On Etheria elliptica LAM. and the Course of Evolution, Including Assumption of Monomyarianism, in the Family Etheriidae (Bivalvia: Unionacea)

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The family Etheriidae (Unionacea) consists of four apparently monotypic genera, *Etheria*, *Bartlettia*, *Acostaea* and *Pseudomulleria*. All inhabit moving, often turbulent, river waters, almost entirely within the tropics in South America, Africa and India.

Etheria elliptica, found in the basins of the Niger, Congo and Nile and also in Madagascar, was studied living at Jinja, Lake Victoria. It is cemented indifferently by either valve (i.e. attachment by way of the mantle/shell) becoming bilaterally asymmetrical. It is also very irregular where attached to an uneven surface.

The mantle margins are singularly free, being briefly fused, by way of the inner mantle folds only, at the posterior end of the ctenidia. Unlike other etheriids, and the Unionacea generally, the mantle/shell is elongated dorso-ventrally with consequent effects on the adductors. The ligament, as probably throughout the Unionacea, has no fusion layer, consisting (apart from a periostracum which is early worn away) of anterior outer, inner, and posterior outer, ligament layers. Owing to a localized transverse 'pinching', the last named is compressed and extended to a corresponding extent laterally into the valves. This feature is characteristic of all the Etheriidae.

Consequences of these changes in form of the mantle/shell are the dorso-ventral extension of the visceral mass, also of the ctenidia the anterior end of which is withdrawn far from the mouth with correlated enlargement of the palps. Ciliary currents on the ctenidia resemble those in *Anodonta* and other Unionidae but with an additional oralward current along the margin of the outer demibranch, possibly of advantage to animals living in water with usually little suspended material. Pseudofaeces collect widely around the margin of the inhalant chamber.

Despite the absence (certainly in the adult) of a foot, there are well-developed posterior pedal retractors and very small anterior retractors. The oesophagus is unusually long, the stomach

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resembles that of the Unionidae, the midgut is extremely wide and the rectum passes dorsal to the pericardium. Pedal ganglia and statocysts are retained.

Although the course of development is unknown, cementation and change to adult asymmetry occur during early growth, the youngest animals being apparently typical bilaterally symmetrical (i.e. equivalve although inequilateral) unionids. Possibly they possess a foot and, in view of the habitat (on hard substrata in running water), also a byssus.

The elliptical cemented shell shows surprising development in *E. elliptica* var. *cailliaudi* where the dorso-ventrally elongated shell is strikingly asymmetrical with a dorsal beak prolonging the under valve which, in all, may be four or more times longer than the upper, free valve. The great part of the beak is composed of valvular, as distinct from ligamental, material owing to extension of the region between the anterior adductor and the ligament. The almost straight ligament, which runs down one side or other of the beak according to which valve is attached, is probably unequalled in depth throughout the Bivalvia. In this variety (as taxonomists are agreed in regarding it) the tendency towards dorso-ventral extension which appears shortly after initial attachment in *E. elliptica*, continues throughout life.

Bartlettia stefanensis, an inhabitant largely of the Amazon basin, has the same basic type of ligament but, as in the unionids generally, this is opisthodetic. The shell is markedly inequilateral with the posterior end enlarged and globular, the anterior end reduced but capable of localized extension, the animal being heteromyarian. Little is known about the animal which is reported to retain the foot. There is no evidence of cementation although the animal is attached to the substratum (typically in turbulent waters) apparently by insertion of the anterior end of the shell into a crevice and its subsequent growth within the space available. The adult shell is invariably most irregular. Here also early attachment by byssus is a probable precursor to the adult habit.

Acostaea and *Pseudomulleria*, which closely resemble each other, are inhabitants respectively of South America and India and represent the culmination of evolution within the Etheriidae. Like *Etheria* they are cemented indifferently by either valve. Beginning life as 'Anodon-like, equivalve and dimyarian' (Jackson), they attain great bilateral asymmetry with accompanying loss of the anterior adductor. Monomyarianism is here attained by exclusively posterior growth accompanied by major bilateral asymmetry due to change in the disposition of the mantle margins following cementation of one valve. The early symmetrical valves are retained (in *Acostaea*) at the tip of a 'talon' attached to the lower valve. No account of the animal of *Acostaea* exists, but that of *Pseudomulleria* resembles that of *Etheria* with loss of the anterior adductor and pedal retractors.

Assumption of monomyarianism in these genera is associated with cementation and a horizontal posture and here again it may possibly be preceded by a short phase of byssal attachment (when still in the vertical posture). Comparison is made with conditions in the monomyarian Anisomyaria and in the Tridacnidae. The three different manners in which the anterior adductor has been lost are clearly indicated in the nature of the pallial attachments.

The process of evolution within the Etheriidae is discussed and is illustrated in table 1. Although all species live in turbulent water, the diversity of adaptive radiation is surprising, the constituent genera being isomyarian, heteromyarian or monomyarian while cementation is associated with both dorso-ventral and posterior extension of the mantle/shell.

In the Etheriidae cementation occurs later in the life history than in any other bivalve apart from *Hinnites* (Pectinidae) but, unlike this genus and probably all other cemented bivalves, they begin post-larval life bilaterally symmetrical and only later, after exchanging a vertical for a horizontal posture, do they become asymmetrical. As species, they are the only bivalves to attach indifferently by either valve which makes the more remarkable the consequent asymmetry, not surpassed in any other bivalves, especially in *E. elliptica* var. *cailliaudi* and in *Acostaea* and *Pseudomulleria*. In their early bilaterally symmetrical unionid form followed by later assumption of a horizontal posture and the cementation accompanied by asymmetry, the Etheriidae (excluding *Bartlettia*) appear quite literally to recapitulate in the life history of each individual the evolutionary history of the species. Asymmetry appears as a direct consequence of cementation.

Despite their great specialization and very scattered, discontinuous distribution—both indicating age—there is no evidence of the existence of the Etheriidae earlier than the Pleistocene. The problem is discussed and the conclusion reached that, on present knowledge of structure and life history, the Etheriidae must be regarded as a natural group.

INTRODUCTION

Interest in the family Etheriidae was initially stimulated by examination of living specimens of the 'freshwater oyster' *Etheria elliptica* Lamarck at the laboratory of the East African Fisheries Research Organization at Jinja, on Lake Victoria, in March 1953. Further study was made during subsequent visits (all on behalf of the Colonial Fisheries Advisory Committee) while additional material, both living and preserved, was obtained from Mr C. C. Cridland and Dr G. Fryer of the staff of that Organization. It is pleasant to acknowledge the help of the then Director, Mr R. S. A. Beauchamp, and of other members of his staff. Knowledge was increased by the acquisition of shells of the related *Bartlettia stefanensis* (Moricand) from Dr W. J. Clench of the Museum of Comparative Zoölogy, Harvard. During preparation of this paper, the author was most fortunately put in touch with Mr F. H. Woodward who, with Mr T. Pain, had just completed a taxonomic revision of the Etheriidae (Pain & Woodward 1961). He had a most informative correspondence with Mr Woodward and also had the great advantage of seeing a manuscript copy of the joint paper and of examining their collections of shells of *B. stefanensis* and, more important still, of the remaining species of the family, *Acostaea rivoli* (Deshayes) and *Pseudomulleria dalyi* (Smith). The manner in which the monomyarian condition has been assumed in these last two species had previously been very inconclusively discussed (Yonge 1933 *a*). Examination of these shells along with others received on loan from the National Museum of Wales (Tomlin Collection) and from Liverpool Museum led to development of the new interpretation of the remarkable change in form undergone during growth by these species which is presented in this paper. Important additional information followed a study of shells of the elongated *Etheria elliptica* var. *cailliaudi* obtained from the British Museum (Nat. Hist.) through the kind offices of Mr Norman Tebble. Final thanks are due to colleagues in Glasgow especially to Dr G. Owen and to the author's research assistant, Miss J. I. Campbell, supported by a grant from the Department of Scientific and Industrial Research, who was responsible for the preparation of sections, for dissections and for the majority of the figures which illustrate this paper.

