FUNCTIONAL MORPHOLOGY, ECOLOGY, AND EVOLUTIONARY CONSERVATISM IN THE GLYCYMERIDIDAE (BIVALVIA)

by R. D. K. THOMAS

ABSTRACT. Since its appearance near the beginning of the Cretaceous, the family Glycymerididae has retained the same simple shell form. Variation among species is largely restricted to differences in size and external sculpture. This evolutionary conservatism can be explained in terms of the morphology and ecology of *Glycymeris*. Bivariate and multivariate studies of interactions among shell characters show that individual parameters of the shell are closely interrelated; there are rigid geometrical and mechanical constraints on deviations from the simple form. Relative growth of most characters is not strongly allometric; where marked allometry does occur, notably in the growth of the ligament, it is directly related to the over-all size of the animal. Thus the potential for evolutionary change in shell form by heterochrony is limited. Glycymerid soft-part anatomy is unspecialized and the animal is functionally less efficient in several respects than more advanced bivalves. Glycymerids have apparently always occupied the same current-swept marine environments. They evolved as functional generalists, adapted to a physically rigorous environment. The compromises that were essential to this adaptation left the group with insufficient flexibility of form to radiate into a wide variety of environments, whence its conservatism.

EVOLUTION in the Glycymerididae has given rise to a group of species which is particularly conservative in its morphological diversity. These bivalves have always been adapted to the same narrow range of physically rigorous environments. The purpose of this paper is: (1) to document these assertions; (2) to review the soft-part anatomy of *Glycymeris* in relation to its functions; (3) to determine interrelationships among shell characters, and to develop an analysis of the geometrical constraints on glycymerid shell form; (4) to demonstrate relationships between shell form and mode of life; and (5) to argue that morphological compromises required by geometry and functional adaptation have made a significant contribution to the evolutionary conservatism of this group of bivalves.

The generic name *Glycymeris* is used in a broad sense here, to refer to all the species that properly belong to the Glycymerididae. Many other generic names are available but generally unsatisfactory, since they are not based on evolutionary relationships, which are largely unknown. *Glycymeris* is a generalized, free-burrowing descendant of the Arcoida, which was established as a distinct group early in the radiation of the Bivalvia. The animal has filibranch gills, subequal adductor muscles, unfused mantle margins, and a large axe-shaped foot. Its shell is subcircular or somewhat trigonal, usually symmetrical about the umbones, with a chevron ligament and an arched series of taxodont hinge teeth. The shell bears flat ribs and a heavy periostracum, or much more prominent ribs.

This paper is based on a detailed investigation of the Miocene–Recent glycymerids of eastern North America (Thomas 1970), and on the accumulated knowledge of the group as a whole. It presumes to be a synthesis, and sets out to provide a conceptual and methodological framework for future studies of evolution in the Glycymerididae. At the same time, many of its conclusions apply in varying degrees to other groups of bivalves.

EVOLUTION AND ENVIRONMENT

The purpose of this section is primarily to document the evolutionary conservatism of the Glycymerididae. This group has developed a narrow range of morphologies in its 130 million year history. Furthermore, the environments preferred by fossil glycymerids are essentially identical with those occupied by the group in present-day seas. This ecological information is important in the functional interpretation of glycymerid shell morphology.

Evolution of the shell. It has been convincingly shown, on the basis of shell morphology and stratigraphic ranges, that the glycymerids evolved from another arcoid family, the Cucullaeidae (Nicol 1950). The oldest known glycymerids occur in early Cretaceous sediments of northern France (Gillet 1924) and northern California (Stanton 1895). In both cases these rocks are now thought to be of latest Valanginian age (Corroy 1925; Debrenne 1954; Imlay 1959; Jones, Bailey and Imlay 1969). Well-documented Aptian and Albian glycymerids have been described from Europe and Japan. During the Upper Cretaceous the group achieved a world-wide distribution, but glycymerids of this age are only common in local areas.

The earliest glycymerid shells already have all the essential characteristics of the family (Pl. 38, figs. 11, 12). They are strongly convex, the shell material is relatively


EXPLANATION OF PLATE 38

Figs. 1-5. *Glycymeris subovata waltonensis* Gardner, all × 1·5. Series showing allometric growth of the ligamental area and increasing posterior elongation of the shell during ontogeny. Allometric growth of the ligament is required by function in all large glycymerids; posterior elongation is a burrowing adaptation developed only in some populations and species. Note isometric growth of the adductor scars, and progressive overgrowth of the hinge plate by the ligamental area. MCZ 17850. Shell Bluff, Walton County, Florida (loc. 10, Thomas 1970). Shoal River Formation, Miocene.

Fig. 6. *Glycymeris pulvinata* (Lamarck), × 1. A typical Eocene species. Note preservation of partially calcified ligament. BMNH LL 90512. Bracklesham Bay, Hampshire, England. Bracklesham Beds.

Fig. 7. *Glycymeris subovata* (Say), × 1. A large shell from its population, showing well-buttressed adductor scars and extensive disruption of hinge teeth by the ventrally expanding ligamental area. MCZ 17852. Colerain Landing, Bertie County, North Carolina (loc. 21, Thomas 1970). Yorktown Formation, Miocene.

Fig. 8. *Glycymeris americana* (Defrance), × 1. MCZ 17877. Dredged in 25 m of water off Cape Fear, North Carolina (loc. 49, Thomas 1970). Living.

Fig. 9. Periostracum of *G. americana*, × 45. Concentric rows of recurved barbs parallel the growth lines of the shell (vertical here). Radial rows of the same barbs are inserted in fine striations on the shell ribs (horizontal here). Barbs catch sand grains, helping to stabilize the shell in burrowing. Geol. Paläont. Inst. Tübingen, Scanning Electron Micrograph 40889/3029/1. Specimen from same population as fig. 8.

Fig. 10. *Glycymeris americana* (Defrance), × 1. Note striations, in which periostracum was inserted, on the low ribs. MCZ 17878. Winnabow, Brunswick County, North Carolina (loc. 39, Thomas 1970). Waccamaw Formation, Pliocene.

Figs. 11, 12. *Glycymeris umbonata* (Sowerby), × 1·5. Early glycymerids already had all the shell characters of later forms with low striated ribs. BMNH LL 27664, 27665. Blackdown, Dorset, England. Blackdown Sand, Albian, Cretaceous.

Fig. 13. *Glycymeris pectunculus* (Linné), × 1. A typical tropical species, with prominent unstriated ribs. BMNH 197445. Ceylon. Living.

All specimens are right valves, except fig. 7.

All coated with ammonium chloride, except figs. 9 and 13.

Specimens are lodged in the collections of the Museum of Comparative Zoology, Harvard (Invertebrate Paleontology) and the British Museum (Natural History; Mollusca and Invertebrate Palaeontology).

PLATE 38
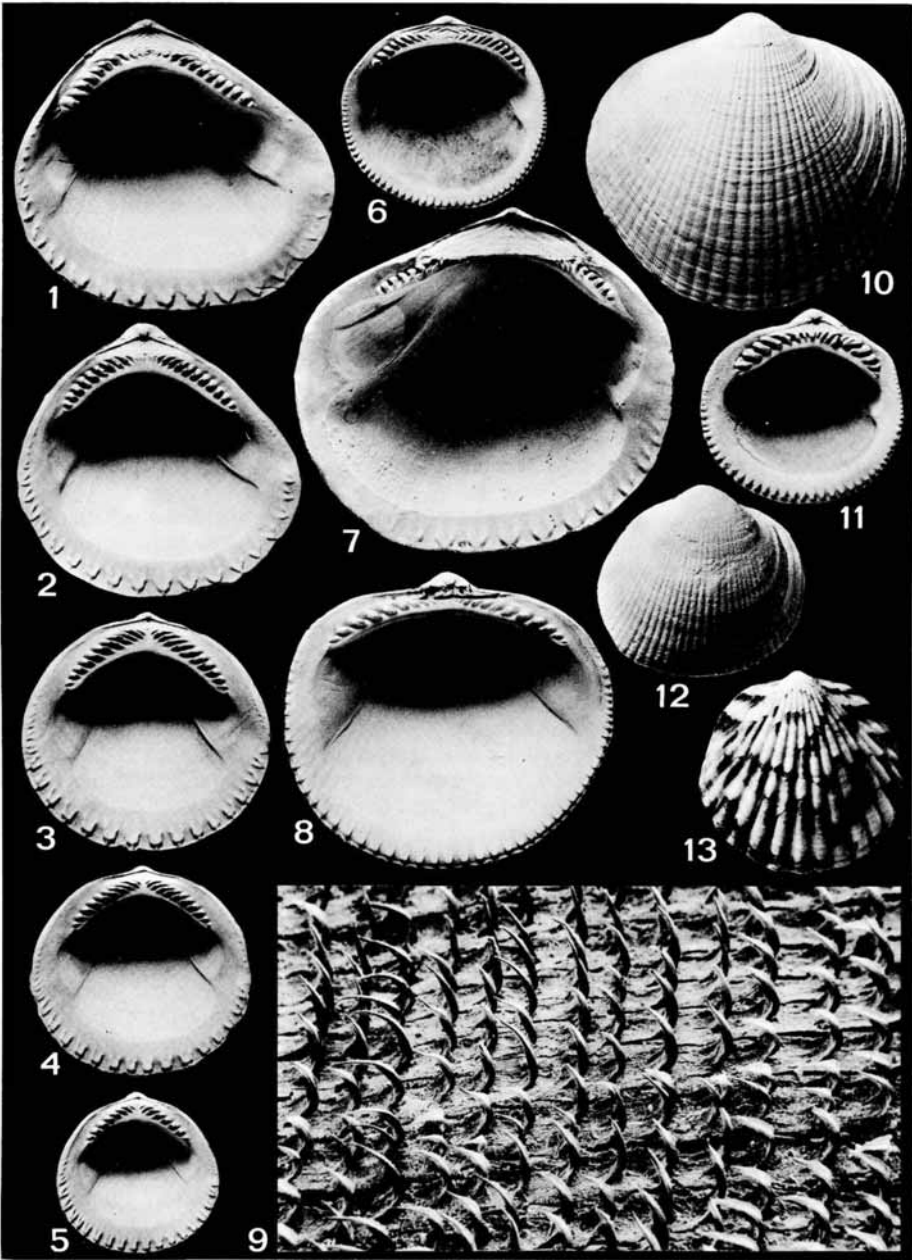
THOMAS, *Glycymeris*

thick, and they are more or less subcircular in shape. The adductor muscle scars are subequal, and the interior margins of the shell interlock by means of strong crenulations. The arched hinge plate bears similar anterior and posterior series of simple teeth, which may be straight, curved, or chevron-shaped, depending largely on the shape of the hinge plate and their positions on it. The large triangular ligamental area is symmetrical, and bears alternating chevron-shaped ridges and grooves, to which the duplivincular ligament was attached. The Cretaceous glycymerids are more particularly characterized by their modest size, a slight posterior truncation of the shell in several species, and their external sculptures. Apart from one or two uppermost Cretaceous species, their heights, or lengths, rarely exceed 25 mm. The posterior truncation may be compared with the flattened posterior margin of the ancestral cucullaeids; in contrast, several later glycymerid species tend to become slightly elongated postero-ventrally. The sculptures of the Cretaceous glycymerids are very subdued; they have low, rounded or flat radial ribs, generally bearing fine striations in which rows of periostracal hairs were inserted. In short, the Cretaceous glycymerids exhibit very little morphological diversity, and they can be assigned to relatively few species, although, like later members of the family, they frequently show considerable intraspecific variation.

During the Cenozoic the diversity of glycymerid species increased substantially, first in the Eocene, and then to a greater extent in the Miocene. The principal morphological modifications involved in this radiation were changes in size and shell sculpture. Species considerably larger and very much smaller than those of the Cretaceous appeared. Radial shell sculptures diversified in several different ways, the most notable development being the advent of forms with smaller numbers of prominent, unstriated ribs. As Nicol (1956) has shown, nearly all living glycymerids can be assigned to one of two broad groups of species. The group with subdued, striated ribs and well-developed periostracum (e.g. *G. glycymeris* and *G. americana*, Pl. 38, fig. 10) ranges from the tropics to the cool-temperate waters of Alaska and southern Chile. In contrast, the group with prominent unstriated ribs and little or no periostracum (e.g. *G. pectunculus*, Pl. 38, fig. 13, and *G. pectinata*) is confined to the tropics. The systematic relationships between species of the two groups have not been worked out, but it is clear that the Cenozoic radiation of glycymerid species occurred largely in tropical and subtropical waters.

