones of the Western Tethys (Central and Southern Europe)* (W. J. ARKELL)

Stages	Zones
Tithonian (upper)	*Virgatosphinctes transitorius (Berriasella chaperi, B. delphinensis)*
(middle)	*Semiformiceras semiforme*
(lower)	*Berriasella ciliata, Anavirgatites palmatus* *Subplanites vimineus* *Taramelliceras lithographicum, Hybonoticeras hybonotum*
Kimmeridgian (middle and lower)	*Hybonoticeras beckeri* *Aulacostephanus pseudomutabilis* *Streblites tenuilobatus*
Oxfordian	*Epipeltoceras bimammatum* *Gregoryceras transversarium* *Cardioceras cordatum* *Quenstedtoceras mariae*

persistent and unchanging stock, with the longest range of all ammonoids; they survived from the Early Triassic until the Late Cretaceous, with only minor changes in their form, mode of coiling, ornament, and highly peculiar sutures.

What were the causes of the final extinction at the end of the Cretaceous can only be conjectured, and speculations in this field would hardly be appropriate in this *Treatise*. It must be said, however, that a hypothesis

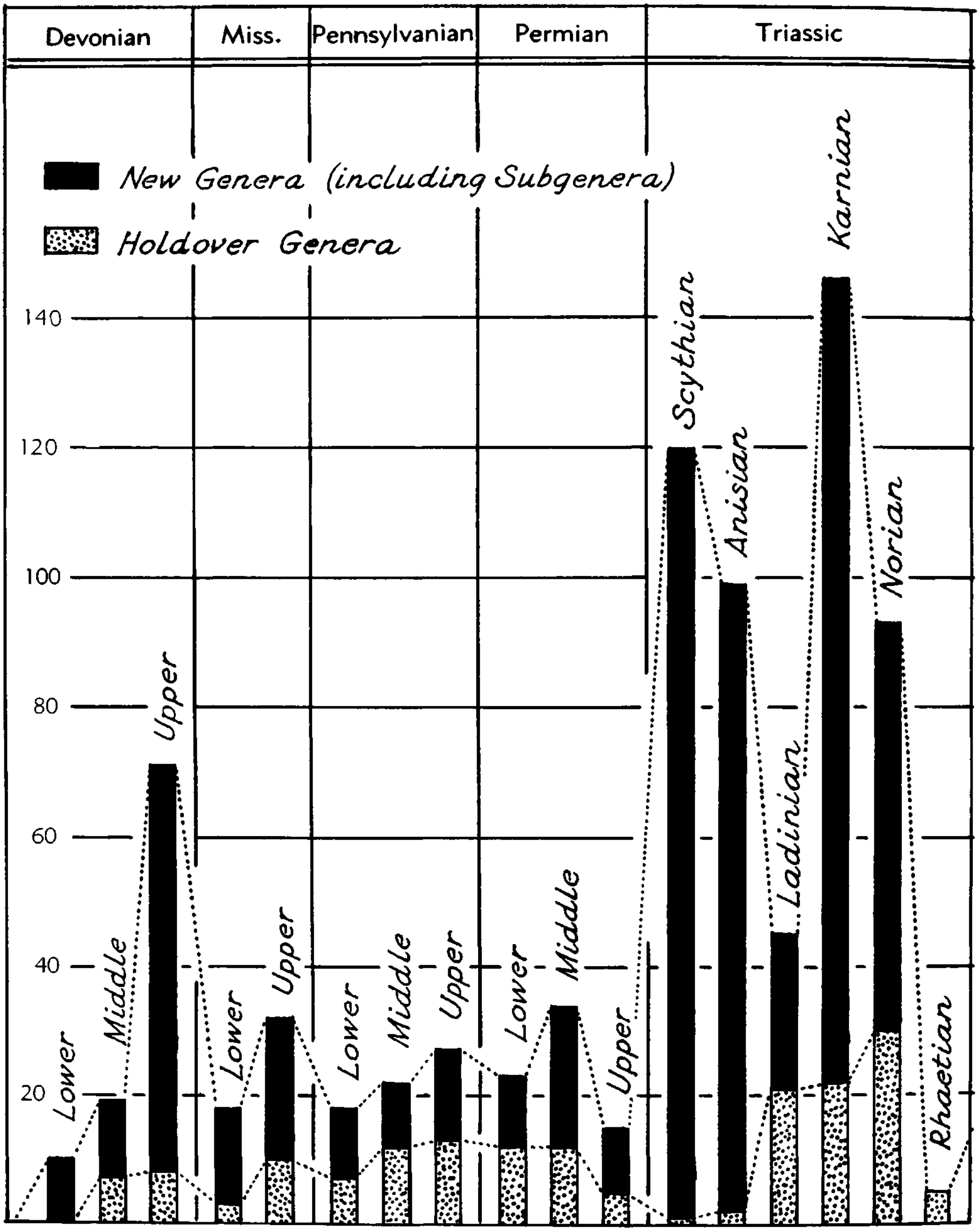

FIG. 159. Number of Ammonoid genera recorded in *Treatise* in main divisions of Paleozoic and Triassic rocks containing them, showing new genera introduced in each and holdover genera (MOORE).