FAMILY ETHERIIDAE

This family is composed of the four monotypic genera, *Etheria* Lamarck 1807 (= *Aetheria*), *Bartlettia* Adams 1866, *Acostaea* d'Orbigny 1851 (= *Mulleria*) and *Pseudomulleria* Anthony 1907. Full synonymy is provided by Pain & Woodward (1961) whose elevation of *Pseudomulleria* from the subgeneric rank proposed by Anthony (1907) and accepted by Thiele (1935) is here supported. The first genus occurs in Africa, including Madagascar, the second and third in South America, and the last in peninsular India. Like all other members of the Unionacea, to which this family is assigned (Thiele 1935), these genera are confined to fresh waters. They occur almost entirely within the tropics. In all the shell is characteristically irregular with a dark periostracum and nacreous within; the hinge is toothless. With the exception of *Bartlettia*, all become firmly cemented, indifferently by either valve, to a hard substratum. They are all inhabitants of moving and often turbulent river waters. *Etheria* and *Bartlettia* retain the two adductors, the latter being somewhat heteromyarian, but the other two are monomyarian reaching this condition in a manner totally distinct from that which occurs either in the Anisomyaria (e.g. *Pecten*, *Anomia* or

Spondylus) or in the Tridacnidae (Yonge 1953*a*). With the exception of *Bartlettia*, the foot has been lost.

The bulk of knowledge about this family comes from the work of Anthony (1905, 1907) who was particularly concerned with the effects of lateral (pleurothetic) fixation. A similar interest is present in this study which is also concerned with the evolution of form, involving interaction of mantle/shell and body, within this most unusual family of bivalves.

Etheria elliptica Lamarck

Distribution

This species occurs in a broad belt across tropical Africa south of the Sahara, extending to the Mediterranean along the Nile Valley and also penetrating into the rivers of north-west Madagascar but being absent in Somaliland (see map in Pilsbry & Bequaert 1927, p. 448). Thus in the main it is an inhabitant of the Nile, Congo and Niger basins. Two subspecies or races, *E. tubifera* and *E. cailliaudi* (figures 9, 10), characterized respectively by spinose and elongate shells, are recognized, the former being found mainly in West Africa, the latter in the Nile basin and East Africa.

Dealing with its distribution in Uganda, Mandahl-Barth (1954) states that *E. elliptica* occurs 'in several places in Lake Victoria (Ilemera, Entebbe, Dagusi) and in the Victoria Nile (Ripon Falls and Owen Falls), but is not known from Lake Albert or Lake Edward or the smaller rivers and lakes'. He found it to be larger in Lake Victoria, with lengths of up to 70 mm, than in the (Victoria) Nile. Personal collections, however, include a shell 85 mm long, while Mandahl-Barth reports that von Martens recorded a specimen 99 mm long from Masanza. In the Nyanda River at Kisumu (Kenya), Mr Cridland found empty shells 120 mm long by 80 mm high, and specimens almost 200 mm long have been taken in the Congo.

Habitat

Knowledge of the habitat is based largely on the field notes in the Congo basin of H. Lang reported in Pilsbry & Bequaert (1927). Although these 'river oysters' are there widespread, they 'were only found on certain rocky sections about rapids and falls of fair-sized streams, where they form "banks" in stony and generally turbulent places, often ten feet and more below the surface of the running floods. Even when the rivers are at their lowest level, as happens during the dry seasons, the uppermost shells alone become exposed. The mollusks attach themselves by one valve to the rock and also to other shells of their kind. In some places they are about three and four deep and sometimes so hemmed in that probably not a few are thus suffocated, as many shells close to the rock base contain no animal.' Although they are up to 8 in. long, Lang notes that they are difficult to see in the brownish water while, like the surrounding stones, they are usually covered with encrusting bryozoans and sponges amongst which live other animals including small bivalves and snails.

Etheria is of some economic importance. In certain regions of the Congo it is collected as food, usually after drying and smoking. After European occupation the resultant mounds of empty shells provided valuable local sources of lime for the manufacture of mortar or for limewashing houses.

Shell

To quote from the detailed description by Pilsbry & Bequaert (1927), the shell is 'irregular, inequivalve, oyster-like, covered with a dark periostracum, attached by either valve; beaks anterior, that of the fixed valve often lengthened. Interior nacreous but rather dull, usually blistered or cellular. Hinge without teeth; ligament thickened inwardly posteriorly, forming a resilium, terminated by a deeply entering, narrow sinulus. Two large adductor impressions.' Only in the description and interpretation of the structure of the ligament (given later) need this description be significantly altered.

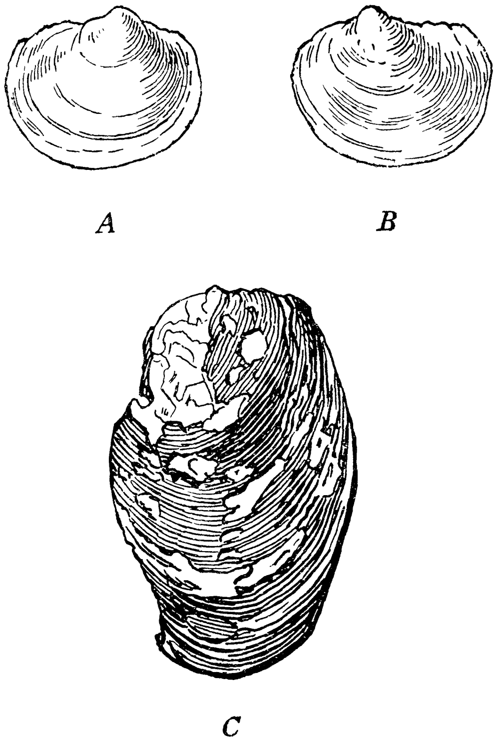

FIGURE 1

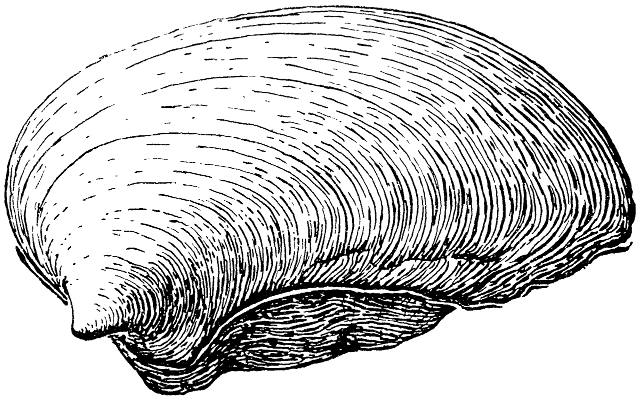

FIGURE 2

FIGURE 1. *Etheria elliptica*. *A*, *B*, young individuals attached to smooth surface by right and left valves respectively; *C*, old shell (containing living animal) showing erosion of surface with pitting of both periostracal and calcareous layers of upper (right) valve, also dorso-ventral extension of shell. (Magn. × 1.)

FIGURE 2. *Etheria elliptica*. Specimen 5·2 cm long attached to smooth surface by the left valve and viewed from the dorso-posterior aspect to show the under valve, there unattached. The shell is becoming dorso-ventrally extended.

The specimens personally examined, ranging in length from 10 to 85 mm, were all from Lake Victoria. They were attached indifferently by either valve (figure 1). Anthony (1907) states that they cement themselves only by the anterior half of the under valve but in young shells this entire surface is effectively attached although in older ones the under valve is raised somewhat clear of the substratum along the hinge line and especially along the posterior margin where shell secretion tends to be more upward than outward (figure 2). Where attachment is to a flat surface, e.g. of concrete, the under valve is correspondingly flat and the upper externally very convex (figure 2).

The shells are inequilateral with the umbones nearer to the anterior end and pointed in that direction. Although at attachment and for some time subsequently (figures 1 *A*, *B*; 2), the shells are elongated antero-posteriorly as in a typical unionid, they later become extended dorso-ventrally (figure 1 *C*). The outline is basically oval (figure 3) like that of an elliptical leaf with the ligament corresponding to the petiole. As in the specimen shown in figure 3, the oval may be skewed to a greater or less extent in a posterior direction with a corresponding inclination of the ligament. The form of the mantle/shell in *Etheria* is responsible for the dorso-ventral elongation of the adductors (figure 3), the posterior extending the more ventrally, the anterior the more dorsally.

