22.9 cm. (Fig. J14). [EATON, GRANT, & ALLEN, 1941, expl. pl. 4, fig. 3].

8) *Crassostrea virginica* (GMELIN, 1791), subfossil from shell mound (Pleist.), Damariscotta River, southern Maine, USA: H. 35.5 cm.; L, 11 cm. [INGERSOLL, 1881, p. 82, pl. 30, fig. 22].

9) *Crassostrea virginica* (GMELIN, 1791), living (Rec.), Boothbay Harbor, Lincoln County, Maine, USA: distance from hinge to ventral border, 20.6 cm.; H (left ligamental area), 5.5 cm.; H (right ligamental area), 4.5 cm.; L, 9.7 cm.; W (near hinge), 6.5 cm.; Wt (shell), 1175 gm.; Wt (soft parts), 35.8 gm.; Wt (enclosed liquid), 19.2 gm.; Wt (total), 1230 gm. [GALTSOFF, 1964, p. 20-21].

10) *Exogyra (Exogyra) erraticosta* STEPHENSON (1914), Pecan Gap Chalk (Campan.), Austin-Manor road, Travis County, Texas, USA: max. dimension, 20.1 cm.; Wt (both valves and internal mold), 3939.5 gm. [STENZEL, personal collection].

11) *Hyotissa hyotis* (LINNÉ, 1758), living (Rec.), New Caledonia: H, 28.5 cm.; L, 23.4 cm.; W, 19.0 cm. [Mus. Natl. Hist. Nat., Paris, France].

12) *Hyotissa hyotis* (LINNÉ, 1758) [= *Ostrea cristagalli* ROUGHLEY, 1931 (*non* LINNÉ, 1758)], living (Rec.), Great Barrier Reef, Queensland, Australia: H, 24.8 cm.; L, 15.6 cm.;

W, 11.4 cm.; Wt (shell), 1885 gm. [ROUGHLEY, 1931].

13) *Hyotissa hyotis* (LINNÉ, 1758), living (Rec.), Direction Island (Cocos-Keeling Is.), Indian Ocean, depth 10-20 ft.: H, 28 cm.; L, 28 cm.; W, 15 cm.; Wt (right valve), 1673 gm.; Wt (left valve), 2750 gm. [Philadelphia Acad. Nat. Sci.].

14) *Ostrea edulis* LINNÉ (1758), living (Rec.), estimated age 26-27 yrs., near Bergen, Norway: Wt (shell), 1228 gm.; Wt (soft parts), 55 gm.; Wt (enclosed liquid), 67 gm.; Wt (total), 1350 gm. [BJERKAN, 1918].

15) *Ostrea edulis* LINNÉ (1758), living (Rec.), age 10+ yrs., Salcombe Estuary near Salstone, Devonshire, England: H, 17.6 cm.; L, 19.8 cm.; W, 5.9 cm.; Wt (shell), 1038 gm.; Wt (soft parts), 94 gm.; Wt (enclosed liquid), 133 gm.; Wt (total) 1265 gm.; mantle cavity volume, 130 cm³. [ORTON & AMIRTHALINGAM, 1930].

16) *Rastellum (Arctostrea) aguilerae* (BÖSE, 1906) [= *Arctostrea atkinsi* RAYMOND, 1925], Habana Formation (Maastricht.), 1 km. NW of Dos Hermanos on road to Abreus, Santa Clara Prov., Cuba: diameter tip to tip, 23.5 cm.; W (right valve), 7.0 cm. [SOHL & KAUFFMAN, 1964, p. 414-419].

TERMS, CHIEFLY MORPHOLOGICAL, APPLIED TO OYSTERS

Terms regarded most important are in boldface type (as **adductor muscle**); use is not recommended of those printed in italics (as *epidermis*). Some nonmorphological terms have been included for aid to biologists and zoologists who may not be familiar with them. These are enclosed by square brackets. Many terms have general application to Bivalvia (*Treatise,* p. N102); additional ones considered by H. B. STENZEL to be especially applicable to oysters are accompanied by an asterisk (*).

aboral*. Pointing away from mouth.

adductor muscle*. Single posterior muscle connecting the 2 valves, tending to close them.

adoral*. Pointing toward mouth.

alate. With wings or auricles.

alivincular. Type of ligament not elongated in longitudinal direction nor necessarily situated entirely posterior to beaks, but located between cardinal areas (where present) of respective valves, with lamellar layer both anterior and posterior to fibrous layer; example, *Ostrea.*

[**allochthonous***.] In structural geology, pertaining to rock masses that tectonic forces have transposed to rest on a strange base.

allometric growth*. Growth by unequal rates in different parts of an animal.

[**allomorph** (noun)***.] Any of 2 or more diverse crystalline forms of the same chemical substance.

[*allomorphic* (adj.)***.] Pertaining to allomorphs. *See* xenomorphic.

allomorphism. See xenomorphism.

allopatric*. Pertaining to 2 or more species living in different regions.

amphidetic. Extending on both anterior and pos-

terior sides of beaks (applied to ligament or ligamental area); example, *Arca.*

anachomata. *See* chomata.

anisomyarian. With one adductor muscle (anterior) much reduced or absent.

anodont. Lacking hinge teeth. Same as edentulous.

anterior*. Direction parallel to hinge axis more nearly approximating to that in which mouth of animal faces.

anterodorsal margin. Margin of dorsal part of shell in front of beaks.

aorta*. Large tubular blood vessel which carries blood from heart toward other organs.

appressed*. Pertaining to thin foliaceous parts of shell separated from main part of shell by narrow vacant space.

[aragonite*.] Rhombic-holohedral or pseudohexagonal allomorph of calcium carbonate.

arborescent*. Resembling branched tree.

auricle. Earlike extension of dorsal region of shell, commonly separated from body of shell by notch or sinus.

auriculate. With auricles.

[authigenic*.] In mineralogy, pertaining to minerals that have grown in place within sediment.

[autochthonous*.] Having originated in place.

automorphic*. Same as idiomorphic.

beak. Noselike angle, located along or above hinge margin, marking point where growth of shell started.

[beekite.] Concentrically structured silicification center.

bialate. With 2 wings or auricles.

bilobate*. With 2 distinct bulges.

biocoenosis (pl., **biocoenoses**)*. Natural ecologic unit composed of diverse, but mutually dependent organisms.

biostrome*. Flat extensive biocoenosis composed of sedentary organisms that have hard skeletons or shells and sediment derived from them.

biotope*. Region of uniform environmental conditions and animal populations.

blood sinus* (blood-filled sinus, or blood lacuna). Irregularly shaped blood vessel without special confining walls.

body of shell. In alate or auriculate shells, entire shell with exception of wings or auricles.

Bojanus, organ of*. Kidney of Bivalvia.

bourrelet. Either of two portions of bivalve ligamental area flanking resilifer on its anterior and posterior sides; each comprises growth track and seat of the lamellar ligament. [The posterior bourrelet is flattish in all oysters except the Exogyrinae, in which it is a narrow sharp-crested spiral ridge on the LV and a corresponding groove on the RV.]

branchia* (pl., **branchiae**). Gill.

branchial passage*. Conduit confined by gills carrying parts of exhalant water stream.

branchitellum (pl., **branchitella**). Point on posteroventral shell margin of oysters nearest to pallio-branchial fusion, commonly forming conspicuously projected posteroventral tip on LV, especially in sickle-shaped oysters; aboral end of gills points toward it.

buttress*. Internal shelly projection supporting resilifer or adductor muscle.

buttressed*. Provided with internal shelly projection for support of resilifer or adductor muscle.

byssal gland*. Gland on foot of Bivalvia which secretes byssus.

byssiferous. Possessing a byssus.

byssus. Bundle of hairlike strands by which temporary attachment of bivalve can be made to extraneous objects.

[calcite*.] Rhombohedral-holohedral allomorph of calcium carbonate.

cardinal axis*. See hinge axis.

carina. Prominent keel-like ridge.

carinate. With carina or sharp angulation.

cartilage. Old term for internal ligament.

catachomata*. *See* chomata.

catch muscle*. White, opaque, opalescent, tonic portion of adductor muscle.

[chalk*.] Earthy, crumbly limestone.

chalky deposits*. Parts of shell resembling chalk.

chemoreceptor*. Sense organ sensitive to chemical stimuli.

chomata (sing., **choma**). Collective term for anachomata, which are small tubercles or ridglets on periphery of inner surface of RV, and catachomata, which are pits in LV for reception of anachomata; both generally restricted to vicinity of hinge, but may encircle whole valve.

clasper* (or clasping shelly process). Narrow extension of shell tending to attach to extraneous objects.

cloacal passage*. Passage in exhalant mantle chamber into which excrements and gonadal products are discharged.

commissural plane*. Imaginary plane drawn through valve commissure.

commissural shelf*. Peripheral, shelflike part of shell adjoining commissure.

commissure. Line of junction of 2 valves.

compressed. Relatively flattened.

concentric. With direction coinciding with that of growth lines. (By no means concentric in literal and geometrical sense of the term.)

conchiolin. Material (protein) of which periostracum and organic matrix of calcareous parts of shell are composed.

[conchological*.] Pertaining to conchology (shell science).

[conchology*.] Study of shell shapes.

convexity. Degree of inflation.

costa. Moderately broad and prominent elevation of surface of shell, directed radially or otherwise.

costella. Rather narrow linear elevation of surface of shell.

costellate*. Having costellae.

costule. Same as costella.

crescentic*. Curved like crescent moon.

crossed-lamellar. Type of shell structure composed of primary and secondary lamellae, latter inclined in alternate directions in successive primary lamellae.

demibranch*. One half of gills.

demiprovinculum*. Half-provinculum.

*denticle**. Small rounded toothlike protuberance on shell. *See* chomata.

dentition. Hinge teeth and sockets, considered collectively.

dichotomize*. To divide by dichotomy.

dichotomous*. Divided by dichotomy.

dichotomy*. Forking of a line or rib into 2 equal parts.

dimyarian. With 2 adductor muscles.

dioecious*. Having male and female reproductive organs in separate individuals.

diphyletic*. Pertaining to group of animals descended from 2 originally diverse ancestral lines.

discordant margins. Margins of closed valves not in exact juxtaposition, but one overlapping other.

disjunct pallial line. Pallial line broken up into separate, mostly unequal muscle insertions.

dissoconch. Postlarval shell.

distal. Pointing or situated away from animal's center.

divaricate. Type of ornament composed of pairs of rather widely divergent costules or other elements.

[dog-tooth spar.] Pointed elongate crystal form of calcite.

dorsal. Pertaining to region of shell where mantle isthmus was situated and valves are connected by ligament (i.e., to region of hinge).

D-shaped larval stage. Stage of larval growth in which valve outline resembles a D and hinge is long and straight.

dysodont. With small weak teeth close to beaks (as in some Mytilacea).

ear. Small extension of dorsal region of shell, commonly separated from body by notch or sinus. Same as auricle.

ecomorph. Infraspecific growth form of species in response to special environment.

ecomorphic. Pertaining to ecomorphs.

edentulous. Lacking hinge teeth.

epidermis. Term used by some authors for periostracum.

equilateral. With parts of shell anterior and posterior to beaks equal in length or almost so.

equivalve. With 2 valves of same shape and size.

euhaline. Pertaining to sea water of normal salinity (around 35 permille).

euryhaline. Capable of living in sea water of a broad range of salinities including brackish waters.

excurrent. See exhalant.

exhalant. Applied to water current within mantle cavity from gills on out and the spaces from which it is departing.

exogyroidal (exogyrate). Shaped like shell of *Exogyra,* that is, with left valve strongly convex and its dorsal part coiled in posterior direction, with right valve flat and spirally coiled.

extrapallial space. Narrow mucus-filled space between mantle lobe and interior face of valve.

[facies.] In stratigraphy, sediment characterized by special mineral assemblage, bedding, and fossil organisms but differing from adjacent contemporaneous deposits.

falciform. Sickle-shaped.

fibrous ligament. Part of ligament characterized by fibrous structure and in which conchiolin is commonly impregnated with calcium carbonate; secreted by epithelium of mantle isthmus and elastic chiefly to compressional stresses.

fingerprint shell structure*. Shell structure, as yet unexplored, resembling thumb prints.

fixation. Process of animals permanently attaching themselves.

fold. Rather broad undulation of surface of shell, directed either radially or commarginally.

foot. Protrusible muscular structure extending from mid-line of body, anteroventrally in more typical bivalves, and used for burrowing or locomotion.

fringe*. Extension of the periostracum conchiolin beyond calcareous part of shell.

[fringe reef.] Crowded oysters growing in band parallel to nearest shore line.

gape. Localized opening remaining between margins of shell when valves are drawn together by adductor muscles.

gashes, radial*. Radial, sharp-edged incisions common on upper valves of some Gryphaeidae.

genital pore*. Opening through which gonadal products issue into cloacal passage.

[glauconite.] Family of soft, green, iron-bearing minerals of diverse compositions, usually in pellet shapes.

globose. Tending toward spherical shape.

growth line. Line on surface of shell, one of usually irregularly arranged series, marking position of margin at some stage of growth.

growth ruga. Irregular wrinkle on surface of shell of similar origin to growth line but corresponding to more pronounced hiatus in growth.

growth squamae*. Scaly extensions of shell arising from shell surface parallel to growth lines.

growth thread. Threadlike elevation of surface of similar origin to growth line.

growth welt. Elongate elevation parallel to growth lines.

gryphaeate. Shaped like shell of *Gryphaea,* that is, with left valve strongly convex and its dorsal part incurved and with right valve flat.

gryphaeiform*. Resembling a *Gryphaea.*

gryph-shaped*. Same as gryphaeiform.

height. Largest dimension obtained by projecting the extremities onto the mid-axis of shell.

hermaphrodite. Animal producing both male and

female gonadal products, not necessarily simultaneously.

heteroclite (adj.)*. Commissural plane that is folded or twisted is heteroclite.

heteromyarian. With one adductor muscle (anterior) much reduced.

hinge. Collective term for structures of dorsal region which function during opening and closing of valves.

hinge axis. Imaginary straight line about which valves rotate.

hinge line. Same as hinge axis.

hinge plate. Shelly internal platform bearing hinge teeth, situated below beak and adjacent parts of dorsal margins, and lying in plane parallel to that of commissure.

hinge tooth. Shelly structure (usually one of a series) adjacent to dorsal margin and received in socket in opposite valve; hinge teeth serve to hold valves in position when closed.

[homeomorph.] Two unrelated species or genera or larger taxa that are superficially similar.

homomyarian. With 2 adductor muscles equal in size or almost so.

[homonym.] Identically same word applied as name for 2 different taxa.

hyote spines. Hollow, tubular and cylindrical shell outgrowths open distally at their tips as well as on their distal flanks, arising periodically from thin edges of shell margin of oysters. [The tip ends are rounded, ear-shaped openings, typically developed on *Hyotissa hyotis* (LINNÉ, 1758).]

[hyperhaline.] Pertaining to waters of higher salinities than normal sea water; above 40‰ salinity.

[hypertely.] Evolution carried beyond the point of optimal adaptation.

hypostracum. Term used in 2 different senses; 1) inner layer of shell wall, secreted by entire epithelium of mantle (original sense); 2) part of shell wall secreted at attachments of adductor muscles and pallial line muscles (later sense: *see* myostracum).

idiomorphic (or automorphic)*. Configuration of valves normal for species and not deformed by crowding or attachment to other objects.

imbricate. Overlapping like tiles or shingles on a roof.

imbrication. Part of shell overlapping like tile on roof.

imprint. Impression on valve left by an organ (either gill or muscle).

incremental line. Same as growth line.

incrustation*. Tight attachment of oysters to rock or other substances.

incubatory*. Pertaining to oysters that incubate their young larvae.

inequilateral. With parts of shell anterior and posterior to beaks differing appreciably in length.

inequivalve. With one valve larger than other.

inflated. Strongly convex.

inhalant. Applied to water current entering mantle

cavity from outside, but before it has passed through gills and to spaces in which it moves.

inner layer of ligament. Same as resilium.

insertion. Place of attachment for a muscle.

interspace. Depression between adjacent costae or other linear surface elevations.

isodont. With small number of symmetrically arranged hinge teeth; examples, *Spondylus, Plicatula*.

isomyarian. With 2 adductor muscles equal in size or almost so; same as homomyarian.

isthmus (or mantle isthmus). Dorsal part of mantle connecting the 2 mantle lobes.

keel. Projecting ridge; same as carina.

labial palp*. One of four lappet-shaped organs to either side of mouth.

lacuna (pl., lacunae)*. Irregular, blood-filled gaps between various organs in mantle and visceral mass.

lamella. Thin plate.

lamellar ligament. Part of ligament characterized by lamellar structure and containing no calcium carbonate; secreted at mantle edge and elastic to both compressional and tensional stresses.

lamelliform. Like thin elongate plate.

lamina. Thin plate.

left valve. Valve of oyster homologous to valve on left side of mobile Bivalvia.

length. Largest dimension obtained by projecting shell extremities onto hinge axis.

lenticular. Shaped like biconvex lens.

[leptopel*.] Extremely fine material floating in sea water, dead or alive, organic or inorganic.

ligament. Horny elastic structure or structures joining 2 valves of shell dorsally and acting as spring causing them to open when adductor muscles relax.

ligamental area*. Area between umbo and ligament showing growth track of ligament.

longitudinal. Direction parallel to that of cardinal axis.

mantle. Integument that surrounds vital organs of mollusk and secretes shell.

mantle chamber*. One of 2 spaces in mantle cavity between gills and mantle lobes.

mantle fold*. One of 3 small folds at periphery of a mantle lobe.

mantle lobe*. One of 2 flat thin extensions of mantle adjoining the valve.

mantle/shell*. Covering organ system of a bivalve consisting of shell and mantle lobes.

[marcasite.] Iron-sulfide mineral forming rhombic-holohedral crystals; allomorph of pyrite.

[marl.] Earthy, crumbly sedimentary rock about halfway in composition between chalk and clay.

metamorphosis. Process by which larva changes into adult form.

mid-axis*. Imaginary straight line drawn in commissural plane at right angles to hinge axis and beginning at mid-point of ventral margin of resilifer.

[minette iron ore.] Sedimentary oolitic iron ore of Jurassic age in Lorraine and Luxembourg.

monoecious*. Having male and female reproductive organs in the same individuals. Same as hermaphroditic.

monomyarian. With only 1 adductor muscle (posterior).

monophyletic. Pertaining to group of animals descended from only one ancestral line.

morph*. Group of variants of a species united by one or several common characters, but not forming a true population.

mouth-anus axis*. Imaginary straight line drawn through mouth and anus of animal.

muscle imprint. Impression on valve left by a muscle at its place of insertion.

myostracum. Part of shell wall secreted at attachments of adductor muscles.

nacreous. Having a shell structure producing mother-of-pearl luster.

[neontology.] Study of living animals.

[neoteny.] Condition of having immature traits prolonged in later life.

[neozoology.] Same as neontology.

nepionic. Pertaining to early postlarval stage.

nodose. Bearing tubercles or knobs.

nonincubatory*. Pertaining to oysters that do not incubate their larvae.

oblique*. Most extended in direction neither parallel nor perpendicular to hinge axis.

obliquity. Angle between straight dorsal margin and line bisecting umbonal angle (in terminology of some authors); or between dorsal margin and most distant point of ventral margin (in terminology of others).

[olistostrome.] In structural geology, allochthonous layer of disordered rock masses.

operculiform. Shaped like a lid or operculum.

opisthocline*. Sloping in posterior direction from hinge axis (term applied to body of shell).

opisthodetic. Located wholly posterior to beaks (term applied to ligament).

opisthogyral (or opisthogyrate)*. Curved so that beak points in posterior direction (term applied to umbones).

orbicular*. Shaped as an orb; less regular than circular.

orthocline*. Perpendicular to hinge axis or almost so (term applied to body of shell).

orthogyral (or orthogyrate)*. Curved so that beak points at right angles to hinge axis.

ostia*. Tiny holes in walls of gills letting a water current through.

ostracum*. Entire calcareous part of oyster shell.

outer ligament*. Same as lamellar ligament in oysters.

ovate. Shaped like longitudinal section of egg.

pad*. Thin aragonite layer on which adductor muscle is inserted.

pallial. Pertaining to the mantle.

pallial curtain. Innermost of 3 mantle folds at periphery of mantle lobe.

pallial line. Line or narrow band on interior of valve close to margin, marking line of attachment of marginal muscles of mantle.

pallial region. Marginal region of shell interior adjacent to pallial line.

pallial retractor muscles*. Muscles which withdraw peripheral edge of mantle lobe in proximal direction.

palliobranchial fuson.*. Place at which aboral ends of gills and 2 mantle lobes are firmly joined.

[patch reef*.] Reef in outline of a patch.

pedal. Pertaining to foot.

pedal muscles. Muscles activating motions of foot.

[pellet*.] Small, rounded, somewhat elongate body.

pericardium*. Saclike organ enclosing heart.

periostracal glands*. Glands at base of middle mantle fold from which base layer of periostracum issues.

periostracal groove*. Groove housing periostracal glands, between middle and outer mantle fold.

periostracum. Dark, horny, conchiolinic substance covering outside of shell.

phasic muscle*. Flesh-colored, semitranslucent portion of adductor muscle which reacts quickly but does not endure.

pivotal axis*. Axis at ligament around which valves rotate when closing.

pleurothetic*. Resting on its side.

plica. Fold or costa involving entire thickness of wall of shell.

plication. Same as plica.

polychotomous*. Divided into many branches.

[polyhaline*.] Pertaining to brackish water of 16 to 30‰ salinity.

polyphyletic. Pertaining to group of animals derived from diverse ancestral stems.

polytypic. A species encompassing 2 or more geographic subspecies or 2 or more widely divergent ecomorphs.

porcelaneous. With translucent, porcelain-like appearance.

posterior*. Direction parallel to hinge axis more nearly approximating to that in which anus faces and exhalant current issues.

posterior flange*. Flange at posterior of left valve of Gryphaeidae separated from main body of valve by posterior radial groove.

posterior ridge. Ridge passing over or originating near umbo and running diagonally towards posteroventral part of valve.

posterior slope. Sector of surface of valve running posteroventrally from umbo.

posterodorsal margin. Margin of dorsal part of shell posterior to beaks.

primogenitor. Ancestor.

prismatic shell layer*. Layer consisting of many tiny prismatic bodies of calcite.

prodissoconch. Shell secreted by the larva or embryo and preserved at beak of some adult shells.

promyal passage*. Exhalant water passage lying on right side of animal between adductor muscle and mantle isthmus.

prosocline. Sloping (from lower end) in anterior direction (term applied to hinge teeth and, in some genera, to body of shell).

prosogyrate. Curved so that beaks point in anterior direction (term applied to umbones).

protandric*. Pertaining to hermaphrodite animal in which male gonad develops and functions before female one does.

protostracum*. Shell of D-shaped larval stage.

provinculum. Median part of hinge margin of prodissoconch, usually bearing small teeth or crenulations.

proximal*. Pointing or situated near animal's center.

proximal gill wheal*. Low ridge on inner valve surface outlining position of proximal edge of gills.

pseudofeces*. Refuse ejected from mantle cavity that has not passed through intestinal tract.

pseudosiphon*. Outline of 2 opposing mantle edges in form of slit or hole.

pyriform. Resembling shape of pear.

[pyrite.] Iron-sulfide mineral forming cubic-paramorph crystals; allomorph of marcasite.

quadrate. Square, or almost so.

Quenstedt muscles*. Pair of small muscles inserted on valves near mouth of animal.

quick muscle*. Same as phasic muscle.

radial. Direction of growth outward from beak at any point on surface of shell, commonly indicated by direction of costa or other element of ornament.

reniform. Kidney-shaped.

resilifer*. Place of attachment of resilium and its growth track on ligamental area. Term introduced by DALL (1895, v. 3, p. 499).

resilium*. Inner layer of ligament or fibrous ligament. Term introduced by DALL (1895, v. 3, p. 498, footnote).

rib. Moderately broad and prominent elevation of surface of shell, directed radially or otherwise; same as costa.

riblet. Rather narrow linear elevation of surface of shell; same as costella.

right valve*. Valve of oyster homologous to valve on right side of mobile Bivalvia.

sagittal plane*. Anteroposteriorly directed plane of symmetry dividing animal into left and right side.

[sapropel*.] Slimy sediment consisting largely of dead plant and animal debris.

scale*. Thin, flat local projection of outer shell layers.

sculpture. Regular relief pattern present on surface of many shells.

secondary riblet. On shell with riblets of different orders of strength, riblet that appears somewhat later in ontogeny than primary ones and remains weaker than these.

self-cleansing*. Process of removal and ejection of pseudofeces.

self-sedimentation*. Sedimentation produced by self-cleansing process and ejection of feces.

semilunar*. Shaped like half-moon with both ends sharp.

shell fold*. Outer one of 3 mantle folds at periphery of mantle lobe.

sinus. Indentation, embayment.

socket. Recess for reception of hinge tooth of opposite valve.

spatulate. Shaped like a spatula.

speciation. Originating of one or more species by evolution.

spine. Thornlike protuberance of surface of shell.

spirogyral (or spirogyrate)*. Curved so that beak is in a distinct spiral.

squamae*. Thin, long, concentric imbrication.

squamose. Bearing scales.

[stenohaline*.] Capable of living in sea water of a narrow range of salinities.

straight-hinge veliger or protostracal veliger*. Same as D-shaped larval stage.

stria. Narrow linear furrow or raised line on surface of shell.

[string reef*.] Crowded oysters in a narrow greatly elongate accumulation.

sulcus. Radial depression of surface of shell.

sulcus, radial posterior*. Groove dividing posterior flange from main body of valve, in left valve of Gryphaeidae.

superspecies*. Monophyletic taxon consisting of several allopatric species too diverse morphologically for inclusion in one single species, but not distinct enough to be raised to status of genus.

surface ornament. Regular relief pattern present on surface of many shells.

sympatric*. Pertaining to 2 or more species occupying the same territory.

taxon (pl., **taxa**). Group of organisms recognized as formal taxonomic unit of any hierarchical level.

tentacular fold*. Middle one of 3 mantle folds at periphery of mantle lobe.

terminal. Forming most anterior or posterior point of valve; term applied to beak.

thickness. Used by some authors to denote the shell measurement here termed inflation, but also commonly applied to the distance between the inner and outer surfaces of wall of shell.

thread. Narrow elevation of surface of shell.

tonic muscle*. White, opalescent, opaque portion of adductor muscle which contracts slowly and can retain tension for long periods of time; same as catch muscle.

transverse. Direction perpendicular to that of cardinal axis in plane of valve margins.

trigonal. Three-cornered.

truncate. With curvature of outline interrupted by straight cut.

tumid. Strongly inflated.

umbo. Region of valve surrounding point of maximum curvature of lontidudinal dorsal profile and extending to beak when not coinciding with it. (Many authors treat beak and umbo as synonymous, but with most shells two distinct terms are needed.)

umbo-veliger*. Last larval stage of oysters.

umbonal cavity*. Part of interior of left valve that lies in umbonal region beneath ligamental area of oysters.

umbonal region*. Part of valve including umbo and its vicinity.

urogenital opening*. Opening through which gonadal products and excretions from organ of Bojanus issue into cloacal passage of exhalant mantle chamber.

valve. One of the calcareous structures (2 in most bivalves) of which shell consists.

veliger*. Velum-bearing larval stage of oyster.

velum*. Large, ciliated, disc-shaped swimming organ of larva.

ventral. Pertaining to or located relatively near to region of shell opposite hinge, where valves open most widely.

ventricle. Heart chamber receiving blood from auricles.

ventricose. Strongly inflated.

vermiculate. Of wiggly outline.

vesicular. Containing small cavities or vesicles.

visceral mass*. Mass of organs from mantle isthmus to adductor muscle.

visceral pouch*. Small pouch-shaped extension of visceral mass on anterior flank of adductor muscle.

width. Largest dimension obtained by projecting shell outline onto a line that is at right angles to hinge axis and mid-axis.

wing. More or less elongate, triangular, distally acute or obtuse, terminal part of dorsal region of shell in Pteriacea, Pectinacea, etc.

xenomorphic (adj.). Pertaining to xenomorphism.

xenomorphism. Special sculpture at the umbonal region of the unattached valve resembling the configuration of the substratum onto which the attached valve is or was originally fixed. Known in the Anomiidae, Gryphaeidae, Ostreidae and other pleurothetic and cemented families. It is on the right valves in oysters and on the left valves in *Anomia* (*see* STENZEL, KRAUSE & TWINING, 1957, p. 98-99). Erroneously called allomorphism by some authors.