Evolution within the Glycymerididae has led to considerable elaboration of the radial sculpture and large differences in size. Rotation of the plane of spiral growth has given rise, in a few species, to umbones facing anteriorly or posteriorly over asymmetric ligamental areas. Other variations are limited to minor, but functionally significant, differences in the convexity and shape of the shell. The fact remains that the fundamental characteristics of the shell, the hinge plate, ligament and muscle scars, have remained very stable.

Evolution of the soft parts. The most striking feature of glycymerid anatomy is that it is so little different from those of other arcoids, which are themselves remarkably undifferentiated. The Glycymerididae have not been shown to have any anatomical characteristics that are unique to the group, apart from the over-all shape of the animal. The similarities extend to quite minor morphological details. For instance,

Purchon (1957) found only minor differences between the stomachs of *Glycymeris* and *Anadara granosa*, while the gills and ciliation of the gill filaments are extremely similar in *G. glycymeris* and *Arca tetragona*, as shown by Atkins (1936). Likewise, variations in the size and number of folds of the labial palps among glycymerid species parallel similar variations among species of both *Arca* and *Anadara*.

The anatomy of *Cucullaea* has not been studied in detail, but the brief accounts of Pelseneer (1911) and Heath (1941) suggest that it is at least as similar to that of *Glycymeris* as those of any of the other arcoids, if not more so. The most apparent difference is that the adult *Cucullaea* retains a byssal cavity, although the animal is not known to secrete a byssus; adult glycymerids all appear to lose the byssal cavity. It is notable that in both *Glycymeris* and *Cucullaea* the ventricle surrounds the rectum. This character is shared with *Lunarca pexata* and *Trisidos* (see Heath 1941), neither of which appeared before the Cenozoic, while in all the other arcoids the rectum passes below the heart. This is not a character of high taxonomic significance, but it does corroborate Nicol's (1950) inference that the Glycymerididae evolved from the Cucullaeidae.

There is very little variation among the soft-part anatomies of even the most widely separated living glycymerid species. Minor variations in the thickness of the gill filaments and the development of the labial palps are apparent. In different species, the shape of the foot may be more or less elongated, and the eyes of the posterior mantle margin may be more or less numerous. These variations have yet to be systematically related either to adaptation to slightly different habitats, or to evolutionary relationships within the group. It is clear that very little diversification of the soft parts has occurred in the Glycymerididae.

Ecology of living species. Living glycymerids occur in normal marine, subtidal environments of the continental shelves. Although isolated individuals may be quite widely distributed, large populations occur sporadically in a narrow range of habitats. These environments are physically rigorous, and harbour faunas of low diversity, including few bivalve species at any one time and place.

The habitats of glycymerids with flat striated ribs and a hairy periostracum are quite well known. The geographic distribution of *G. glycymeris* in the English Channel has been mapped by Holme (1966, p. 409), who observed: 'In much of the western Channel the offshore areas consist largely of shelly sands or shell gravels, with many dead *Glycymeris* shells. The fauna is rather sparse. . . .' He goes on to note (p. 411) that this species prefers hard or gravel bottoms, where there is much water movement, and that 'they are common in tide-swept areas of the central Channel where little else occurs. They are absent from samples in the calmer waters with associated finer sediments. . . .' Holme's station data indicate that *G. glycymeris* is abundant on 'clean shell gravel', 'coarse silty sand and stones', and 'muddy fine gravel and shells', at depths between 16 and 100 m. Many earlier authors have recorded similar observations. Cabioch (1968) also found this species to be common on shell gravel bottoms, in what he calls 'le facies appauvrissement' on account of its limited fauna. *G. glycymeris* is sometimes common on firm sand bottoms, but the species does not occur today off the Dutch coast (Eisma 1966), where, although strong tidal currents occur, the bottom sediments are mostly fine and muddy sands.

Similar unstable sand and gravel habitats are preferred by *G. undata* in the Caribbean, *G. americana* off the eastern United States, and *G. modesta* around New Zealand. Data on these and other species have been compiled elsewhere (Thomas 1970). The environmental distribution of glycymerids with flat striated ribs is quite consistent from one region to another, and we may make the following generalizations. These species occur in both tropical and temperate waters, at depths between 3 and 130 m, although they are not usually common in water shallower than 10 m. They are found on clean sand, clean shell gravel, or muddy gravel bottoms. They favour turbulent waters and strong currents, but are intolerant of turbidity. They are typically associated with bottom communities of low faunal diversity. These factors will be related to the mode of life of *Glycymeris* in later sections.

Much less is known about the habitats of the tropical glycymerids with prominent unstriated ribs and little or no periostracum, so the distribution of *G. pectinata* around the Florida Keys may or may not be typical for these species. Stanley (1970) notes that: '*G. pectinata* prefers coarse, often grass-covered substrata in subtidal environments.' My own more extensive observations (Thomas 1970) indicate that this species occurs in three different situations. Occasional individuals are very widely distributed on off-shore, unstable, poorly sorted skeletal sands, in 2–5 m of water. The species is more common on very shallow subtidal gravel banks. These banks consist largely of broken branches of the coral *Porites*, together with mollusc shells and coarse skeletal sand; they are usually partially overgrown by *Thalassia* 'grass', and are often swept by strong tidal currents. However, *G. pectinata* was found to be most abundant in three sheltered bays, on the north sides of islands (text-fig. 1).
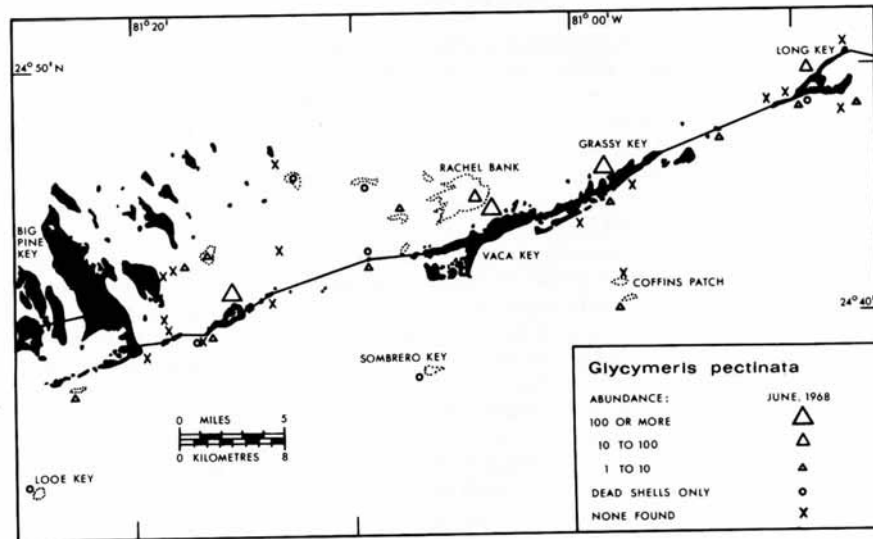
TEXT-FIG. 1. Distribution of *Glycymeris pectinata* (Gmelin) along the middle Florida Keys.

Here the animals were living, in the absence of other bivalve species, in very quiet water at depths of 1–4 m. The bottom sediment consisted of a thin, irregular veneer of poorly sorted coarse skeletal sand, and occasional shell gravel, overlying an eroded limestone platform. This environment is rather different from others in which glycymerids are known to occur, particularly in the absence of strong currents. However, like the current-swept shell gravels, it is an environment which is physically inhospitable to more specialized bivalves. The thin layer of sand provides insufficient cover for infaunal burrowers, but it is enough to inhibit those epifaunal forms which would attach to bare rock. The mobile shallow-burrowing glycymerid is able to take advantage of an otherwise empty habitat.

The environmental range of *G. pectinata* appears to be wider than those of other glycymerid species that have been studied. A similar Japanese species has been reported from coarse sand and shell gravel bottoms at 100–200 m (Okutani 1963). *G. laticostata* also has raised ribs, although they are not very prominent; this is a common species on hard, clean, shell gravel substrates in channels, off New Zealand (Powell 1936). Clearly, there are not enough data for generalizations to be made about the habitat preferences of the glycymerids with prominent unstriated ribs. The limited data suggest that they are not greatly different from those of the glycymerids with flat ribs, their different shell forms notwithstanding. The ecological differentiation of broadly sympatric glycymerid species has yet to be investigated, but it might be expected to shed some light on this problem.

Palaeoecology. It can be shown that glycymerid species have flourished, at least throughout the Cenozoic, and probably since they first evolved, in physical environments essentially identical with those enjoyed by their living descendants. This conclusion is based on lithological and palaeoecological observations; it specifically does not depend on analogy with the habitat of the living animals, or on arguments based on shell form.

I have made a detailed study of the occurrence of *G. americana* and *G. subovata* in the Neogene sediments of the Atlantic coastal plain of the United States (Thomas 1970). These species are abundant in shell beds, consisting of mixtures of broken, worn, and fresh molluscan shells, with a matrix of sand or muddy sand. The assemblages include species derived from a variety of environments, but the predominant species have usually not been transported very far (see Warme 1969; Hallam 1967; but cf. Fagerstrom 1964). Three main lines of evidence confirm that the glycymerids lived on these shell gravels and on unstable sandy bottoms. (1) The glycymerids are abundant in the shell beds, but they are only occasionally found in associated fossiliferous sands and clays. (2) Although the smallest shells have sometimes been winnowed or leached out of the assemblages, frequently complete size ranges, above about 5 mm, are represented. (3) Articulated valves are common in many of the shell beds. Where these are found with the valves gaping, limited transport might have occurred, but these shells are easily disarticulated (Craig 1967). More often, the shells occur with the valves closed, indicating that the animals were buried alive. Since these shells do not often appear to be in life position, it seems likely that the animals were washed out of their shallow burrows and suddenly buried during the last major reworking of the shell gravel in which they are entombed.

These observations confirm that, at least since the early Miocene, species in the
G. americana and *G. subovata* lineages have lived on subtidal sand and shell gravel
bottoms, often swept by fairly strong currents. Palaeogeographic considerations and
palaeoecological studies of several authors (reviewed in Thomas 1970) further
indicate that these sediments accumulated in inner-shelf environments at depths of
up to 50 m.

Similar palaeoecological conclusions have been reached by Báldi (1973), with
regard to *G. latiradiata*. This species is locally very abundant in shell gravels and
medium- or coarse-grained sands of the Hungarian Oligocene. These sediments
accumulated in turbulent, shallow subtidal environments. In the Paris Basin,
G. obovata is a characteristic species of the shallow-water sediments of the type
Stampian. Alimen (1936) describes this species as being very common, often with the
valves articulated, in fine shelly sands and fine gravels. One of the commonest species
in the Gosport Sand (Eocene) of Alabama is *G. staminea*. This glycymerid occurs in
a coquina of shells and shell fragments, with a matrix of clean sand, which is often
highly glauconitic. Gardner (1957) concludes that these sediments were laid down on
a firm, current-swept bottom, at a depth of less than 38 m. *Glycymeris* is also abundant
in sandy sediments of Palaeogene age on the Russian Platform (Semenova 1969).

Less information is available on the habitats of the Cretaceous glycymerids. In
the Nacatoch Sand (Maastrichtian) of Texas, *G. rotundata* occurs in indurated lenses
of shelly and glauconitic sand; it has not been found in the associated argillaceous
sediments. One of the earliest records of abundant, well-preserved glycymerids is
from the Upper Greensand (Albian) of south-western England (see Pl. 38, figs. 11, 12).
At the classic Blackdown locality, which has never been well exposed, *G. umbonata*
is the predominant fossil in Bed 7 of Downes (1882), who observes that the shells
occur in clusters, with the valves almost always attached. Downes was of the opinion
that the sandy sediment was deposited in still water, on account of the articulated
shells, and the lack of breakage and rolling of the fossils. However, the thickness of
the shells of several species, the abundance of glauconite (Tresise 1960), and the
grain size of the sediment suggest considerable water movement. Higher up in the
section, *Glycymeris* is again common, in lenticular bands of mostly broken and water-
worn shells.

Fossil glycymerids do occur in sediments other than those described above.
Nevertheless, these examples are representative of the situations in which they are
most abundant, and apparently in or near their preferred habitats. The physical
habitats have been emphasized here, since much less is known of the biological inter-
actions of *Glycymeris*, living or fossil, with other organisms. Off the east coast of the
United States a coherent group of species, which I have referred to as the *Eucrassatella-
Glycymeris* community (Thomas 1970), has existed at least from the early Miocene to
the present day. The Upper Oligocene *G. latiradiata* community, recognized in
Hungary by Báldi (1973), has much in common with the former community, includ-
ing the abundance of *Eucrassatella* and the presence of the deep-burrowing *Panopea*.
These communities, as well as those in which *Glycymeris* thrives today, belong to
the group of '*Venus* communities' recognized by Thorson (1957). *Glycymeris* has
apparently always been associated with communities of this type. Some more specific
interactions can also be recognized. Throughout the Neogene, the American

glycymerids *G. americana* and *G. subovata* were subject to similar, albeit very variable, rates of predation by gastropods, principally naticids. Over the same period, their liability to infestation by the shell-boring polychaete *Polydora* showed no directional change (Thomas 1970).