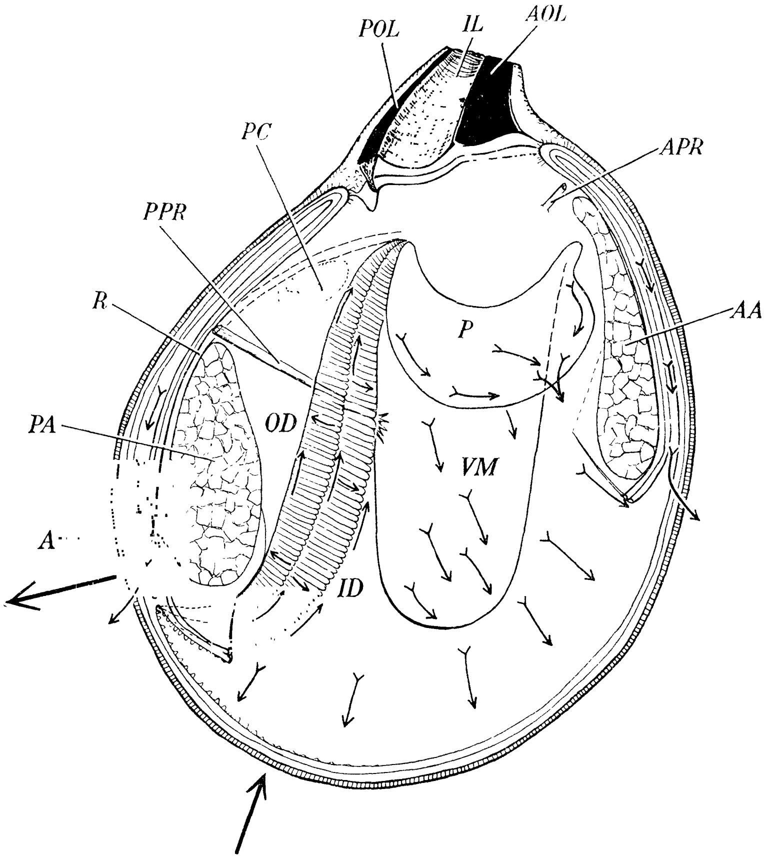

FIGURE 3. *Etheria elliptica*. Body and ligament viewed after removal of upper (right) valve and mantle lobe. (Magn. ×1½.) *A*, anus; *AA*, anterior adductor; *AOL*, anterior outer ligament layer; *APR*, anterior pedal retractor; *ID*, *OD*, inner and outer demibranchs of right ctenidium; *IL*, inner ligament layer; *P*, palp; *PA*, posterior adductor; *PC*, pericardium; *POL*, posterior outer ligament layer; *PPR*, posterior pedal retractor; *R*, rectum; *VM*, visceral mass. Large arrows indicate position of inhalant and exhalant currents, smaller arrows currents on ctenidium, feathered arrows cleansing currents.

Where attachment is to an uneven surface, as in nature is usually the case, the shells become highly irregular both in outline and in contour owing to the extensive attachment of the under valve, to the irregularities of which the upper valve must conform.

The general surface of the free valves is covered with numerous series of low irregular concentric ridges. The periostracum is golden yellow in young specimens and may remain entire in shells up to 4·5 cm long. Older (not always larger) shells are often deeply eroded (figure 1 *C*) with both periostracum and outer calcareous layer extensively pitted and with even the inner, nacreous layer superficially penetrated.

Mantle lobes

The somewhat fleshy mantle lobes (figure 3) are bordered by the characteristic three marginal folds (Yonge 1957) which are darkly pigmented. All are unusually small. The outer, as always, is attached to the margin of the shell by a thin sheet of periostracum secreted along its inner surface (the outer surface producing the outer calcareous layer of the shell). The middle fold is no more than a narrow ridge and, as certainly in *Anodonta* and possibly throughout the Unionacea, it is the inner muscular, and *not* the much more usual middle, fold which bears the single row of small tentacles. These are best developed around the inhalant and exhalant openings. Anterior and posterior to these they fade into insignificance.

The two lobes are singularly free from attachment to one another. Only at the posterior end of the ctenidia is there brief union by way of the inner mantle folds only. The ctenidia are attached here, ensuring complete separation of inhalant and exhalant chambers. Otherwise the three marginal mantle folds are everywhere free, extending unfused (figure 5) dorsal to the adductors into the depths of the embayments at either end of the ligament and so leaving the rectum and anus exposed on the hind surface of the posterior adductor (figure 3).

As already noted, both adductors (figure 3) are greatly extended dorso-ventrally and this can be interpreted both as a result of the elliptical form of the shell and as a response to the mechanical needs of closure in a shell of this form which is also cemented. Their total length is about half that of the entire mantle margin. They do not, as indicated in section in figure 5, extend dorsally to the ends of the ligament, the regions of hypertrophied pallial muscle represented by the adductors having moved somewhat from their primitive position, as in other bivalves with similar mechanical needs such as the Solenacea (Owen 1958, 1959). Between the adductors there is firm attachment by the orbicular muscles along a pallial line set so far back that it encloses little more than half of the inner surface of the valve. But, as in other Unionacea, although unlike various other groups of bivalves, secretion of the characteristic nacre forming the inner calcareous layer of the valve is *not* bounded by the pallial line but extends almost to the margin of the shell.

Ligament

In the depths of the embayments at each end of the ligament, the outer surface of the outer mantle fold—which elsewhere forms the outer calcareous layer of the valves (Yonge 1957)—lengthens anteriorly and broadens posteriorly and secretes the corresponding outer ligament layers. There is *no* fusion of outer mantle margins, as for instance in *Pinna* (Yonge 1953 *b*), and so *no fusion layer* which represents secondary extension of the primary ligament in many bivalves (Yonge 1957). The Etheriidae, and probably all Unionacea, possess a purely primary ligament consisting of superficial periostracum (where not worn away) with anterior and posterior outer ligament layers and between (initially also beneath) these the inner ligament secreted by the mantle isthmus. Without knowledge of their distinct origins, Anthony (1907) noted the presence of these regions of the ligament (figure 8), referring to the marginal areas as being non-elastic and the central region as calcified but elastic. Lack of any anterior splitting of the ligament, such as exists to greatest extent in *Glossus* (*Isocardia*) (Owen 1953 *b*) and the Chamacea and to a less extent in the Cardiidae (Owen 1953 *a*) and the Mytilidae (Yonge 1955) indicates the absence of any tangential component in shell growth such as occurs in those bivalves. This is undoubtedly true of all the Unionacea.

The ligament of *Etheria* is shown viewed from the ventral aspect in figure 4 and in side view after removal of the upper (here right) valve in figure 3. Outer and inner ligament layers are easily distinguished even by the naked eye, the former being dark but translucent, the latter paler but opaque. The asymmetry of the valves appears in the edentulous hinge region including the ligament (see figure 4) which is somewhat larger on the 'free' side of the sinuous mid-line. The ligament also undulates in the longitudinal horizontal plane, the under surface of the inner ligament in particular being convex (figure 3). The most striking feature of the ligament, however, and one characteristic of this family of the Unionacea, is the compression and lateral extension into the valves at the posterior end. As shown in figure 4, this affects the posterior outer layer which is short but penetrates deeply into each valve. This, as shown in figure 5, is due to compression of the secreting surface of the outer surface of the outer mantle folds posteriorly and so represents a transverse pinching of the mantle/shell in this region.