DISTRIBUTION

CONTENTS

Today oysters live off the shores of all continents except Antarctica. They exist under various marine climates except the polar ones. Some species have succeeded in colonizing shores of isolated oceanic islands.

Oysters originated in euhaline waters, and to this day the Gryphaeidae are restricted to them. However, among the Ostreidae, groups have evolved that were able to penetrate into brackish estuaries and lagoons. Some species can exist in salinities as low as 10 permille.

DISPERSAL

The best means of dispersal of oyster species are their planktonic larvae. In special cases, however, dispersal is possible even after the oysters have become fixed.

Whenever oysters settle on movable objects or animals they can be carried considerable distances. Driftwood carries oysters. Such oysters can reach sexual maturity, because young oysters become capable of reproduction in a few months when they are 2-3 cm. large and still very thin-shelled. The method of dispersal by driftwood is important wherever mangrove swamps and dense tropical rain forests line the shores.

Sea turtles of the family Cheloniidae, but not *Dermachelys,* often carry attached oysters (W. T. NEILL, letter of May 16, 1964). Jurassic ammonites, dead or alive, carried oysters grown onto their shells (STAFF & RECK, 1911; SEILACHER, 1960) and may have floated considerable distances, before they sank or stranded. How far dead cephalopod shells can float has been shown on *Nautilus* by STENZEL (see *Treatise,* p. K90, Fig. 67).

Although such dispersals are only sporadic and haphazard, they may happen often enough to be quite effective in time, that is, during the geologic life span of a species. Such sporadic dispersals may add 1,000 to 3,000 km. to the geographic spread of a species each time they are successful.

Larvae are the chief means of dispersal, because they are produced in great swarms during every breeding season and because they are planktonic, so that they can be carried far by ocean currents. The larvae remain planktonic up to 33 days (IMAI, HATANAKA, *et al.,* 1950, p. 75) or even 50 days (ERDMANN, 1934, p. 7).

Tidal and oceanic currents distribute and transport the larvae. In some cases great distances are covered. To estimate how far currents can carry oyster larvae one must ascertain the maximal possible velocity of the current that is sustained over the duration of the larval period. Successful long-distance dispersal may be possible only under exceptionally optimal conditions and may happen only once in a century.

Assuming a current velocity of 200-250 cm. per second (=173-216 km. per day), which has been recorded for the Gulf Stream (WORTHINGTON, 1954), and a free-swimming larval period of 6 days, the computed travel distance amounts to 1,000-1,300 km. A short larval period has to be assumed, because only in warm waters do larvae have a good chance to survive and in such waters larval periods are short. Therefore, maximal distance for successful dispersal of an oyster species by its larvae planktonic in an ocean current is about 1,300 km. Evidently, oysters have good dispersal and geologic migration rates.

Euhaline oysters have better chances of survival during dispersal than those which require brackish waters. The latter must find brackish waters at the end of larval transport and such waters are hardly available around isolated oceanic islands.

With such dispersal distances possible, oysters can cross large bodies of water by island hopping. A species established around many islands and over large oceanic areas nevertheless can maintain occasional gene flow from one isolated island to the other so that the species may remain intact and attain an enormous geographic spread during long periods of geological history.

A living example is the euhaline, shallow-water gryphaeid species *Hyotissa hyotis* (LINNÉ, 1758). It lives in warm tropical to subtropical waters from southern Japan in the north to the Persian Gulf and Red Sea in the west, to Inhaca Island, Mozambique, off the east coast of Africa in the southwest, and the Tuamotu Islands and Clipperton Island (HERTLEIN & ALLISON, 1966, p. 139) in the southeastern Pacific Ocean.

Because of these abilities to spread it is not surprising to find the giant Miocene brackish-water oyster *Crassostrea gryphoides* (VON SCHLOTHEIM, 1813) in so

many places along the shores of the Miocene Tethys Sea and its bays. No island hopping was required, because continuous coastlines were available from the western outlet of the Tethys Sea at the Atlantic Ocean to the eastern ends on the Indian and Pacific Ocean shores.

The high migration rates of oysters explain also certain former geographic ranges.

The euhaline Cretaceous exogyrine genus *Gyrostrea* is well represented during the Turonian and Campanian in central Asia (MIRKAMALOV, 1963) and there is a lone species in southwestern Texas and adjoining Mexico, *G. cartledgei* (BÖSE, 1919) from the Del Rio Clay (early Cenoman.). This species appears to have neither ancestors nor descendants in the latter region; its appearance and disappearance here is best explained by migrations.

Very closely related and approximately contemporaneous species of *Exogyra (Exogyra)* are found in Late Cretaceous deposits of North Africa (*E. overwegi* BEYRICH, 1852) and of the Atlantic and Gulf coastal plains of North America (*E. costata* SAY, 1820, and its closest relatives). These two allopatric groups are morphologically more similar to each other and probably more closely related than they are to other, collocal but not contemporaneous species of *Exogyra*.

The sudden appearance of *Gryphaea arcuata* LAMARCK (1801) in western and central Europe and possibly in other less well-known regions during the early Liassic is probably best explained by migration from afar, as was first suggested by HALLAM (1962, p. 574).

LIMITATIONS TO DISPERSAL

In spite of the excellent means of dispersal available to them, today's shallow-water oyster species are bound by very definite limitations to their dispersal. They are the open-water barriers, climate barriers, and salinity barriers. Similar limitations must have been effective in the geologic past.

OPEN-WATER BARRIERS

Open-water barriers are stretches of open oceanic water not "bridged" by shoals or island chains. Too wide to be crossed in one direction, they are also too long to be outflanked in any way. Their two ends, at the north and south, are closed off by climate barriers so that outflanking becomes impossible.

The Atlantic Ocean today is such a barrier. Both ends abut against polar or at least cold-climate areas too rigorous for shallow-water oysters. All shallow-water oyster species, except one, are restricted to one or the other side of the Atlantic and no species has succeeded in crossing it since the beginning of the Pleistocene or earlier, in spite of the swift and far-reaching Gulf Stream. The only species living on both sides of this ocean is the warm-water *Lopha cristagalli* (LINNÉ, 1758) ecomorph *folium* (LINNÉ, 1758). This tropical and subtropical oyster grows on octocorallian branches and has a worldwide equatorial range. It must have had good means of spreading in the near geologic past, perhaps during the Miocene, but has not evolved since then into a chain of separate, provincial species.

The East-Pacific open-water barrier separates the Hawaiian and Tuamotu Islands on the west and coasts of the Americas and Galápagos Islands in the east (EKMAN, 1934). This barrier limits the species-rich, shallow-water, marine fauna of the Indo-Pacific. Island hopping is possible and has taken place in the past from the shores of Persia, Arabia, and East Africa to this barrier. East of the barrier, on the west coasts of the Americas, the IndoPacific species are replaced by other, in many cases quite similar, separate species. For example, the Indo-Pacific warm-water species *Hyotissa hyotis* (LINNÉ, 1758) is replaced along the shores of the Americas by *H. fisheri* (DALL, 1914), found from Mexico to Ecuador, off the Galápagos Islands, and in the Gulf of California.

At some periods of the geologic past, island hopping may have been much easier than today. Islands existed where only seamounts or submarine ridges now are left.

CLIMATE BARRIERS

Temperature tolerances are different in the various oyster species. The extreme limit of specific temperature tolerance of a given species is its climate barrier. Such barriers are of two different kinds (HUTCHINS, 1947): 1) summer temperatures,

meaning the critical warm temperatures that must be reached before reproduction can take place and ontogeny be completed, 2) winter temperatures, meaning the critical low temperatures below which mature individuals of the species die.

These two critical temperatures become evident particularly where they inhibit the poleward dispersal of a given species. Dispersal poleward is limited by whichever of the two factors is the more restrictive.

SUMMER TEMPERATURES

Wherever temperatures during the summer are too low to induce spawning or stay warm enough for too short a time span for the larval period to reach a successful finish, the species cannot propagate itself and becomes extinct. In marginal regions, the oyster species may be able to propagate successfully only once in ten years. Once the period of time between successful years becomes longer than the median life span of the species in that region, however, the species must disappear. Consequently, the poleward limit of a species fluctuates backward and forward with secular climatic changes.

The northwestern European oyster *Ostrea edulis* requires summer temperatures of only 15°C. for success in propagation. It breeds in the chilly Kattegat once in about 10 years and survives there only with difficulty. Farther north, in northern Norway, it survives only in a few isolated, especially favorable localities. These places have a hothouse effect. They are in narrow waters exposed to the full sun and protected by hills or mountains so that water temperature can rise while cold winds or water currents cannot reach them. The oysters originally reached these scattered localities during a former climatic optimum; they are relics.

Because of the Gulf Stream and the low summer temperature requirements of *Ostrea edulis* this species reaches the Arctic Circle in Norway. Its most northerly populations are recorded from Troena Island, just south of the Arctic Circle, and from near Rodoyosen on Tjotta Island, off the Norway coast at 65° 50′ N. The species is not known from Iceland, Spitsbergen, and the Faeroes Islands, but lives off the Shet-

land and Hebrides Islands. Because its summer temperature requirements are extremely low for oysters, the species is the only one that can survive on the coasts of Europe north of France. *Crassostrea angulata* (LAMARCK, 1819), the other European species, propagates successfully on the coasts of southwestern Europe and France, but only rarely when it is transplanted to England.

Similarly, in the northeast Pacific, *Ostrea conchaphila lurida* CARPENTER has the lowest summer-temperature requirements of any oyster and it is the only oyster able to survive north of San Diego, California. It is reported from as far north as Sitka, Alaska.

Some species of *Ostrea s.s.* appear to have in common their ability to spawn and to complete their larval periods at lower summer temperatures than species of other genera. Species of *Crassostrea* require higher summer temperatures for successful propagation. For example, *C. virginica* requires about 20°C. before it will begin to spawn. Because *Ostrea s.s.* is incubatory and *Crassostrea* is not, and because larvae of incubatory oysters finish their larval periods in shorter time, it is likely that incubation in *Ostrea s.s.* is used as an adaptation that makes it feasible for some species to spread poleward into regions not accessible to other oysters.

WINTER TEMPERATURES

Most oysters are quite sensitive to winter air temperatures, because they live in shallow waters. Those living between tide levels are exposed directly to air temperatures at low tides.

Some species of *Crassostrea* can tolerate repeated freezing and long exposure to freezing. At the Canadian and New England end of its long geographic range, *C. virginica* becomes exposed in the winter to frigid air or to very low water temperatures during low tides. It can withstand freezing near-solid for 4 to 6 weeks (NELSON, 1938, p. 55; KANWISHER, 1955). Although as much as 54 percent of their body fluids become ice at −15°C., the animals survive. Ice masses form between muscle fibers within the adductor muscle. The fibers are pushed aside by ice crystals and clumped into separate bundles. As ice forms the

remainder of the body fluids become richer in NaCl and other electrolytes, and this raises their freezing temperature. Only euryhaline oysters can stand such changes of internal salinity (KANWISHER, 1959).

Crassostrea virginica ranges on North America's east coast farther north than any other species. It reaches the Baie des Chaleurs of the Gulf of St. Lawrence, Canada. *Ostrea equestris* SAY, 1834, ranges poleward only to near the entrance to Chesapeake Bay (37° 37' N, 74° 19' W, 60 fathoms; GALTSOFF & MERRILL, 1962, p. 241). It is the second one as regards poleward range on this coast.

Similar conditions prevail on the northeast coasts of Asia. There, *Crassostrea gigas* (THUNBERG) ranges farther north than any other oyster, including *Ostrea denselamellosa* LISCHKE, 1869, living off Japan and Korea. The former reaches poleward to near the town of DeKastri in Khabarovskiy Kray (Khabarovsk Territory), USSR, and the south end of the narrows Poliv Nevelskogo at 52°N, between the island Sakhalin and the Asian mainland (SKARLATO, 1960, p. 125, fig. 61).

It is evident that poleward limits of the ranges of *Crassostrea virginica* and similar species of this genus are not fixed by their inability as adults to survive extreme winter temperatures. Rather, at their northern range limits, summer temperatures do not suffice for successful propagation.

In contrast, freezing kills the adults of any species of *Ostrea*. The freezing point of seawater, −1.7° C., is the lowest temperature they can tolerate. They die if they become exposed to cold winter air during low tide. *Ostrea edulis* is intertidal only in the frost-free, southern part of its range, but must live at several meters depth in Norway. *Ostrea equestris* lives between tides or just below low tide level at many places in the Gulf of Mexico and off the Carolinas. However, at the north end of its range, off Maryland, it must live at 60 fathoms. Poleward limits of the ranges of *Ostrea* species are the result of the inability of the adults to survive freezing.

SUMMARY

Some species of *Crassostrea* tolerate extreme cold in winter and require quite warm summer temperatures. In other words, they are adapted to a so-called continental climate offshore. In the northern hemisphere such climates are found on the eastern coasts of continents. In contrast, some species of *Ostrea s.s.* require mild winters and can tolerate cool summer temperatures, that is, they are adapted to a more equable climatic regimen. Such climates are found on the western coasts of continents in the northern hemisphere where warm ocean currents tend to equalize the seasons. For these reasons, *Crassostrea* is the better adapted to penetrate poleward on one side of a continent and *Ostrea s.s.* on the other side. In the southern hemisphere, conditions are reversed. In southern Argentina, *Ostrea puelchana* D'ORBIGNY, 1842 (Paléontologie vol., p. 162), reaches poleward to the Golfo San Matías and is the most southerly oyster species found there.

These observations apply only to some species of the two genera. Other species of both genera do not live outside the tropical and subtropical climatic belts. The warm-temperate and cold-temperate climatic belts have only two shallow-water oyster genera, namely *Crassostrea* and *Ostrea;* in addition, the deep-water genus *Neopycnodonte* lives in those belts. Many additional genera are found living offshore in the arid, subtropical, and tropical climatic belts. Very little is known about their geographic distributions and climatic barriers, however. Only one of them, *Hyotissa,* is discussed below (see p. N1040).

SALINITY TOLERANCES

Salinity tolerances and optima can be established by two methods: 1) the more exact method of measuring salinities in experiments or in the vicinity of live animals in their natural environments, and 2) the less exact method of inferring salinities from their biocoenoses using general knowledge of their natural environments. As might be expected, the first method has been applied to only a few commercially important species in scientifically advanced countries. Although inexact, the second method is the more important because it can be applied neatly to both living and extinct species.

Crassostrea seems to be the most euryhaline oyster genus. In *C. virginica* neither
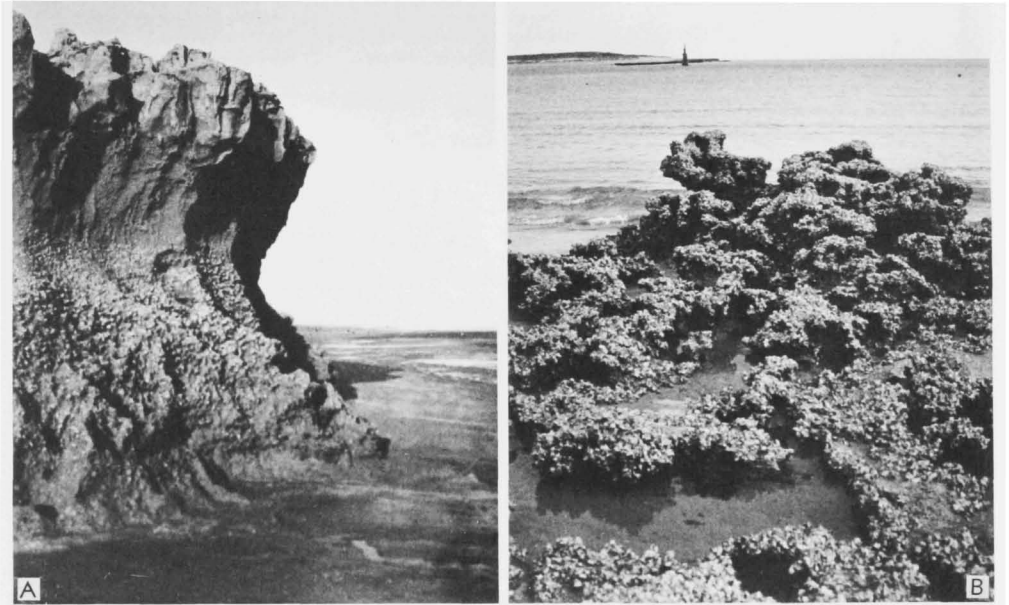
Fig. J50. Incrustations of the rock oyster *Saccostrea cucullata* (von Born, 1778) on eolian rocks facing open Indian Ocean near Port Hedland, Western Australia. Photographs taken at low tide by H. V. Howe.—*A.* Wave-cut cliff.—*B.* Wave-cut platform.

eggs nor functioning spermatozoa develop unless salinity exceeds 7.5‰. Larvae and young adults grow best at 17.5‰ and tolerate 10 to 40‰. Although nearly all oyster reefs of this species grow in brackish waters, some reefs occur in hyperhaline environments near the south end of the Laguna Madre in southern Texas. In general, the species seems not well adapted to euhaline and hyperhaline salinities, however, and at the southern limits of its range, where a hot climate provides elevated salinities in evaporative lagoons, it is replaced by *C. rhizophorae* (Guilding, 1828), the mangrove oyster of Central America and the Caribbean Islands.

In Laguna Rincón near Boqueron, southwestern Puerto Rico, *Crassostrea rhizophorae* is very numerous and reproduces prolifically although salinities are above 35‰ through 11 months of the year. There, salinities are mostly 38‰. The larvae tolerate even 40.5‰ (Mattox, 1949, p. 348).

Ostrea is polyhaline to euhaline and less euryhaline than *Crassostrea*. *Ostrea edulis,* for example, lives in the basin of the Oosterschelde, an abandoned tributary channel of the Schelde River in the Rhine-Maas-Schelde delta in the southwestern Netherlands, where salinities average 27.5‰ (Korringa, 1941, p. 24-32) and drop to 24 or rise to 31‰. However, *O. equestris* Say at Aransas Pass, Texas, lives in salinities that range from 28.3 to 38.4‰. During the drouth years 1950-57 it thrived in Mesquite Bay north of Aransas Pass, Texas, in salinities of 34.6 to 45.3‰ (Hoese, 1960, p. 331). In most situations, *Ostrea* prefers brackish waters of higher salinities than *Crassostrea.*

Saccostrea is restricted to tropical and subtropical waters of normal salinities; measurements of 35.1-35.45‰ are recorded for it at one place (Macnae & Kalk, 1958, p. 3). It is a rock oyster, growing on hard substrata and on mangrove trees. On the east side of Inhaca Island at the entrance to the Bay of Lourenço Marques, or Delagoa Bay, Mozambique, Portuguese East Africa, *S. cucullata* (von Born, 1778) grows in profusion on sea cliffs exposed to the open Indian Ocean; there too, the waters must be euhaline.
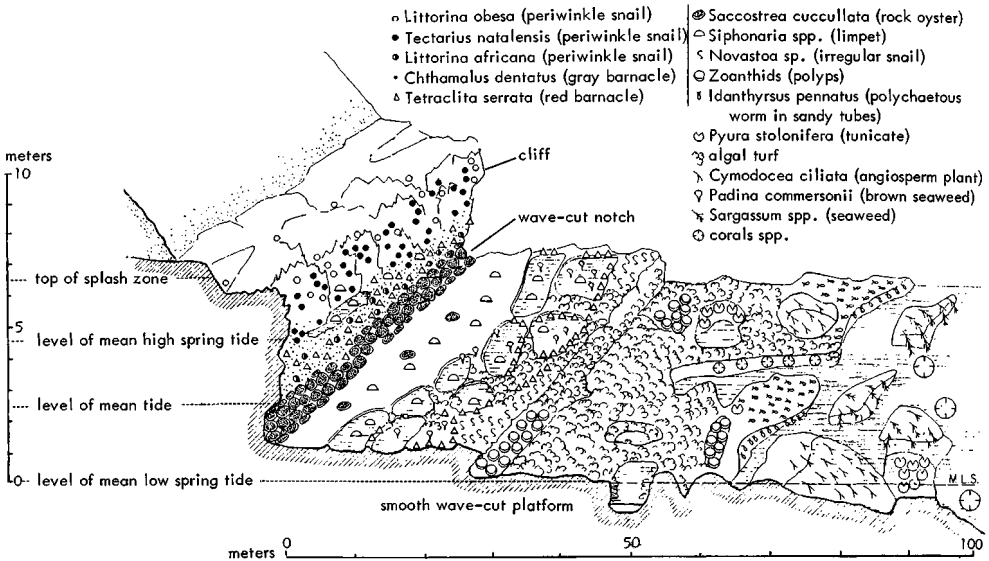
Striostrea appears to live in euhaline

FIG. J51. Intertidal rock-incrusting oyster *Saccostrea cuccullata* (BORN, 1778) on sea cliffs at north end of Inhaca Island, Mozambique, fronting on subtropical Indian ocean and fully exposed to strong wave action, as seen at low water of spring tides, vertical exaggeration, ×2.4 (after Macnae & Kalk, 1958).

waters. Salinities of 33.2-35.0‰ are recorded for *S. margaritacea* (LAMARCK, 1819) at one place (KORRINGA, 1956, pl. 10). It thrives at such salinities at the mouths of the Knysna River and Svartvlei Lagoon alongside the Indian Ocean, Republic of South Africa.

The genus *Hyotissa* is strictly euhaline. Exceedingly few salinity measurements have been made, however. On the west side of Inhaca Island it lives near reef corals, and a salinity of 35.45‰ has been recorded there (MACNAE & KALK, 1958, p. 3, 129). Among the Cocos-Keeling Islands in the Indian Ocean, *Hyotissa,* growing to enormous size, has been found living at depths of 0.6 to 6.0 meters on fine lime sand among coral heads and slabs on the reefs (VIRGINIA ORR, personal communication, September, 1963). On Australian coral reefs, it grows submerged just below low spring tide level (THOMSON, 1954, p. 162). Considering its common association with colonial corals there is no doubt that it is a euhaline, warm-water genus. The extinct species of the genus in Tertiary deposits and their fossil associates fully confirm these conclusions. Fossil remains of this genus, so easily identified, are quite valu-

able indicators of warm euhaline environments.

The other living genus of the Pycnodonteinae, *Neopycnodonte,* has a nearly worldwide distribution. It lives in deeper waters and mostly far removed from land. At all places where it has been dredged from the sea bottom it must have been living in oceanic euhaline waters.

Therefore, all living Pycnodonteinae appear restricted to oceanic euhaline waters. This conclusion applies also to the great number of extinct species of the family Gryphaeidae. All of them are found in sediments and in company of faunas that indicate open euhaline seas. Not a single case is known where the association of fossils and sediments indicates brackish water environments for the Gryphaeidae.

SALINITY BARRIERS

Limits of salinity tolerances of a given species serve as salinity barriers to its geographic spread. There are two kinds of barriers: 1) elevated salinities, and 2) lower salinities. The former may be produced by evaporation of sea water along arid coasts or they may consist of merely a

lack of brackish water lagoons and estuaries along the coast. Lowered salinities are produced by the influx of fresh waters from rivers.

ELEVATED-SALINITY BARRIERS

Highly elevated salinities arise wherever high evaporation overbalances influx of fresh river water and precipitation of rainwater. In shallow coastal regions and in bays or lagoons with restricted inlets, water currents are often inadequate to fully replenish the evaporated sea water. Then aridity barriers arise. Such areas lie in desert climates and may form unbridgeable barriers to the spread of shallow-water oyster species not adapted to elevated salinities.

The best example is *Ostrea edulis*. Its southernmost known occurrence (LECOINTRE, 1952, p. 39) is off Cape Rhir (or Ghir), 30° 40′ N, near Agadir on the Atlantic coast of Morocco, where it was dredged from a depth of 80 m. This place marks the southernmost place of its geographic range, because here the arid coast on the west flank of the Sahara is highly evaporative and lacks fresh-water streams. South of this aridity barrier many different oyster species and genera thrive on the tropical West African coast.

Another kind of elevated-salinity barrier seems to be responsible for the southern limit to the geographic range of *Crassostrea virginica*. It is not so much an aridity barrier as it is a lack of extensive brackish waters.

South of Yucatan *Crassostrea virginica* is replaced by *C. rhizophorae*. South of the Yucatan Peninsula no large rivers drain from the Central American land bridge into the Caribbean Sea, so that local brackish water environments are rare and occupy only small areas. Because of this lack of suitable brackish habitats the larvae of this species perhaps have difficulties in spreading southward from North America to South America.

On the other hand, *Ostrea equestris*, being adapted to higher salinities, has no such difficulties. It has been able to spread along the east coasts of the Americas from Maryland to the Golfo de San Matías, Argentina.
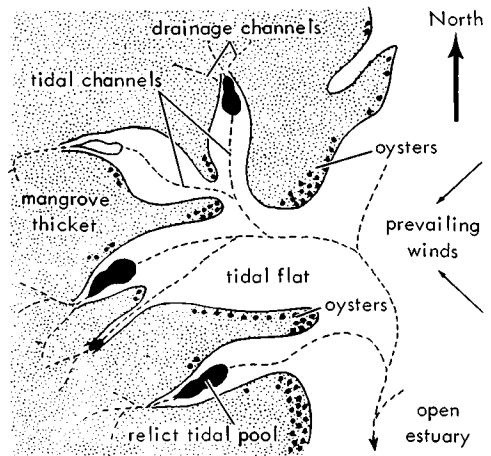

FIG. J52. Diagrammatic map of Mida Creek estuary on tropical coast of Kenya, East Africa, showing distribution of mangrove oyster *Saccostrea cuccullata* (BORN) attached to stilts of mangrove bushes (*Rhizophora mucronata*) (Someren & Whitehead).

INCRUSTATIONS AND REEFS

Incrustations are oysters attached to rocks, cliffs, or mangrove stems and root stilts. These oysters apparently do not accumulate to form thick layers. Only euhaline intertidal species make incrustations.