Synthesis. Glycymeris is a mobile shallow-burrowing bivalve. It lies at shallow to intermediate depths on the continental shelf, and no glycymerid is known to have ventured either into brackish water or the deep oceans. Large populations of gly-cymerids occur in patches on clean sandy or coarse bottoms, often swept by strong currents. These are physically rigorous environments which support biocoenoses of low diversity. Glycymerids are in every respect typical opportunistic species (MacArther 1960; Levinton 1970). The distributions of their populations in time and space, within the environmental ranges of the species, are determined by variable and unpredictable factors. The establishment and extirpation of these local popula-tions are presumably largely controlled by random spatfalls (cf. *Mulinia lateralis*, Levinton 1970) and the stability of the substrate. Salinity and the availability of sufficient dissolved oxygen are essentially invariant in the environments preferred by glycymerids, while temperature variations should rarely exceed the tolerances of the species. The fact that most opportunistic bivalves are suspension feeders implies that fluctuations in food supply may also limit their distribution. The availability of suit-able phytoplankton is likely to be particularly critical for glycymerid veligers and spat, primarily limiting recruitment and the establishment of new populations.

The fossil record of glycymerid shells and the soft-part anatomies of the living animals, expressions of the limited morphological diversity of the Glycymerididae, confirm the evolutionary conservatism of this family. Palaeoecological observations show that these animals have lived as opportunistic species in similar environments for most, if not all, of their history. In the following sections the morphology and physiology of *Glycymeris* will be considered in terms of environmental adaptation, and related to this evolutionary conservatism.

GENERALIZED ANATOMY AND PHYSIOLOGY

The soft parts of *Glycymeris* are quite unspecialized, and there is little differentiation among the living species that have been studied. This lack of specialization reflects both its derivation from the ancient arcoid lineage and its own secondary adaptations. The following discussion of some functionally significant points is based on many detailed studies of *G. glycymeris*, several accounts of other species, and my own observations of *G. americana*, *G. pectinata* (text-fig. 2), and *G. glycymeris*.

Glycymeris is a mobile burrower in resistant sands and gravels. As such, it has a massive muscular foot, which is suspended from the shell by four large pedal retractor muscles. The pedal retractors, together with the pedal protractor muscles, form a muscular sheath which encloses the foot and viscera. The interior of the foot and the visceral cavity are crossed by bundles of transverse muscle fibres, which with the muscles of the sheath control the hydrostatic dilation and retraction of the foot (Heath 1941). The haemocoele extends ventrally into the foot, and the blood constitutes the fluid of this fluid/muscle system (Ansell and Trueman 1967). The base
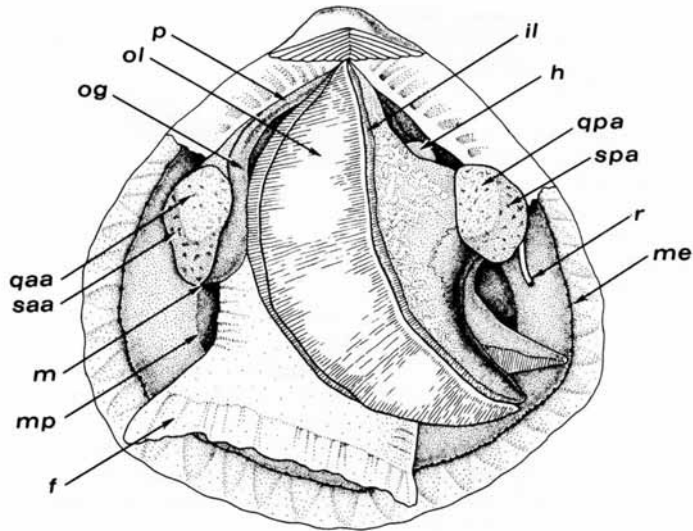
TEXT-FIG. 2. Gross anatomy of *Glycymeris pectinata* (Gmelin), ×4·5. *f*, foot;
mp, inner mantle surface; *m*, mouth; *saa*, *qaa*, slow and quick anterior adductor
muscle; *og*, oral groove; *ol*, ascending lamella of outer demibranch; *p*, labial palps;
il, descending lamella of outer demibranch; *h*, heart; *qpa*, *spa*, quick and slow
posterior adductor muscle; *r*, anus; *me*, eyes on the second fold of the (retracted)
mantle margin. Drawing by Laszlo Meszoly.

of the foot is divided by a deep longitudinal cleft into left and right lobes, which are
spread sideways to form the pedal anchor in burrowing (see p. 242). There is no
byssus or byssal gland in the foot of the adult glycymerid.

Notwithstanding its impressive foot, *Glycymeris* is a slow burrower (Ansell and
Trueman 1967; Stanley 1970). The foot takes a long time to probe the substrate,
largely because the ligament is weak and unable to brace the shell firmly against the
sediment. When *G. glycymeris* is more than one-third buried the ligament is not
strong enough even to open the valves against the sand, and they have to be forced
apart by the foot (Trueman 1968). Unlike bivalves in which the viscera lie up against
the shell, *Glycymeris* is unable to use its adductor muscles in the extension and dila-
tion of its foot, since the mantle cavity extends dorsally almost to the umbones (Ansell
and Trueman 1967). Moreover, since the mantle margins are entirely unfused,
closure of the shell by the adductors cannot be used to raise the hydrostatic pressure
in the mantle cavity; in many bivalves such pressure also helps to force blood from the
viscera into the expanding foot (Trueman, Brand and Davis 1966). In *Glycymeris*
the highly developed muscular sheath and transverse muscles of the foot and visceral
cavity partly compensate for the lack of these special adaptations.

Although the burrowing of *Glycymeris* is slow and mechanically inefficient, com-
pared with that of more specialized bivalves, the animal does move around a good

deal, principally at night. When washed out of their shallow burrows, or otherwise disturbed, glycymerids plough considerable distances along the sediment surface in search of a suitable new substrate, leaving meandering furrows behind them (Thomas 1970; Stanley 1970). Lacking siphons, glycymerids are normally just covered by the sediment, with their posterior-ventral mantle margins exposed at the sediment surface. In gravel they may burrow deeper, and can apparently obtain adequate feeding and respiratory currents through the sediment (Ansell and Trueman 1967). The attachment of several epifaunal species to the posterior-ventral margins of many living glycymerids (Thomas 1970) and the presence of well-developed mantle eyes in this region confirm that they are normally exposed at the surface. In the case of fossil glycymerids, the same conclusion can be drawn from the frequent abundance of polychaete shell-borings with their openings along this part of the shell margin.

Glycymeris is a suspension feeder, with large filibranch gills that have been described in great detail by Ridewood (1903) and Atkins (1936). The gill axes are attached dorsally to the mantle, very high up, under the hinge plate (text-fig. 2). They extend steeply downwards to the posterior-ventral margin, reaching it at the point where the two mantle lobes remain in contact during feeding, and thereby separating the posterior inhalant and exhalant currents. The individual gill filaments are attached to one another by interlocking cilia, but their distal ends are not attached to either the mantle or the wall of the visceral cavity. As a result, the inhalant and exhalant chambers of *Glycymeris*, like those of other arcoids, are not as effectively separated as they are in more advanced bivalves.

In addition to the posterior inhalant current, *G. glycymeris* has a subsidiary anterior inhalant current (Atkins 1936). This anterior current, which is thought to represent the primitive bivalve condition (Yonge 1953, 1955), is typical of byssally attached arcoids such as *Arca tetragona* and *Anadara antiquata*, but it is lost in many burrowing forms (Lim 1966). It is not known whether most or only some *Glycymeris* species have such an anterior inhalant current, but those which do must be restricted to coarse, clean, permeable substrates, as noted by Stanley (1970). *Glycymeris* and the other arcoids are also unusual in that they have rejection currents which run posteriorly along the lower margins of the demibranchs, carrying denser particles to the mantle margin, where they are discarded as pseudofaeces (Atkins 1936). The direction and function of these currents may be related to the ancestral anterior-to-posterior direction of the feeding currents; in almost all other living bivalves these currents run anteriorly, carrying food to the labial palps.

All the glycymerid species so far described have very simple palps, with only three or four weakly developed folds. This condition is primarily responsible for their intolerance of fine-grained substrates and turbid water. Furthermore, the Caribbean species *G. pectinata*, which does live in rather more turbid water (see p. 223), has more substantial palps, with a dozen or more clearly defined folds. A similar relationship between the development of the palps and turbidity is seen in other arcoids, and has been well demonstrated among species of *Anadara* by Lim (1966).

Food particles collected by *Glycymeris* travel a roundabout route in order to reach the stomach. They are collected and carried postero-dorsally on the gill filaments, and then dorsally up the gill axis to the labial palps, at the very top of the animal. They must then return ventrally down the long oral groove to the mouth,

whence they are carried dorsally again by the oesophagus and into the stomach. In many more advanced bivalves the oral groove is shortened or lost, bringing the palps and the ends of the gills much closer to the mouth. In most bivalves food is carried towards the mouth along both the top and the bottom of each gill lamella, but in *Glycymeris* the ventral margins are occupied with the removal of rejected particles, as noted above.

The structure and function of the glycymerid stomach have been exhaustively described, most recently by Reid (1965). Authors agree that this stomach, which does not differ greatly from those of other arcoids, is simple and unspecialized compared with those of most other bivalves. It is likely that easily digested naked phytoplankton, as opposed to forms with thick cell walls, are the principal source of food for suspension-feeding bivalves such as *Glycymeris* (Jørgenson 1966).

Most bivalve tissues have low oxygen requirements, and it has been generally assumed that the gills are potentially more efficient as respiratory organs than is necessary for the life of the animals (e.g. Ghiretti 1966). Food gathering is certainly the primary purpose of their hypertrophy and specialization. On the other hand, great improvements in the pattern of blood circulation through the gills have been made in the more advanced bivalves, suggesting that the more primitive gills were not in every circumstance more than adequate to fulfil their respiratory function. In *Glycymeris*, as in all arcoids, both the afferent and the efferent blood vessels are located in the gill axis. As a result, blood flowing into each filament must travel down the descending limb and up the ascending limb of the filament, and then all the way back, the two streams being separated by a median septum. Clearly this is an inefficient system compared with those of *Mytilus* and the eulamellibranch bivalves, where the oxygenated blood flows into efferent vessels which run along the distal margins of the demibranchs.

Haemoglobin has been found in the blood of some species of *Glycymeris*, but in others it appears to be absent (Manwell 1963). In a single population of *G. violacescens*, some animals were found to have dark-red blood, others had less haemoglobin, and some had none at all (Kruger 1958; his *G. nummaria*). On the basis of its haphazard distribution among closely related molluscs, and because its occurrence is not correlated with life in oxygen-poor habitats, Read (1966) infers that haemoglobin is of minor importance to these animals. However, in view of the limitations of the respiratory circulation discussed above, it is surely significant that the occurrence of haemoglobin is far more widespread in the Arcoida than in other bivalve groups (data in Read 1966).

Little is known about the reproduction of *Glycymeris*. In common with most other bivalves, these animals show no sign of sexual dimorphism in their shells, and they have been assumed to be truly dioecious. However, Lucas (1964, 1965) has presented evidence that is suggestive of protandry in *G. glycymeris*.

Although the Glycymerididae did not appear until the Cretaceous, *Glycymeris* can nevertheless be regarded as a primitive bivalve in the sense that it is an anatomically and functionally generalized descendant of an ancient and very conservative stock. As such, its potential for evolutionary radiation into new environments has been severely limited by its unspecialized burrowing, feeding, and respiratory mechanisms. On the other hand, the particular combination of adaptations acquired

by *Glycymeris* evidently serves it well in the limited range of habitats it prefers. *Glycymeris* is at least as well adapted for life in these physically rigorous environments as any other bivalve.

FORM AND FUNCTION OF THE *GLYCYMERIS* SHELL

The glycymerid shell is a geometrically very simple structure. Nevertheless, it must fulfil three different functions simultaneously: it is at once a protective armour, a skeletal support for the soft tissues, and a burrowing plough. As in other molluscs, the morphology of this shell is determined both by functional requirements and by the constraints of accretionary growth (Stasek 1963; Raup 1966). Growth of the shell is largely isometric, the adult proportions being established in most cases by the time it is about 5 mm high. Relative growth in the early shell has not been studied, but two kinds of allometry, with consequent changes in shape, occur in later ontogeny.