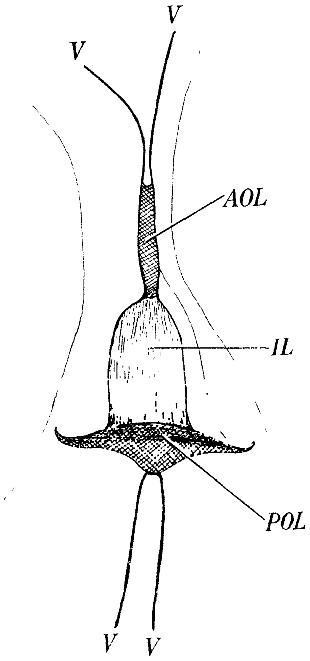

FIGURE 4. *Etheria elliptica*. Ligament viewed from ventral aspect, attached (right) valve on left, free valve on right. (Magn. × 4.) *V*, margin of valves. Other lettering as before.

The ligament increases greatly in thickness with growth. In the youngest shells the two outer layers extend dorsally to meet above the intervening inner layer and beneath the umbones, but following attachment there is intense secretion by the dorsal mantle surfaces with formation of additional ligament by the mantle isthmus and the outer mantle folds and of further nacreous substance to the valves by the adjacent mantle surfaces. This causes a ventralward movement of the animal within the containing shell. Such movement is an inevitable consequence of cementation; only in this way can internal width be increased dorsally as it must be during growth. Precisely the same thing happens in the similarly cemented Ostraeidae, in *Spondylus* and in the 'rock scallop', *Hinnites* (as figured in Yonge 1951), although not in the very similar but non-cemented species of *Pecten* or *Chlamys*. In all cemented species continuous secretion of ligamental material occurs throughout life with extensive areas of old ligament persisting dorsal to the functional layers. These uppermost, exposed, areas become eroded and their attachments to the valves exposed in older shells. The state of affairs in *E. elliptica* is shown in figure 3 and the exaggerated condition found in *E. elliptica* var. *cailliaudi* in figures 9 and 10.

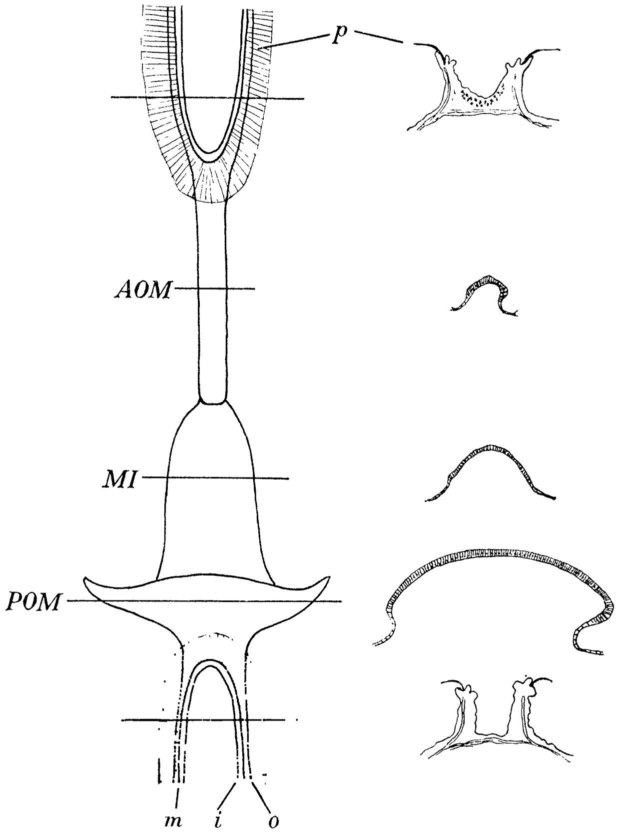

FIGURE 5. *Etheria elliptica*. Mid-dorsal region showing mantle isthmus (*MI*) with anterior and posterior outer surfaces of the outer mantle folds (*AOM*, *POM*) responsible respectively for secretion of inner, and of anterior and posterior outer, ligament layers. Anterior and posterior embayments of mantle lobes shown with unfused inner (*i*), middle (*m*) and outer (*o*) marginal folds with periostracum (*p*) secreted by inner surface of last. Transverse sections through each region, at positions indicated by horizontal lines, shown on right. (Magn. × 3.)

Mantle cavity

The general appearance of the animal after removal of the right valve and mantle lobe is shown in figure 3. Between the elongated adductors and roughly parallel to them lie the visceral mass and the ctenidia, the latter extending from beneath the ventral surface of the posterior adductor almost directly dorsal to their anterior extremity at the posterior end of the visceral mass. Connexion is there made with the relatively far-distant mouth by way of conspicuously large, crescent-shaped, palps, the inner demibranchs terminating just within the opposed lamellae.

The disposition of the major organs thus conforms to the pattern set by the mantle/shell. The elliptical form of this is responsible for the dorso-ventral elongation of the adductors, as already noted, and also for that of the visceral mass and the ctenidia. The pinching transversely of the posterior end of the dorsal region of the mantle has the added effect of pulling back the anterior end of the ctenidia and so extending the palps antero-posteriorly. Thus the ctenidia, losing the close proximity with the anterior adductor customary in dimyarians, become closely applied to the posterior adductor, a condition normally found in monomyarians.

Ctenidia and palps

The plicate ctenidia are very firmly attached to the mantle marginally and to one another or, antero-dorsally, to the interposed visceral mass (figure 3). The axes are free for the posterior quarter of their length. The inner demibranch is somewhat larger than the outer. Grooves run along the margins of both and also along the axes and between the mantle surface and the edge of the outer demibranchs. Frontal ciliation is the same on ordinary and principal filaments, i.e. on the crests of the plicae and in the deep intervening furrows.

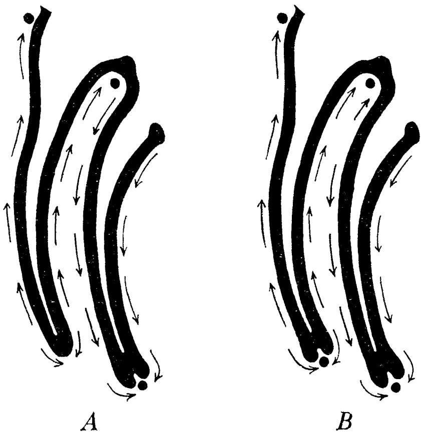

FIGURE 6. Diagrammatic sections through left ctenidia of *A*, *Anodonta* (typical of Unionidae) and *B*, *Etheria elliptica*, to show nature of ciliary currents (indicated by arrows), on the frontal surfaces of the demibranchs and of oralward tracts (indicated by dots) along margins of demibranchs and dorsally. (*A*, after Atkins 1937.)

The nature of the ciliary currents is indicated in figure 6*B*. On the inner demibranch cilia beat to the margin except in the region near to the axis. On the inner ('descending') surface of the outer demibranch, cilia also beat towards the axis except near the free margin where they carry particles into the groove. The same arrangement holds on the outer surface where only cilia adjacent to the margin beat towards the groove while over the remainder they carry particles towards the line of attachment to the mantle. Here, and along the axis, and within the two marginal grooves, cilia beat towards the palps and it will be noted in figure 6*B* how each of these oralward tracts receives particles collected over a significant proportion of the total frontal surface with the marginal groove of the inner demibranch being the most liberally supplied.

This pattern of gill ciliation differs from any previously described. It is, however, nearest to that in the Unionidae (Type D of Atkins 1937), although in this there is no current towards the axis on the descending lamellae of the inner demibranch. Moreover, there are but three oralward currents (figure 6*A*), there being no marginal groove along the outer demibranch. Conditions in *Etheria* may be regarded as derived from those in the Unionidae (e.g. *Anodonta*), the changes increasing efficiency so that most of the material which is carried on to the surface of the gill reaches the palps. The animals inhabit stony regions where there will be little suspended matter except following rain storms, and then any excess of material will cause sudden contraction of the plicae and rejection of particles on to the mantle surface, there to be accumulated and expelled as pseudofaeces.

The anterior ends of the inner demibranchs barely penetrate between the posterior margins of the pairs of very large, crescent-shaped palps. The opposed surfaces of the latter are covered with very numerous rows of correspondingly small ridges. These organs also would appear especially fitted for the selection of the very finest particles from those collected by the ctenidia. The long passage to the mouth is made either in the depth of grooves between the pairs of palps (lateral oral groove) or across the summits of the lamellar folds with, as always, the larger particles drawn into the furrows and passed to the margins of the palps for rejection and incorporation into the pseudofaeces.