Reefs are natural accumulations of oyster shells, dead or alive, that rise above the general level of the substratum they are built on. Only coastal brackish-water species form reefs.

ROCK INCRUSTATIONS

Intertidal rock-incrusting oysters live in an extremely severe environment, because low tides expose the animals to air and direct sunlight leading to desiccation, interrupted feeding, and excessive temperatures. During low tides the shells must remain tightly closed. In cold-temperate climates only *Crassostrea* is able to stand this environment with its freezing temperature (see p. N1037).

In tropical and subtropical climates only two genera are known to be living in this sort of environment, namely *Saccostrea* and *Striostrea*. The former, represented by the living superspecies *S. cuccullata* (VON BORN, 1778), preferentially grows on rocks and cliffs and is called the rock oyster (Fig.
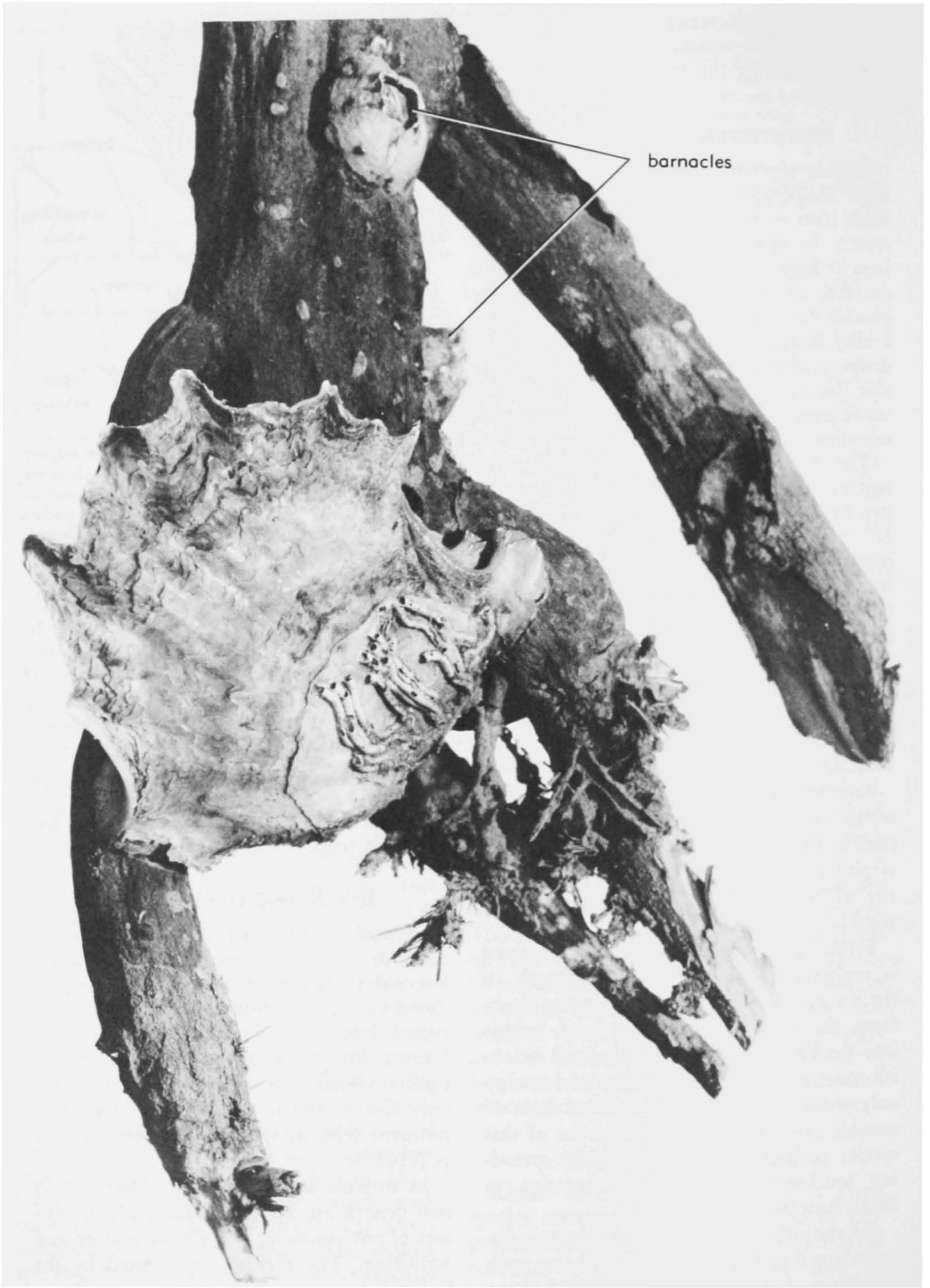
Bivalvia—Oysters

barnacles

FIG. J53. A mangrove oyster *Crassostrea virginica* (GMELIN, 1791) growing in crotch of mangrove stilt, near Comalcalco, State of Tabasco, Mexico, ×1.4 (Stenzel, n. Specimen donated by J. D. STOEN).
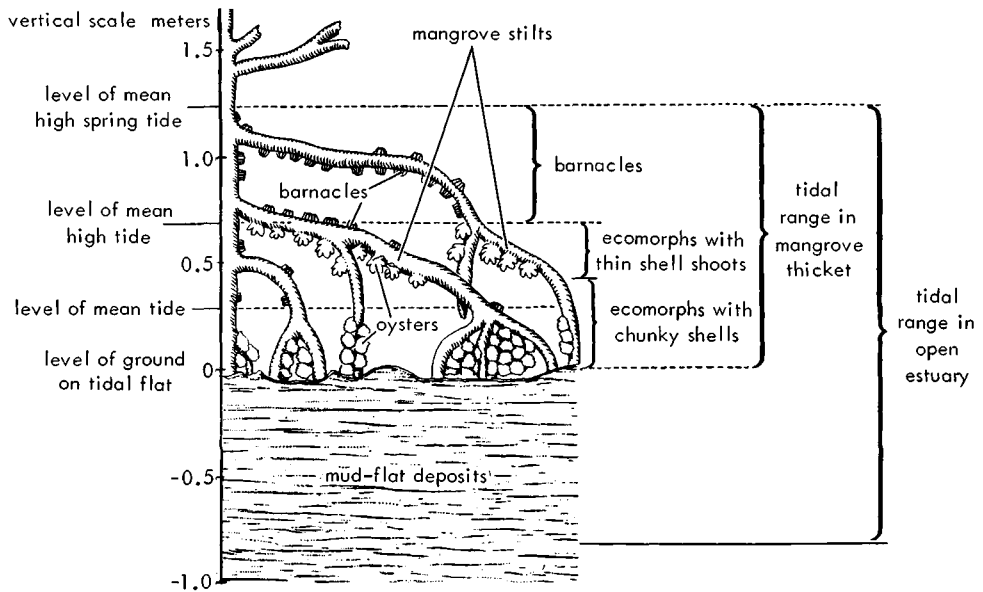
Fig. J54. Vertical zonation of mangrove oyster *Saccostrea cucullata* (Born) incrusting mangrove stilts in Mida Creek estuary on tropical coast of Kenya, East Africa (Someren & Whitehead).

J50). It grows intertidally just above the upper limit of seaweed cover and below the splash belt occupied by littorinid snails and certain barnacles. Where they are exposed to heavy wave action the oysters occupy a belt 1 meter across, just above the wave-cut rock platform at the base of the cliff (Fig. J50). Where wave action is less strong, the oysters are not limited to such a narrow belt. They grow at various levels below the splash belt occupied by littorinid snails down to mean low spring-tide level (Fig. J51). These incrustations do not differ greatly from those on mangrove where wave action is even weaker.

Exposure to air, sunshine, and sea water bleaches and corrodes the outside of the shells, even while the animals are alive; strong wave action breaks off all protruding delicate growth imbrications and shell-shoots or prevents them from forming. Corrosion and corrasion are very active and dead shells disappear quickly.

MANGROVE OYSTERS

Mangrove trees and bushes grow in much exposed places, and the plants are sensitive to freezes so that they are restricted to frost-free, tropical and subtropical climates, although their distribution is circumglobal. They grow on shallow, intertidal, protected mudflats wherever wave action is minimal. The tangle of stems and stilt roots slows down waves and currents. Therefore, mangrove-covered shores are the sites of deposition of muds. The muds are very dark and rich in organic matter derived from animals and plants. The muds produce hydrogen sulfide gas.

Salinity in the mangrove swamps tends to be 36-38‰ in those parts where oysters grow. Most mangrove swamps have little river water entering them and have high evaporation rates so that salinity can rise to 40-42‰ during dry seasons. Water temperatures are around 31-34° C. in the hot season and 20-30° C. during the cooler, rainy season.

Oysters incrust the mangrove stems and stilt roots only in a narrow band up to 4 m. wide at the edges of the swamps facing open water of tidal channels or of the center of the lagoon (Someren & Whitehead, 1961, p. 9). Edges of swamps facing prevailing winds have more oyster incrustations than the more protected edges. Oys-
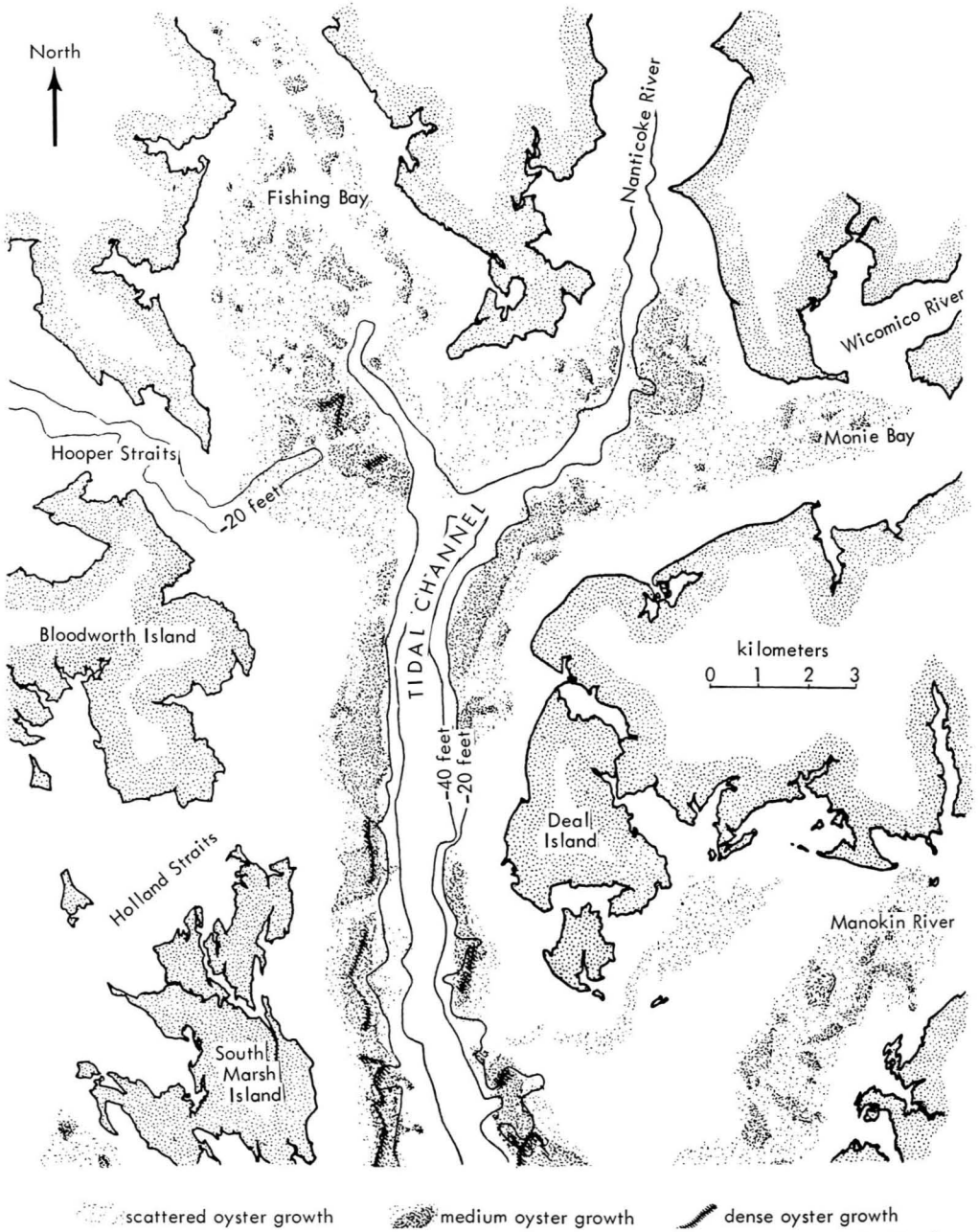
FIG. J55. Fringe reefs of *Crassostrea virginica* on the shoulders at margins of tidal channels in Tangier Sound on east side of Chesapeake Bay, Maryland, USA. Surveyed in September, 1878. From data given by WINSLOW (Winslow, 1882).

ters are absent in the centers of the swamps (Fig. J52; see Fig. J54).

Mud is the reason for these distributions of oyster incrustations. Wherever wave ac-

tion is feeble, mud settles out on the mangrove, and oyster larvae avoid settling on mud-covered substrata. For the same reason oysters tend to colonize the undersur-

faces of inclined mangrove stems rather than their top surfaces. The crotch on the underside of tripod-like mangrove stilts is commonly free of mud and is the favorite place for oysters to grow on (Fig. J53).

Incrustations are restricted to between tides. Below low tide level the oysters remain covered by water continuously and therefore, remain exposed to such predators as crabs and fish continuously. These predators are so numerous that they eliminate all young and thin-shelled oysters. Above average high-tide level oysters become exposed to air and sunshine too long to survive; only barnacles can survive there. Periodic exposure of the intertidal oysters to air and sunshine has a strong influence on their growth habits. Oysters do not grow on mud bottoms except where such firm and not mud-covered substrata as gastropod shells are available.

Many different oyster genera have invaded the mangrove biotope: *Crassostrea* through *C. rhizophorae* (GUILDING, 1828) in the Caribbean and West Indies; *Lopha* through *L. folium* ecomorph *cristagalli* (LINNÉ, 1758) in the region from the Indian Ocean to southwestern Japan; and *Saccostrea* through *S. cuccullata* (VON BORN, 1778) and its subspecies in tropical West Africa and East Africa to Honshu, Japan. The situation is indicative of multiple, noncontemporaneous, separate invasions, each by a different genus, and the last invasion probably was by *Crassostrea*.

The various mangrove oysters have several ecomorphic features in common. They tend to be thin-shelled and fragile. They tend to produce thin fragile scalelike shell imbrications or shell shoots and delicate protruding frills (Fig. J53, J54). There is a tendency to clasping shell extensions, which become auxiliary holdfasts. Many of the mangrove oysters have xenomorphic sculpture.

The delicate and thin-shelled features are caused by scarcity of free calcium ions and by abundance of planktonic food in these waters. Shell growth must be rapid, but material to build shell walls is scarce. In addition, the oysters must shut their valves during low tide for some time. During this period their blood tends to become more acid and must be buffered. This is done

FIG. J56. Dagger Reef in San Antonio Bay, Texas, a string reef built by *Crassostrea virginica*. Photograph by courtesy of R. M. NORRIS, Univ. of California at Santa Barbara, Calif.

by some of the calcium carbonate of the shell. In other words, during low tide the shell wall not only quits increasing in thickness but must lose thickness. Because wave action is minimal in mangrove swamps, delicate and thin-shelled features remain undamaged and are not greatly disadvantageous to the animal. In fact, they may be advantageous in keeping enemies at a distance.

REEFS

On the basis of their configurations and the independence of the configurations from the nearest shore line, reefs are classified as fringe, string, and patch reefs. As to their configuration, fringe reefs are the least and patch reefs the most independent from the nearest shore line.

FRINGE REEFS

Fringe reefs are adjacent to the shore. They are common features along the finger-like branches of estuaries, that is, in drowned river valleys and their drowned tributaries. In most of them there is a tidal channel along the axis of the estuary. The axial channel increases downstream in depth from 3 to 30 m. or more and in width from 370 to 750 m. or more. Tidal scour excavates the axial channel and keeps it deep and free of oysters and sediments. At its sides the axial channel is flanked by fringe reefs. Their surface slopes gently
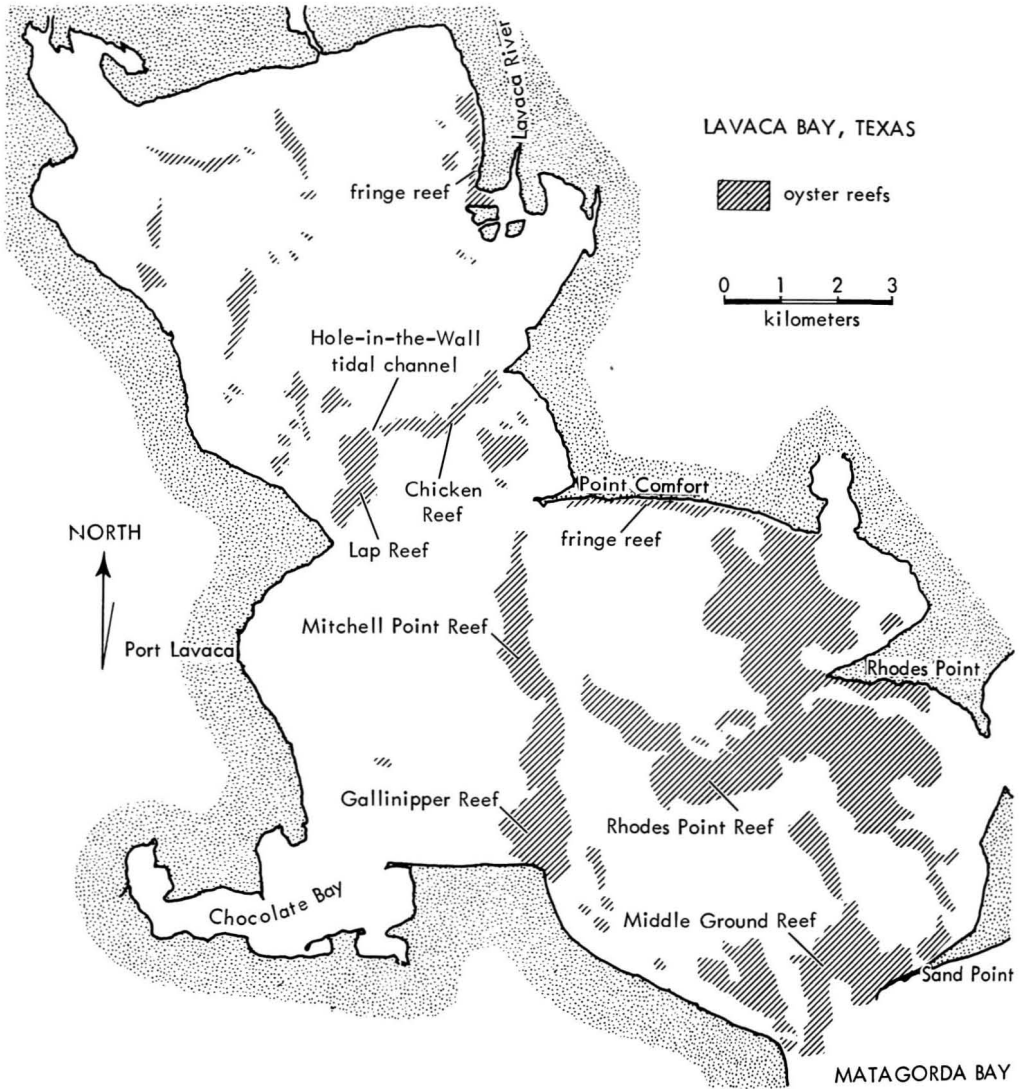
LAVACA BAY, TEXAS

oyster reefs

0 1 2 3
kilometers

fringe reef

Lavaca River

Hole-in-the-Wall
tidal channel

Chicken
Reef

Point Comfort

Lap Reef

fringe reef

NORTH

Port Lavaca

Mitchell Point Reef

Rhodes Point

Gallinipper Reef

Rhodes Point Reef

Chocolate Bay

Middle Ground Reef

Sand Point

MATAGORDA BAY

Fig. J57. String reefs and fringe reefs in Lavaca Bay, Texas, composed of *Crassostrea virginica* (Moore & Danglade, 1915).

from the shore toward the shoulder alongside the channel. The densest oyster populations are on the shoulders close (275-650 m.) to the edge of the channel (Fig. J55).

The fastest tidal currents are in the channels. As the water spreads during a rising tide from the channel over the adjacent shoulder it must slow down very much. Where it slows down most of the planktonic oyster larvae drop down and settle out, giving rise to the fringe reefs.

STRING REEFS

String reefs have fairly narrow crests, which may become exposed for a width of 10 m. when the tide is low. Crests are straight or curved as garlands. Many are arranged in an en echelon series maintaining nevertheless a straight alignment. Others are more loosely arranged and form various odd-shaped islands at low tide.

A straight series of crests is Panther Reef in San Antonio Bay, Texas, which is 10 km.
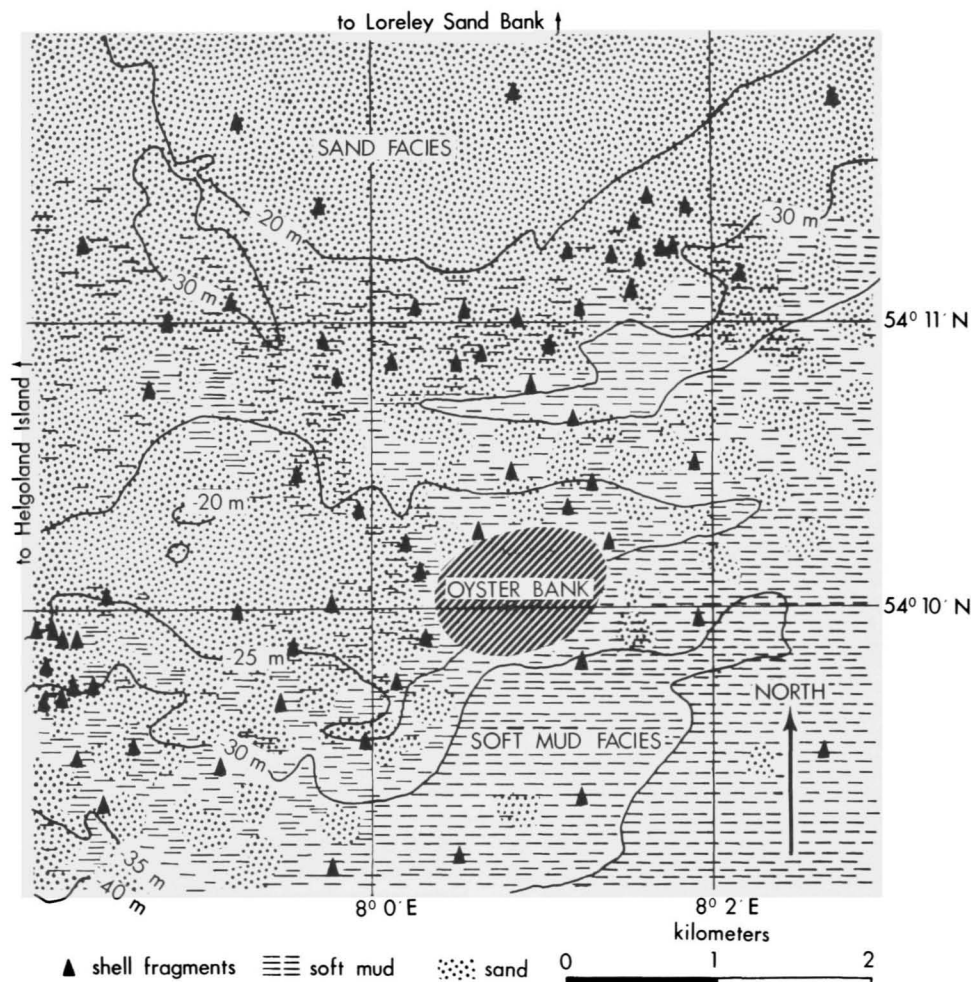
FIG. J58. Patch reef of Helgoland in the North Sea, composed chiefly of *Ostrea edulis*. (From data given by Caspers, 1950.)

long and originates at Panther Point on the bayward side of Matagorda Island. Tidal channels separate several looped crests called Long Reef, Halfmoon Reef, Grass Island Reef, and Pier Reef. They form a string reef 12 km. long across Aransas Bay from St. Joseph's Island to Lamar Peninsula on the Texas mainland. The longest string reef known is nearly 42 km. long in a straight line and forms a discontinuous barrier separating Atchafalaya and East Côte Blanche Bays on the Louisiana shore from the open Gulf of Mexico. All these were built by *Crassostrea virginica* (Fig. J56).

No true string reef is built by euhaline oysters. String reefs are found only in brackish lagoons or as barriers between sea and brackish bays.

Most string reefs are at right angles to the nearest shore, as first noted by GRAVE (1901). Actually, the string reefs are normal to the direction of tidal currents. These in turn are guided by the shape of the lagoon and the placement of the passes to the open sea. Lagoons that are long and straight and have straight shores on both flanks tend to establish regular tidal currents parallel to the long flanks. In such situations string reefs develop best and be-

come arranged at right angles to the nearest shore. Many of them become partial barriers across the lagoon. Good examples are string reefs in the lagoons along the Texas coast (Fig. J57).

PATCH REEFS

Patch reefs grow far from shore and have irregular but fairly compact outlines. Their sizes and locations depend mainly on availability of an appropriate substratum.

A good example is Helgoland Oyster Bank in the German Bight of the North Sea about 15 km. east of Helgoland Island and 50 km. from the nearest mainland shore. It covers an area of 800,000 sq. m.; its larger east-west axis is 1,150 m. and its north-south axis 750 m. long (CASPERS, 1950). The reef is 23-28 m. below sea level and is built almost exclusively by *Ostrea edulis* LINNÉ. The reef is now much depleted by over-fishing but nevertheless has about 1.5 million full-grown and half-grown oysters (Fig. J58). ZENKEVITCH (1963, p. 449) reports 14 million oysters on the Gudaut bank of the east coast of the Black Sea.

The distribution of sedimentary facies and biocoenoses around Helgoland Oyster Bank is characteristic for oyster banks of nearshore oysters, and generalizations of the local situation are in order. At the north is Loreley sand bank, less than 10 m. below sea level, composed of coarse sand and gravel. The sand bank is all that is left of a former island.

Sea bottom slopes gently from the sand bank southward and the bottom sediments become successively finer grained. Thus the bottom sediments are arranged in successive facies belts surrounding the sand bank. The oyster bank is at the deeper, down-slope end of the sand facies. Farther down the slope the bottom sediments consist of soft muds.

These muds are too soft for oyster larvae to find a suitable substratum for attachment. In contrast, the oyster bank sits on firm sand mixed with soft mud, mollusk shells, and their fragments.

On the muds south of the oyster bank the oysters are replaced by the mussel *Mytilus edulis* LINNÉ, because the mytilid mussels have a competitive advantage over oysters on a soft mud bottom, because they can attach themselves by many separate byssus threads anchored all around on seaweeds and other objects. Vice versa, oysters have the advantage wherever the substratum is firm and has shells or shell debris for the oyster larvae to settle on (ZENKEVITCH, 1963, p. 442).