The size of the ligamental area increases exponentially relative to that of the shell as a whole, during ontogeny. This allometry is a functional necessity, as will be shown below, so it occurs in all glycymerid shells except perhaps for very small species. Exponential growth of this kind has its greatest effect when the animal is large, and it places strict limits on potential size increase, as long as the rates of relative growth are unchanged. In contrast, the posterior-ventral margin of the shell may become relatively elongated with increasing size, as a result of differential, but linearly related, growth rates. This allometry is not required by the basic mechanics of the shell, so the adaptation only appears in some species and populations. Here the greatest change in proportion occurs when the shell is small, and no limitation is placed on size increase.

The forms of individual elements of the glycymerid shell will be considered here in relation to their functions. Much of what follows is based on detailed studies of about fifty samples from populations in the *G. americana* and *G. subovata* lineages, from the Neogene sediments of the eastern United States. Parameters measured and referred to here are shown in text-fig. 3 and Table 1. More of the statistical data of this study is given in Thomas (1970). A similar study of one of these populations, of *G. parilis*, has been made by Brower (1973). The following analysis is based on these studies, and on more general observations of a wide range of living and fossil glycymerids. It will become clear that different functions make conflicting demands upon the shell, and that its simple geometry results from a series of compromises among these requirements. Such compromises have left *Glycymeris* well adapted to its particular habitat, but with little evolutionary flexibility, due to the high degree of morphological integration of its shell characters.

Adductor muscle scars. Glycymeris is the archetypical dimyarian. Its subequal adductor muscles are symmetrically disposed behind and in front of the umbones, and are essentially equidistant from the hinge axis. Quick and slow muscle are present in both adductors. As in most dimyarians, the quick muscle constitutes the more dorsal portions of the adductors, where a smaller contraction is necessary to close the valves completely, and hence quickly (cf. the position of the adductors in *Ensis* (Trueman 1967) and the quick muscle in scallops (Gould 1971)). At the same time,

TABLE 1. Definitions of terms and measured parameters, shown in text-fig. 3 (numbers in column A) and referred to in the text. Computer codes in column B, used in multivariate studies, identify the variables of Tables 2 and 3. Variables were measured in the following units, with the precisions given: shell thickness (measured with caliper), 0·1 mm; all other linear variables (measured on a rectangular vernier stage), 0·1 mm; compound variables are ratios and products of these measurements; internal volume (measured by displacement weighing), 1 mm³; shell weight, 0·001 g.

A	CHARACTER	B
1	Height of shell (measured from umbo)	HTLGSP
2	Height of anterior extremity	HANTEX
3	Height of posterior extremity	HPOSEX
4	Length of shell	LENGTH
	Linear measure of size, square root (height × length)	RTHXL
5	Anterior length	A LEN
18	Posterior length	P LEN
	Asymmetry = A LEN/P LEN (text-fig. 12)	
6	Height of ligamental area	HTLIG
7	Length of ligamental area	LENLIG
8	Median height of hinge plate (directly below umbo)	HTHING
	Height of ligamental area/height of hinge plate	LIGHIN
15	Height of anterior tooth row	HT ATO
16	Height of posterior tooth row	HT PTO
14	Distance between last anterior and posterior teeth	DISTET
9	Height of anterior adductor scar	HT AAD
10	Length of anterior adductor scar	LENAAD
	Area of anterior adductor scar	HXLAAD
11	Height of posterior adductor scar	HT PAD
12	Length of posterior adductor scar	LENPAD
	Area of posterior adductor scar	HXLPAD
13	Distance between inner margins of adductor scars	DISTAD
	Adductor moment = sum of adductor scar areas × mean distance from hinge axis	MOMENT
17	Height of crenulated, extra-pallial, margin	HTCREN
	Width of margin outside anterior adductor	EX AAD
	Width of margin outside posterior adductor	EX PAD
	Shell thickness (between tops of adductor scars)	THICK
	Convexity = maximum perpendicular distance, plane of commissure to exterior surface of shell	CONVEX
	Internal volume (of single valve)	INTVOL
	Approximation for volume = height × length × convexity of shell	HXLXC
	Weight of shell (excellent preservation only)	WEIGHT
	Displacement of mid-point of ligamental area from umbo	UMBO
	Number of crenulations between inner adductor margins	CRENS
	Number of anterior hinge teeth	ATEETH
	Number of posterior hinge teeth	PTEETH
	Number of anterior ligamental chevrons	ACHEV
	Number of posterior ligamental chevrons	PCHEV

the more ventral position of the slow muscle gives it a greater mechanical advantage about the hinge axis, enabling it to hold the valves the more tightly closed against opening forces exerted by the physical environment or potential predators. Glycymerid adductors are extremely strong, absolutely and for their sizes. Plateau (1883) found that *G. glycymeris* took a weight of 2·7 kg, hung at the shell margin, before the valves would open 1 mm. Among the species he studied, Plateau found
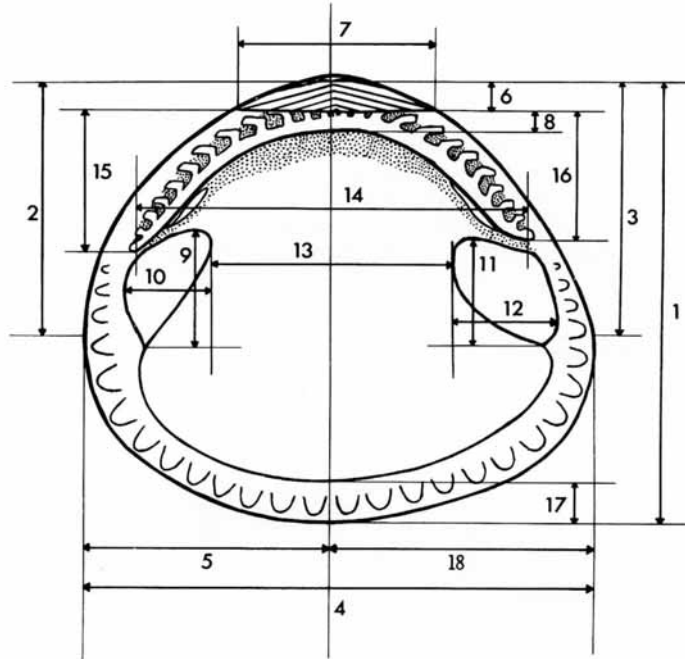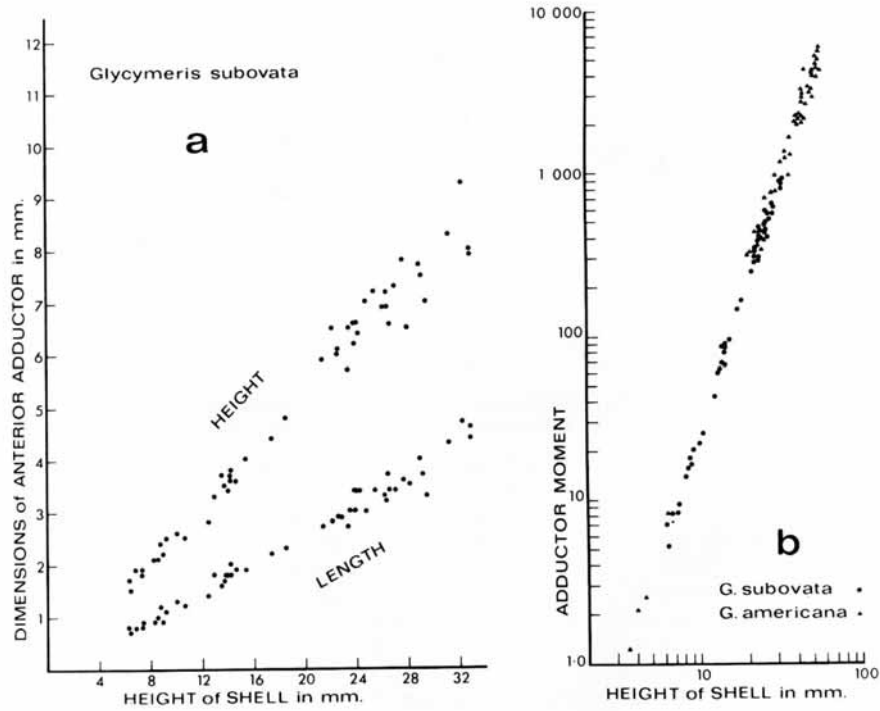
TEXT-FIG. 3. Parameters of the *Glycymeris* shell measured in quantitative studies and referred to in the text. Terms applied to these characters are given in Table 1.

that the strength per unit cross-sectional area of the adductors of *G. glycymeris* was exceeded only by that of *Venus verrucosa*.

In most glycymerids the muscle scars are situated on low buttresses, which are produced by the secretion of thick wedges of adductor myostracum. Kauffman (1969) has suggested that these buttresses serve to strengthen the shell against the stresses developed by the adductor muscles. Buttressed adductor scars are also more nearly perpendicular to the lengths of the adductor muscles than scars flush with the curved surface of the shell. This may improve the effective adhesion of the muscles to the shell by reducing the shear component of adductor stress acting on their attachments. The posterior buttress, like that of *Cucullaea*, often forms a distinct flange, overlapping a groove along the inner margin of the adductor scar (Pl. 38, fig. 7). This groove, which extends back towards the umbo, tracing the line of growth of the adductor margin, appears to have yet another function. Atkins (1936, p. 237) shows a subsidiary ciliary rejection current on the mantle of *G. glycymeris* in this position. The groove forms a distinct channel for this current, away from the food-bearing stream that runs dorsally along the extremity of the outer demibranch of the gill.

The forces exerted by the adductor muscles of fossil glycymerids can be estimated

from projections of the areas of their adductor scars on to the commissural plane; these projections represent the cross-sectional areas of the muscles. The estimates do not take account of ontogenetic changes in the proportions of quick and slow muscle, which are not seen on the undifferentiated muscle scars, and which have not been investigated in the living animals. Although one would expect the strength of the adductor muscles to increase in proportion to the weight of the animal, the relative sizes of the adductor scars of *Glycymeris* remain essentially constant during ontogeny (text-fig. 4*a*). The area of the anterior adductor was plotted against a linear measure of shell size ($^2\sqrt{}$ (height × length)) for forty-eight samples from the *G. subovata* and *G. americana* lineages, and log–log reduced major axis regressions were calculated.

TEXT-FIG. 4. Isometric growth of adductor muscles. A, growth of the anterior adductor of *Glycymeris subovata* (Shoal River Formation, Miocene, Florida). Linear dimensions of the muscle cross-section, measured as parameters of a projection of the muscle scar on to the plane of the commissure, increase as linear dimensions of shell size. B, growth of the adductor moment of *G. subovata* (same population as above) and *G. americana* (Duplin Formation, Miocene, North Carolina). The closing moment exerted by the adductors is taken to be proportional to the sum of their cross-sectional areas (mm^2) multiplied by their mean distance from the hinge axis (mm), which is here plotted against shell height. Regressions for these samples are $\log y = 3.016 \log x - 1.632$ and $\log y = 2.915 \log x - 1.499$ respectively. The adductor moment increases as the cube of shell height, as does the weight of the animal, so growth is almost isometric.

The mean of the slopes of these lines is 2·017 (standard deviation, 0·099), where a value of 2 represents no allometry between an area and a linear parameter. However, the adductors do not simply hold two independent valves together. Rather, they operate a lever system, in which they exert a moment about the hinge axis (Thomas 1970; Gould 1971; Brower 1973). The closing moment developed by the adductors depends on their distances from the hinge axis as well as on the forces they exert. Relative to a linear dimension X, since the cross-sectional areas of the muscles increase as X^2, and since their distances from the hinge axis increase as X, the total moment increases as X^3, keeping pace with weight, and no allometry is required to maintain functional similarity.

The sum of the areas of the two adductor scars, multiplied by their mean distance from the hinge axis, was plotted against the linear measure of size for the same forty-eight samples (text-fig. 4*b*). In this case, the mean of the slopes of the log–log regression lines is 2·915 (standard deviation, 0·091), compared with a theoretical value of 3 for isometry. The moment exerted by the adductor muscles increases almost linearly with the volume or weight of the animal, implying that there is no major change in adductor function during ontogeny.

It is significant that the magnitude of the total moment does not quite keep up with weight, although the sizes of the muscles themselves do, as shown by the slopes of the regressions. This is largely the result of a negative interaction between two size-correlated shell parameters. The distance between the adductors and the umbo increases linearly with size, but the height of the ligamental area has to increase allometrically (see below). As a result, the hinge axis moves ventrally with increasing size. This displacement is fairly small compared with the distance from the hinge axis to the adductors, but it slightly reduces what would otherwise be the linear increase of that distance. The moment is thus somewhat reduced in larger shells by this ventral movement of the hinge axis; the needed increase in the relative size of the ligament impinges on the volume-related growth of the adductor moment.