Currents in the mantle cavity

The positions of the inhalant and exhalant openings are shown in figure 3, the former being restricted to the mid-ventral region owing to apposition of the mantle margins anteriorly. Owing to the absence of fusion of the inner mantle folds, cilia occur along the outer surfaces of the adductors. Particles are carried to the ventral margins of these muscles and there rejected. The currents concerned with accumulation of pseudofaeces in the inhalent chamber are unusually simple. Both on palps and visceral mass, material is conveyed antero-ventrally (figure 3) where it briefly accumulates and then falls on to the mantle surface. There, cilia beat toward the margin where particles collect; there is an unusual absence of currents carrying these pseudofaeces posteriorly. In *Etheria*, as to a more limited extent in the unrelated Ostraeidae or true oysters (Yonge 1926) with their similar habit, pseudofaeces collect over a wide area prior to expulsion by periodic contractions of the adductors. In this way material rejected from the surface of the ctenidia and palps, and which collects on the surface of the visceral mass and mantle, is removed from the inhalant chamber. The exhalant current carries with it the faeces and the renal and reproductive products.

Internal anatomy

The principal anatomical features are shown in figure 7 confirming and supplementing previous descriptions notably by Anthony (1907) and Sassi (1910). Despite the total absence, at any rate in the adult, of a foot, there are well-developed posterior retractor muscles (*PPR*) and very much smaller anterior ones (shown only in figure 4, *APR*). The latter muscles have not previously been noted and may well be functionless in the adult but the large posterior muscles probably pull back the visceral mass and the ctenidia when the valves close. The mouth (*M*) is situated just below the dorsal end of the long anterior adductor. It is a wide slit and leads into a long oesophagus (*O*) of corresponding width. The stomach (*S*) was not examined in life but from the appearance in preserved specimens is essentially similar to that of *Anodonta*, i.e. a type 4 stomach (Purchon 1958). As shown in figure 7, the gut (*G*) is much coiled within the visceral mass the substance of which it effectively fills. Absorption in the Bivalvia occurs in the tubules of the digestive diverticula and the probable reason for the exception diameter of the gut in *E. elliptica* is the need to consolidate as faeces great quantities of inedible matter. The rectum (*R*) passes dorsal to the pericardium as it does in all Etheriidae of which the structure is known. This may be connected with the posterior pinching of the mantle/shell (of universal occurrence in the family) but hardly with the dorso-ventral extension found only in *Etheria*. Exposure on the posterior wall of the adductor of the final section of the rectum and of the anus, due to non-fusion of the mantle margins, has already been noted.

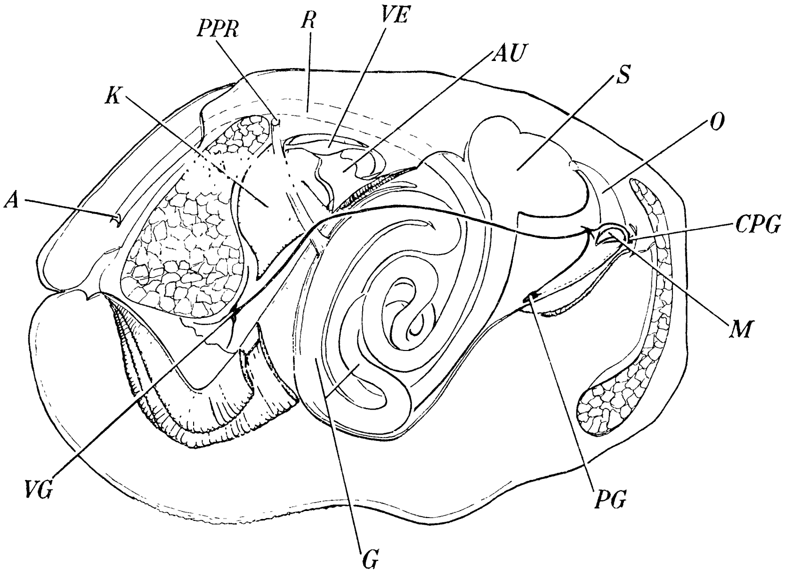

FIGURE 7. *Etheria elliptica*. Dissection of animal from right side to expose internal anatomy; in particular course of gut and of nervous system. (Magn. × $1\frac{1}{2}$.) *AU*, auricle; *CPG*, cerebro-pleural ganglion (left); *G*, coils of gut in visceral mass; *K*, kidney; *M*, mouth; *O*, oesophagus; *PG*, pedal ganglia; *S*, stomach; *VE*, ventricle; *VG*, visceral ganglia. Other lettering as before.

The cerebro-pleural ganglia (*CG*) are small with exceptionally long connectives over the wide oesophagus; the small pedal ganglia (*PG*) lie close to them at the anterior end of the visceral mass. As noted by Sassi (1910), statocysts are retained. The visceral ganglia (*VG*), situated as always on the ventral surface of the posterior adductor, are enlarged as in the other, unrelated, pleurothetically attached bivalves. Sassi (1910) describes the excretory and circulatory systems, the former involving pericardial glands as well as kidneys (*K*). As observed by Anthony (1907), and here confirmed, the small eggs are retained briefly within the exhalant chamber mainly, although not exclusively, within the water tubes of the more capacious inner demibranchs, and there development proceeds. Unfortunately nothing is known about the course of development which presumably involves a stage parasitic on fish. Whether this is a glochidium as in the Unionidae or the very different and much further modified haustorial larva recently described by Fryer (1959, 1961) in *Mutela*, or is even of a type unique to the Etheriidae, remains to be discovered.

Characteristics of *Etheria*

Lack of knowledge about larval development in *Etheria* does not, fortunately, affect our understanding of the significant features of adult structure because these are assumed unusually late, in the period accompanying and following initial attachment. Anthony (1907) states that young *Etheria* resemble young *Anodonta* or the tropical *Spatha* (= *Mutela*), i.e. are typical unionids, a group in which the shell is equivalve but inequilateral with the umbones well towards the anterior end. Examination of the ligaments, both superficially and in serial transverse sections, of *Anodonta cygnea* and *Mutela* sp. (obtained from Lake Victoria) revealed the presence in both of a narrow elongated anterior outer ligament layer, a long inner ligament layer of medium width and a posterior outer ligament layer both wider and shorter than the anterior outer layer. In *Mutela*, where the posterior outer layer is wider, conditions are somewhat nearer to those in *Etheria*. Despite the contrary statement of Beedham (1958) for *A. cygnea*, no fusion layer was found. There was no indication of an anterior splitting of the ligament, i.e. there is no tangential component in shell growth. The ligament is opisthodetic with great posterior extension of all layers, of anterior outer layer under the inner layer and of this under the posterior outer layer so that near the centre of the ligament all three layers appear in the same section (as in *Bartlettia*, see figure 13).

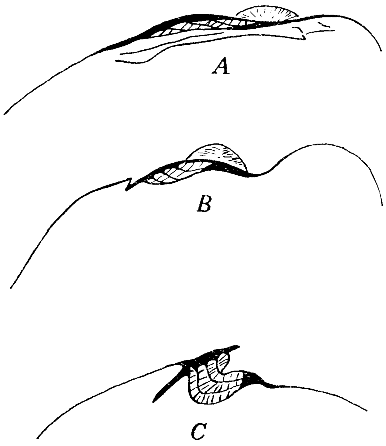

Figure 8. Disposition of ligament in *A*, *Unio*; *B*, young *Etheria* shortly after attachment; *C*, adult *Etheria*. (From Anthony 1907.)

Anthony (1907) gives an interesting comparison between the ligament in *Unio* (essentially the same as in *Anodonta* and *Mutela*) and in recently attached and adult *Etheria* (figure 8, *A*–*C*). The pronounced folding and posterior compression of the ligament in adult *Etheria* which develops after attachment (cf. figure 8*B* and *C*) he attributed to a process of what he terms 'pseudo-plicature' in which the dorsal border of the shell folds back on itself. This process has been here described as the result of a transverse 'pinching' at the posterior end of the mantle/shell. It is, as will be shown, *the* characteristic feature of the Etheriidae.