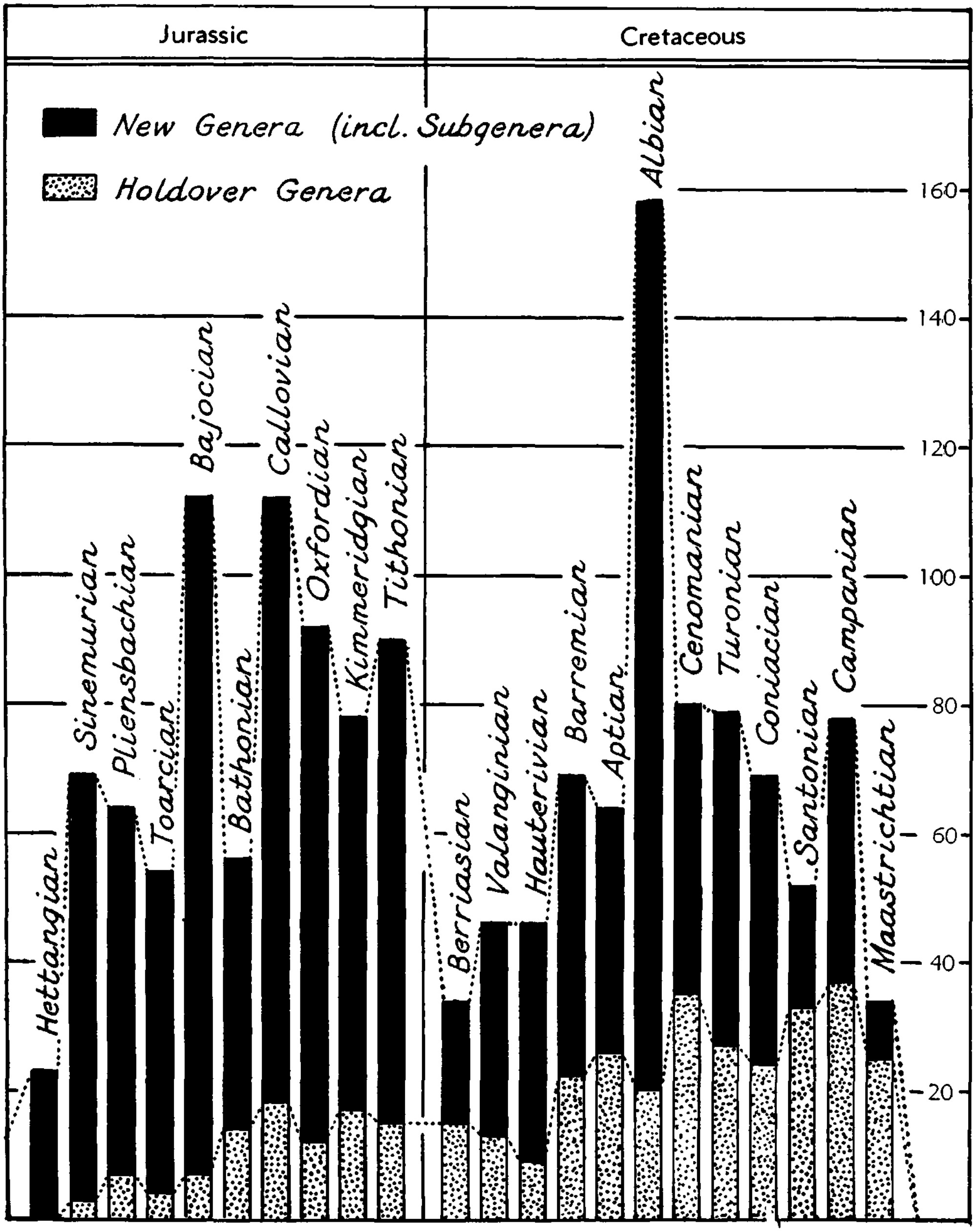

FIG. 160. Number of ammonoid genera recorded in *Treatise* in main divisions of Jurassic and Cretaceous rocks, showing new genera introduced in each and holdover genera (MOORE).

TABLE 4. *Standard Stages and Ammonite Zones of the Cretaceous of Classic Areas of Western Europe*[1] (C. W. WRIGHT)

	Stages	Zones
UPPER CRETACEOUS	Maastrichtian	*Sphenodiscus* sp.
		Pachydiscus neubergicus
	Campanian	*Hoplitoplacenticeras vari*
		Menabites delawarensis
		Diplacmoceras bidorsatum
	Santonian	*Placenticeras syrtale*
		Texanites texanus
	Coniacian	*Paratexanites emscheris*
		Barroisiceras haberfellneri
	Turonian	*Subprionocyclus neptuni*
		Collignoniceras woollgari
		Mammites nodosoides
		Metoicoceras whitei
	Cenomanian	*Utaturiceras vicinale*
		Acanthoceras rhotomagense
		Mantelliceras mantelli
		Mantelliceras martimpreyi
LOWER CRETACEOUS	Albian (upper)	*Stoliczkaia dispar*
		Mortoniceras inflatum
	(middle)	*Euhoplites lautus*
		Hoplites dentatus
	(lower)	*Douvilleiceras mammillatum*
		Leymeriella tardefurcata
	Aptian (upper)	*Diadochoceras nodosocostatum*[2]
		Parahoplites nutfieldensis
		Cheloniceras martini
	(lower)	*Deshayesites deshayesi*
	Barremian	*Costidiscus recticostatus*
		Heteroceras astierianum
		Crioceratites emericianus
	Hauterivian	*Pseudothurmannia angulicosta*[3]
		Subsaynella sayni
		Crioceratites duvali
		Acanthodiscus radiatus
	Valanginian	*Kilianella roubaudiana*
		————[4]
	Berriasian	*Thurmanniceras boissieri*

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[1] Since the characteristic exposure of the stages or the best-described ones are in different areas, the zones given in the table do not apply over the whole of western Europe.

[2] This zone is often placed in the lower Albian.

[3] This zone is sometimes placed in the Barremian.

[4] There seems to be an unnamed gap here in the classic zones of southern France.