Brower (1973) has suggested that the adductors of *G. parilis* exhibit preparatory growth, being larger than necessary to perform their required function in the young animals. He observed that small shells in his sample have relatively large adductor scars, the areas of which grow at significantly less than the rate needed to maintain isometry with respect to shell height (exponent=1·79 as opposed to 2; my results for the same population are rather higher). In this case it is the rate of growth of the adductors themselves, and not the relatively modest allometric growth of the ligament, that reduces the rate of increase of the adductor moment below that needed to maintain isometry (Brower's exponent=2·84; my data for the same population, 2·81). Clearly these samples are not exceptional, for their parameters lie well within the range of variation among my populations.

The inference that the size of the juvenile adductors is preparatory, rather than immediately functional, is implicitly based on the assumption that the function of the adductors is primarily to close the shell against the ligament, which is small in the early stages of its allometric growth. In fact, the adductors are much stronger than the ligament at all growth stages. *Glycymeris* needs strong adductor muscles to articulate its thick, heavy shell in burrowing. They also serve to keep the valves tightly closed when the animal is washed out and rolled around under turbulent conditions.

B

Their importance in resisting predators is unknown, although experiments of Hancock (1965) suggest that rates of starfish predation vary with the strength of bivalve adductor muscles. The nearly isometric growth of the glycymerid adductor moment, with only small variations among populations and species, shows that in ontogeny its strength is critically related to shell size, and restrained from deviating far from it.

Ligamental area. The accretionary growth of bivalve ligaments, together with the need to separate the umbones so that the valves may open, constitutes a fundamental limitation on their form and function (Stasek 1963; Raup 1966). As Trueman and Ansell (1969) have observed, bivalves such as *Tellina* with opisthodetic, parivincular ligaments have solved this problem most effectively, although even this type of ligament may be relatively weak in forms such as *Glossus* where the umbones curve sharply away from one another (Owen 1953). For a bivalve of its size and shell thickness, *Glycymeris* has a particularly weak ligament (Trueman 1964).

In common with most arcoids, *Glycymeris* has a 'chevron-type' or duplivincular (Newell 1942) ligament. This ligament is all but entirely external, the valves being articulated about an axis just within its ventral margin. In most species it is symmetrically distributed, before and behind the umbones (amphidetic). It consists of parallel layers of lamellar conchiolin and partly calcified fibrous material. The fibrous layers, which typically lie in chevron-shaped grooves on the ligamental areas of the valves, are elastic only under compressional stress. The lamellar layers, which exert the opening moment of the ligament, are elastic under both tensional and compressional stress (Newell 1937). A ligament consisting of such alternating layers is unspecialized in the sense that the materials of which it is composed are not set apart in positions where they can best perform their different mechanical functions.

The ontogeny of the ligamental area of *G. obovata* (Oligocene, France) has been described by Bernard (1896). In the early post-larval shell the ligament, which is set in a small triangular fossette at the centre of the hinge, is entirely internal (text-fig. 8). As the cardinal platform develops, the hinge axis moves ventrally, and the ligament divides into the first anterior and posterior grooves. Subsequent chevron-sheets of lamellar and fibrous ligament are added alternately beneath the umbones, growing ventrally and outwards from the centre along the hinge axis. At the same time the ligamental area expands ventrally over the upper part of the hinge plate, and the earlier hinge teeth are overridden by a thin wedge of crossed-lamellar shell material, to the surface of which the ligament is attached.

As a result of the considerable inter-umbonal growth of *Glycymeris* the earlier, more dorsal sheets of lamellar ligament are stretched across a wider and wider gap during ontogeny. Up to a point this increases the tension they exert, but finally they break below the umbones. Thus in the larger shells of many species only the latest chevrons and the anterior and posterior ends of the earlier ones are functional, as in other arcoids (Newell 1937; Stasek 1963). In most glycymerids the successive chevron-sheets are added parallel to one another, and are of a similar thickness. Thus, after the earlier stages of growth, the relative proportions of lamellar and fibrous ligament do not change. The number of such ligamental chevrons has nothing to do with the age of the animal, as suggested by Hayasaka (1962), but rather is

linearly related to the size of the ligamental area. In a few species the individual sheets thicken ventrally, and new chevrons are added less frequently.

The size and shape of the ligamental area of *Glycymeris* change allometrically with the growth of the shell to a far greater extent than any other character (text-figs. 5a, 6; Pl. 38, figs. 1–5). This allometry is necessitated by the dorsal breakage of the ligament. It is not explained by the fact that the ligament moment is inadequate to open the valves, or by any geometrical constraint on the relative size of the ligament in small shells, as supposed by Brower (1973, pp. 83, 89) in his study of the ontogeny of *G. parilis*. The ligament opens the shell by exerting a moment about the hinge axis, opposite to the closing moment exerted by the adductors when they contract. As long as the ligament remains unbroken, the tension it exerts must increase at least as its cross-sectional area (the detailed mechanics are more complicated; Thomas, in preparation), while the moment arm increases as a linear dimension in the absence of allometry. Like the adductor moment, the ligament moment would scale as X^3, maintaining its relationship with the weight of the shell it must articulate, without any allometry, but for the fact that the ligament breaks dorsally. The allometric growth of the internal ligament of *Argopecten*, described by Waller (1969), is required by the changing demands of swimming with increasing size (cf. Gould 1971). In contrast, the allometry of the glycymerid ligament is required by its inability to maintain functional similarity, due to its mode of growth.

The area of the ligamental attachment was plotted against a linear measure of shell size ($^2\sqrt{}$ (height × length)) for forty-eight samples of the *G. americana* and *G. subovata* lineages, and log–log reduced major axis regressions were calculated. The average slope of these regressions is 2·641 (standard deviation, 0·279), compared with a value of 2 for isometric growth. The slope for a collection of *G. parilis* is 2·499, in close agreement with the slope of 2·45 obtained by Brower (1973) for a least-squares regression on the same characters of a collection from the same locality. It is not possible to estimate ligament moments, because of the partial breakage of the ligament. However, it is clear that the size of the ligamental area increases allometrically to compensate for this breakage.

Since the dorsal part of the ligament breaks in larger shells, a more efficient ligament would be produced by increasing its length rather than its height. In fact, the shape of the ligamental area usually changes little during growth; its length increases allometrically with shell size, but slightly less rapidly than its height. There is a functional compromise here, in that a longer ligament can be produced only by ventral displacement of the hinge axis, or by increasing the length of the shell at the hinge axis. However, a dorsally longer shell would be less well adapted for the rocking locomotion of *Glycymeris* (see p. 242).

The height of the ligamental area, L, increases logarithmically relative to the height of the shell, but the distance from the umbo to the base of the hinge plate immediately below it, $L+H$, increases linearly with size (text-fig. 5). As a result, the height of the median part of the hinge plate, H, increases at first, stops, and then decreases absolutely during growth, as the hinge plate is overgrown by the rapidly expanding ligament (text-fig. 7). In large shells of some populations the ligamental area may actually extend to the base of the median hinge plate, separating the anterior and posterior series of hinge teeth completely (Pl. 38, fig. 7). This relative growth of the
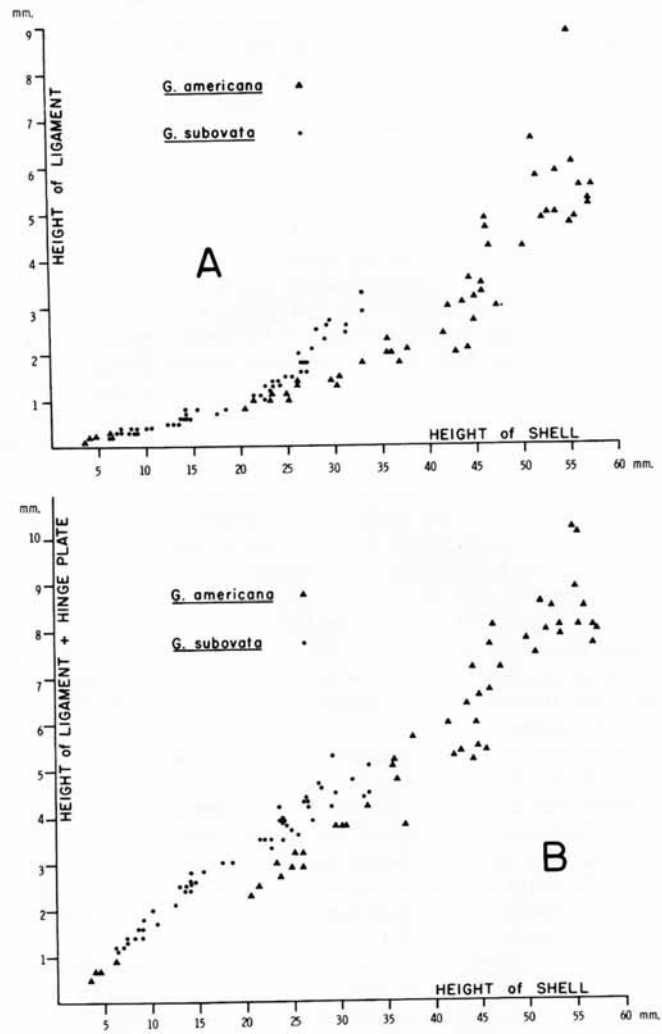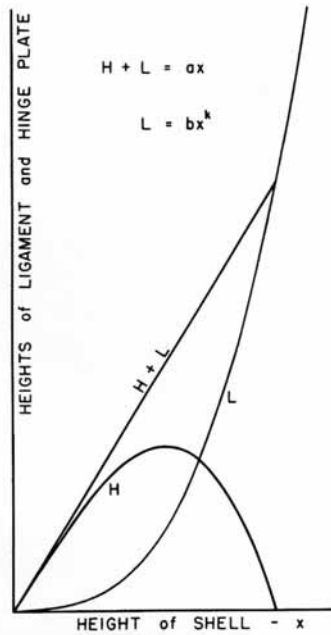
TEXT-FIG. 5. Growth of the ligament and hinge plate. A, strongly allometric growth of the ligament, shown by the relationship between the height of the ligamental area and the height of the shell. B, isometric growth of the total space between the umbo and the median base of the hinge plate. Same populations as in text-fig. 4.
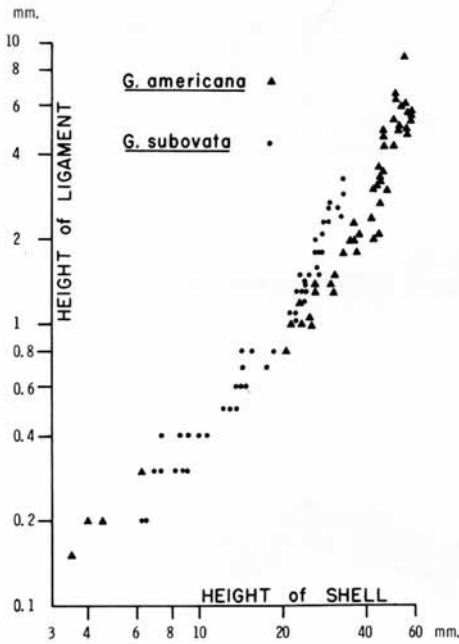
TEXT-FIG. 6. Double logarithmic plot of the height of the ligamental area against the height of the shell. The curves show that the exponent in this logarithmic relationship itself increases with size in later ontogeny. Same populations as in text-fig. 4.

TEXT-FIG. 7. Idealized relationship between the growth of the height of the ligamental area (L), the height of the median hinge plate (H), and their sum, against the height of the shell (x).

ligament considerably reduces the number and effectiveness of the hinge teeth; Brower (1973) gives a simple parabola as the equation of best fit for the number of teeth versus shell height in *G. parilis*. Evidently the strength of the ligament is more critical than the precise alignment of the valves in large glycymerids. The larger ligament could be accommodated without interfering with the hinge if the entire hinge plate were to be displaced ventrally during ontogeny. This would reduce the size of the mantle cavity, increase the weight of the shell, and move the centre of gravity of the animal dorsally. These disadvantages evidently outweigh the need for a complete series of teeth in larger shells.

The ligament of *Glycymeris* is poorly designed for its purpose, especially compared with those of more advanced bivalves. New organic material must continually be secreted to replace that which has lost its function. Yet, despite its allometric growth, the ligament is still one of the weakest among the bivalves. It serves adequately to articulate the valves and to open them during feeding, but is relatively ineffective in bracing the shell against the sediment during the probing phase of burrowing (Ansell and Trueman 1967).

Hinge teeth. The hinge teeth of most bivalves serve two functions. One is to guide the gaping valves into perfect apposition as they close. The other is to prevent the disarticulation of the closed valves by any shearing stress in the commissural plane which might be exerted upon them. The variety of types of bivalve hinge teeth, even amongst animals with a similar mode of life, indicates that these functions can be fulfilled, perhaps equally well, in several different ways. The more advanced heterodonts have developed specialized teeth to perform each function, while in the taxodonts both purposes are served by a large number of similar teeth.