Up the slope the oysters are replaced by other, unattached bivalves most of which are forms that plow through or dig in the sand. Many of them are venerids. They have a competitive advantage over oysters because they can adjust to shifting sands, whereas oysters must have a stable and firm substratum. Thus oysters are confined to a specified facies belt, where waves and currents are too weak to induce shifting of the sands and too strong to let muds accumulate. This belt must be a fair distance away from shore and down the sea-bottom slope.

Salinities there stay below 34‰ because of the slightly brackish western European Continental Coastal Water Current. The current is high in nutrients and turbidity, follows the coast northward and northeastward, and originates from the influx of many large rivers in Belgium, The Netherlands, and West Germany.

PHYLOGENY

CONTENTS

BEGINNINGS

ALLEGED OYSTERS FROM PALEOZOIC

No Paleozoic fossils are known today that are definitely identified as remains of oysters or that can be shown to be their direct ancestors. In the past, however, several authors have described remains claimed by them to be oysters or ancestors of oysters. The following list, possibly not complete, enumerates them (Fig. J59).

Ostrea costata STEININGER, 1831, from Eifel Mts., W. Europe. Description inadequate, no illustration (see STEININGER, 1834, p. 366).

Ostrea matercula DE VERNEUIL, 1845, from Magnesian Limestone (Perm.) near Itchalki on the banks of Pyana River, Gorkiy (formerly Gouvernement Nishniy Novgorod), Russian Soviet Federated Socialist Republic (VERNEUIL, 1845, p. 330-331, pl. 21, fig. 13a-c; NECHAEV, 1894, p. 188, pl. 7, fig. 1-2). This enigmatic form is now placed questionably in *Annuliconcha* NEWELL, 1937, family Aviculopectinidae, Pectinacea.

Ostrea nobilissima DE KONINCK, 1851, from Visé Limestone (Visean), at Visé, Belgium. First, DE KONINCK (1851, p. 680, pl. 57, fig. 10) described it as *Ostrea,* but later (DE KONINCK, 1885, p. 201-202, pl. 40, fig. 1-5) he made it the type species of *Pachypteria* DE KONINCK, 1885, family Aviculidae.

Pachypteria has also been found in Carboniferous limestones of Derbyshire and Yorkshire, Eng-
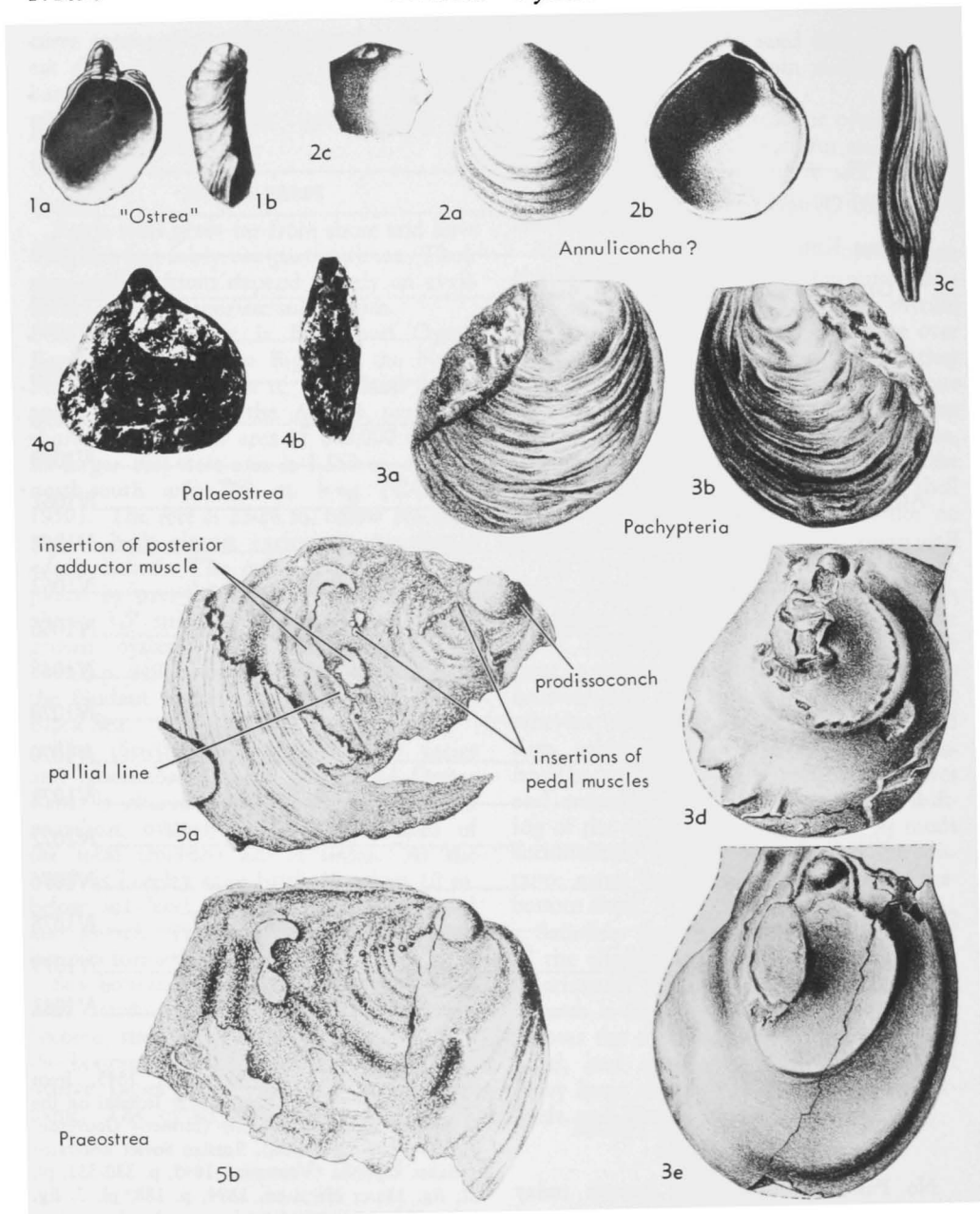
FIG. J59. Alleged oysters from the Paleozoic.

1. "*Ostrea*" *patercula* WINCHELL, 1865, from sandstone at base of Burlington Ls., Miss., at Burlington, Iowa, USA; *1a,b,* inside and ?posterior or ?anterior views. (Original of figure by courtesy of L. B. KELLUM, Museum of Paleontology, Univ. Michigan.)

2. *Annuliconcha? matercula* (DE VERNEUIL, 1845) from Magnesian Ls., Perm., of P'yana River, Gorkiy, USSR; *2a-c,* lower valve, outside and inside views; valve of young specimen (de Verneuil, 1845).

3. *Pachypteria nobilissima* (DE KONINCK, 1851) from Visé Ls., L.Carb.(Visean), at Visé, Belg. (*3a-e*) (de Koninck, 1885).

4. *Palaeostrea sinica* GRABAU, 1936, from Maping Ls., Perm., of Kwangsi, China (*4a,b*) (Grabau, 1936).

5. *Praeostrea bohemica* BARRANDE, 1881, from Kopanina F., U.Sil., of Jinonice-Butovice, Hájek, Bohemia, Czech.; *5a,b,* internal molds of RV (Kříž, 1966).

land. A second species, *P. ostreiformis* MAILLEUX, was described from the Frasnian of Belgium and a third species *P. gevini* TERMIER & TERMIER, 1949, from yellow sandy marls (late Visean) of Kerb en Neggar, 65 km. NW. of Aouinet Legra in the western Sahara. The genus was discussed by GEVIN (1947), DECHASEAUX (1948), and TERMIER & TERMIER (1949). The TERMIERS placed it in the Pseudomonotinae. The Saharan species has a small attachment area on the right umbo; the valves are mostly equivalve, but one of the left valves collected has greater inflation; the hinge is rectilinear and lacks teeth, has a depressed resilifer at the anterior end, and the single muscle insertion is subcentral; radial ribs and two auricles are present in the young. Although this animal was attached, it cannot be classed with the Ostreidae according to DECHASEAUX and hardly can be an ancestor. Such similarities between *Ostrea* and *Pachypteria* as are visible must be convergence features caused by attachment. According to NEWELL (personal communication, 1963), *Pachypteria* is a junior synonym of *Pseudomonotis* BEYRICH, 1862, family Aviculopectinidae, Pectinacea (see p. N342). It is attached by its right valve and has an aragonitic shell; it is unlikely that it is an ancestor of oysters.

Ostrea patercula WINCHELL, 1865, from sandstone at base of Burlington Limestone (Miss.) at Burlington, southeastern Iowa (Fig. J59,*1*). Described by WINCHELL (1865, p. 124) and figured by WHITE (1884, p. 288, pl. 34, fig. 1-2). Possibilities of contamination were good at Burlington, which was at the time a major Mississippi River port and railroad terminal (letter from B. F. GLENISTER, February, 1962). Figure and description are insufficient to recognize this form with certainty as a mollusk, let alone to place it in the Ostreidae. The type was deposited at the University of Michigan, but cannot be found today (letter from L. W. KELLUM, February, 1963).

Ostrea prisca HOENINGHAUS, 1829, from Visé, Belgium. This is a *nomen nudum* in both publications (1829, p. 14; 1830, p. 237).

Palaeostrea sinica GRABAU, 1936, from Maping Limestone (Perm.) of Kwangsi, China. GRABAU (1936, p. 284-286, pl. 28, fig. 1) claimed that this fossil shell cannot be distinguished from a Mesozoic oyster and made the separation purely on a stratigraphic basis. No information on the muscle imprint was given and the material at hand consisted of a single valve resting on rock matrix and a fragment of the umbonal part of another fossil (Fig. J59,*4*). It appears to be wholly unidentifiable. This species is the type species of *Palaeostrea* GRABAU, 1936, by original designation.

Praeostrea bohemica BARRANDE, 1881, and *P. bohemica* var. *simplex* BARRANDE, 1881, from Late Silurian (Kopanina Formation) of Karlstejn (formerly Karlstein), southwest of Praha, and Lochkov and Dlauba Hora, Bohemia, Czechoslovakia. BARRANDE (1881a, p. 147, pl. 3, fig. 1-2,

and pl. 3, fig. 3-4, respectively; 1881b, p. 233-234) (Fig. J59,*5*). The type species is *P. bohemica* by monotypy, because *simplex* was regarded merely as a variety by BARRANDE. JIŘI KŘÍŽ of the Charles University, Praha, recently monographed the genus (KŘÍŽ, 1966). According to him, the genus is the only one classed in the Praeostreidae KŘÍŽ (1966) and assignable to the superfamily Mytilacea RAFINESQUE (1815). This Silurian-Lower Devonian form cannot be considered as an ancestor of the oysters.

EARLIEST KNOWN FOSSIL OYSTERS

The most ancient fossils known today that are undoubtedly oysters are Carnian (Late Triassic).

Before 1880, several authors had described bivalves from earlier (Middle Triassic) beds which they, following general practice, claimed were oysters and described as *Ostrea* or *Ostracites*. For example, GOLDFUSS (pt. 2, p. 1833-44) figured 10 species from the Muschelkalk (M.Trias.) of Germany as *Ostrea* and ROEMER (1851, p. 312, pl. 36, fig. 19) described *Ostrea willebadessensis* as a new species from an oolitic limestone layer of the upper Muschelkalk (Ladin.) quarried on the road from Cloister Willebadessen to Altenheerse, about 3 km. south of the town of Driburg on the southeastern foothills of the Teutoburger Wald, State of Nordrhein-Westfalen, West Germany.

Later studies of various supposed oysters from the Muschelkalk of Germany, however, led to the realization that these supposed oysters were attached by their right valves, rather than by left. The first one to emphasize this observation and to conclude that these bivalves could not be true oysters was NOETLING (1880, p. 321-322). His stand has found approval by many authors since 1880 (PHILIPPI, 1898, p. 617; WAAGEN, 1907, p. 172-175; COX, 1924, p. 65-66) and is generally accepted today.

These observations led BITTNER (1901, p. 72) to propose the genus *Enantiostreon*, and many Mid-Triassic bivalves which had been called oysters before were transferred to it. SCHMIDT (1928) reviewed the entire fauna of the Muschelkalk of Germany and regarded *Ostrea willebadessensis* ROEMER (1851) as one of the many variants of *E. difforme* (VON SCHLOTHEIM, 1820). He
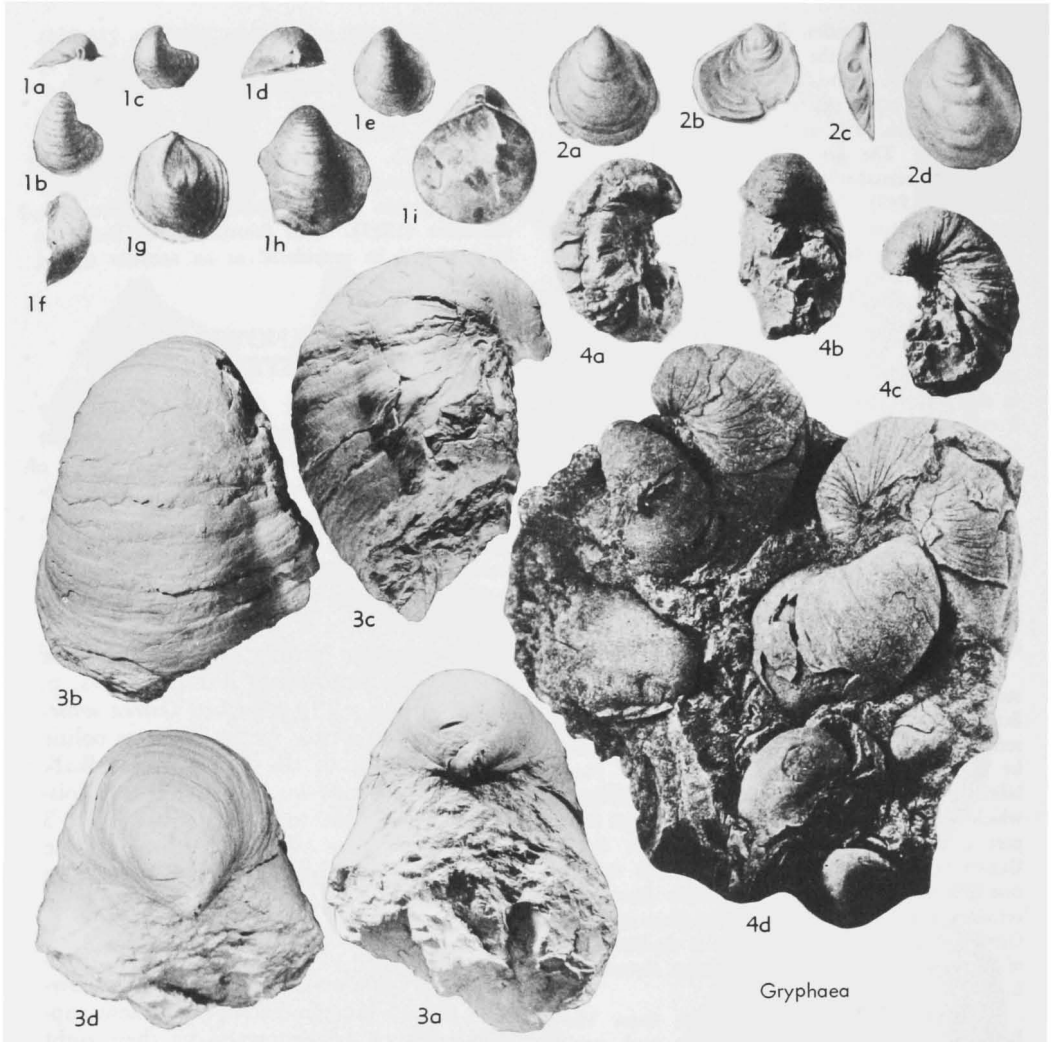
FIG. J60. Earliest fossil oysters known; *Gryphaea* from Triassic sea of Arctic.

1. *G. keilhaui* Böhm, 1904, *Myophoria* Sandstone, Carn., Bjørnøya Island; *1a-i,* ×1 (Böhm, 1904).
2. *G. skuld* Böhm, 1904, *Myophoria* Sandstone, Carn., Bjørnøya Island; *2a-d,* ×1 (Böhm, 1904).
3. *G. chakii* McLearn, 1937, Pardonet Formation, Carn.-Nor., Sikanni Creek, B.C., Canada; *3a-d,*

×1 (Stenzel, n. Specimen by courtesy of Shell Oil Company of Canada, Ltd.).
4. *G. arcuataeformis* Kiparisova, 1936, Carn., Korkodon River, far eastern Siberia; *4a-d,* ×1 (Kiparisova, 1938).

placed the 10 supposed oysters described by Goldfuss from the Muschelkalk in the following genera: *Enantiostreon* Bittner, 1901, family Terquemiidae; *Placunopsis* Morris & Lycett, 1853, ?Terquemiidae; and *Pseudomonotis* von Beyrich, 1862 [=*Prospondylus* Zimmerman, 1886], Pseudomonotidae. To these one might add *Atreta* Étallon, 1862 [=*Dimyopsis* Bittner, 1895], Plicatulidae.

Plicatulidae and Spondylidae living today are attached by their right sides, but have strong interlocking hinge teeth. On the other hand *Enantiostreon, Placunopsis, Pseudomonotis,* and *Atreta* are devoid of interlocking teeth although they are attached by their right valves as determined by the position of the adductor muscle insertions.

The removal of the various Mid-Triassic

bivalve species from true oysters to other families has left only a few species that, for lack of incisive investigation, are still carried as *"Ostrea"* by some authors. In short, no bivalves are known from Mid-Triassic or older beds that can be demonstrated to have been attached by their left valves and can be assigned to the oysters with complete certainty.

However, NAKAZAWA & NEWELL (1868) have described two species of bivalves from the Permian of Japan which they place confidently in the family Ostreidae and questionably in the genus *Lopha sensu latissimo*. Unfortunately, the specimens available are too poorly preserved to allow one to distinguish the right from the left valves with complete confidence. Thus their generic and even their familial taxonomic positions are uncertain.

Only three oyster genera are known from the Upper Triassic. However, not all of them are closely related to each other and thus they prove that even before Late Triassic time oysters had attained considerable evolutionary divergence and that we have not yet discovered any fossil remains representing the very earliest oysters and the missing ancestors that were the links connecting the Late Triassic genera. Or, the Late Triassic oysters are really not so closely related, because they are polyphyletic, and the differences between the Late Triassic genera are rather the consequences of their polyphyletic origins rather than the results of evolutionary divergence from a common ancestor.

GRYPHAEA LAMARCK, 1801

The various species from Triassic deposits described as *Gryphaea* and examined independently and repeatedly by several authors have diagnostic generic features of *Gryphaea* and are quite correctly placed in this genus (Fig. J60). One of them, namely *G. arcutaeformis* KIPARISOVA (1936), is quite similar to *G. arcuata* LAMARCK (1801), type species of the genus, as was pointed out by KIPARISOVA (1936, p. 100-102, 123-125, pl. 4, fig. 1-2, 4, 6-10; 1938, p. 4, 33-34, 38, 46, pl. 7, fig. 17-21, pl. 8, fig. 1-2, 11) and affirmed by VYALOV (1946).

Triassic species of *Gryphaea* have been found at the following places, arranged from east to west. ——1) Kolyma River drainage basin in Magadan-

skaya Oblast [Province], far eastern Siberia, USSR. Described by KIPARISOVA (1936, 1938) and VYALOV (1946).——2) Bjørnøya [Bear Island], south of Svalbard [Spitsbergen], Norway. Here Triassic gryphaeas were discovered for the first time (BÖHM, 1904).——3) Ellesmere Island, Arctic Canada (KITTL, 1907; TROELSEN, 1950; TOZER, 1961; TOZER & THORSTEINSSON, 1964).——4) Borden and Prince Patrick Islands, Queen Elizabeth Islands, Arctic Canada (TOZER, 1961; TOZER & THORSTEINSSON, 1964).——5) Rocky Mountain foothills along the Peace and Pine Rivers, east-central British Columbia (McLEARN, 1937; WESTERMANN, 1962) and the region of the Sikanni Chief River, B.C., Canada (McLEARN, 1946; 1947).——6) Cedar Mts. in east corner of Mineral County, west-central Nevada, USA. Here S. W. MULLER discovered *Gryphaea* in the Luning Formation (Carn.).——7) Gammaniura in the mountain group of the Monte Judica, about 40 km. west of Catania, eastern Sicily. Several species of *Gryphaea* have been described by SCALIA (1912) from an oolitic limestone exposed there. Although the species as described by SCALIA are mostly ill-founded, there is little room for doubt that the genus is correct. No one seems to have investigated this locality since 1912. The rock may be part of the autochthonous Mufara Formation (U.Trias.) or part of the Lavanche Olistostrome, a chaotic allochthonous sheet of blocks which are Cretaceous to early Miocene in age (letter from Paolo Schmidt de Friedberg of Novara, March 17, 1964). The supposed Triassic age of the gryphaeas may be erroneous.

Most of the Triassic gryphaeas have a circumpolar distribution and are from the Triassic sea that occupied the Arctic region. Localities in British Columbia and Nevada are from deposits in oceanic passages connecting at the north with the Triassic Arctic realm. The Sicilian locality must be set aside as dubious until it has been reinvestigated.

It is probably a safe conclusion that the Triassic home and place of origin of *Gryphaea* was the sea that during Late Triassic time occupied the Arctic region and the seaways that opened into it. The genus first showed up during the Carnian.

LIOSTREA DOUVILLÉ, 1904

Small, smooth oysters that probably are representatives of *Liostrea* have been found in many places in Rhaetian deposits (Zone of *Rhaetavicula contorta* (PORTLOCK, 1843)) of Europe. Such an oyster has been reported from the upper part of the Sully Beds (L.Rhaet.) at Cadoxton, Glamorganshire, southern Wales. It has been inadequately described and only a single view of one broken valve was figured as *"Ostrea*
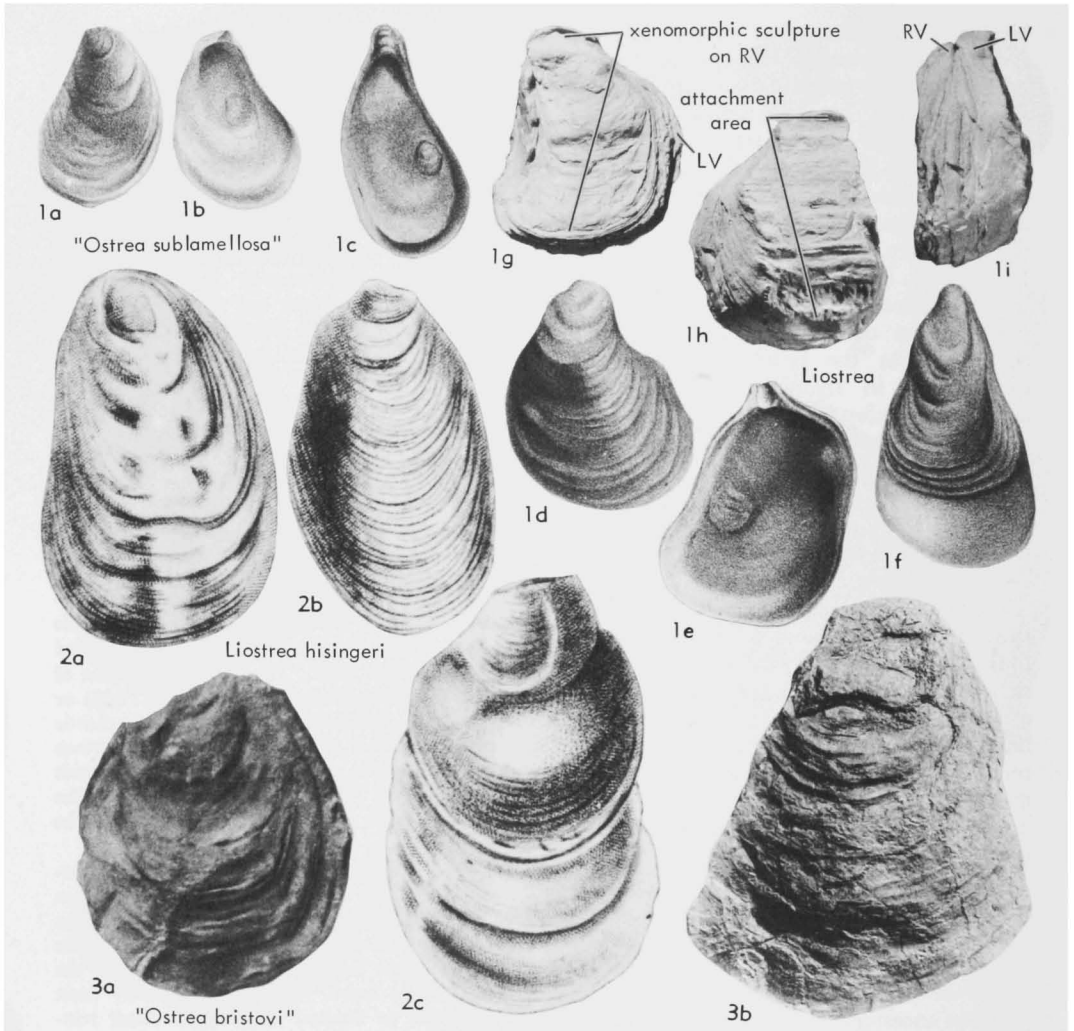
FIG. J61. Earliest fossil oysters known: Triassic-Liassic *Liostrea hisingeri* (NILSSON, 1832) from northwest Europe.

1. *"Ostrea sublamellosa"* DUNKER, 1846, Lias., Germany (West).—*1a-f*. Specimens from vicinity of Halberstadt, ×1 (Dunker, 1846).—*1g-i*. Specimens from vicinity of Hildesheim, Hettang., Zone of *Scamnoceras angulatum,* both valves seen from right, left, and front, ×1 (Stenzel, n. Specimen by courtesy of F. TRUSHEIM, Hannover).

2. *L. hisingeri* (NILSSON, 1832), L. Högenäs Series, Hettang., Skåne, Sweden; *2a-c,* ×2 (Lundgren, 1878).

3. *"Ostrea bristovi"* RICHARDSON, 1905, Sully Reds, low. Rhaet.; Glamorganshire, Wales; *3a,b,* ext., ×0.8, ×1 (Richardson, 1905; Arkell, 1933).

Bristovi ETHERIDGE ms." by RICHARDSON (1905, p. 422, pl. 33, fig. 4). The species remains nondescript, notwithstanding its listing by ARKELL (1933, p. 97). Seemingly, these oyster remains are stratigraphically the earliest in England and Wales. One or more species have been described from the Kössener Schichten (Rhaet.) of the Alps

and are widely distributed in homotaxial formations of the Rhaetian in the Alps and Carpathians (DIENER, 1923; KUTASSY, 1931) (Fig. J61).