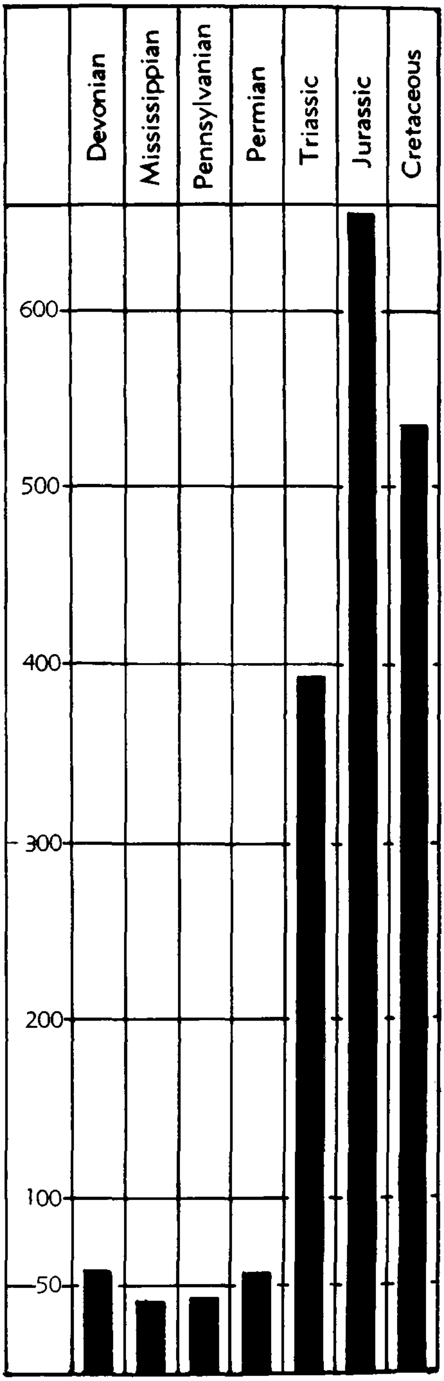

FIG. 161. Bar graph showing number of ammonoid genera (including subgenera) as recognized in the *Treatise*, occurring in each geologic period (MOORE).

TABLE 5. *Ammonite Zones of the Volgian* (W. J. ARKELL)

Stages	Zones
Volgian (upper)	*Riasanites rjasunensis* *Craspedites nodiger* *Craspedites subditus* *Craspedites fulgens*
(lower)	*Lomonossovella blakei,* *Epivirgatites nikitini* *Virgatites virgatus* *Zaraiskites scythicus* *Dorsoplanites dorsoplanus*

postulating that the ammonites suddenly cast away their shells and that their descendants are to be found at the present day as the Octopoda or other Dibranchiata, has no evidence to support it.

Nor is this the place for a discussion of the nature and scope of ammonoid zones or ages; that is a stratigraphical matter. The principal zones, and the stages in which they are grouped for purposes of the *Treatise,* will be found in Tables 1-5. It should be noted in connection with the tables that the zones of the Paleozoic are not comparable with Mesozoic zones but are more in the nature of the "ages" sometimes distinguished in the Mesozoic, namely, periods dominated by certain genera or families. The distribution of genera in time is shown in Fig. 161.

SYSTEMATIC DESCRIPTIONS

By W. J. ARKELL, BERNHARD KUMMEL, and C. W. WRIGHT

INTRODUCTION

AUTHORSHIP

The systematic descriptions of all Triassic taxa in following pages have been prepared by BERNHARD KUMMEL. In general, W. J. ARKELL is the author of all Jurassic ammonoid taxa and C. W. WRIGHT of all Cretaceous units, but because some families contain both Jurassic and Cretaceous genera, contributions to the text by ARKELL and WRIGHT are intermixed in some places. In the section mainly devoted to description of Jurassic forms, WRIGHT is author of the text on Protetragonitidae (p. L199), Macroscaphitidae (p. L204), Cicatritidae (p. L205), Aconeceratinae (p. L285), as well as diagnoses of Cretaceous genera assigned to otherwise Jurassic families of Phylloceratina and Lytoceratina. Descriptions of the Neocomitinae (p. L356), Oosterellidae (p. L362), and Spiticeratinae (p. L345) are the product of collaboration by ARKELL and WRIGHT.

Because of placement in the predominantly Paleozoic suborder Prolecanitina, the Triassic family Sageceratidae has been described by MILLER & FURNISH in the preceding section of this volume on Paleozoic Ammonoidea, and conversely, Permian genera of the Xenodiscidae and Otoceratidae, included in the predominantly Triassic Ceratitina, have been described by KUMMEL.

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Special appreciation is expressed here for help furnished by L. F. SPATH in connection with KUMMEL's work on Triassic ammonoid taxa, both during studies at the British Museum in 1951-1952 and through subsequent correspondence.

Valuable help with Liassic families and genera was received at all stages of preparation from Dr. D. T. DONOVAN, University of Bristol. Assistance in connection with Cretaceous units by providing important specimens for study, by furnishing advance copies of manuscripts, or by advancing publication of their own work on various ammonoids was given by Vicomtesse ELIANE BASSE DE MÉNORVAL (Paris), G. BOTERO-ARANGO (Colombia), RAYMOND CASEY (London), W. A. COBBAN (Colorado), J. P. CONLIN (Texas), TATSURO MATSUMOTO (Japan), R. A. REYMENT (Nigeria), and Comtesse DE VILLOUTREYS (Monaco). All illustrations that accompany systematic descriptions of Mesozoic ammonoids have been prepared by RAYMOND C. MOORE. Appreciation of the aid furnished by these individuals and various others who are unnamed is expressed here.