The ontogeny of the hinge teeth of *G. obovata* has been minutely described by Bernard (1896). As the cardinal platform begins to develop, the first true teeth are formed, *parallel* to the hinge axis (text-fig. 8). Subsequent teeth are added ventrally
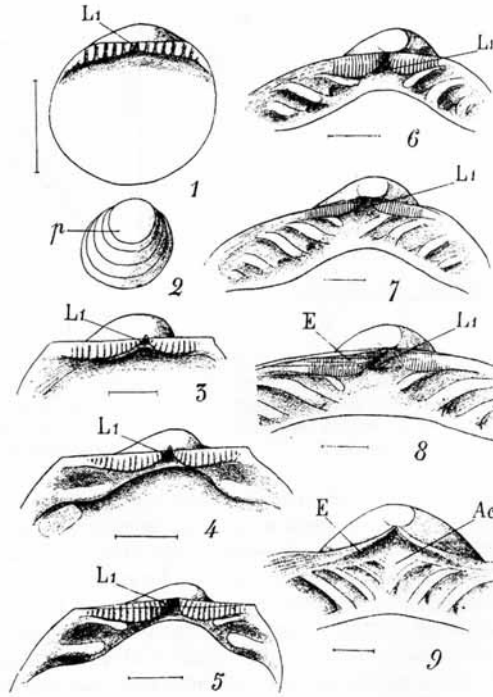
TEXT-FIG. 8. Ontogeny of the hinge and ligamental area of *Glycymeris obovata* (Lamarck) from the Oligocene of the Paris Basin. 1, prodissoconch, right valve. 2, early dissoconch, exterior right valve. 3-9, growth of the left valve. Scale-bars all represent 0·1 mm. Key: *p*, prodissoconch; Li, primary internal ligament; E, first chevron of lamellar ligament; Ac, region where tooth rows meet, and are subsequently overgrown by the ventrally expanding ligamental area. (From Bernard 1896, p. 60.)

to the expanding cardinal platform by successive bifurcations of the terminal teeth. The new teeth are always subparallel to the hinge axis, but as the shell grows and they occupy progressively more dorsal positions on the hinge plate, they swing around, becoming oblique or chevron-shaped. The earliest teeth ultimately grow perpendicular to the hinge axis, along which they are gradually overgrown by the ventrally expanding ligamental area. In some cases their dorsal margins are cut off sharply against the base of the ligamental area, and shell resorption definitely takes place during growth. As noted above, and by Brower (1973), the number of hinge teeth changes in a complex manner during ontogeny, first increasing with size, and later decreasing due to the overgrowth of the ligamental area.

The hinge teeth of large or very thick *Glycymeris* shells commonly become irregular, much reduced, and sometimes fused together (Pl. 38, fig. 7). This led Jeffreys (1863, p. 168) to the amusing observation that 'The teeth occasionally decay and become carious in living specimens'. In a few cases the hinge teeth even obtrude into the lower part of the ligament, indicating that the animals were unable to resorb their summits completely. These observations suggest either that the form of the hinge teeth is no longer critical in securing the apposition of the valves in such large individuals, or, more likely, that this irregularity is an undesirable but unavoidable consequence of the interaction between the growth of the ligament and that of the hinge plate.

The larger teeth of *Glycymeris* are always more or less bicuspate. Their crests are divided by an oblique longitudinal furrow, which is not reflected by a ridge in the corresponding pit. This furrow may provide a passage for the diffusion of materials for shell secretion in the extrapallial fluid, for the two mantle lobes occupy a very narrow space between the interlocking teeth. The sides of the hinge teeth have distinct vertical ridges and grooves, which further promote the perfect interlocking of the valves.

The shape of the hinge teeth depends both on the arching of the hinge plate, and on its width, which is highly correlated with shell thickness. Shells with longer, straighter hinges, like *G. glycymeris* and *G. americana*, have chevron-shaped teeth with most of their lengths parallel to the hinge axis. Shells with shorter, more strongly arched hinges, like *G. pectinata* and *G. subovata*, have chevron teeth with longer vertical components, the two branches of each tooth being more nearly equal in length. This distinction is complicated by the fact that thinner shells have more parallel teeth, while thick shells tend to have equibranched chevron teeth.

While the shapes of the teeth depend on the shape of the hinge plate itself, they are also directly related to function. Teeth parallel to the hinge axis must be particularly important in aligning the closing valves where the position of the hinge axis, in the lower part of the ligament, is not well defined. However, straight teeth parallel to the hinge axis would provide little protection against disarticulation by anterior-posterior shearing stresses between the valves. Likewise, teeth perpendicular to the hinge axis would provide little resistance to dorsal-ventral shearing stresses. Straight teeth perpendicular to the inner margin of the hinge plate would be rather better, where the hinge plate is strongly arched. Clearly, chevron-shaped teeth are superior to all of these in resisting shearing stresses in the plane of the commissure in all directions.

Spiral curvature. Growth of the exterior of the glycymerid shell occurs along one plane spiral and an infinite number of anterior and posterior turbinate spirals, all originating at or near the umbo (see Lison 1949). In most populations and species these spirals are more or less truly logarithmic, and the convexity of the shell changes little during ontogeny, although it varies considerably from one species to another. In two Miocene samples of *G. americana* the convexity of the shell does increase substantially relative to its height, as shown in text-fig. 9. The change in spiral angle involved in this allometry, calculated for an individual specimen by the formula of Lison (1949, p. 20), is shown in text-fig. 10. The significance of this allometry is not clear. In terms of the model of shell growth proposed by Carter (1967) this kind of change would occur if the rate of shell secretion was maintained while the rate of proliferation of new mantle cells decreased. The shells in these two collections are relatively thick, and their later growth lines are very closely spaced. Increased convexity and shell weight would be quite disadvantageous in terms of burrowing, but they may have a stabilizing function in current-swept environments, as suggested by Stanley (1970, p. 69).

As in other arcoids, considerable shell secretion occurs right up to the glycymerid hinge line, and the growth of the ligamental area also describes a spiral transverse section (Stasek 1963). The curvature of this spiral in *Arca noae* is much stronger than that of the shell exterior, as the umbones of the two valves grow very far apart. In contrast, the allometric growth of the ligament is directed ventrally in *Glycymeris*, and its attachment area shows a shallower curvature than the shell exterior. Paradoxically, the interumbonal growth which ultimately leads to the breakage of the ligament is in the first instance necessary, to stretch the passive elastic ligament between the valves, so that it can exert tension between them. Interumbonal growth is also necessary to separate the opposing umbones, which would otherwise grow together and prevent the valves from opening (Stasek 1963). This problem is evidently not completely solved for *Glycymeris*, in that the umbones frequently exhibit abraded facets at the point where they meet when the valves gape widely.

Shape of the shell margin. It has been suggested that 'The rounded form exemplified by *Glycymeris* is suited to a relatively inactive bivalve . . .' (Purchon 1968, p. 157), but this view is inconsistent with both the form and habits of the animal. The symmetrical shape of the *Glycymeris* shell is in fact related to its mode of locomotion, as will be shown here.

Glycymeris is not a quick or mechanically efficient burrower. However, the animal is able to burrow into firm substrates and to move around a great deal on the surface by means of its exceptionally muscular foot. The movements of *G. glycymeris* have been described by Deshayes (1858), Vlès (1906), and Ansell and Trueman (1967); recently Stanley (1970) and Thomas (1970) have observed the locomotion of *G. pectinata*. At the surface, the animal supports itself in a furrow, with its commissure vertical. From this position the foot probes anteriorly down into the sediment. When fully extended it is dilated, and two ventral lobes, which had been held tightly together during probing, are spread sideways, at right angles to the axis of the foot. The foot thus forms a stable anchor, with the shape of an inverted mushroom. The valves are then sharply closed to about half their previous gape, forcing water out of the mantle
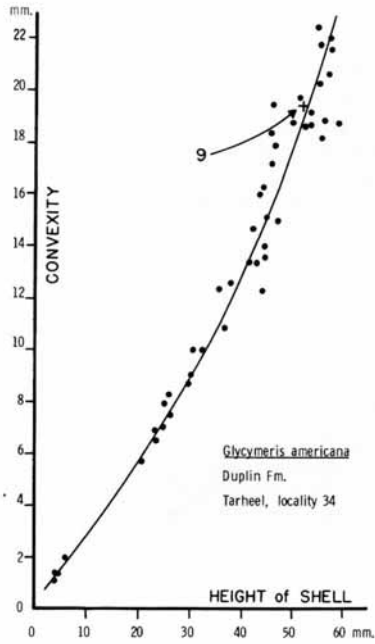
TEXT-FIG. 9. Allometric change in the spiral curvature of a *Glycymeris americana* population during ontogeny, shown by the changing relation of height and convexity of the shell. Curvature of specimen 9 is illustrated in text-fig. 10.
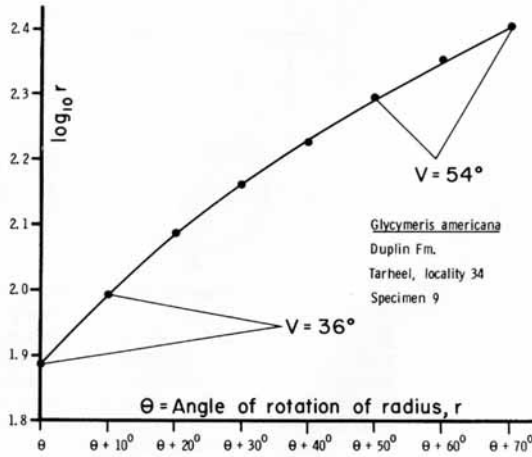

TEXT-FIG. 10. Allometry of the spiral angle, shown by the changing value of log r with increasing θ. Values of V calculated, for increments shown, by the formula of Lison (1949, p. 20). Radii were measured from the pole of the spiral, by the projection method described in Maclennan and Trueman (1942).

cavity into the surrounding sediment, loosening it and making it more easily penetrable.

The action of the pedal retractor muscles in moving *Glycymeris* forward against its pedal anchor is shown diagrammatically in text-fig. 11*a*. From position I to II the bivalve simply rocks forward about its centre of gravity by the contraction of its anterior pedal retractor. From II to III the contraction of the posterior retractor draws the shell forward and down; the median axis is now back in the vertical position. If the animal is to bury itself in the sediment probing now begins again, and these steps are repeated serially (see text-fig. 11*c*). Alternatively, if the animal is to move along the surface, a further contraction of the posterior retractor serves to rock the shell backwards and upward (III–IV). Finally, the anterior retractor and the release of the pedal anchor bring the animal back into a vertical position at the same horizontal level as it began (V). The effect of serial repetition of these movements is shown in text-fig. 11*b*. Such rocking locomotion is characteristic of both *G. glycymeris* and
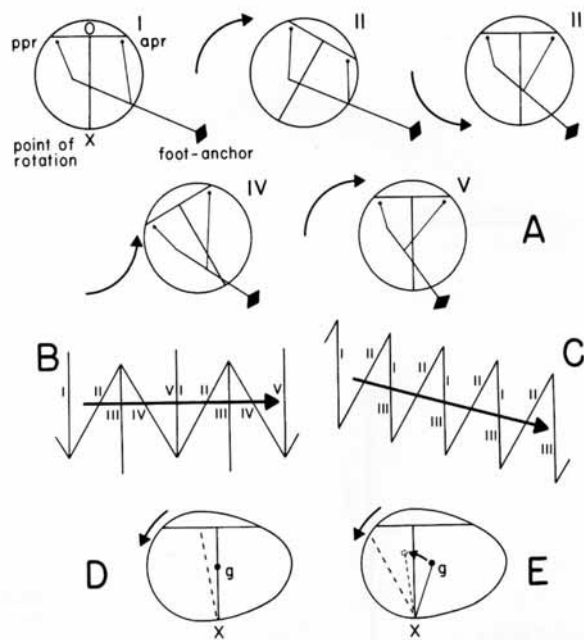
TEXT-FIG. 11. Burrowing movements and shell form. A, rocking loco-
motion of *Glycymeris. apr, ppr*, anterior and posterior pedal retractor
muscles. B, locomotion on the surface, diagrammed as changes in the
position of the line *OX*. C, similar diagram of downward locomotion,
leading to burial in the sediment. D and E, rocking locomotion and the
asymmetric shell. D, the animal rocks about its centre of gravity, *g*.
E, the animal rocks about a point anterior of its centre of gravity. These
diagrams are more completely explained in the text.

G. pectinata, although Stanley (1970) has stated that the latter species burrows with its hinge line horizontal. The pedal retractors are assisted in these manipulations by transverse muscles in the foot and visceral cavity, and pedal protractor muscles which extend across the foot from beneath the anterior adductor (see also p. 225). The pedal retractors themselves are securely attached to buttressed scars at the ends of the relatively thick hinge plate.