Triassic liostreas have been found (KIPARISOVA, 1938, p. 33, pl. 7, fig. 16a-b; VYALOV, 1946, p. 27-28, pl. 1, fig. 1a,b) near the Arctic Circle in far eastern Siberia
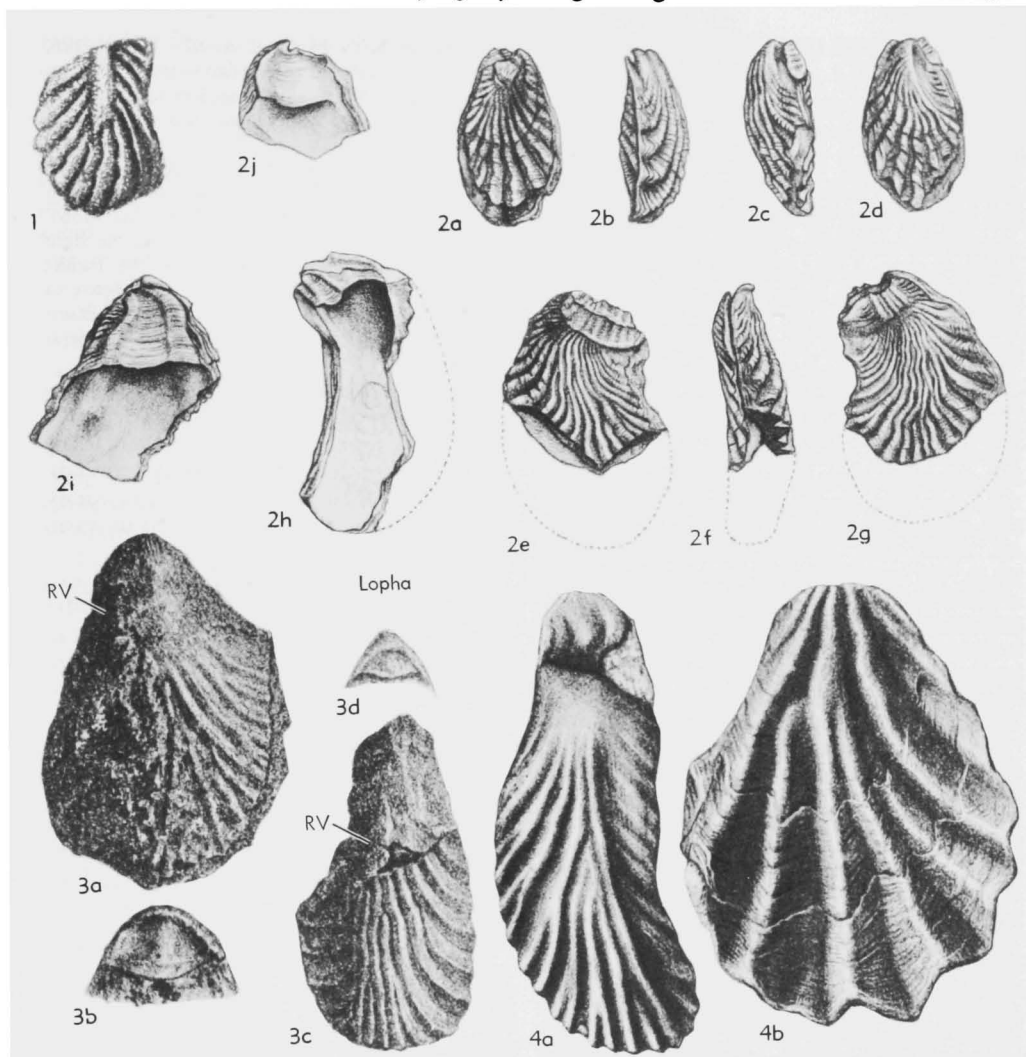
Fig. J62. Earliest fossil oysters known; Triassic *Lopha* from Mesogena seas of Alps.

1. L. medicostata (Wöhrmann, 1889), *Cardita* Oolite, Carn., ×2 (Wöhrmann, 1889).

2. L. montiscaprilis (Klipstein, 1843), St. Cassian Formation, Carn.; *2a-j,* ×0.9 (Bittner, 1912).

3. L. calceoformis (Broili, 1904), *Pachycardia* Tuff, Carn.; *3a,c,* ×2; *3b,d,* enl. (Waagen, 1907).

4. L. haidingeriana (Emmrich, 1853), Kössen Formation and its homotaxial equivalents, Rhaet.; *4a,b,* ×1 (Martin, 1860).

[Assignments of stratigraphic stages according to Diener and Kutassy.]

at the Andesite Springs of the headwaters of the Agidzha River, a tributary to the Zyryanka River, Yakutsk Autonomous Soviet Socialist Republic. The liostreas are accompanied there by *Entomonotis ochotica* (Keyserling in Middendorf, 1848) in interbedded gray limestones and calcareous shales (Norian).

It is probable that the stratigraphically earliest liostreas were Norian and were restricted to the Triassic sea that occupied the Arctic realm. The earliest *Liostrea* in Europe seems to be Rhaetian. Beginning with the Rhaetian *Liostrea* was widespread in Europe and the Mesogean territories.

What species names are to be applied to the Rhaetian liostreas in Europe is debatable (see p. *N*1103 under *Liostrea*).

LOPHA RÖDING, 1798 (SENSU LATISSIMO)

Recognition of *Lopha* found in Triassic deposits is difficult. Externally the lophas are quite similar to some species of *Enantiostreon, Atreta, Placunopsis,* and *Pseudomonotis*. The former are attached by their left and the latter by their right valves. The distinction cannot be made unless location of the adductor muscle insertion is clearly visible. However, most specimens found in Triassic deposits have tightly closed valves (Fig. J62).

The following lophas are known from the Triassic.——1) *L. calceoformis* (BROILI) from the Pachycardien tuff (Carn.) of the Seiser Alp (BROILI, 1904, p. 195, pl. 23, fig. 10-11). Originally described from only two considerably corroded left valves it was redescribed from another alpine locality by WAAGEN (1907, p. 116, pl. 34, fig. 37-38) and critically reinvestigated (Fig. J62,3). All valves described are unsatisfactory as to preservation.——2) *L. haidingeriana* (EMMRICH) from the Kössener Schichten (Rhaet.) from several localities in the northern Alps, including the type locality of the formation, 3 km. from the Bavarian border in northeastern Tirol, Austria (EMMRICH, 1853, p. 377). The same species was described as *"Ostrea" marcignyana* MARTIN (1860, p. 90, pl. 6, fig. 24-25) from Rhaetian arkoses [Grès et Schistes à *Avicula contorta*] at Marcigny-sous-Thil, on the left bank of the Armançon River, and at Montigny-sur-Armançon, Départment Côte d'Or, eastern France (Fig. J62,4). MARTIN (1865, p. 248) later conceded that his species name was a junior subjective synonym of *L. haidingeriana* (EMMRICH, 1853), this correction has been accepted by later authors (DIENER, 1923; KUTASSY, 1931). The species has been found in southern Bavaria and adjoining Austria, western Switzerland, the Carpathian Mountains of Poland, the Bihar Mountains of northwestern Rumania. Very similar remains have been found in Burma (HEALEY, 1908, p. 37, pl. 5, fig. 17-19).——3) *L. mediocostata* WÖHRMANN, 1889, p. 201, pl. 6, fig. 5) from the "Cardita Oolith" (Carn.) from the Salzberg near Hall in Tirol, Austria (Fig. J62,1).——4) *L. montiscaprilis* (KLIPSTEIN, 1843, p. 247, pl. 16, fig. 5) from the Kassianer Schichten (Carn.) of the Monte Caprile [or Zissenberg] in the Lombardy Alps, Italy. It was redescribed by WÖHRMANN (1889, p. 200, pl. 6, fig. 1-3) and BITTNER (1912, p. 70, 74-75, pl. 6, fig. 14-18) (Fig. J62,2). The latter pointed out that WÖHRMANN had confused the right with the left valve. The species has been reported from Tunisia, Tripolitania, Sicily, Bavarian Alps, Slovenia, Hungary, the Jordan River valley, Singapore Island, and the Luning Formation of Nevada, USA.——5) *L. parasitica* (KRUMBECK, 1913, p. 47-48, pl. 3, fig. 4-7) from the Fogi Beds (U.Trias., probably Nor.) of western Buru Island, Molucca Archipelago, Indonesia.——6) *?L. blanfordi* (LEES, 1928) was described as *"Ostrea" (?Exogyra)* from the Elphinstone Formation (Nor.) in the Elphinstone Inlet in Muscat and Oman, at the north tip of the Arabian Peninsula. This is a U-shaped plicate form known only from left valves.——7) *?L. tinierei* (RENEVIER, 1864, p. 80-81) was described as *"Ostrea"* from the right bank of the Tinière River, opposite the hamlet Placundray near Les Chainées above Villeneuve at the east end of Lac Léman, Canton Vaud, Switzerland. It is a U-shaped form recalling *?L. blanfordi* (LEES) found in Rhaetian beds.

Triassic lophas are restricted to the Mesogean and Pacific realms. They appeared for the first time during the Carnian. They are commonly associated with crinoids, echinoids, brachiopods, sponges and corals, even compound corals. They lived in warm euhaline waters.

Although much of the Triassic and earlier deposits are yet to be searched for oyster remains, data at hand indicate that the earliest, Carnian oyster genera were *Gryphaea* (home and probable place of origin: the Triassic Arctic realm) and *Lopha (sensu latissimo)* (home and place of origin: the Triassic Mesogean and Pacific realms). *Liostrea* appeared later, in the Norian, in the Triassic Arctic realm. Indications that *Liostrea* might have evolved from *Gryphaea* are certain anatomical similarities and its later appearance and early restriction to the Arctic realm, the home of *Gryphaea*.

Gryphaea did not spread from its home area until the early Liassic. *Gryphaea* and *Lopha* at first did not live side by side, except in the oceanic connecting passage (Luning Formation of the Cedar Mts. in Nev., USA), where Arctic and Mesogean faunas intermingled.

The great geographic distance between the places of origin of *Gryphaea* and of *Lopha* are believed to be indicative of diphyletic origins of these two oyster genera.

DIPHYLETIC ORIGINS

Phylogenetic chains documented by innumerable species described from countless stratigraphic levels are fairly common in the oysters so that one is tempted to build up long phylogenies from these chains. One must be cautious in selecting the links between such chains, however.

In going from one link to the next, one

must select the one species that is both in correct stratigraphic sequence and among all available species morphologically the most similar to its predecessor species. Internal anatomical and morphological features are the more important ones in this procedure (STENZEL, 1959), and one must avoid a purely provincial outlook when searching for a missing link, because oysters are capable of spreading from one depositional basin to another.

In this fashion the Gryphaeidae can be traced from the Triassic species of *Gryphaea* to their descendants living today: *Neopycnodonte cochlear* (POLI) [=*Ostrea cochlear* POLI, 1795, v. 2, p. 179, 255, 261], living circumglobally in cool, deeper, euhaline waters, and *Hyotissa hyotis* (LINNÉ) [=*Mytilus hyotis* LINNÉ, 1758, p. 704, no. 207] and three more, congeneric species, all living geographically separated from each other in shallow, warm tropical, euhaline waters. The Gryphaeidae, always euhaline, never were rich in genera at any one time, and only two genera survive today.

Similarly it is possible to trace the Lophinae from the Triassic species of *Lopha (sensu latissimo)* to their descendants living today: *L. folium* ecomorph *cristagalli* (LINNÉ) [=*Mytilus crista galli* LINNÉ, 1758, p. 704, no. 206] a euhaline, warmwater species, living in the western Indo-Pacific Ocean, which is the type species of the genus, and several other species. Thus, two separate phylogenetic stems of oysters are traceable from their very first appearance in the Late Triassic to today. All known oyster species, fossil and living, are either offshoots or parts of these two separate phylogenetic stems. As concerns tangible evidence documented by fossil remains, the oysters are diphyletic.

The problem reduces itself to the question whether the very first oysters, that is, pre-Late Triassic ones, were truly monophyletic or were diphyletic. Because remains of oysters that ancient have not yet been discovered, the problem must be attacked by other means than fossil remains and becomes subject to speculation. Certain anatomical features of the Gryphaeidae are significant in the question and are discussed below. Other differences between the Gryphaeidae and the Ostreidae are given in the systematic portion (see p. N1096).

PELSENEER (1896, pl. 3, fig. 4-5, pl. 4, fig. 7-8; 1911, p. 94, pl. 9, fig. 8-9) was the first to discover that in two living oyster species now placed in the Gryphaeidae by me the intestine passes through the pericardium and through the ventricle of the heart itself. This arrangement has been confirmed by HIRASE (1930, p. 38), RANSON (1948b, p. 5), THOMSON (1954, p. 161), and HAROLD W. HARRY (by anatomical dissection, 1966) so that it is reliably documented in both genera. In contrast, all representatives of the Ostreidae that have been dissected have the intestine bypassing the pericardium on the dorsal side of the latter. Peculiar as it may seem, the arrangement found in the Gryphaeidae is not unusual for the Bivalvia. The great majority of the Bivalvia have the same arrangement (PELSENEER, 1906, p. 223).

This being so, one is forced to conclude that it is the original arrangement in the Bivalvia and in the ancestors of the oysters as well. Thus it is the primitive arrangement in the oysters, as PELSENEER (1911, p. 93-94) pointed out, and the arrangement of the intestine bypassing the pericardium is an evolutionary achievement of later date or an "advanced" feature.

Also, the living Gryphaeidae are probably nonincubatory, because they all have a large promyal passage. No direct observations on incubation or on ejection of eggs are really available for this family, but the promyal passage has been demonstrated in all Gryphaeidae which have been dissected and its presence has been confirmed by HARRY (dissections made in 1966). The tie-in of promyal passage with nonincubatory propagation in the oysters appears to be reliable, although reasons for it are obscure.

In the Ostreidae, some genera, notably *Ostrea,* are incubatory. Again, the vast majority of Bivalvia are nonincubatory and only a scattering of genera have progressed to incubation. Nonincubatory propagation must be the primitive situation, so general considerations demand, and the Gryphaeidae are primitive in this respect. In contrast, the Ostreidae are in part incubatory and must be regarded, in part at least, as progressive in regard to propagation.

By and large, the living representatives of the Gryphaeidae have retained more of the primitive features than the rest of the

oysters. This being so, one is perhaps justified in expecting that most, and perhaps all, features by which the Gryphaeidae differ from the Ostreidae are primitive and were present in the very oldest, Triassic, representatives of *Gryphaea,* even if those primitive features did not leave any recognizable traces on the fossil shells. These primitive features are: 1) nonincubatory mode of reproduction, 2) presence of a promyal passage, 3) penetration by the intestine of the pericardium and ventricle of the heart, 4) orbicular outline of the insertion of the adductor muscle, and 5) position of this insertion comparatively closer to the hinge than in the Ostreidae. The last two are visible on fossil specimens and for that reason assume extraordinary importance in any phylogenetic inquiry.

The adductor muscle has many functions indispensable to the survival of the individual oyster (see p. N999). For that reason it is so large and powerful and must be capable of reacting instantaneously. In order to accomplish all these functions it must be copiously and unceasingly supplied with fresh oxygenated blood. However, heart and circulatory system in the oysters are rather poorly organized, and delivery of fresh oxygenated blood is hardly efficient. This inadequacy has been improved upon in the oysters through the anatomical position of the heart: it is placed as close to the muscle as possible and the artery supplying fresh oxygenated blood to the muscle (posterior aorta of AWATI & RAI, 1931, p. 59, fig. 31, and YONGE, 1960, p. 48) is as short as possible.

In other words, heart and adductor muscle are functionally tied together in the oysters. If for some reasons of adaptation the adductor muscle has to shift position within the shell cavity, heart and pericardium must move with it irrespective of the location of other organs in the shell cavity. For instance, if there is need for the adductor muscle to shift toward the venter, that is, away from the hinge, the heart and pericardium would shift in exactly the same way so as always to stay adjacent to the muscle, whereas the intestine would remain unaffected and be left behind. If this shift were to take place, heart and pericardium would become disengaged

from the intestine. They would follow the muscle and leave the intestine behind so that the intestine would come to be on the dorsal side of the pericardium. For some reason or other this is what happened early in the phylogenetic history of the Ostreidae but not in that of the Gryphaeidae, which retained the original, primitive, arrangement of the oyster ancestors. The reason for this shift of the muscle is unknown. One might speculate that leverage of the muscle becomes better the farther away it comes to lie from the fulcrum, the hinge axis. The shift must have enhanced leverage of the muscle, and functions of the muscle must have been made easier and more efficient.

Whatever may have been the reason behind the shift of the muscle, it is obvious that the anatomical position of the muscle is clearly marked on fossil specimens by the position of the muscle imprints. Or, fossil oysters that have muscle imprints comparatively close to the hinge (see STENZEL, 1959, p. 28, fig. 19, for exact measurements) must have had the intestine passing through the pericardium and ventricle of the heart while they were alive. All Gryphaeidae, including Triassic species, have such a position of the muscle imprints. This must be expected of them, if the observations on the anatomy of their descendants, the living species, are correct, and if our conclusion that the arrangement found in the living species is a conservative trait is correct.

On the other hand, the Triassic species of *Lopha,* that is, the oldest known representatives of the Ostreidae, have muscle imprints that have crescentic to reniform outlines and are placed closer to the ventral shell margin. It is to be expected that these oldest known representatives of the Ostreidae had the intestine passing by the dorsal side of the pericardium. In other words, this evolutionary achievement was already an established fact in the Ostreidae during Late Triassic time and must have happened before that time.

During Carnian time, when first the oysters showed up as recognizable fossils, already two separate stems were discernible: Ostreidae represented by various species of *Lopha* and Gryphaeidae by various species of *Gryphaea.* The two stems were already far apart in anatomy and other important

features. So far no earlier intermediate forms are known to us which one might interpret as ancestors of both stems. Thus further investigation of the phylogeny has to rest on speculation.

There are two possibilities to consider: 1) derivation was monophyletic, that is, both stems descended from a single common ancestor which would have to be classified as an oyster; 2) derivation was diphyletic, that is, each stem descended from a different genus, but the two ancestral genera were not oysters. The two ancestral genera were closely related to each other and are to be found in the same extinct family. At present, neither possibility can be claimed proved or even provable. However, I believe the second possibility is more likely.

NEWELL (1960, p. 81) has indicated that some of the late Paleozoic and Early or Middle Triassic Pseudomonotinae resemble true oysters so closely as to suggest that the former may indeed be ancestral to the latter. Accordingly, the oysters may have arisen either from a genus of the Pseudomonotinae (monophyletic hypothesis) or from at least two genera of the same subfamily (diphyletic hypothesis). If the monophyletic hypothesis is correct, there would have to have been a long chain of transitional species starting with an ancestral pseudomonotine genus, evolving into an ancestral oyster genus, progressing by dichotomy and divergence in the two stems discussed above. This phylogeny must have been long drawn out, because in the Carnian the divergence between the two stems, at the end of the phylogenetic chains, was quite large. Because of its length it is not likely that the chain of transitional oyster species can have entirely escaped detection by searching paleontologists.

On the other hand, if the diphyletic hypothesis is correct, much of the divergence between the two stems was established by evolution within the confines of the subfamily Pseudomonotinae. Thus no lengthy chains of transitional oyster species were necessary to lead from the two pseudomonotine ancestor genera to their respective oyster descendants. Because each chain was short they could have escaped detection easily. This assumption seems to fit the facts discovered so far.

HYPOTHETICAL ANCESTORS

The roots of the phylogeny of oysters are obscure, because they are not documented by fossils or perhaps because there are difficulties in recognizing certain fossils as oyster ancestors. New discoveries of fossil remains may yet expand our knowledge. The most promising area for such discoveries is probably far eastern Siberia, where beds older than Carnian may yield recognizable remains of oyster ancestors.

Until such finds are made we must reexamine ideas concerning characteristics and appearances of these ancestors, thus turning to hypotheses and assumptions. These are presented here with full realization that ultimately they may be refuted. At the present stage of knowledge, however, new hypotheses and ideas to stimulate investigation are needed badly. This is the purpose of the following hypotheses.

We may postulate that ancestors of the Pseudomonotidae and kindred groups were sedentary animals anchored by byssus threads. Because they were not firmly cemented to their substratum but only anchored by fairly long byssus threads, they were subject to waves and currents and were tossed about by them on occasion. During such times the most stable, and therefore the safest, position for them was to lie on their sides (pleurothetic attitude). Hydrodynamics of their environment made more stable and safe bivalves possessing one convex valve and the other one flat, suited to lie on the seabottom. The adaptive advantage of such different convexities of the two valves is that an animal exposed to water currents and anchored by byssus threads but otherwise lying loose with the flat valve on bottom is more stable than would be an animal with two equally convex valves or one resting with the convex valve on bottom and the flat valve on top. This inequality of the valves induced some shifting of internal organs. Then it became heritable and genetically fixed. It so happened that the common ancestor of the superfamilies Anomiacea, Limacea, Pectinacea, Pteriacea, and Ostreacea came to lie on its right side, and the right valve became the flat one.

JACKSON (1888, p. 547-548, pl. 7, fig. 19) convincingly showed that the unequal con-

vexities of valves of oysters, with the left valve normally more convex than the right, are not merely a mechanical result of the individual oyster's attitude during its growth, as HYATT assumed, but must be under genetic control. This important discovery proved that oysters fit quite well with other superfamilies in this respect and it is likely that the feature was inherited by the oysters and kindred superfamilies from common ancestors that were byssiferous and pleurothetic on the right side.

Although the other superfamilies mentioned are pleurothetic, with the right valve on bottom, oysters are cemented onto their substratum and pleurothetic with the left valve on bottom. This singular exception is explained below by the hypothesis that the oyster ancestors were originally pleurothetic with the left valve on top but later reversed their attitude in giving rise to the oysters.

Waves and currents exerted a considerable pull which was transmitted through the anchoring byssus threads to the byssus gland and tissues surrounding it. The pull tended to push these tissues forward, toward the anterior adductor muscle. Restrictions thus exerted on this muscle led to its gradual shift toward the hinge. In this position the muscle became no longer as effective as the other muscle and atrophied by stages. On the other side, the posterior adductor muscle remained unobstructed and was free to shift to its most advantageous position and to take over more and more of the functions of the other muscle. Ultimately the animal became monomyarian (SHARP, 1888; DOUVILLÉ, 1907, p. 97; 1913, p. 430). The presence of a byssus comprised an obstacle to free growth of the valve margins, and a byssal notch had to develop at the place where the byssus passed from the valve margins.

The hypothetical ancestor of the Ostreacea and kindred superfamilies is believed to have been byssiferous, monomyarian, pleurothetic, inequivalve (right valve flat, left convex), and to have been sedentary, anchored by byssus threads. It was nonincubatory; internally, the intestine passed through the pericardium and ventricle of the heart. It was pleurothetic on the right side, had a byssal notch at the margin of the valves, and the byssus threads were fairly long.

Cementation of the shell to its substratum probably was not so difficult an innovation, because no great changes of internal organization were required. This is attested to by the fact that several branches of these monomyarian bivalves attained cementation independently. Cementation may have been preceded by a gradual shortening of the byssus threads. Adaptational needs may have led to a shorter and shorter byssus, until ultimately the shell was so closely held that it could shift no more with reference to its substratum and the growing valve margins came into contact with the hard substratum. At this point cementation became easy.

Possibly cementation came about through adaptation of the ancestral bivalves to life on hard substrata. As long as they lived attached to sea weeds and other flexible and yielding objects, they needed many long byssus threads which could find many widespread points of anchorage. When the animals began to occupy hard, inflexible, or unyielding substrata, a few anchorage points and short byssus threads were sufficient and better.

Once cementation became a permanent way of life, byssus gland and foot became useless to the adult bivalve and were retained only in the larvae. The foot in the adult stage disappeared completely except for a pair of Quenstedt muscles (see p. *N*965). The shell itself was free to grow where the byssal notch had indented the valves, and the notch disappeared.

There remains the question of reversal of the pleurothetic attitude in the ancestor of the oysters. The monomyarian bivalves enumerated above, including the oysters, have so many anatomical features in common that it appears beyond doubt that they are of monophyletic derivation. If most of them are pleurothetic on their right sides, it would seem that this attitude is the original one among them, inherited from their common ancestor, and that the reversed attitude of the oysters is an innovation imposed upon the original attitude of the oyster ancestor. From these considerations the hypothesis is derived that oysters descended from ancestors that were byssiferous and pleurothetic on their right sides.

Perhaps reversal of the ancestral pleurothetic attitude has something to do with

cementation. One innovation may have favored or entrained the other. Among bivalves that have one flat and one convex valve, a great adaptive mechanical advantage accrues to bivalves cemented with the larger, more capacious, more convex valve on bottom. The upper valve has to be lifted up by the animal every time it opens its shell.

As long as these bivalves were only loosely attached by byssus threads, and had fairly light shells, hydrodynamics of the environment precluded their lying with the convex valve on bottom. However, as soon as they became cemented, hydrodynamics of their environment lost influence and mechanical advantage could prevail. If oyster ancestors already had valves of unequal convexity before they adopted cementation as a way of life, thicker shells and cementation of the more convex valve at the bottom must have been an advantage to them.

Several different branches of this group of monomyarians came to achieve cementation independently, but only those that accomplished it with the more convex, left, valve on bottom became oysters. The others, cemented with the right valve on bottom, never became biologically as successful as the oysters.

If several different branches of this group of monomyarians were able to achieve cementation by the right valve independently, it stands to reason that it was equally well possible for more than one branch to do so with the left valve. In other words, a polyphyletic origin of the oysters is not impossible.

ATROPHY OF HINGE TEETH

Among the Bivalvia, mechanically strong shells equipped with strong hinge plates carrying large hinge teeth and corresponding sockets are developed in taxa that move about actively and plow through the sand or mud of the substratum. Such taxa have for their locomotor organ a large turgid foot activated by hydrostatic pressures of the blood in the foot produced by powerful muscles compressing the blood lacunae in foot and mantle. To accommodate a large foot when it is withdrawn into the shell, these animals must have an inflated, copious shell and must be able to open their valves wide enough to extrude the turgid foot.

When these animals plow through the sand, silt, or mud of the substratum, the valves, opened wide, easily could be wrenched out of juxtaposition so that quick shutting of the shell would be made impossible unless there are structures that effectively keep the two valves in their proper juxtaposition and that guide them when they are being shut. Such structures are of two kinds: 1) interlocking serrate valve margins, which are an auxiliary but less effective means of guidance for the valves, and 2) hinge teeth and sockets situated on a support, the hinge plate, which are a very effective means of preventing the valves from wrenching out of correct juxtaposition.

Teeth and sockets must be large and strong and their height (or rise from the hinge plate) must be sufficiently large to keep the valves in correct juxtaposition, even when the animal opens its valves to their fullest. In turn, high and strong teeth and sockets require a strong hinge plate for their support.

Animals that neither plow through the substratum nor burrow into it do not really need a large active foot. Their foot either can atrophy or must modify to take over functions other than plowing or burrowing. The oysters have followed the former of the two pathways of evolution. They have no foot when they are adult, although their larvae have a very active foot. Adult oysters need not open their valves very much, because they lack a foot and have no need for teeth, sockets, and hinge plates. Consequently, oyster larvae, which have a foot with a byssus gland, hinge plates, teeth, and sockets, lose them very soon as they undergo metamorphosis and begin to assume the adult shell form.