With it are associated changes in growth gradients around the margin of the shell. In the genus *Etheria* (but not in the other genera) the effect of these is to produce a dorso-ventrally elongated shell.

With these alterations in form comes change in habit, from burrowing to cementation, although at what point in evolution *Etheria* came to lie on one side and become cemented it is impossible to say. Certainly the dorso-ventral elongation enabled the contained body to 'grow away from' the ligament and was also responsible for the corresponding extension of the visceral mass and ctenidia, the posterior 'pinching' also causing posterior withdrawal of the latter with a functionally compensating enlargement of the palps.

It is not improbable that young unattached equivalve *Etheria* possess a foot and, in view of the habitat—in running and often turbulent water—possibly a byssus for temporary attachment in a vertical posture. But cementation is certainly *not* here preceded by a horizontal posture associated with byssal fixation (i.e. by way of the body) as it is in anisomyarians (e.g. *Hinnites*) and which predetermines by which valve attachment must inevitably be made (right valve in all but the Ostraeidae). Such preceding byssal fixation is also accompanied by a reduction in the anterior half of the body (Yonge 1953 *a*) which does not occur in *Etheria*. Here attachment is the sole responsibility of the mantle/shell with presumably local conditions determining by which valve this shall be. The habit of life so imposed would permit loss of a now unwanted foot.

The elliptical cemented shell is capable of surprising modification, most strikingly where intense secretion by the dorsal mantle tissues produces the enormously extended 'beak' found in *E. elliptica* var. *cailliaudi*. The beak is a part of the cemented under valve which, owing to this great bilateral asymmetry, may be more than three times as long as the upper valve (figure 9). Modification of form is here so great as to demand special description.

E. ELLIPTICA VAR. *CAILLIAUDI*

Observations on this variety have been made on two shells from the British Museum, one attached by the right valve (figure 9), the other by the left (figure 10); neither is complete but the former more nearly so with a total length of 43 cm. Of this 30 cm is occupied by the beak which if intact would probably have exceeded 40 cm. The upper valve, which dorsally overlaps the margin of the under valve as indicated by the dotted line in figure 9 *A*, is only 16 cm long. The second specimen retains little more than the portion of the beak shown in figure 10 *A*, but the upper valve and the space occupied by the animal in the attached valve are approximately the same size as the other specimen. A much smaller specimen, attached to the free distal portion of the under valve of the first specimen, is shown in figure 9 *E*; it has been omitted from the drawing of the complete valve (figure 9 *B*).

Both valves show successive stages in growth, temporary cessation being accompanied by the production of tubular extensions of the shell margin secreted presumably by temporary extensions of the mantle. Similar extensions, but more closely set in the absence of any such elongation of the shell, are characteristic of *E. elliptica* var. *tubifera* as illustrated in Pilsbry & Bequaert (1927). Areas of attachment (figure 9 *B*, *AT*) are few but may have been more extensive on the missing apical region (as they are in the younger shell shown in figure 9 *E*), and the immediate impression is that these exceptionally large and rather fragile shells grow in relatively quiet water.

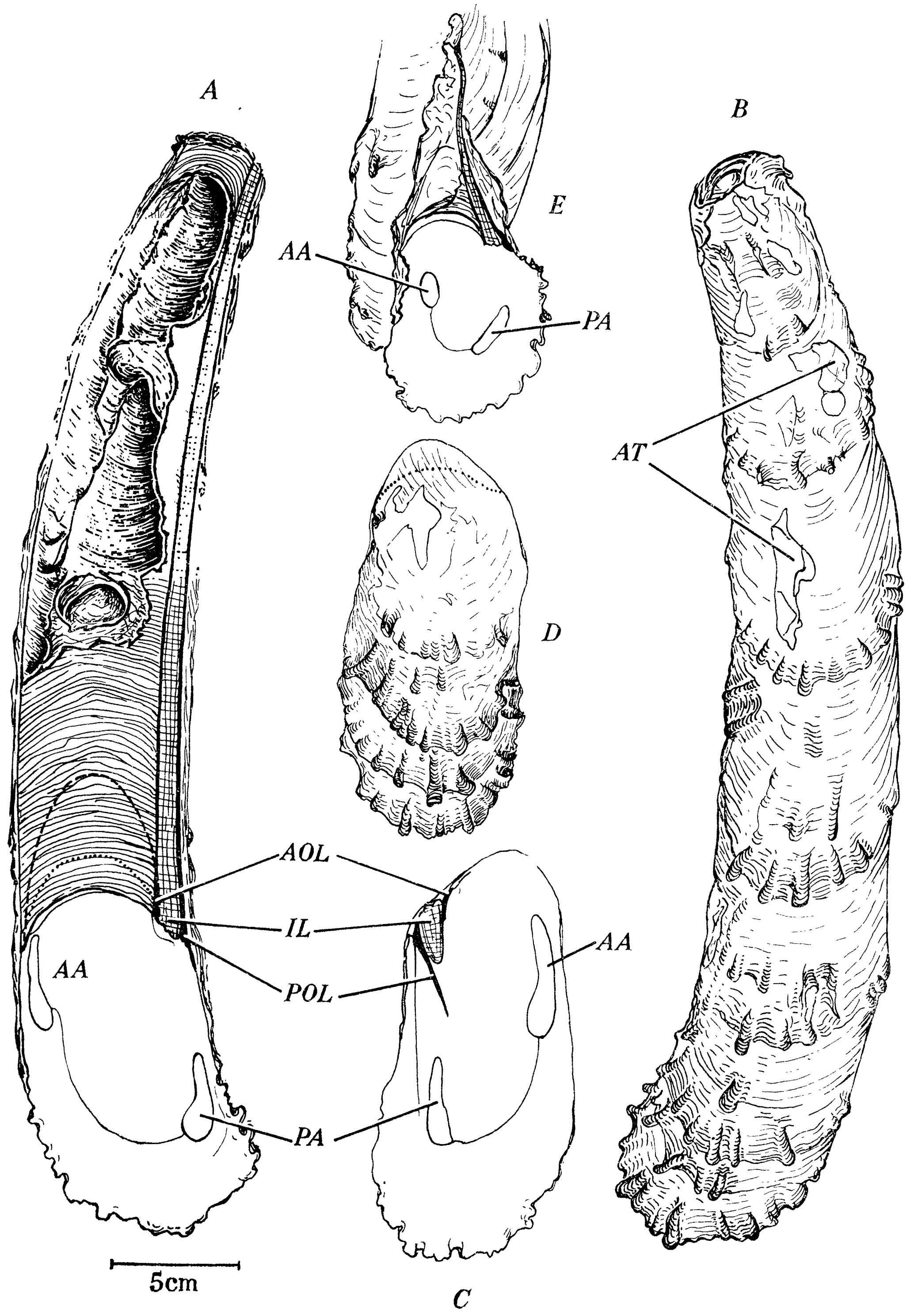

FIGURE 9. *Etheria elliptica* var. *cailliaudi*, attached by right valve. *A*, upper surface of under valve showing great dorsal extension of beak, broken at apex and much eroded with ligament running down right side (when viewed as in the figure), broken line indicates extent of cavity within beak, dotted line extent of overlap of upper valve; *B*, under surface of same valve showing areas of attachment (*AT*) and tubular extensions indicating stages in growth; *C*, *D*, inner and outer surfaces of upper valve, dotted line indicating extent of overlap of under valve dorsally; *E*, attached valve of shell of young specimen with intake beak. Lettering as before.

The beak is formed by the continued, and presumably relatively rapid, ventralward growth of the animal, new shell being produced marginally and additional layers continuously added dorsally. A slight curvature is retained in the larger specimen (figure 9) which is somewhat concave on the posterior side, but specimens figured by Anthony (1905, 1907) are almost straight. Much the greater part of the beak is composed of valvular, as distinct from ligamental, secretion. It largely consists of concave layers of shell secreted by the outer surface of the outer mantle fold at the margin of the attached valve in the region, here greatly extended, between the dorsal extremity of the anterior adductor (*AA*) and the depth of the anterior embayment where this surface secretes the anterior outer ligament (cf. figures 3, 10*A*).