The rocking locomotion of *Glycymeris* provides a functional explanation for the anterior-posterior symmetry of its shell, and for its nearly circular shape. If the animal were posteriorly elongated it might rock about a point below its centre of gravity, which would be behind the median axis, but it could not rock through a very large angle (text-fig. 11*d*). Alternatively, it could rock through a larger angle about a more anterior fulcrum (text-fig. 11*e*) but now it would have to do additional work to lift its centre of gravity, which would be behind the fulcrum. An anteriorly elongated animal would suffer even more acutely from these mechanical problems. Hence the paradigm for an animal with the rocking locomotion of *Glycymeris* (or *Divaricella*, which moves vertically down into the sediment, Stanley 1970) is a symmetrical, circular form, which allows a maximum of rotation while keeping the centre of gravity always directly over the rotational fulcrum.

Since more rocking is involved in moving about on the sediment surface than in burrowing into it, we may infer that the maintenance of a symmetrical, circular shape over a long period of evolution by *Glycymeris* represents a continued need for mobility. Such mobility may be required in searching for suitable new burrowing sites, since the animals are surely often washed out in turbulent environments. However, it is also clear that they move about considerably of their own accord.

In some species, and populations within species, the glycymerid shell does become somewhat elongated posteriorly during ontogeny. This allometric growth is particularly well seen in *G. subovata* from the Shoal River Formation (Miocene) of Florida (Pl. 38, figs. 1–5). In this population the smallest individuals have slightly more of their lengths in front of the umbo than behind it, but posterior length increases more rapidly during ontogeny, and many of the larger shells are quite posteriorly elongated. This asymmetry is a very variable character, as can be seen in text-fig. 12, but the linear increase in posterior elongation is quite clear. In contrast with the growth of the ligamental area, the shape of the juvenile shell is here progressively modified by the difference between two linear growth rates, and not by any relative change in the rates themselves. Where allometric changes are required by linear–surface–volume relationships, as in the case of the glycymerid ligament, linear parameters may be related exponentially; changes in bivalve shell shape required by other kinds of problems seem most often to be achieved by differential linear growth (Thomas 1970). The anterior shape of the juvenile *G. subovata* may be related to the accommodation of the large foot, while the posterior elongation of the adult allows deeper burial, with the posterior margin still in contact with the sediment surface.

The degree of posterior elongation varies greatly among populations of some glycymerid species, and is probably correlated with environmental factors. Purchon (1939) found populations of *Cardium edule* from quieter water to be, on average, more elongated than those from wave-swept marine sand. Holme (1961) found the
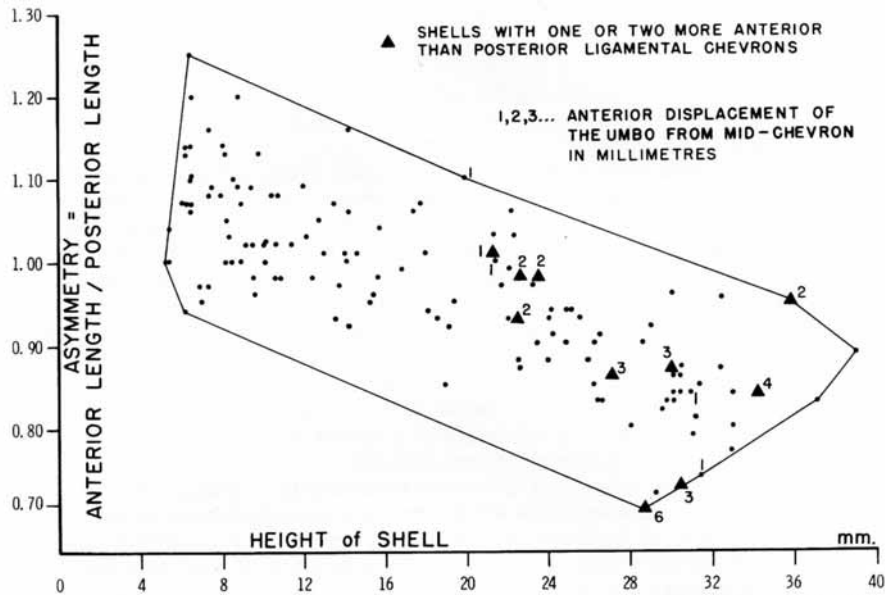
TEXT-FIG. 12. Asymmetry of *Glycymeris subovata* from the Shoal River Formation (Miocene, Florida). Plot shows that: (1) asymmetry increases linearly with size, in ontogeny; (2) individual variation in the degree of asymmetry is very great; (3) this asymmetry is not produced by pseudo-turbinate spiral growth; more orthogyrate shells, with additional anterior ligamental chevrons, are not necessarily the most asymmetric shells.

shells of *Venerupis rhomboides* from deeper water to be more elongated than those from shallower water. In the case of *Glycymeris*, the orbicular shells are well adapted for locomotion and reburial, following frequent rolling on coarse gravel bottoms. Elongation of the shell allows slightly deeper burial, with the posterior-ventral margin still at the sediment surface, in more stable sand substrates. Moreover, contact with the sediment surface may not always be necessary in open-framework gravels (see p. 227), whereas it is certainly essential in sand. Available ecological and palaeoecological data are suggestive of such a relationship between shell shape and turbulence or sediment type, but by no means conclusive. The functional arguments for it are more compelling.

Intraspecific variation in the posterior shell shape of *Glycymeris* does not affect the whole shell; that is, the elongated shell is not a simple transformation (Thompson 1942, p. 1026) of the orbicular form. Only the posterior radial ribs are modified in elongated shells; they broaden and swing postero-dorsally during ontogeny, while the anterior and median ribs remain simply radial, like those of orbicular shells. The posterior adductor muscle scar also rotates postero-dorsally with these ribs. Elongation is not produced here by changes in the spiral curvature of the whole shell, as further shown in text-fig. 12. Some specimens of *G. subovata* in this population are

planispirally coiled, while others are slightly pseudoturbinate (Carter 1967), the umbones pointing just posteriorly. Pseudoturbinate coiling leads to the development of one or two more anterior than posterior ligamental grooves, and to the posterior displacement of the latest chevrons relative to the umbo. It is clear that the pseudo-turbinate shells are not significantly more asymmetric than the planispirally coiled shells.

Differences in shell shape among glycymerid species do often take the form of transformations of the whole shell, and may involve changes in the spiral curvature. It appears that the direction of spiral coiling is relatively invariable and under close genetic control, while changes in the spiral angle and local modifications of the shape of the shell margin may occur within species under the influence of environmental factors.

Ribs, periostracum, and crenulations. The shells of different species of *Glycymeris* bear variously developed radial ribs. Most have either very low, flat ribs bearing fine striations and a heavy periostracum, or prominent, usually rounded, ribs lacking striations, with little or no periostracum. It appears that the periostracum is func-tionally important to the first group, while raised ribs are of some utility to the second.

Bivalve ribs have generally been considered as corrugations whose primary func-tion is to strengthen the shell. The radial patterns of glycymerid ribs are not obviously related to the stresses developed by the ligament and adductors, but they are simple to program and generate in the accretionary growth of the shell. Bivalve shell is a com-posite material, and much stronger than has been recognized until recently (Taylor and Layman 1972). On the other hand, some bivalves are capable of breaking their own shells by adduction, if they are artificially prevented from closing (Wainwright 1969). Ribs may also increase the shell's resistance to external stresses, exerted on it by predators or the physical environment. Kauffman (1969) has suggested that the prominent ribs of *G. pectinata* enable it to withstand considerable rolling by waves and currents; they may also deter predators, such as crustaceans and some fishes, which crush their bivalve prey. Raised ribs, particularly the steeper, sharper ones, must also make it more difficult for starfishes and boring snails to grasp potential prey; naticids are said to bore relatively smooth-shelled bivalves (Carriker and Yochelson 1968). The ribs of shallow infaunal bivalves help to stabilize the shell in the substrate (Kauffman 1969), and aid in burrowing even where they are not optimally designed for this purpose (Stanley 1970). In *G. pectinata* the ribs assist the weak ligament in bracing the shell against the sediment, which more than offsets the disadvantage of their resistance to the downward pull of the securely anchored foot. It is clear that glycymerid ribs are not specialized for any one function; they have several different roles, and their simple pattern is governed largely by the process of accretionary growth.

The interior shell margin of all species of *Glycymeris* is lined with distinct crenula-tions, which alternate with the exterior ribs and are formed by the same micro-structural elements of the outer shell layer. These crenulations serve, in conjunction with the hinge teeth, to align and interlock the valves. Carter (1968) has postulated another possible function for such crenulations: they may make it more difficult for

a starfish to intrude its stomach into the bivalve by sliding it around the shell margins after entry has been gained at one point.

The periostracum is variably developed in the flat-ribbed glycymerids. It usually extends around most of the shell margin, being progressively worn off towards the umbones. This periostracum has often been described as 'hairy' or 'velvety' on account of the numerous tiny barbs which stand up from its surface. These are arranged in a regular pattern, as radial rows set in the striations on the ribs, and as concentric rows corresponding to growth lines (Pl. 38, fig. 9). In *G. americana* the barbs are apparently secreted in a horizontal position, as blades pointing away from the umbo. Once complete the blades spring up, normal to the surface of the shell. They are not straight, but rather curve back towards the umbo. In this position the tiny barbs catch against sand grains and help to prevent the shell from slipping upwards and backwards as the foot probes the sediment during burrowing. This is presumably a valuable adaptation to a burrowing bivalve with a weak ligament, and hence an otherwise poor shell anchor. Here then is a function both for the periostracum itself, and for the striations in which the rows of barbs are set. The presence of a barb-bearing periostracum in fossil glycymerids can be inferred from the presence of fine radial striations on the ribs.

Multivariate analyses. A principal components analysis of the growth of *G. parilis* by Brower (1973) and several R-mode factor analyses of samples of *G. americana* and *G. subovata* (Thomas 1970) have yielded very similar results. These techniques distinguish clusters of closely related variables (see review by Gould 1970, and references therein) on the basis of linear correlations. Logarithmic transformation of the measured parameters facilitates the recognition of simple allometric as well as rectilinear relationships. The parameters used in my studies are shown in text-fig. 3 and Table 1.

The most striking result of these analyses is the extremely high intercorrelation of all the variables. In Brower's study the first principal component accounts for 93% of the correlation matrix variance, while the first component in some of my analyses explains as much as 97% of the data. Certainly these correlations result partly from the large amount of redundancy among the parameters used. Nevertheless, the intercorrelation among the variables with increasing size is so strong that correlations independent of size are largely swamped, even in the oblique factor matrix. As a result, groups of characters differentiated by R-mode analyses of different samples are not always consistent, being sometimes rather arbitrary divisions of a single tight cluster of vectors.

Certain patterns do recur, and these are accentuated in an analysis of a sample of twenty-two specimens of *G. subovata*, all between 30 and 33 mm in height (compare Tables 2 and 3). With the much-reduced influence of size, the first principal component for this sample explains only 46% of the data. Measurements of the ligamental area form a cohesive group, together with the length of the posterior half of the shell, which also increases allometrically with size (Axis 4). The characters affected by the overgrowth of the hinge plate by the ligamental area, and ventral movement of the hinge axis, form a group which naturally tends to be negatively correlated with the former one (Axis 2). The convexity, thickness, and internal volume of the shell are

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TABLE 2. Factor analysis. Reordered oblique projection matrix of 28 variables in 6 axes. Variables were measured on 72 right valves of *Glycymeris subovata* representing a complete growth series. Shoal River Formation, Miocene, Florida. For explanation of character codes, see Table 1.