Reduction of teeth and sockets are fairly easily accomplished during evolution of the oysters from their immediate ancestors, because the latter themselves already had weak dentition and were largely immobilized byssiferous monomyarian bivalves.

Quite a different evolutionary path was taken by the rudists. Although they became attached like oysters, their hinge retained teeth and sockets and even enlarged their height. However, rudists descended from mobile bivalves with prominent teeth
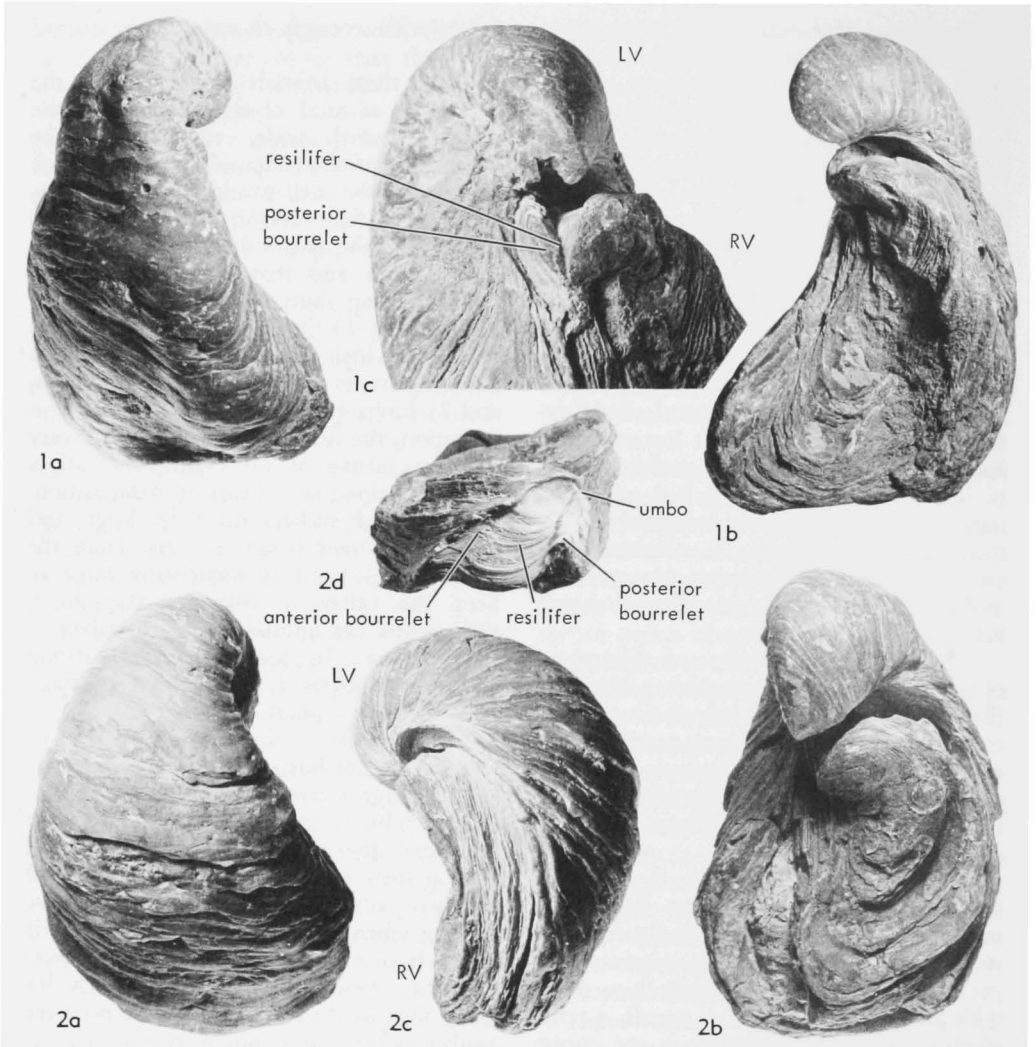
FIG. J63. The *Gryphaea* homeomorph *Aetostreon imbricatum* (KRAUSS, 1843), from Sundays River beds of Uitenhage Series, L.Cret.(Neocom.), Sondags River, Cape Province, Republic of South Africa (Stenzel, n).

1a,b. LV and RV views, ext., *ca.* ×0.6.—*1c.* Umbonal view, *ca.* ×1.
2. *"Gryphaea" imbricata* (KRAUSS) of SHARPE (1853, pl. 23, fig. 3) (BMNH no. LL 15898).—

2a-c. LV, RV, and edge views, ext., *ca.* ×0.6.—
2d. RV ligamental area, *ca.* ×0.1.
[Photographs by courtesy of J. D. TAYLOR and British Museum (Natural History), London.]

and sockets. It was easier for them to retain and readapt their teeth and sockets than to suppress them and to evolve entirely new structures ensuring proper closures of the valves.

EVOLUTION OF GRYPHAEA AND HOMEOMORPHS

The phylogeny of *Gryphaea* has aroused considerable interest and there is an exten-

sive literature on this and related subjects. Good lists of references of this literature are found in SCHÄFLE (1929) and BURNABY (1965). However, much of the literature is repetitious, and several misconceptions have gained currency and even acceptance, without sufficient critical reexamination.

FEATURES IN COMMON

The following features are common to the gryph-shaped oysters, that is, *Gryphaea,*

some of its descendants, and its homeomorphs (Fig. J63, J64, J65; see J73, J74, J80, J81, J83, J84, J87).

1) Exceptionally small attachment area at the tip of the left umbo,

2) Spirally inrolled growth pattern of left valve,

3) Large and highly convex, spirogyral left valve and small, flat or concave, operculiform right valve lacking a conspicuous umbo,

4) Growth squamae closely appressed to contour of left valve,

5) Lack of chamber formation in umbonal part of left valve,

6) Lack of umbonal cavity under hinge area of left valve, and

7) Presence of radial sulci dividing left valve.

Most of these seven characteristics are surficial or external.

Many authors have commented on the extraordinarily small size of the attachment area at the tip of the left umbo in gryph-shaped oysters (JACKSON, 1890, p. 317, pl. 24, fig. 22-24). From SWINNERTON's (1939, p. xliv and lii; 1940, p. xcviii, fig. 8; 1964, p. 419-420) data one can calculate the numerical average (2.1 mm.) of the maximal diameter of the attachment area and the average size (less than 4.5 square mm.) of the area (Fig. J35). These figures pertain to *Gryphaea arcuata* LAMARCK, 1801, from clay shales in the Zone of *Scamnoceras angulatum* (VON SCHLOTHEIM, 1820) in the Granby Limestones (latest Hettang., Lias.) south of Granby, Lincolnshire, England.

In *Gryphaea* itself no individual has been found to lack an attachment area. However, some species in other homeomorphous genera are regularly free of an attachment area (e.g., *Odontogryphaea thirsae* (GABB, 1861) (Fig. J64) from the Nanafalia Formation (Sparnacian) of the northern Gulf coastal plain (Ala. to Mexico) and possibly other congeneric species).

Evidently, larvae of nearly all gryph-shaped oyster species were like those of common oysters living today in that they could not grow into adults without first becoming attached to a firm substratum at the proper time. After growing over the substratum for a short period of time, the gryph-shaped oysters built their shells steeply upward and away from the substratum. This happened early in life so

that the attachment areas remained very small in most individuals.

Perhaps, the substratum was so small a piece that the postlarval oyster soon finished spreading over all of it and had to grow freely upward. Or perhaps, the gryph-shaped oysters were genetically predisposed to growing steeply upward from their bases after they had spread over a small area on the substratum. The latter idea is borne out by certain individuals of *G. arcuata* grown one on the other, such as the one figured by SCHÄFLE (1929, pl. 2, fig. 8) and copied by many authors. In this example the younger one of the two had really much more of a substratal area available than it managed to spread over. It is also possible that the gryph-shaped oysters did not succeed to spread over larger areas of their substratum, because they were in competition with encroaching mud or algal mats covering the substratum around them while they grew.

Whatever the situations may have been, gryph-shaped oysters were able to grow to final size without using a large attachment area on a firm substratum. Some species (e.g., *Odontogryphaea thirsae*), had evolved even further and had attained the ability to grow from planktonic larva to final size without ever becoming attached.

The highly incurved growth pattern of the left valves has always attracted attention. THOMPSON (1917, p. 534) surmised that the spiral curve of the lower valve in *G. arcuata* approaches a logarithmic or equiangular spiral. This suggestion has been followed up by TRUEMAN (1922, p. 260-261), MACLENNAN & TRUEMAN (1942), JOYSEY (1959, p. 313-314), HALLAM (1959), and BURNABY (1965). These authors have found several flaws, when they tried to fit specimens to mathematically constructed logarithmic spiral curves. It is not surprising that such flaws exist, rather it is surprising that individuals of *Gryphaea* in growing freely came so close to fitting a logarithmic spiral.

In some of the homeomorphs the curve of the left valve is quite regular; in others, notably in *G. arcuata* the regularity is obscured by many narrow transverse grooves and rounded ridges caused by the expanded end of the many growth squamae as seen in thin section (see Fig. J73,*1*). Finally, there are those that have nearly rectilinear
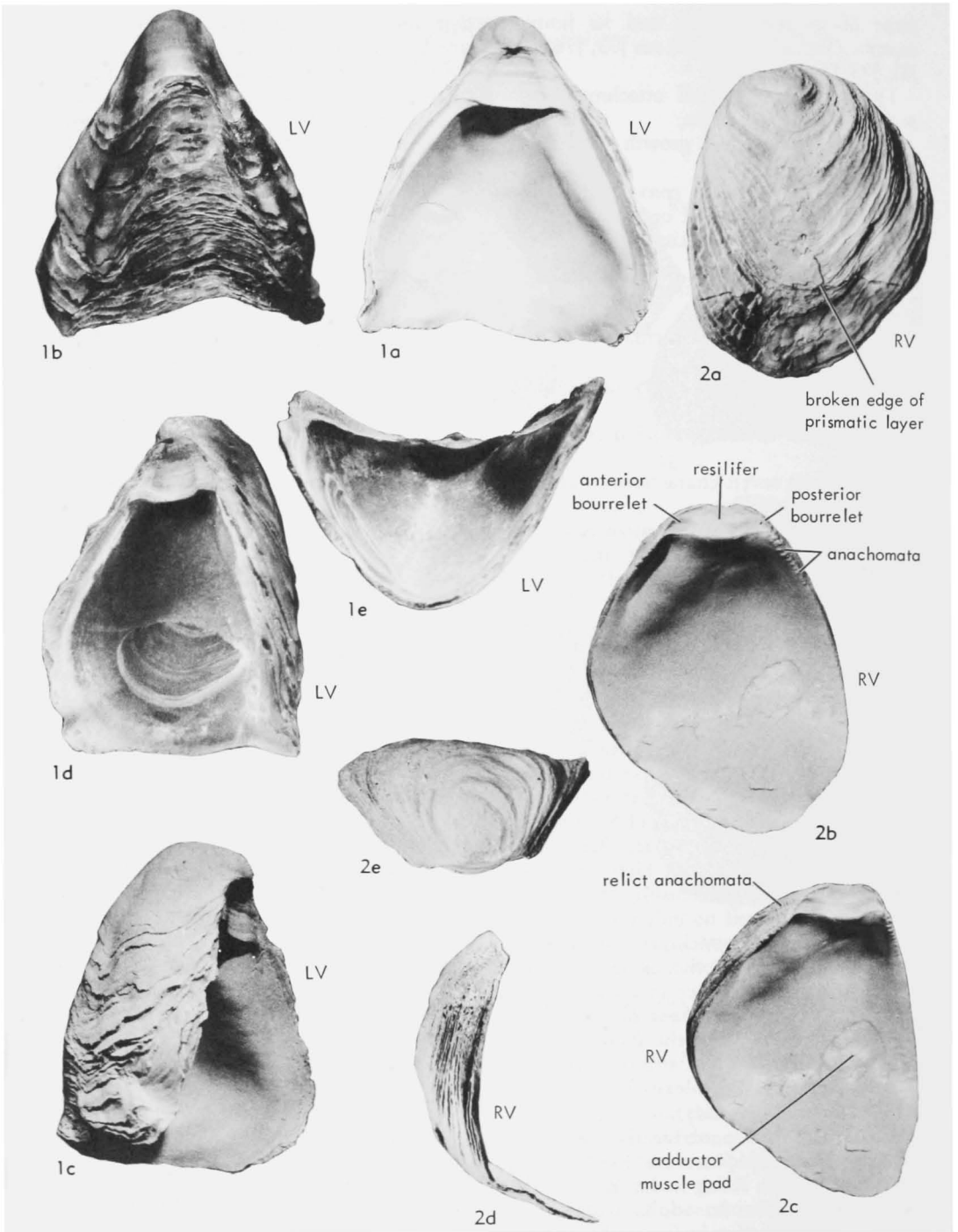
Bivalvia—Oysters

FIG. J64. *Gryphaea* homeomorph *Odontogryphaea thirsae* (GABB, 1861) from oyster bed of Nanafalia Formation, Wilcox Group (low. Eoc.), near Shoal Creek, south of Camden, Wilcox County, Ala., USA (Stenzel, n).

stretches of the periphery and have one such stretch leading over to the next one by a bend, comp. *Texigryphaea roemeri* (MARCOU (see Fig. J87,*1c*).

The spiral growth pattern is difficult to investigate with sufficient precision. Only in the anteroposteriorly compressed later Jurassic Gryphaeas and the early Cretaceous Texigryphaeas is the periphery convenient to define, because these have a rounded keel. The others, including *G. arcuata,* have hardly a keel so that the course of the spiral is difficult to follow. Also, the spiral is not two-dimensional, making it difficult to obtain precise results. JOYSEY and HALLAM pointed out other difficulties.

The left valves are highly convex in both directions from dorsum to venter and from anterior to posterior margin. In the latter direction they are commonly more convex than in the former. Their right valves are flat and in many species they are concave in one or another direction. The distribution of the concave areas can be highly complex in some species.

Growth squamae of the left valve generally are tightly appressed to the contour of the valve so that they are rather difficult to see and the outer surface of the valve is smooth. Even in the radially ribbed Eocene genus *Sokolowia* the surface of the left valve is smooth and free of outstanding growth squamae, because crests of the ribs and interspaces between them are smooth in radial direction and growth squamae are appressed. Smoothness and appressed growth squamae are lost near the end of growth in old individuals.

Sections through the left beak of *G. arcuata* show no voids or shell chambers there (see Fig. J73,*2a*) as in many other homeomorphs. This situation is quite different in ordinary oysters. If the latter have a prominent left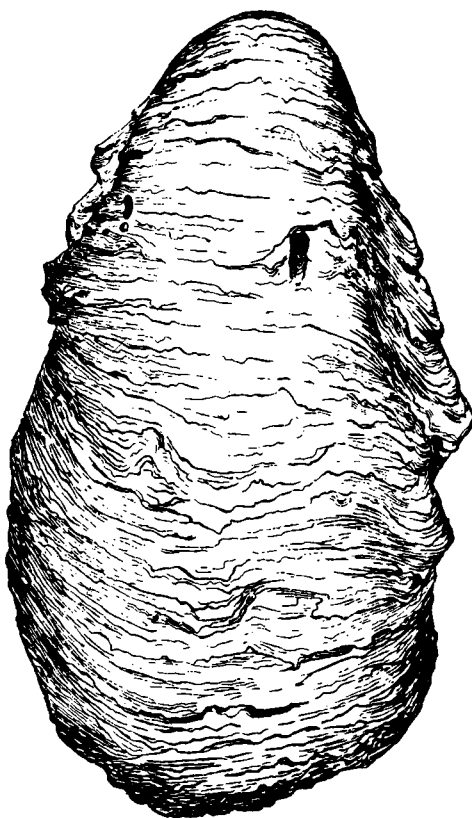 beak, they commonly have many irregularly spaced shell chambers filling in the space under the ligamental area of the left valve.

FIG. J65. *Gryphaea* homeomorph *Sokolowia buhsii* (GREWINGK, 1853) subsp. *gamma* (VYALOV), up. Eoc., Turkestanian (Trk₃) Central Asia, SSSR; LV ext., ×0.5 (Gekker, Osipova, and Belskaya, 1962).

Oysters that have great disparity between the two valves and have a prominent left umbonal region commonly have a pronounced umbonal cavity, or recess, under the hinge plate or ligamental area of the left valve. Good examples are *Crassostrea* and *Saccostrea.* From time to time the umbonal cavity is closed off by a thin shell wall, resulting in a chamber. Continued

FIG. J64. *(Continued from facing page.)*

1. LV; *1a,* specimen seen from right side, whitened for photography, showing lack of attachment area at beak, ×1; *1b,* external view of same specimen, not whitened, showing traces of coloration and many growth squamae at rooflike terebratuloid fold, ×1; *1c,* oblique view of same, whitened, ×1; *1d,* oblique view of same, not whitened, showing very thin dorsal calcite cover of muscle pad partly broken out so that false convex dorsal margin of pad is suggested, ×1; *1e,* ventral view of same showing deep terebratuloid fold, ×1.

2. RV; *2a-e,* several views of specimen whitened for photography, ×1.

growth produces a series of such chambers, arranged somewhat irregularly, infilling the left umbonal region. The gryph-shaped oysters, however, have a very shallow umbonal cavity or none at all and chambers are not developed in the left umbonal region. Their left beak is solidly filled with shell material.

Radial sulci are common features in these oysters and are known from such diverse taxa as *Gryphaea (Gryphaea), G. (Bilobissa), Texigryphaea, Pycnodonte, Odontogryphaea,* and others. The sulci of the Gryphaeinae and Pycnodonteinae are homologous, but those of *Olontogryphaea* are only analogous to the former. These sulci are deeply incised in some species and shallow in others. Their depth is a specific to subgeneric feature. They set off flanges or separate parts of the shell which serve to concentrate and deflect the inhalant or exhalant water current and are needed as improvements to the sanitation of the animals.

PROBLEM OF FORM GENUS

Similarities between the various gryph-shaped oysters appeared so persuasive to many authors that they rather uncritically classed or described diverse species under the generic name *Gryphaea* without making an effort to search for less obvious features that might set apart one group of related species from another. KITCHIN (1908, p. 79) was first to express the idea: "It is highly probable that the shells classed as *Gryphaea* do not represent a homogenetic group, but are polyphyletic in origin, including repeated offshoots from an ostrean stock."

Accordingly two avenues of procedure were open. Either accept *Gryphaea* as a form genus or investigate the various gryph-shaped oysters so as to disentangle the polyphyletic groups of species in order to establish several separate monophyletic genera, each furnished with a nomenclaturally valid name. The first avenue is not recommended. Temporarily it is a convenient expedient allowing one to set aside pressing problems and a cover for the lack of incisive basic work on them. However, if the first procedure is used, repeated often, and maintained for decades, it discourages searching inquiries into phylogenetic rela-

tionships among the various genera involved in homeomorphy.

At first KITCHIN (1908, p. 77-82) followed the second avenue and proved that one of the homeomorphs, previously classed by one author as "*Gryphaea*" and by another one as "*Pycnodonta*" (DOUVILLÉ, 1904a, p. 215), is really an exogyrine related to *Aetostreon latissimum* (LAMARCK) [=*Gryphaea latissima* LAMARCK, 1801, p. 399, =*G. couloni* DEFRANCE, 1821, =*G. sinuata* JAMES SOWERBY, 1822, =*Griphea aquila* BRONGNIART, 1822, in CUVIER & BRONGNIART, p. 332]. This particular homeomorph is *Aetostreon imbricatum* (KRAUSS) (KRAUSS, 1843, p. 129; 1850, p. 460, pl. 50, fig. 2a-d) from the Sundays River Beds, Uitenhage Series (Neocom.), of the region around the Coega, Sondags, and Swartkops Rivers near Port Elizabeth, Cape Province, Republic of South Africa (Fig. J63; see Fig. J92).

The species is rather variable. Some local populations have a broader shell shape (length to height ratio fairly large) and obviously exogyrine coiling of the left beak. These have been correctly classified as Exogyras by all authors who had such specimens at hand. In common with *A. latissimum* they all have many nonappressed growth squamae on the left valve. Other local populations have shells of small length and large height looking like a tall hook-shaped *Gryphaea*. KITCHIN discovered that their attachment area was not at the tip of the left umbo as in *Gryphaea*, but was situated on the posterior flank of the beak as in the Exogyrinae. In addition, the left ligamental area has its posterior bourrelet greatly reduced in length so that it is a narrow sharp ridge rising above the general level of the ligamental area. The two features prove the species is one of the Exogyrinae.

Although in this case KITCHIN was successful in disentangling one of the homeomorphs from the form genus and in showing the true affinities of the homeomorph, he changed his mind (KITCHIN, 1912, p. 59-60) and reported:

He [Mr. PRINGLE] obtained a fine series of shells [from the Lower Liassic of Fretherne, Gloucestershire], which should prove of value in helping to elucidate the nature and origin of those ostrean forms which have hitherto been roughly

TABLE 1. *Gryph-shaped Oysters.*

Name	Subfamily & relationship to *Gryphaea*	Stratigraphic time range	Geographic distribution
Aetostreon imbricatum (KRAUSS, 1843) (Fig. J63)	Exogyrinae, homeomorph	Neocomian	East and South Africa
Gryphaea LAMARCK, 1801 (*see* Fig. J74)	Gryphaeinae, homeomorph	Late Carnian-Kimmeridgian	Nearly worldwide
Odontogryphaea VON IHERING, 1903 (Fig. J64; *see* Fig. J127)	Ostreinae, homeomorph	Late Maastrichtian-early Lutetian	Nearly worldwide
Pycnodonte FISCHER DE WALDHEIM, 1835 (*see* Fig. J80-J84)	Pycnodonteinae, descendant	Early Albian-Miocene	Nearly worldwide
Sokolowia BÖHM, 1933 (Fig. J65; *see* Fig. J121-123)	Ostreinae, homeomorph	Late Lutetian-Auversian	Transylvania and central Asia
Texigryphaea STENZEL, 1959 (*see* Fig. J87)	Pycnodonteinae, descendant	Mid-Albian-Cenomanian	Southwestern North America

classed together as *Gryphaea.* Many of these specimens show well the transitional stages between the ancestral simple oysters of flattened forms, with prolonged attached stage, and the extreme morphological type characterized by a greatly reduced attached stage and a strongly arcuate left valve. . . . He believes that the specimens comprised in this collection contribute some valuable evidence in support of this view that the features usually considered to characterize *Gryphaea* are not those of a long-lived genus but of a similar evolutionary stage which has appeared repeatedly and independently in various ostrean stocks. It is evident that in the Lower Lias alone there were two or three separate derivations for such forms. The evolution of analogous gryphaeate stages was repeated in other stocks in various Jurassic and Cretaceous horizons . . . .

Here he regarded *Gryphaea* as a stage name or form genus. His statement marks the turning point in the attitude some paleontologists took toward the problem. TRUEMAN (1922, p. 264) epitomized this attitude:

Indeed it is extremely likely that these gryphaeiform shells have been evolved repeatedly during the Jurassic and Cretaceous from species of *Ostraea* [*error pro Ostrea*] that are similar and are presumably closely related. In other words, "*Gryphaea*" is a polyphyletic group, containing species evolved along many different lines. Therefore, the name *Gryphaea* can only be applied strictly to *one* of these series, and each such series should receive a separate generic name; but until more of these characteristics are known, at least, it appears undesirable to add to the existing confusion by creating new names for each group. Indeed, as homeomorphs in some of the series are almost or quite identical, it would probably be impossible to distinguish many of the genera even though names were available.

SCHÄFLE (1929, p. 79) agreed in regarding "*Gryphaea*" as a nonhomogenetic group. ARKELL (1934, p. 58-59) quoted TRUEMAN with obvious approval.

Thus it came to pass that from 1922 onward many preferred to consider *Gryphaea* as a collection of hardly distinguishable genera, a so-called pseudogenus or form genus (MORET, 1953, p. 31, 373 footnote 2; SIMPSON, 1953, p. 183). It was rather unfortunate that from that time on no more concerted efforts were made to disentangle monophyletic groups of species from the form genus.

It is my contention that every effort must be made to disentangle the various monophyletic groups of species and to provide each group with a valid name until there are only monophyletic genera at hand. This task has largely been completed, and it is now possible, and highly advisable, to regard *Gryphaea* as a monophyletic genus tied to its well-known type species. This monophyletic genus is clearly separable from similar genera, be they its descendants or its homeomorphs, and is definable on the basis of features of anatomy, morphology, and shell structure (Table 1).

KITCHIN (1912, p. 59) maintained that among the lower Liassic gryphaeas there were two or three separate derivations from ostrean ancestors, that is, that the lower Liassic gryphaeas were polyphyletic. In more than 50 years no one has substantiated this extreme viewpoint, believed to be erroneous, and the lower Liassic gryphaeas are regarded as diversified species of a monophyletic genus.

By reason of ICZN Opinion 338, the monophyletic genus *Gryphaea* LAMARCK, 1801 (p. 398-399), has for its type species *G. arcuata* LAMARCK, 1801 (=*G. incurva* J. SOWERBY, 1815). The type species is widespread in western Europe, from southern Sweden to northern Italy and the high Tatra Mountains in southern Poland. The species ranges stratigraphically from the Zone of *Scamnoceras angulatum* (VON SCHLOTHEIM, 1820) in the Hettangian to the Zone of *Caenisites (Euasteroceras) turneri* (J. DE C. SOWERBY, 1824) in the Sinemurian. Extensive descriptions of the species were given by JONES (1865) and SCHÄFLE (1929, p. 26-37, pl. 10, fig. 7-17; pl. 11, fig. 1-4, 9).

ANCESTORS OF GRYPHAEA

DOUVILLÉ (1910, p. 118; 1911, p. 635) apparently was the first to express himself concerning the ancestry of *Gryphaea*. He suggested that the group of simple oysters of flattened shape with prolonged attachment stage found in Late Triassic and Early Jurassic beds of western Europe is the immediate ancestor of Liassic *Gryphaea*. He bestowed the name *Liostrea* to the supposedly ancestral group and used *Liogryphea* [*error pro Liogryphaea* FISCHER, 1886 (=*recte Gryphaea* LAMARCK, 1801)] for Liassic gryphaeas. This phylogenetic derivation has become a generally accepted hypothesis. For example, PHILIP (1962, p. 337) and SIMPSON (1950, p. 153) have accepted it.

Nonetheless, it never was more than an assumption without good proofs. The bases for the assumption, not explicitly stated, seem to be two: 1) *Liostrea* is found in western Europe in beds older than the *Gryphaea*-bearing Lower Liassic beds and in them it is the sole oyster genus present in this region. If one looks for an ancestor of *Gryphaea* in western Europe, *Liostrea* appears to be the only oyster genus available. 2) *Liostrea* has a simple, flattened shape which, it seems logical to assume, is more primitive than the spiral-shaped *Gryphaea*. To this day it remains to be seen whether these two ideas are sound.

PRINGLE and KITCHIN (1912, p. 59-60) claimed to have discovered good proof for this hypothetical phylogenetic derivation.