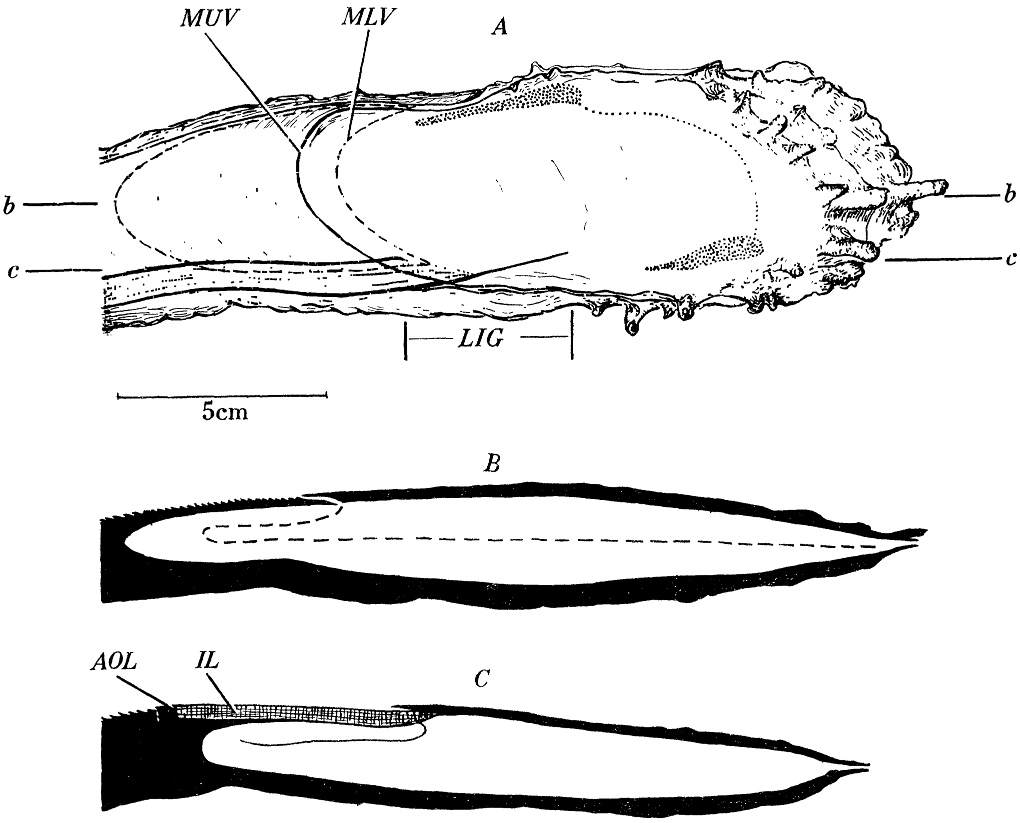

Figure 10. *Etheria elliptica* var. *cailliaudi*, attached by left valve. *A*, viewed from above with upper valve *in situ* but, except ventrally, shown as though transparent to reveal extent of ligament, adductors and pallial line stippled. *LIG*, extent of ligament attaching the valves, anterior outer layer on left; *MLV*, *MUV*, margins of lower and upper valves (broken and entire lines respectively). *B*, dorso-ventral longitudinal section through valves along line indicated by *b* in *A*, broken line indicating approximate mid-line of contained body. *C*, similar section through valves and ligament along line indicated by *c* in *A*. Lettering as before.

Although this margin of the shell is 'dorsal' to the ligament itself the contained animal is not bounded by it. The cavity of the attached valve penetrates for a considerable distance beneath the surface layers of the beak, as shown by the broken lines in figures 9*A* and 10*A* and still more clearly in the 'dorso-ventral' sections of the shell shown in figures 10*B*, *C*. The actual distances to which the beak is so penetrated are respectively 4·5 and 5·4 cm.

The almost straight ligament, extended to a depth probably unparalleled in any other genus of the Bivalvia, runs along one side or other of the beak according to whether the shell is attached by the right (figure 9) or the left valve (figure 10). Compared with *E. elliptica* (figure 3), the anterior outer ligament (*AOL*) is very narrow while the inner layer (*IL*) is well developed and forms the greater part of the ligament. As indicated in figure 10*C*, it extends along a ridge of shell in the lower valve. The narrow posterior outer layer (*POL*) diverges to penetrate, as in all etheriids, into each valve although to a notably greater extent in the upper valve (figures 9*A*, *C*). But owing to the exceptional dorso-ventral extension of the shell, the posterior ligament layer runs more nearly parallel to the posterior margin of the valves than in any other etheriid.

The ligament extends laterally into the upper valve for distances increasing from the anterior end backwards. As shown in figure 9*C* and also in figure 10*A* where the upper valve is shown *in situ* but, except marginally, is portrayed as though it were transparent, the inner ligament layer extends laterally for only a very short distance and the posterior outer layer much further. This is, of course, due to the transverse extension of the secreting surfaces which here affects the mantle isthmus as well as the outer surface of the outer mantle fold in the posterior mantle embayment. In other words, greater dorso-ventral extension is accompanied by a correspondingly greater 'pinching' of the posterior pallial region. This may also account for the extension of the anterior shell margins around the 'dorsal' surface.

The extremely short ligament—in such great contrast to the elongated opisthodetic ligament of the ancestral unionid (and of the allied etheriid *Bartlettia* described below)—is confined to what now appears to be the postero-dorsal corner although it is, strictly speaking, the central area of a dorsal surface which extends between the two adductors. These are elongated as in *E. elliptica* (figure 3) but the anterior adductor is here carried much further dorsally and the posterior adductor much further ventrally (cf. figures 3, 10*A*). This again is associated with the intensified 'pinching' in *E. elliptica* var. *cailliaudi*.

The remarkable bilateral asymmetry is strikingly displayed in the form of the two valves, the upper (figures 9*C*, *D*) being almost flat and forming what is effectively an opercular plate over the opening of the concave lower valve with its deep dorsal extension within the beak (figures 10*B*, *C*). Although the margins of the two valves coincide around the ventral surface, the upper valve overlaps the margin of the lower valve for some distance in the region between the anterior adductor and the ligament (cf. *MUV* and *MLV* in figure 10*A*, and dotted lines in figures 9*A*, *D*). As indicated in figure 10*B*, continued growth will here push the lower valve under the upper one, marginal areas of the latter continually breaking away following the withdrawal of the mantle tissues from them.

There must be a corresponding asymmetry of the contained animal, unfortunately never described. This will be greatest in the region anterior to the ligament, i.e. in that part of the body which occupies the deep 'dorsal' cavity within the beak and which will consist largely of the 'under half' of the body (whichever side this may be). The probable line of division between the two sides of the body is indicated by the broken line in figure 10*B*. Examination of the body of *E. elliptica* var. *cailliaudi*, still better of the living animal, would be most rewarding.

The only data about changes during growth are provided by the small shell (without upper valve) shown in figure 9 *E*. Here the beak is only about half the length of the entire shell the cavity of which is more rounded than in the larger specimens and the position of the adductors less modified. Comparison with figure 9 *A* reveals thatin the course of growth the length of the beak may be increased by four to five times but the corresponding length of the shell opening (disregarding the internal cavity) by little more than half as much again.

In both shell length and the position of the adductor scars it is clear that the tendency towards dorso-ventral extension which becomes apparent some little time after attachment in *E. elliptica* continues, and indeed, probably increases, throughout life in *E. elliptica* var. *cailliaudi*. Elongation here is in most interesting contrast to that in the monomyarian etheriids, *Acostaea* and *Pseudomulleria*, where, as described later, the posterior end is extended, the animal at the same time twisting from a vertical to a horizontal posture with resultant loss of the anterior adductor (see figure 19).