CODE	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6
HTHING	1.000	0.000	0.000	0.000	0.000	0.000
THICK	0.911	0.652	-0.038	0.082	-0.532	0.077
HT ATO	0.543	0.164	-0.043	0.101	0.298	0.004
HT PTO	0.490	0.103	0.022	-0.012	0.401	0.054
CONVEX	0.423	0.353	-0.015	0.129	0.044	0.166
WEIGHT	0.363	0.321	0.010	0.168	0.132	0.100
LENLIG	0.353	0.350	0.089	0.077	0.214	0.009
LIGHIN	0.000	1.000	0.000	0.000	0.000	0.000
HTLIG	0.427	0.674	0.001	-0.002	0.011	0.004
AR LIG	0.395	0.527	0.041	0.036	0.105	0.006
DISTAD	0.000	0.000	1.000	0.000	0.000	0.000
EX AAD	0.000	0.000	0.000	1.000	0.000	0.000
EX PAD	0.167	0.340	0.125	0.894	-0.781	0.346
HTCREN	0.169	0.114	-0.012	0.576	0.393	-0.221
HT AAD	0.000	0.000	0.000	0.000	1.000	0.000
HXLAAD	0.047	0.008	-0.010	0.028	0.944	-0.005
LENAAD	0.091	0.015	-0.019	0.054	0.884	-0.010
HT PAD	0.155	0.133	0.023	0.013	0.778	-0.065
HXLPAD	0.145	0.123	0.018	0.023	0.724	0.007
LENPAD	0.136	0.114	0.013	0.031	0.673	0.071
A LEN	0.104	0.074	0.035	0.258	0.560	0.008
HTLGSP	0.216	0.203	0.012	0.156	0.427	0.049
INTVOL	0.217	0.232	0.018	0.144	0.381	0.076
LENGTH	0.156	0.159	0.041	0.252	0.379	0.072
HXLXC	0.259	0.232	0.013	0.181	0.294	0.095
P LEN	0.192	0.217	0.043	0.250	0.251	0.117
PCHEV	0.000	0.000	0.000	0.000	0.000	1.000
ACHEV	0.075	0.078	0.026	-0.134	0.073	0.896

highly intercorrelated (Axis 3). The parameters of the adductor scars form distinct groups (Axes 1 and 5), their lengths not being highly correlated; however, it is notable that their heights are strongly correlated, directly with one another and inversely with the size of the ligamental area. Clearly the allometric growth of the ligament does impinge on the space available inside the shell. Measures of the extra-pallial margin fall together (Axis 7) and are correlated with the shell-thickness group. The numbers of anterior and posterior ligamental chevrons form a separate group (Axis 6) largely because they are discrete variables, but would otherwise join the parameters of the ligamental area. The main linear measures of shell size, such as height, length, anterior length, and distance between the adductors, are similarly correlated with several groups in which their appearance has no particular significance (Axis 8 and others).

Aside from the relationship of all variables with size, two groups of characters

TABLE 3. Factor analysis. Reordered oblique projection matrix of 28 variables in 8 axes. Variables were measured on 22 specimens of *Glycymeris subovata*, all between 30 and 33 mm high. Shoal River Formation, Miocene, Florida. For explanation of character codes, see Table 1.

CODE	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8
HXLAAD	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
LENAAD	0.915	0.171	0.270	0.483	-0.611	0.066	0.368	0.193
HTLGSP	0.467	0.100	0.323	0.143	0.082	0.356	0.465	0.137
HTHING	0.000	1.000	0.000	0.000	0.000	0.000	0.000	0.000
HT ATO	-0.009	0.810	0.229	-0.219	-0.169	-0.091	-0.245	0.206
HT PTO	-0.238	0.713	-0.099	-0.234	-0.061	-0.022	-0.174	0.468
LIGHIN	0.093	-0.746	0.057	0.398	-0.094	0.068	0.023	-0.133
CONVEX	0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000
THICK	-0.358	0.248	0.857	0.180	-0.205	0.123	0.022	-0.162
WEIGHT	-0.012	0.733	0.836	0.244	0.003	0.104	0.346	0.081
HXLXC	0.221	-0.022	0.592	0.190	0.092	0.189	0.353	0.183
INTVOL	0.256	-0.177	0.555	0.115	0.091	0.077	0.181	0.270
AR LIG	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000
LENLIG	-0.278	0.342	-0.117	0.853	0.362	-0.193	-0.069	0.395
HTLIG	0.195	-0.197	0.116	0.818	-0.191	0.138	0.046	-0.270
P LEN	0.086	0.057	0.283	0.552	0.192	0.186	0.429	-0.014
HXLPAD	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000
HT PAD	-0.075	-0.330	0.269	-0.378	0.910	-0.219	-0.127	0.169
LENPAD	0.066	0.293	-0.234	0.334	0.906	0.194	0.114	-0.147
HT AAD	0.582	-0.170	-0.240	-0.418	0.725	-0.273	-0.244	0.083
PCHEV	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000
ACHEV	-0.117	0.313	-0.287	0.473	0.334	0.755	-0.179	-0.304
HTCREN	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
EX AAD	-0.008	-0.502	0.476	-0.099	-0.248	-0.035	0.805	0.290
EX PAD	-0.265	-0.043	0.296	0.576	-0.101	0.129	0.771	-0.077
LENGTH	0.191	-0.104	0.235	0.311	0.141	0.184	0.461	0.296
DISTAD	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000
A LEN	0.273	-0.283	0.122	-0.078	0.026	0.135	0.382	0.595

are most cohesive: those related to a larger or smaller ligamental area; and those related to a more or less massive hinge plate, together with shell thickness and convexity. The parameters of the ligament group interact negatively with those of the hinge plate, and parameters of both of these groups interact negatively with characters of the shell interior. Shells with larger ligaments have shorter adductor moment arms, and the heights of the adductors themselves are reduced. Likewise, thicker shells with massive hinge plates and broad extra-pallial margins have smaller adductor scars and less internal volume, despite the fact that more work must be done by the adductors to manipulate a heavier shell. Evidently the advantages of a more massive shell in resisting stresses generated by predators or the physical environment must be offset against disadvantages in locomotion and the need for a mantle cavity large enough to accommodate both large gills and a massive foot.

Factor analysis shows that metric characters of a single structure or functional complex of the *Glycymeris* shell are in general more closely interrelated than characters of different complexes. The same conclusion has been reached by Gould (1967, 1969) for pelycosaurian reptiles and pulmonate snails, and by Olson and Miller (1958) for the blastoid *Pentremites* and a variety of vertebrates. In his study of *G. parilis*, Brower (1973) has suggested that 'the animals might have genetically programmed their growth with two genetic complexes, one devoted to overall size ontogeny and the other assigned to development of the teeth'. However, it is clear that the growth pattern of the hinge plate is the result of interaction between more or less isometric growth typical of the shell as a whole, and the allometric growth of the ligament. The interaction of these two growth patterns is determined by functional considerations and the constraints of shell geometry, as we have seen. Genetic complexes surely control morphology by means of growth gradients and patterns, rather than by direct determination of unit characters, which are often arbitrarily defined in any case. It does not necessarily follow from this that intercorrelated parameters of morphology are controlled by corresponding groups of genes.

With respect to bivalve shell form, the most significant feature of the relationships among parameters of the glycymerid shell is that the same associations occur in ontogeny, in variation within and between populations, and among species. An R-mode factor analysis of specimens of *G. subovata* and *G. americana* treated as one sample reveals much the same character groups as the two species analysed separately. Analyses using ratios of variables also yield similar groupings, indicating that allometric changes in the variables during ontogeny are interrelated in the same way as the variables themselves. The constancy of these interrelationships is a function of the geometric simplicity of the glycymerid shell, and the fact that any considerable change in one character impinges more or less directly on several others. The glycymerid shell as a whole shows a very high degree of morphological integration.

Synthesis. These observations on the form and function of the *Glycymeris* shell lead to two general conclusions. (1) This shell is a geometrically very simple structure; as such its various characters are closely interrelated, and are not free to change independently of one another, in either ontogeny or phylogeny. The size and shape of the ligament affect the disposition of the hinge teeth and the closing moment that the adductors can exert. The shapes of the hinge teeth depend largely on the shape of the hinge plate, which also interacts with the size of the adductors and the volume of the mantle cavity. Both the length of the ligament and the shape of the hinge plate affect the position of the animal's centre of gravity, and hence its locomotion. The evolution of the shell is limited in that any substantial change in one character has a major effect on the shell as a whole. (2) The growth of the *Glycymeris* shell, apart from its ligament and the posterior elongation of some forms, is largely isometric. This limits size in ontogeny and phylogeny, and reduces the opportunity for new adaptations to evolve by heterochrony, a process which Stanley (1972) has shown to be a major factor in bivalve evolution.

The survival of *Glycymeris* for over 100 million years attests that it is well adapted to its particular ecological niche. However, in a number of mechanical respects the animal is less efficient than more specialized bivalves. The ligament is weak and

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unable to brace the shell firmly against the sediment in which the animal burrows. Radial ribs strengthen the shell, but are not well designed for burrowing. Their mutual abrasion shows that the apposed umbones limit the opening of the valves. The soft parts are functionally inefficient in a variety of ways. In short, *Glycymeris* is a much compromised organism. The compromises which have adapted it to its restricted niche have been made at the expense of the flexibility, or range of possible variations on the theme, necessary for an evolutionary radiation into diverse environments.

CONCLUSIONS

Evolution in the family Glycymerididae has given rise to a modest diversity of species with a very narrow range of morphologies. This conservatism is not exceptional, although certainly greater than average, compared with other bivalves. It is the result of both extrinsic ecological factors and intrinsic morphological factors discussed in this paper. Glycymerids have always been opportunistic species, members of unstable, low-diversity communities inhabiting physically rigorous environments. They are morphologically unspecialized, and the characters of their shells are constrained to be highly intercorrelated by the requirements of function and accretionary growth.

Conservatism in the evolution of a group of species lineages implies survival as well as the absence of change. *Glycymeris* is clearly very well adapted to its particular habitat, from which more specialized forms are excluded by the vagaries of the physical environment. It occupies an ecological niche which is narrow with respect to substrate preference, but broad in terms of the animal's ethology and tolerance of physical instability. This pattern is typical of slowly evolving groups, which tend to be 'adapted to some ecological position or zone with broad but rather rigid selective limits' (Simpson 1944, p. 140; see also Stebbins 1949).

Most authors consider ecological factors to be of primary importance in determining rates of evolution. Stanley (1973) has recently argued most convincingly that differences in the intensity of competition are primarily responsible for the difference in evolutionary rates between bivalves and mammals in general. Low levels of inter-specific competition, and consequently low selection pressures, among bivalves have permitted extensive overlap of ecological niches, and the radiation of advanced groups without the extinction of more primitive forms. Population levels are limited by the physical instability of the environment and often by intense predation, rather than by competition. *Glycymeris* could well be taken as the type, perhaps extreme, example for these generalizations. There is no clear evidence of niche partitioning among glycymerid species, and they are subject to variable, sometimes very heavy, predation by naticid gastropods (Thomas 1970). The physical factors which largely define the glycymerid niche are frequently random rather than selective in their effects on populations. Perhaps more important, this physically determined niche has remained constant throughout the evolution of the group. *Glycymeris* did not have to evolve in order to 'keep up with the Joneses', as must organisms whose adaptive zones involve more specific biological interactions with evolving neighbours (Simpson 1944, p. 190; Van Valen 1973). Where an organism is primarily adapted to a constant physical environment, selection tends to be centripetal (Simpson 1944)

and is a positive factor in conservatism. As the environment fluctuates, glycymerid lineages change back and forth with it, within the limits set by morphology and behaviour (Thomas 1970).

The principal purpose of this paper has been to determine these limitations. Although extrinsic factors have been stressed in most discussions of evolutionary conservatism, Simpson (1949) clearly recognized the significance of morphological complexity for rates of evolution, again contrasting bivalves and mammals.

The more differentiated an animal is, the more ways there are in which it can evolve without fundamental modifications of its organization, particularly if its organ systems or skeletal parts can change independently of one another. While organisms with complex skeletons such as *Limulus* and *Latimeria* may evolve slowly for other reasons, organisms with very simple skeletons must be conservative, unless they can make large, rapid changes in morphology and adaptive zone, such as occur in the origin of higher taxa. The rudistids are exceptional among bivalves in that they made such an adaptive shift, and were able to maintain high rates of morphological change in their uniquely complex shells, in the course of rapid speciation. In contrast, the high degree of morphological, essentially functional, integration of the simple glycymerid shell does not allow the independent modification of individual characters. Eldredge and Gould (1972) have drawn attention to the importance of homeostatic mechanisms (Lerner 1954) in maintaining the morphological stability of individual species in time as well as space. These mechanisms must be most effective where morphological integration does not allow independent variation or change of characters. While genetic homeostasis can only act directly to stabilize individual species, similar systems of canalized development must be shared by the species of conservative genera and families, such as the Glycymerididae.

Glycymeris is a generalized descendant of the ancient arcoid lineage, which is itself very conservative in its fundamental anatomy, but remarkably diverse in the range of its adaptations. Evidently the glycymerid adaptation is not necessarily an evolutionary dead-end, for the parallelodontids, and hence all later arcoids, are thought to have evolved from Palaeozoic cyrtodontids very much like *Glycymeris* in form and inferred mode of life (Pojeta 1971, and earlier authors cited therein). Thus *Glycymeris* has secondarily reverted to an ancestral free-burrowing adaptation, a phenomenon which Stanley (1972) has recognized in both the Arcoida and the Carditacea. The adaptation and pattern of evolution of the Glycymerididae are in many respects comparable with those of other shallow-burrowing bivalves, to which many of the conclusions of this study should also apply.

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