They claimed to have found in lower Liassic beds at Fretherne transitional evolutionary stages connecting the two genera. Thus they opened a lively discussion of these supposedly transitional stages of evolution. TRUEMAN (1922), in one of the first papers to use statistical data and variation diagrams in paleontology, strongly supported these claims and published a graph in their support (TRUEMAN, 1922, fig. 5). The graph shows the amount of incurving of the left umbonal region, called number of whorls by TRUEMAN, in each of five collections coming from five different stratigraphic levels. The lowest one is based on a *Liostrea,* the others on *Gryphaea arcuata* going progressively higher up in the stratigraphic section. MACLENNAN & TRUEMAN (1942) furnished additional, improved graphs based on specimens from Loch Aline, Argyllshire, Scotland. The two papers were acclaimed by many, for example, by PHILIP (1962, p. 334), and regarded as the ultimate paleontologic proof that successive evolutionary stages connected *Liostrea,* the ancestor, with *Gryphaea,* the descendant, in the stratigraphic section of the lower Liassic of the British Isles.

Objections were raised early by SCHÄFLE (1929, p. 76, 78 and footnote 2) who explicitly took issue with TRUEMAN in stating that in southwestern Germany no transition between the two genera can be found, although one could hardly deny close relationships between them.

HALLAM reexamined statistically the supposed proof presented by TRUEMAN (1922) and MACLENNAN & TRUEMAN (1942) with the aid of specimens from various localities in the British Isles. He found no such transition connecting the two genera and concluded: "While the presumption must remain that the Jurassic *Gryphaea* evolved in some way from an *Ostrea*-like ancestor a convincing evolutionary series has yet to be demonstrated" (HALLAM, 1959a, p. 107). This contradiction added much to the interest in the question and more papers (GEORGE, 1953; HALLAM, 1959b, 1960, 1962; JOYSEY, 1959, 1960; PHILIP, 1962; SWINNERTON, 1932, 1939, 1940, 1959, 1964; TRUEMAN, 1940; WESTOLL, 1950) discussed several aspects of the problem. Particularly, the formulae and statistical methods em-

ployed so far were thoroughly criticized and improved.

It was recognized that the amount of incurving of the left umbonal region as expressed through the number of whorls was not a good measure, because it depended on the age or size of the individual oyster. The larger the individual oyster, the more of a coil or coils it has.

The progressive increase in number of coils from lower to higher beds noted by TRUEMAN (1922) does not necessarily indicate an increase in the tightness of the coiling, it may merely indicate a progressive increase in the size or age of the individuals, whereas the tightness of coiling was the feature whose evolution supposedly had led from *Liostrea* to *Gryphaea*.

Finally, the ultimate, most refined statistical approach was used by BURNABY (1965), who was able to use HALLAM's original samples. BURNABY proposed a new method of measuring tightness of coiling, thereby avoiding the influence of size on the results. His study showed that there is a slight trend from lower to higher beds toward less tightly coiled left valves in *Gryphaea arcuata*. The trend expresses itself in a reduction of a few millimeters in the length of the spiral periphery of the left valve as measured from the tip of the umbo to an arbitrarily selected point on that periphery at which the radius of the valve spiral is 2.0 cm. Thus the increase of apparent coiling noted by TRUEMAN (1922) is best explained by the increase in size of the shells toward the upper part of the section.

Because BURNABY proved that there is no evolutionary tendency to tighter coiling within the species *Gryphaea arcuata,* the stratigraphically lowest specimens are no less tightly coiled and no nearer to *Liostrea* than specimens in higher beds. Therefore, no likelihood of a transition between *Liostrea* and *Gryphaea* is inferred. This conclusion reinforces SCHÄFLE's observation, and the hypothesis of derivation of one genus from the other remains unproved and unlikely.

In all these discussions of the hypothetical derivation of *Gryphaea* from *Liostrea* various authors have made no use of the Triassic gryphaeas, although some have mentioned them. SCHÄFLE (1929, p. 78, footnote

1), who is one of these, refused to regard the Triassic gryphaeas as true *Gryphaea*. The reason for neglect of the Triassic gryphaeas presumably was that no Triassic *Gryphaea* is known in western Europe and everyone has sought to find the ancestor in beds beneath the Liassic *Gryphaea*-bearing beds of this region.

Since TRUEMAN's early work, more and better Triassic gryphaeas have been described by KIPARISOVA (1936; 1938), Mc-LEARN (1937), VYALOV (1946), and others. All of these fossils came from areas difficult to reach, in the present-day polar region. No wonder they were ignored by those working on the ancestry of *Gryphaea*.

Triassic gryphaeas are smaller than the large forms of *Gryphaea arcuata* from the Liassic of Europe, but otherwise they are similar and have features diagnostic of the monophyletic genus *Gryphaea*. In particular do *G. arcuataeformis* KIPARISOVA (1936, p. 100-102, 123-125, pl. 4, fig. 1-2, 4, 6-10; 1938, p. 4, 33-34, 38, 46, pl. 7, fig. 17-21, pl. 8, fig. 1-2, 11) from late Carnian to Norian beds on the left bank of Korkodon River, a right-hand tributary of Kolyma River in Magadanskaya Oblast [Province], far eastern Siberia, USSR, and *G. chakii* McLEARN (1937, p. 96, pl. 1, fig. 8) from the Schooler Creek Group (Carn.-Nor.) in foothills along Peace River in east-central British Columbia, Canada, come close in morphology to *G. arcuata* LAMARCK, 1801, from the Liassic of Europe. To disregard the evidence they present or to deny them a place in the monophyletic genus *Gryphaea* would be a serious error. They are the ancestors of the lineage of *G. arcuata,* or are very close to the real ancestors (Fig. J60).

The first appearance of *Gryphaea arcuata* in the fossil record of western Europe was investigated thoroughly by SCHÄFLE (1929, p. 32-35, fig. 5). He was obviously puzzled by the abrupt appearance of this species, without any antecedents known to him, in the "Angulatenschichten," that is, in the Zone of *Scamnoceras angulatum* (VON SCHLOTHEIM) at the top of the Hettangian Stage, early Liassic (*cf.* ARKELL, 1933, p. 117). HALLAM (1959a, p. 106-107) and BURNABY (1965, p. 258) recognized that wherever *G. arcuata* first appears in the
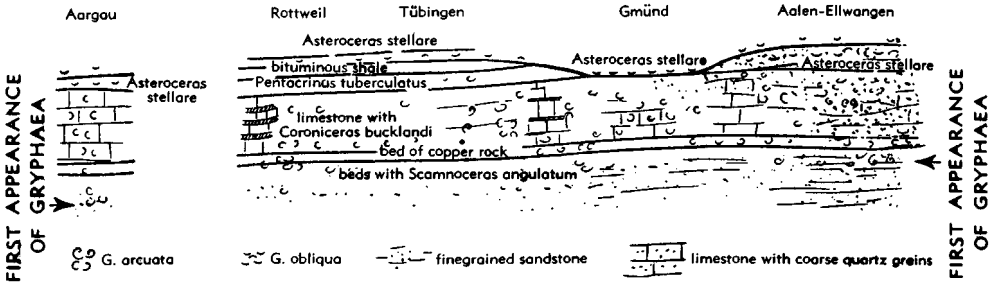
Fig. J66. First stratigraphic appearance of *Gryphaea* in western Europe (Schäfle, 1929).

fossil record of western Europe, it does so with dramatic suddenness (Fig. J66).

An abrupt appearance of a marine species within a section of continuously deposited marine beds speaks against local or provincial evolution of the species in the same depositional basin; rather, it is indicative of immigration. It is to HALLAM's credit that he was first to suggest (HALLAM, 1962, p. 574), as one of the alternatives in the problem of the origin of *Gryphaea arcuata,* that the genus might have migrated swiftly into the west European area following gradual evolution elsewhere.

The Triassic homeland or place of origin of *Gryphaea* is the Arctic region: the Kolyma River basin in far eastern Siberia, Bjørnøya Island, the Canadian Arctic Archipelago, and British Columbia, Canada. This sea basin was landlocked on all sides except in the region of British Columbia and Nevada, where it connected with the Pacific basin. In this sea basin, the first gryphaeas probably evolved from pseudo-monotid or other ancestors. There *Gryphaea* made its recorded appearance in the Carnian. During the Triassic an isthmus separated the Arctic sea from the sea in western and central Europe. The isthmus was in part responsible for the widespread deposition of evaporites in western and central Europe during the Triassic. During early Liassic time the sea broke through the isthmus, establishing connection between the two seas and allowing marine faunal exchanges to occur. It was then that *G. arcuata* immigrated from the Arctic region into the western and central European sea. The spread of this species into the new area was rapid, and its first fossil record in the *Scamnoceras angulatum* Zone marks the exact time it happened. Possibly

other species of *Gryphaea* immigrated in the same way.

The environments in this sea were suitable to *Gryphaea* so that the genus became widely distributed there and produced many species and individuals. The Early Jurassic time was one of great flowering of the genus in western and central Europe.

Gryphaea is one of the two oyster genera to make an early appearance in the fossil record. There are no fossil oysters known that antedate it. To judge by its modern descendants, *Neopycnodonte* and *Hyotissa,* it must have had a "primitive" anatomy. For these reasons it is believed that it is an ancestral form of the oysters, or at least of one branch of the stock, the Gryphaeidae. Contrary to widespread opinion, the spiral *Gryphaea* shape probably is not an "advanced" feature, and *Gryphaea* possibly did not descend from a simple, flat *Ostrea*-like ancestor. It may have descended from a spirally shaped genus of the Pseudomonotinae or a related stock.

ADAPTATION AND ENVIRONMENT

SUBSTRATUM

Features that distinguish gryph-shaped from other, normal oysters must be results of adaptation to a special and rigorous environment obviously different from the usual environments in which oysters grow today. Because there are no gryph-shaped oyster species now living, it is not feasible to draw conclusions from modern species in order to explain the gryph shape. It must be concluded that either the special environment does not exist any more or that present-day oysters do not occupy it anymore, if indeed it exists. It seems unlikely that a formerly widespread sea-bot-

tom environment that lasted for a long time has vanished utterly. Perhaps, other more efficient animals have displaced the oysters from that environment.

Gryph-shaped oyster species show less variability of shell shape than normal oysters. Elimination of the unfit as expressed by shell shape must have been rather rigorous among gryph-shaped oysters.

A feature of the environment in which gryph-shaped oysters thrived is its euhaline salinity, for they were euhaline or very nearly euhaline bivalves. *Gryphaea* itself was associated in many places with ammonites, corals, echinoids, or other animals indicative of euhaline waters. Its direct descendants, the Pycnodonteinae, were strictly euhaline and are so to this day, as can be ascertained from those now living. The genus *Sokolowia,* found in upper Eocene (=Biarritzian) deposits of Transylvania, Rumania, and central. Asia, was associated in the region of Căpuş-Gilău of the Transylvanian basin with reliable indicators of euhaline waters, such as nummulites, echinoids, and brachiopods (MÉSZÁROS & NICORICI, 1962).

Taxa that are either strictly euhaline (e.g., Exogyrinae) or polyhaline to nearly euhaline (e.g., *Ostrea s.s., Flemingostrea*) have furnished offshoots that became homeomorphs of *Gryphaea.* On the other hand, taxa that are normally brackish-water oysters (e.g., *Crassostrea*) have not furnished them. In other words, oysters living in brackish-water lagoons or estuaries never evolved into *Gryphaea* homeomorphs. *Gryphaea,* its descendants, and its homeomorphs were always adapted to living in euhaline or nearly euhaline waters of epicontinental seas. There they evolved, because that is where the particular environment they became adapted to existed. The environment is not found in brackish lagoons and estuaries.

Sedimentary rocks in which fossil remains of gryph-shaped oysters are found furnish an important clue to the special environment in which they lived and to which they were well adapted. Nearly all of them lived on sediments of low energy levels, that is, on sediments deposited in fairly quiet waters. Very few have been found growing on pebbles, whereas such overgrowths are not rare among common oysters.

SCHÄFLE (1929, p. 75) pointed out that Jurassic gryphaeas are rarely found in sands, especially pure, not muddy sands. Sediments with which gryph-shaped oysters are most commonly associated are clays, marls, chalks, limestones, and glauconite marls. Originally, before their diagenesis and consolidation, these sediments were either soft, water-logged oozes or contained various amounts of small pellets composed of minette iron ore or of authigenic minerals of the glauconite group. These pellets are the modified excrements of small mud-eating animals. Most of the sediments are dark-colored, because they contain finely divided iron-sulfide minerals (FeS_2, pyrite, or marcasite). For example, *Texigryphaea roemeri* (MARCOU) is found in countless numbers in the Grayson Clay (Cenoman.), a dark gray, very sticky, carbonaceous, calcareous blocky clay shale. *Sokolowia buhsii* (GREWINGK) forms a layer (KOCH, 1896) in a thick, bluish gray, silty clay marl (late Lutet.). Abundance and great proliferation of species of *Gryphaea* during the Liassic of western and central Europe coincides with occurrence of abundant dark, carbonaceous clays in the stratigraphic section. In later Jurassic deposits such clays are much less abundant, and so are the gryphaeas.

Gryphaea, its gryph-shaped descendants, and its homeomorphs lived mostly on sea bottoms composed of soft, water-logged oozes with small fragments of shells, and their distinguishing features are adaptations to this environment. DOUVILLÉ (1911, p. 635) was the first to recognize this. TRUEMAN (1940, p. 81) mentioned it and WESTOLL (1950, p. 490) recognized that *Gryphaea* was adapted for life on unconsolidated sea floors.

ATTITUDE DURING LIFE

The broader, more bowl- or basin-like gryph-shaped oysters (with length/height ratio fairly large, near 1) always had been believed to have lived on the sea bottom with their left valves on bottom and their flat right valves nearly horizontal (ZEUNER, 1933b, p. 308). A different life attitude was postulated for the narrow canoe-shaped *Gryphaea arcuata.* Concerning this species, PFANNENSTIEL (1928, p. 390, 408) claimed

that the longest diameters of the shells were kept close to horizontal and that the left valves were beneath, resting on their posterior flanges, on their posterior sulci, and on the main bodies of left valves. Their right, or opercular, valves opened out like doors, their hinge axes being "more or less vertical."

ZEUNER (1933a) conducted experiments with fossil *Gryphaea* shells lying on a very fine-grained sediment in a flume trough. He showed that currents would tend to bury the shells part way in the sediment with their left valves on bottom and their greatest diameters nearly horizontal. The shells would come to lie with their hinge axes and flat right valves nearly horizontal. Partly sunk into the soft substratum, they would lie immobilized in quite stable positions.

ZEUNER pointed out that PFANNENSTIEL probably had been thinking of a firm unyielding substratum into which the *Gryphaea arcuata* shells could not sink and on which the shells would roll around at the slightest water current. The attitude PFANNENSTIEL described was the one that might be assumed by shells free to roll around on a firm, level substratum. In that case, the shells always would be in labile positions, but would become less labile if they came to rest at a slight posterior tilt on their posterior flanges as outlined by PFANNENSTIEL. In no case could the hinge axes become vertical, however. The premise of an unyielding substratum is rather questionable, and the attitude postulated by PFANNENSTIEL is incorrect. ZEUNER's explanations are well substantiated and must be accepted with only minor modifications.

SIMPSON (1953, p. 284, fig. 35) showed another interpretation of the life attitude of *Gryphaea arcuata* in which both the longest diameter of the shell and the flat right valve are vertical but the hinge axis is horizontal. The interpretation is probably a misunderstanding of data given by WESTOLL (1950). The attitude would be extremely unstable.

It is now believed that the animals lived partly sunk into the soft ooze lying with their valve commissures nearly horizontal (Fig. J67). In this position, the animal's weight, shell and all, was about equal to the weight of the ooze it displaced so that the *Gryphaea* essentially floated in or on

the soft ooze. The animals must have done vigorous self cleansing (see p. N1001) to keep the surrounding ooze from encroaching. The fact that the incurved left beaks of the gryph-shaped oysters did not enclose any fluid-filled chambers and had no umbonal cavities perhaps may have been an adaptation facilitating correct distribution and balance of the load the animals exerted on the ooze so that the growing valve margins surrounding the inhalant and exhalant water currents could remain above the level of the ooze. All the gryph-shaped oysters had in principle the same attitude in life.

ORIGIN OF GRYPH SHAPE

The origin of the gryph shape among oysters was first explained by HENRI DOUVILLÉ (1911, p. 635), whose very brief exposition has been adopted, modified, and expanded by later authors, notably by PFANNENSTIEL (1928, p. 385-386), SCHÄFLE (1929, p. 74-77), and TRUEMAN (1940, p. 81-82). DOUVILLÉ's explanation is well founded, and the expanded exposition given below is based on it.

Euhaline oysters adapted to ooze-covered bottoms have much larger regions accessible to them than brackish-water oysters, for brackish-water regions form only a narrow belt along coasts of continents, whereas ooze-covered sea bottoms stretch far and wide. However, ooze-covered sea bottoms generally are devoid of firm substrata on which oysters can grow. Such firm substrata as are available are mainly small shells or their fragments. This sort of bottom contrasts with the brackish and shallow-water environments in which mangrove roots, large plant debris, or large pieces of shells are plentiful for oysters to grow on. The gryph shape is a mechanical consequence of and an adaptation to this sort of environment, that is, to life in normal-salinity marine sea waters, deep enough to be removed from strong wave action and tidal currents and far enough removed from shore to be outside the influx of fresh or brackish waters, and to life on bottoms covered with soft ooze on which small particles offer the only firm substrata for growing oysters. Such ooze-covered sea bottoms normally are at somewhat greater depth in calm waters with rather
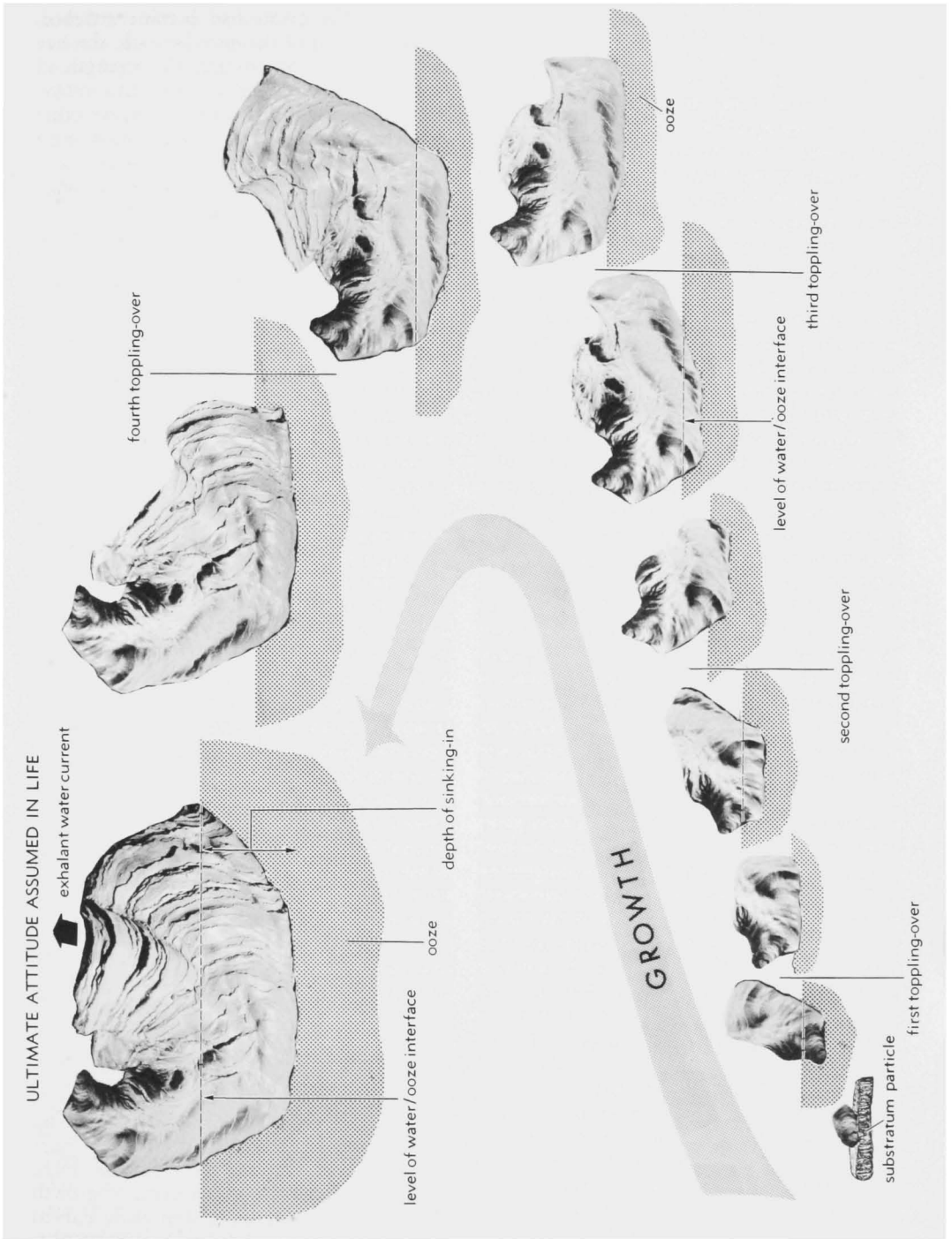
FIG. J67. Origin of the gryph shape of oysters as exemplified by an individual of *Texigryphaea roemeri* (MARCOU, 1862) from the Grayson Clay (Cenoman.), Texas, ×0.75 (Stenzel, n).

stable salinities and stable but low temperatures.

From observations made on living oyster larvae it is well known that they cannot attach themselves successfully on mud-covered surfaces, and many times it has been demonstrated that oyster larvae are selective as to the substratum to which they choose to affix themselves. The larvae of gryph-shaped oysters found extensive soft, ooze-covered bottoms, on which they were unable to settle, except wherever small particles offered suitable substrata. The larvae and postlarval oysters became adapted successfully to such substratum conditions so that it became possible for gryph-shaped oysters to occupy large areas of sea bottom that were unfavorable to colonization by other oysters. Successful they were as is attested to by the vast number of individuals of many species.

The very young postlarval oyster, later to become gryph-shaped, first grew over the small substratum and then grew upward steeply, at an angle of circa 60-70° from the horizontal (Fig. J67). By growing upward so early and so steeply the young oyster managed to bring that part of its shell margins over which the inhalant water current enters the mantle cavity into a position where the sea water was better supplied with oxygen and less polluted with mud and hydrogen sulfide. The water film at the immediate interface between water and bottom sediment was poor in oxygen, because hydrogen sulfide solutions rose from the dark-colored ooze at the bottom. Most of the ooze contained fair amounts of finely divided organic matter, probably derived from dead plankton and the feces and pseudofeces of the oysters themselves, and the water in the pore spaces of the ooze had hydrogen sulfide in solution (Fig. J67).

As the young oyster built up its shell steeply and was attached to a small particle, which in turn rested on a soft and oozy support, the young oyster shell soon reached an unstable attitude and toppled over on its ventral side. As it fell over, the left beak with the small substratum particle attached to it was lifted up off the ooze. The moment when the young oyster shell started to topple over depended on the size or rather weight of the small particle

to which the oyster had become attached, the yield point of the ooze beneath, the size and weight of the oyster, the strength of water currents, vigor of the shell movements made by the oyster, and many other factors. Some young oysters must have reacher an unstable attitude sooner than others, and specific differences in shell shapes may have had their influence.

After the young oyster had toppled over, it continued to build up its shell steeply and thereby shell growth changed direction. This process was repeated several times periodically, and in this fashion the lower valve repeatedly changed direction of growth so that it became convexly curved and its beak became incurved.

The periodicity of this process is well shown on many individuals of *Texigryphaea roemeri* (MARCOU, 1862) from the Grayson Clay (Cenoman.) of Texas (Fig. J67). In many individuals the shell is not continuously and regularly curved, but shows intermittent angular adjustments in direction of growth. Each angular adjustment followed a toppling-over. The specimen figured exhibits three major angular adjustments and some minor ones. The attachment area at the tip of the left beak is roughly triangular and 6 by 10 mm. in size. The original substratum is no longer preserved and had disappeared already before the shell was finally buried in sediment, as attested to by a small colony of Bryozoa, which grew over a small part of the attachment area with many apertures clearly visible. The sedimentary rock in which this species is found is a dark gray, very sticky clay shale containing the finely divided iron sulfide minerals (FeS_2) marcasite or pyrite. The Grayson Clay contains millions of specimens of this species, hardly ever in clusters, and very many of them show angularity of growth.

Other gryph-shaped species show a smoother, more uniformly curved growth. In these species the periodicity of toppling over followed by building up was more frequent and resulted in countless small intermittent angular adjustments of growth which produced a more uniformly curved convex lower valve. It is conceivable that in some species the two, toppling over and building up, were combined into a smooth and continuous process. The very smoothly

curved left valves of many species of *Pycnodonte* may owe their origin to such a smoothly functioning process.

Many factors may exert an influence on the growth process and may tend to produce smoothness of the lower valve. For instance, vigorous repeated valve movements by the animal may keep the oyster, with its shell, from ever attaining much of an unstable attitude and may initiate adjustments of attitude quite often. Also, the ratio of weight of body and shell to that of the small substratum piece, attached at the left umbo, is important in this connection.

The very smoothly curved left valves and the growth squamae closely appressed to the contour of that valve are adaptations to life on ooze. They reduce to a minimum any hindrance to a passive adjustment or slippage of the animal's position on the ooze. Growth squamae extending out ending in frills, such as are found in common oysters, would prevent adjustments of position.

During the periodic process of toppling over and building up, the distribution of weight undergoes a gradual shift. The incurved left beak is produced gradually and comes to lie successively higher and higher above the plane of the valve commissure. In this fashion a counterweight to the growing ventral shell margin is produced. The fact that the umbonal cavity of the left beak in many gryph-shaped species is filled in continuously with solid shell-layers and that the left beak has no chamber building must be of considerable influence in making the umbonal region a more effective counterweight as pointed out by SCHÄFLE (1929, p. 76). The gradual shift in weight distribution tends to slow down the frequency of toppling over and to reduce the size of the adjustment of the direction in which the left valve is growing. These changes and the increase in size of the shell cavity result in a gradual reduction of dorsoventral curvature of the left valve. The valve grows in a spiral rather than along a circular path; at first, the radius of curvature is small, but it gradually increases in size so that the spiral opens up concomitantly. Ultimately, a stage may be reached by an old oyster when no further adjustments of the attitude of the shell are necessary. At this stage, the shell may grow quite irregularly (see SCHÄFLE, 1929, fig. 4).

Extreme-coiling of the left beak has been suggested by TRUEMAN (1922, p. 265; 1940, p. 84) as the cause of extinction in the phyletic lineage culminating in *Gryphaea arcuata*. Many individuals of this species supposedly had continued to grow until they reached a stage when the coiled apical part of the left valve started to press against the opercular right valve beneath. Thus such advanced individuals encountered gradually more and more difficulty in opening their shells to feed and propagate and they became extinct. This idea of hypertely has been adopted by some later authors although no attempt to furnish proof has been made.

One should be able to find many specimens with valves tightly locked, if this manner of death had been widespread enough to cause extinction. So far only one author (HENDERSON, 1935, p. 558) has claimed to have found such specimens. These were collected at Hock Cliff, Fretherne, on the left bank of the river Severn, 9 miles south of Glouster, England, but the specimens have not been illustrated. Other paleontologists who have collected at this locality have not made such a claim, so considerable doubt remains as to the reliability of the observation. So far all shells illustrated in the literature or available for study show a gap between the coil of the left beak and the top of the right valve beneath, provided sufficient care has been taken to remove the sediment matrix completely. The smallest gap seen is 1.5 mm. but in most individuals it is 3 mm. or more.

Many gryph-shaped species, especially those of *Texigryphaea*, have the left beak coiled in a three-dimensional spiral so that the tip of the left beak comes to lie well behind the umbo of the right valve, where this valve is thickest, and allows plenty of space for the valves to open. However, in *Gryphaea arcuata* the three-dimensional arrangement is much less marked, and the spiral comes close to lying in one plane. Nevertheless, even in this species some individuals have the tip of the left beak turned aside so that the thickest part of the right valve at the hinge is not directly opposite the tip of the left beak, if the hinge axis is used as a reference axis. In addition, very

old and large individuals of gryph-shaped species tend to cease growing in a strictly regular spiral and during growth their hinge axis tends to shift ventrally away from the coil of the left beak. This shift allows the left ligamental area to grow in height chiefly and provides more clearance between the two apical parts of the shell. This sort of growth pattern is different than that postulated by TRUEMAN for extreme individuals of *G. arcuata,* but has been clearly depicted by SWINNERTON (1940, p. lvi, fig. 7d), whereas TRUEMAN's postulate has not been illustrated.

It is commonly not realized to what slight extent live oysters open their valves during feeding. Data gathered from *Crassostrea virginica* by W. J. DEMORAN of the Gulf Coast Research Laboratory, Ocean Springs, Mississippi, in August, 1962, show that a living oyster, with shell 106 mm. high, opens its valves 3.5 mm. at their ventral margins, at the best. The largest size of *G. arcuata* listed by SWINNERTON (1940, p. lxxxvi) is 51.5 mm. and the largest specimen available here, graciously sent by Prof. SYLVESTER-BRADLEY, is 75 mm. high. *G. arcuata* has a much smaller shell cavity and a smaller right valve in proportion to the height of its shell than *Crassostrea.* Consequently, it would open its valves to a lesser extent than a *Crassostrea* of the same shell size. It is evident that the largest *G. arcuata,* 75 mm. high, would have to open its valves less than 2.5 mm. at the ventral margins, that is, at the side opposite the coil of the left beak. Directly under the coil the amount of clearance must have been much smaller and must have been in proportion to the distances from the hinge axis, around which the right valve pivots. Calculations show that a clearance of less than 0.6 mm. between the coil of the left valve and the top of the right valve at its thickest point would suffice to let the largest *G. arcuata* open its valves with ease and comparably to living *C. virginica.*

Another argument against TRUEMAN's idea is that the onset of the impinging of the coiled apical part of the left valve onto the top of the right valve beneath must have been rather gradual. During this protracted period of time, the incessant opening and closing of the valves, which live oysters do during feeding, must have made the two valves rub against each other. The rubbing must have resulted in considerable wear of the areas affected and must have resulted in increasing the clearance between the two valves there. It is hardly conceivable that growth and progressive coiling of the lower valve could have been faster than the wear produced by the rubbing together of the two valves, particularly so in old and large individuals. It should be noted that no specimens of *Gryphaea arcuata* have been described showing friction scars on the apical regions of the valves. On the contrary, the individuals are neatly preserved and intact at those places.

TRUEMAN (1940, p. 84) himself discussed one objection to this idea. He pointed out that the sealing of the shell would first show up in aged individuals of the species, and would, therefore, have no harmful effect on survival of the species. Sealing of the shell could have been the direct cause of extinction only if the extreme coiling were to show up in nearly all individuals before they could participate in reproduction. However, living oysters attain sexual maturity as early as 21 days after fixation, and young oysters have been found to contain ripe eggs when they were merely 1.25 by 1.20 cm. in size (see p. *N1002*). Of course, no one has ever found much of a coil developed on such small individuals of *Gryphaea arcuata.*

In summary, it is not likely that *Gryphaea arcuata,* or any other extremely coiled gryph-shaped oyster species, suffered from hypertely and became extinct because of starvation or inability to reproduce caused by impinging valves. It is more probable that this species became extinct because it was in direct competition with at least four other species of the genus living in the same seas.

GRYPHAEA AND DESCENDANTS

After gryphaeas migrated during the early Liassic from the Arctic realm into the sea covering western and central Europe, the chief flowering period of the genus began. Numerous species evolved; their fossil remains are found in the European Jurassic wherever the sedimentary environments were favorable. Among the latest species in that area were *Gryphaea dilatata* J. SOWERBY, 1816 (see ARKELL, 1932-36, p. 160-170, text figs.) from Coral-

lian beds of England, also recorded as far east as Lithuania (KRENKEL, 1915, p. 300-301) and the Negev Desert in Israel, and *G. lituola* LAMARCK, 1819 (see LEMOINE, 1910, fiche 201-201a) from Oxfordian and Kimmeridgian beds of France and England. The disappearance of *Gryphaea* in the highest Jurassic beds of western Europe is probably not so much caused by extinction as by lack of suitable environments in this area.

ARKELL (1934, p. 64) noted several separate branches or lineages among the Jurassic gryphaeas and named them *Bilobata, Dilatata,* and *Incurva.* However, he did it in a manner admittedly unacceptable in formal zoological nomenclature. The three names remain unavailable. Chains of successional species were recognized early (SCHÄFLE, 1929, p. 79; ZEUNER, 1933b, p. 317; DECHASEAUX, 1934). Some of the phylogenetic sequences are reliably reconstructed, because successive species are connected by forms transitional between species (CHARLES, 1949; CHARLES & MAUBEUGE, 1952a; 1953a; 1953b). Four lineages were recognized among species in the stratigraphic section from Hettangian to Bajocian of the Paris Basin, including Belgium, northern France, and Luxembourg by CHARLES (1949) and CHARLES & MAUBEUGE (1952a). However, they refrained from giving formal subgeneric names to them, though they selected a type species for each. According to CHARLES & MAUBEUGE these lineages originated during the Jurassic, but it is quite possible that some of the differentiation took place in the Late Triassic. In any case, they furnish no argument whatsoever in favor of polyphyletic origins.

Among later species of *Gryphaea* in Jurassic deposits, certain traits seemingly foreshadow transitions to *Texigryphaea* and *Pycnodonte.* These traits are a broad and deep posterior sulcus dividing the left valve, an ill-defined smooth rounded radial keel running down the main body of the left valve, a slight amount of compression of the left valve in anteroposterior direction, a three-dimensional spiral growth pattern, a more opisthogyral left beak, and sharp radial grooves or gashes on the right valve. These are traits that are considerably enhanced in *Texigryphaea* and *Pycnodonte* of the Cretaceous. Why should such traits make their foreshadowing appearance on

Late Jurassic species of *Gryphaea,* unless *Texigryphaea* and *Pycnodonte* are the direct Cretaceous descendants of *Gryphaea?*

HILL & VAUGHAN (1898), in reviewing Lower Cretaceous gryphaeas of the Texas region, described species most of which are nowadays classified as *Texigryphaea* (STENZEL, 1959). They were strongly convinced that the texigryphaeas were descended from Jurassic gryphaeas (HILL & VAUGHAN, 1898, p. 32).

In a phylogenetic diagram (HILL & VAUGHAN, 1898, p. 65, fig. 2) they showed only Cretaceous species from the Texas region. For this reason Jurassic ancestors were omitted and the oldest known species from Cretaceous rocks of the Texas region, named *"Gryphaea" wardi* HILL & VAUGHAN, 1898, was entered as the group's primogenitor.

"Gryphaea" wardi (HILL & VAUGHAN, 1898, p. 49-50, pl. 1, fig. 1-16; STANTON, 1947, p. 27-28, pl. 14, fig. 1-3, 6-11, 13) is from the Glen Rose Limestone (Alb.) of western Travis County, central Texas. Its stratigraphic level is about 350 feet (=100 m.) below the top of the formation, which is truncated by a transgressive regional disconformity at the base of the overlying Walnut Formation (mid-Alb.). The latter formation contains countless *Texigryphaea mucronata* (GABB, 1869) [called *G. marcoui* by HILL & VAUGHAN; it is not the *G. mucronata* of HILL & VAUGHN]. The 350 feet of beds between the two is barren of fossil oysters, so that HILL & VAUGHAN's statement that "the two undoubtedly grade into each other" cannot be correct.

HILL & VAUGHAN's diagram and statements have misled later authors to accept *G. wardi* as the ancestor of *Texigryphaea,* and as proof that the latter descended from a line of simpler ostrean ancestors, meaning ancestors that were more primitive than *Texigryphaea* and were *Ostrea*-like, not showing any strong homeomorphy with *Gryphaea s.s.* (KITCHIN, 1912, p. 593; ARKELL, 1934, p. 60; TRUEMAN, 1940, p. 83; GEORGE, 1962, p. 11-12). These authors considered *G. wardi* as one of the last species in a line of simpler ostrean ancestors. ARKELL identified it as a *Catinula,* a genus that had its acme in the Jurassic.

All shells of *G. wardi* are quite small, much smaller than any full-grown *Texigryphaea* from beds above the Glen Rose

Limestone. The largest at hand is 29.6 mm. long and 25.5 mm. high. They have orbicular muscle imprints, vesicular shell structure in both valves, vermicular ridgelets on the commissural shelf of the upper valves, and corresponding pits on that of the lower valves. These features securely place the species in the subfamily Pycnodonteinae and remove it from *Catinula* and from *Gryphaea*. The attachment area of the species is large; in the largest specimen at hand it is 28 by 24 mm. Because of the large attachment area on the left valve, there are equally large areas on the right valve covered with xenomorphic sculpture. The shell rises steeply from the attachment area as in many of the Gryphaeidae. There are scattered rounded radial ribs on the left valve visible where the valve rises steeply from its attachment.

"*Gryphaea*" *wardi* is a neotenous species of *Pycnodonte (Costeina)* and takes its place with the other radially costulated pycnodontes such as *P. (C.) costei* (Coquand) (1869, p. 108, pl. 26, fig. 3-5, pl. 38, fig. 13-14) from Santonian beds of Martigues, France. It is not considered to be a direct ancestor of *Texigryphaea,* but is a separate lineage of the Pycnodonteinae.

Whatever its generic assignment may be, it is not a simple or primitive ostrean, but a fairly advanced species of the Gryphaeidae. As such it differs much from *Liostrea,* the alleged ancestor of *Gryphaea,* so that the two can not be united as a persistent oyster stock of similar primitive oysters from which *Gryphaea* and its homeomorphs are supposed to have evolved by iterative evolution. Rather, *Gryphaea* itself is the ancient monophyletic root-stock of one of the two branches of oysters, namely the Gryphaeidae; several mutually unrelated genera similar to *Gryphaea* have evolved at various times either from *Gryphaea* itself (*Gryphaea* descendants) or from a few not gryphoidally incurved unrelated genera of the Ostreidae (*Gryphaea* homeomorphs).

Texigryphaea probably evolved directly from *Gryphaea,* but the series of transitional species linking the two at the turn from Jurassic to Cretaceous is largely incomplete. *Texigryphaea* first appeared in abundance as an immigrant with the invasion of the sea that deposited the mid-Albian Fredericksburg Group (including the Walnut Formation) in southwestern North America. The last of the *Texigryphaea* species is *T. roemeri* (Marcou, 1862) from the Grayson Clay (Cenoman.) of Texas and northeastern Mexico (Stenzel, 1959, p. 22, fig. 1-2, 6, 13, 17a,b). The most extreme species is *T. navia* (Hall, 1856, pl. 1, fig. 7-10; Stanton, 1947, p. 27, pl. 19, fig. 1-2), which has the most prominent keel and is more oblique and more compressed than the other species. It is from the Kiamichi Formation (mid-Alb.) and synchronous beds in southwestern North America. Geographic distribution of the genus is distinctly provincial. *Pycnodonte* shares vesicular shell structure with *Texigryphaea,* and probably both had a common ancestor which descended from *Gryphaea.* The most ancient *Pycnodonte* species known today are *P. (Costeina) wardi* (Hill & Vaughan) and *P. (Phygraea) vessiculosa* (J. Sowerby, 1822) (see Woods, 1913, p. 374-375, pl. 55, fig. 10-14, pl. 56, fig. 1), which made its earliest appearance in the Shenley Limestone (l.Alb.) of Leighton Buzzard, Bedfordshire, and in Bed 3 of the Folkestone Beds (l.Alb.) of Folkestone, Kent, England (letter from R. Casey, July, 1961). One of the latest species is *P. queteleti* (Nyst) from lower Oligocene beds of Zuid Limburg, Netherlands (Albrecht & Valk, 1943, p. 121-122, pl. 12, fig. 405-407).

Whereas *Texigryphaea* never produced more than a few provincial species, *Pycnodonte* became prolific in species and attained worldwide distribution. In the Miocene it gave rise to *Neopycnodonte,* which is represented today by a living species of circumglobal distribution. *Hyotissa,* also living today, is probably one of the descendants of *Pycnodonte.*

The descendants of *Gryphaea,* the Gryphaeidae, had their acme in the Cretaceous, and have gradually dwindled since that time. Today, they are a small group of only two genera.

SPECIATION

Speciation, or the making of a species, takes place among oysters chiefly in two ways: by successional speciation (Huxley, 1943, p. 172-173, 385-386) and by geographic separation.
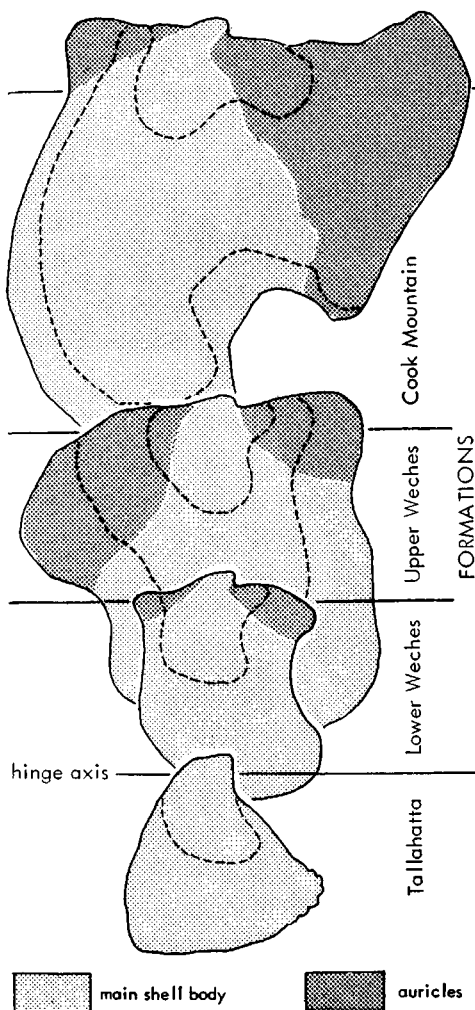
FIG. J68. Evolution and successional speciation in the *Cubitostrea sellaeformis* (CONRAD) stock, mid-Eoc., Gulf and Atlantic Coastal Plain, N. Am., ×0.5 (Stenzel, 1949). [Outlines of LV of large specimens in each species arranged in stratigraphic sequence.]

the ancestor species into two or more separates. Then, lack of gene exchange allows the separate populations to drift apart genetically. It produces two or more descendent species from one ancestor species. The phylogenetic diagram depicting this sort of speciation has a dichotomous, trichotomous, or polychotomous arborescent configuration.

SUCCESSIONAL SPECIATION

Successional speciation among oysters was demonstrated by STENZEL (1949) on the stock of *Cubitostrea sellaeformis* (CONRAD, 1832), consisting of four widespread mid-Eocene species distributed along eastern and southern shores of North America (Fig. J68, J69). Each species is distinguished readily by its morphologic shell features. Transitions between them are not found, because the four species are sepa-

Successional speciation is the very slow and gradual transformation of a large interbreeding population composing a species into a successor species. Time is the main factor at work. It produces a single file of successive species, and the phylogenetic diagram depicting this sort of speciation is a single unbranched line (Fig. J68).

Geographic separation divides a species of extensive geographic range by a barrier and breaks the interbreeding population of
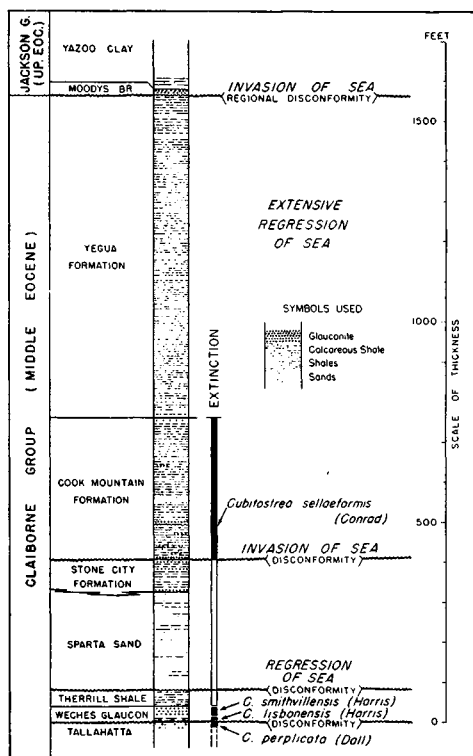

FIG. J69. Stratigraphic distribution of four successional species composing *Cubitostrea sellaeformis* stock in Gulf Coastal Plain of North America (Stenzel, 1949).
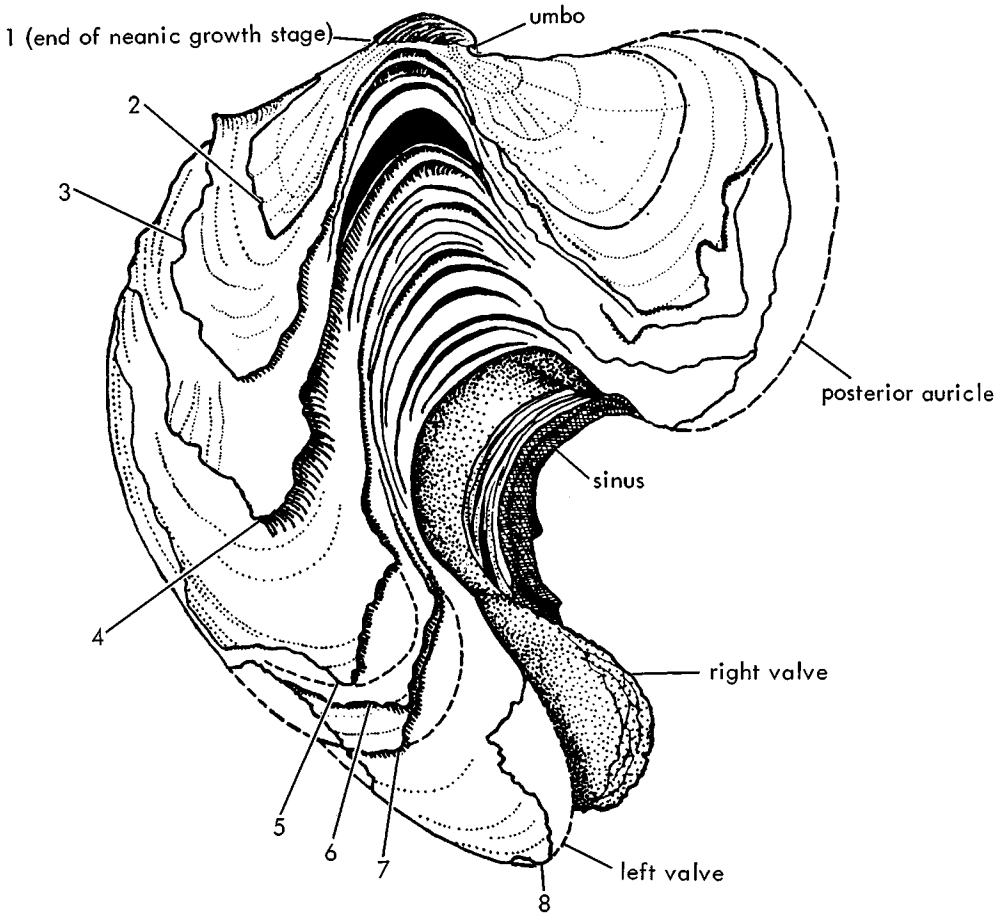
Fɪɢ. J70. Full-grown shell of *Cubitostrea sellaeformis* from Archusa Marl of Cook Mountain (Wautubbee) Formation, mid.Eoc., near Wautubbee, Clark County, Miss., USA, ×0.6 (Stenzel, 1949).

Eight major imbrications, numbered 1-8, probably indicate an age of eight years for this individual. Oblique posterior view seen at approximately 45° to hinge axis, showing very large posterior auricle and very twisted valve commissure. RV largely hidden by LV; RV stippled.

rated by nonmarine deposits containing no oysters or by recognizable disconformities, indicating absence of any deposits.

Among several distinguishing features is the size of each species. A size increase from one species to the next is demonstrable by measuring the maximal sizes (maxima of heights of the shells) obtainable in extensive collections (e.g., *Cubitostrea sellaeformis* (Cᴏɴʀᴀᴅ, 1832), 18.2 cm. (Fig. J70); *C. smithvillensis* (Hᴀʀʀɪs, 1919), 14.7 cm.; *C. lisbonensis* (Hᴀʀʀɪs, 1919), 8.6 cm.; *C. perplicata* (Dᴀʟʟ, 1898), 6.4 cm. (Fig. J43; see Fig. J116, J117)).

The lineage became extinct with *Cubito-*

strea sellaeformis, which is an index fossil of the Cook Mountain Formation and its lateral contemporaneous extensions (Fig. J70).

Because successional speciation involves the entire interbreeding population composing a species, no evolutionary laggards are left and it is impossible for two such species to exist side-by-side simultaneously. If such a situation had been in existence at any time, the two species would have interbred readily and the distinctions between them would have disappeared thereby. As a consequence, successional speciation produces reliable chronologic time markers

and the species can be used as index fossils in stratigraphy.

Two obvious shortcomings affect their use, however. Because transformation in so large an interbreeding population can proceed only very slowly (MAYR, 1942, p. 236), the chronologic time span of each species is fairly large. Therefore, successional oyster species have no great resolving power in stratigraphic chronology.

As illustration of this conclusion, oyster species used in Mesozoic stratigraphy and derived by successional speciation have much larger time spans than ammonites associated with them. An oyster species of this sort runs through several ammonite zones. *Gryphaea arcuata* LAMARCK, 1801, is found in at least three ammonite zones of the Liassic (CHARLES, 1949, p. 40; ARKELL, 1933, p. 120-149).

Nevertheless, STEPHENSON (1933) used species of *Exogyra s. s.* with good success as zone and index fossils to divide the Upper Cretaceous strata of the Atlantic and Gulf Coastal Plains and to trace the zone of *Exogyra (Exogyra) cancellata* STEPHENSON (1923, p. 182, pl. 50, fig. 5-6) for at least 4,000 km.

STENZEL (1949, p. 42-45) proved that all deposits containing *Cubitostrea sellaeformis* from Maryland to Mexico were part of the Cook Mountain Formation or its equivalents and belonged to the middle of the Claiborne Group. Thereby he proved that the Santee Limestone of South Carolina, which contains this species, had been misplaced in the Jackson Group.

The second shortcoming is the provincial distribution of oysters. Oyster stocks undergoing evolution as successional species must remain in a geographically circumscribed province. The *Cubitostrea sellaeformis* stock is found only from Virginia to the Gulf of Mexico, that is, along the ancient eastern and southern coasts of North America. Contemporaneous beds in the Paris or London Basins do not have it. *Exogyra cancellata* is found only along the ancient eastern and southern coasts of the Late Cretaceous North American continent, but is absent from contemporaneous deposits of the Western Interior of North America.

GEOGRAPHIC SEPARATION

This well-known cause of speciation (MAYR, 1942) affects mostly shallow-water oyster species living along shores and can become effective in several ways. Change in climate can make a stretch of the geographic range of a species uninhabitable to this oyster and divide the range into two separate parts. Or, tectonic events or falling sea level may raise a land barrier splitting the range into two.

For instance, the land bridge connecting North America with South America is a comparatively recent result of tectonic movements in Central America. Previously, the Pacific Ocean communicated with the Gulf of Mexico through a sizeable gap, and most probably a species of *Crassostrea* ranged through the gap from the western coast of North America to the Gulf of Mexico and the eastern coast of the continent. As the gap closed, the range of the species became divided, and two separate species arose from the separated populations: *C. corteziensis* (HERTLEIN, 1951) ranges from Panama to the head of the Gulf of California and *C. virginica* from Yucatan to the Gulf of St. Lawrence. The two are daughter species of a common Pacific-Atlantic ancestor species of Miocene and Pliocene age. This is a case of dichotomy by geographic separation.

An interesting case of polychotomous phylogeny is the stock of *Crassostrea gryphoides* (VON SCHLOTHEIM, 1813, p. 52), a gigantic oyster (see p. N1027) of very great west-east range during Miocene time, which has aroused interest since 1763 because of its large size (RUTSCH, 1955). This reef-forming brackish-water ancestral species has received many formal names based on local races and variants in shell shape and has been found in Miocene deposits of the Tethys Sea and its branches from Portugal, Spain, and Morocco in the west to Czechoslovakia, Austria, Cilicia in Asia Minor, and Somalia (AZZAROLI, 1958, as *Somalidacna lamellosa,* see Fig. J102) and into Japan in the east. It is evident that these occurrences from Portugal to Japan are all of the same species, because they fall into a former continuous open west-east seaway

of Miocene time, the ancient Tethys Sea, along which climates were fairly uniform and warm, varying from tropical to desertic. Neither climate nor land barriers existed to prevent this species from spreading the full length of the seaway.

Toward the end of Miocene time and later, tectonic events produced several land barriers across the former seaway, breaking it up into separate sea basins, gulfs, or bays. The separate populations left behind in these broken remnants of the Tethys Sea gave rise to three, or possibly more, local species of *Crassostrea: C. angulata* LA-MARCK, 1819, on the shores of Spain, Portugal, and Morocco; *C. cattuckensis* (NEW-TON & SMITH, 1912) [=*C. madrasensis* PRESTON, 1916] on Indian Shores; and *C. gigas* (THUNBERG, 1793), China, Japan, to Sakhalin Island (see p. *N*1037-*N*1038). At least two of these three daughter species have retained the ability to grow to extraordinary size, a feature that so characterizes their ancestor *C. gryphoides*.

The earth movements that raised the land barriers and broke up the ancient Tethys Sea were synchronous. They were part of widespread tectonic disturbances that were synchronous as far as geologic evidence indicates. Therefore, the three above-mentioned species presumably arose simultaneously. This idea is contrary to the belief that one species can give rise to three descendent species only by two successive dichotomies.

Some aspects of the geologic history of the stock of *Crassostrea gryphoides* have been discussed by DOLLFUS, DOLLFUS & DAUTZENBERG, and RUTSCH (1915; 1920, p. 465-471; 1955). Many formal species names have been proposed and are nomenclaturally available for this species. Some of the names were published in the same work by VON SCHLOTHEIM (1813). The species name used here has been selected by RUTSCH, whose decision as the first reviser must be respected according to *Code* (1961, 1964) Article 24 (a)(i).

CLASSIFICATION

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