The survival value of greatly elongated shells, found in some other cemented bivalves, notably in the Japanese oyster, *Crassostrea gigas*, which also attains lengths of over a foot, probably resides in the added capacity so conferred to maintain contact with the water in regions where there is danger of overgrowth by other individuals.

There remains the question of the status of *E. elliptica* var. *cailliaudi*. Although clearly belonging to the genus *Etheria* the differences in growth and final shell form—including the fact that here it is the under valve which is concave, whereas in *E. elliptica* it is the upper valve—would certainly point to its being a distinct species. However, that is not the opinion of those who have examined a wide series of shells. Thus Pilsbry & Bequaert (1927) write of *Etheria* that 'Many supposed species have been defined, but in the latest considerations of the genus by von Martens (1897),* by Germain (1907),* and by Anthony (1907) all are recognized as forms of one species. *E. tubifera* and *E. cailliaudi* will probably be considered distinguishable subspecies, the former mainly West African, the latter mainly Nilotic and East African.' They add that 'According to Simroth and Germain the spinose forms grow in quiet, the smooth in rapid water. In some places smooth and spinose individuals appear to occur together, or at least are associated in lots with the same field label. A careful study of an *Etheria* colony is needed.' In correspondence Mr F. R. Woodward informed the author that if he were able to examine a large series he 'would find that the two "species" grade into one another'.

Accepting the judgement of those who have studied these large series, it remains to be remarked that the range of variation within the species is indeed remarkable—although, of course, not more so than the great bilateral asymmetry which appears during growth and affects indifferently one side or other. A study of a living *Etheria* colony could certainly be most illuminating.

Bartlettia stefanensis (Moricand)

There is a somewhat baffling lack of precise information about the body, as distinct from the shell, of this most interesting species. The latter has been most fully described by Anthony (1907), Carcelles (1904) and Morretes (1941), the last named under the name of *Rochanaia gutmansi*. Later (1949) he referred this to *Bartlettia* although retaining it as a

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* For references see Pilsbry & Bequaert (1927).

separate species; this view is not supported by Pain & Woodward (1961) or by the present writer. *B. stefanensis* appears to be widely distributed in the rivers of central South America and has been collected in Brazil, Ecuador, Paraguay and Peru (for full details see Pain & Woodward 1961).

Shell

Six shells, two small and four large, obtained from Dr W. J. Clench and coming from Rio San Alejandro near Agua Caliente, Huanaco, Peru, were originally examined; still larger specimens were later borrowed from Mr Pain and Mr Woodward. Certainly up to a length of 34 mm the shell is equivalve and unattached, the uneroded valve surfaces of the specimen shown in figure 11 *A* bearing no sign of attachment. Older shells, the largest examined having an over-all length of 108 mm, are always to some extent inequivalve, but this is due to the exceptional irregularity and twisting of the shell (figure 11 *B*) especially at the anterior end and is certainly not the result of any possible later attachment which could only be by way of marginal areas, as in *Hinnites* (Yonge 1951) which makes late attachment. Irregularity is so great that no two adult shells of *Bartlettia* are alike.

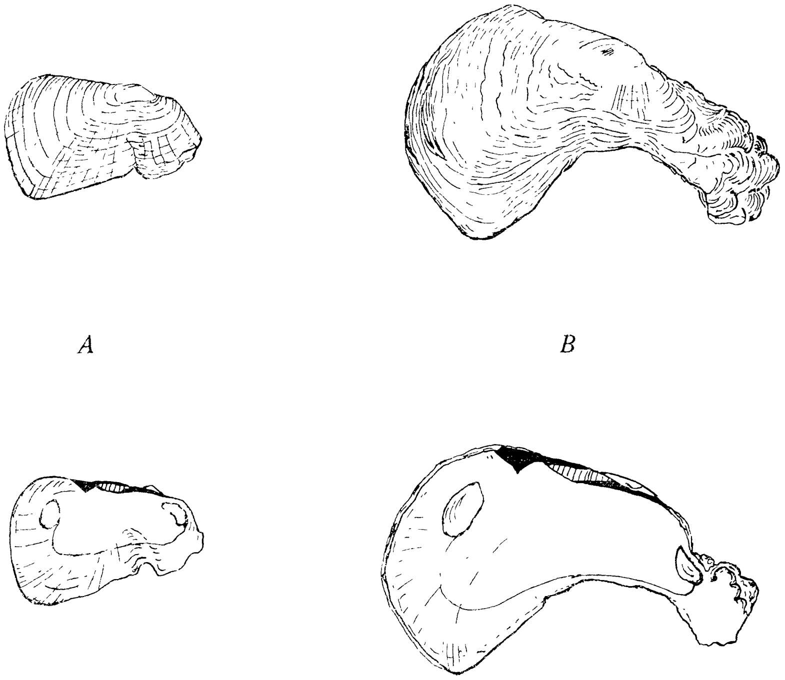

FIGURE 11. *Bartlettia stefanensis*. Outer (above) and inner (below) views of *A*, young and *B*, adult shells. (Magn. $\times\frac{3}{4}$.)

The shell has a distinctive outline. It is inequilateral, an asymmetry which, as shown in figures 11 and 12, increases notably with age. Especially in older shells the posterior end is rounded and both valves externally very convex while the anterior end is reduced although it may also be drawn out to form a narrow, compressed and usually very irregular extension. This is the result of growth marginal to the pallial line (figures 11 *B*, 12) which, as in all Etheriidae, is situated well back from the shell margin. The extent of variability is indicated by comparison of the two shells, one 91 and the other 108 mm long, but of very similar internal capacity, shown in figure 12. Extension of shell anterior to the adductor is four times longer in the latter, 40 compared with 10 mm.

Compared with *Etheria*, the mantle/shell is here extended in a postero-ventral direction with greatest growth gradients in that region. There is, however, a subsidiary centre of shell growth in the anterior territory of the mantle/shell which is responsible for the extension at this end. These two centres of shell growth are separated by an area of very restricted growth with resultant formation of the mid-ventral embayment characteristic of this genus (figures 11, 12). This increases with age, there being only a small embayment in the smaller shell of 34 mm length. Carcelles (1942) states that shells 10 mm long are equilateral and resemble *Anodontites tenebricosus* (= *Anodonta tenebricosa*). Pain & Woodward (1961) think it possible that this may prove to be the young of *B. stefanensis*. But although individual irregularities of shell form and sculpture can certainly be attributed to environmental constraint, the characteristic adult form of *Bartlettia* with reduced but often attenuated anterior end and deep ventral embayment is undoubtedly genetically controlled.

FIGURE 12. *Bartlettia stefanensis*. Inner surfaces of left valves of two shells showing great difference in the form and extent of the anterior prolongation. (Magn. × ½.)

Ligament

This possesses the features noted as characteristic of *Etheria*, namely long anterior outer layer, long inner layer and compressed, transversely 'pinched' posterior outer ligament layer (figure 13). But there is no bilateral asymmetry which would be present if the animal was cemented by one or other valve. Unlike *Etheria*, however, the ligament is opisthodetic, i.e. retaining this original unionid character. As shown in figure 13, the anterior outer ligament layer extends posteriorly under the inner layer and this grows under the posterior outer layer, less than half of the anterior outer layer being situated anterior to the umbo. Lateral extension of the posterior outer layer is greater than in *Etheria*, no doubt in correlation with the greater external convexity of the posterior end of the shell which increases with age. Although well developed in a large shell, the ligament does not exhibit the great thickening found in all types of *Etheria*; there is no indication that the animal grows postero-ventrally within the shell as it would need to do if cemented.

Animal

Unfortunately almost nothing is known about the animal which forms this unusual shell and which is certainly somewhat heteromyarian. Morretes (1941) gives the only account of anatomy but this is confined to statements about the organs revealed by removal of the mantle lobes and illustrated by photographs from which it is impossible even to determine the extent of the ctenidia and palps! As in *Etheria*, the mantle lobes are united at the one point where the ctenidia are attached. No significant information about the ctenidia is given and the palps are merely described as semilunar, nothing is said about their size, so important in view of conditions in *Etheria*. The most important statement concerns the presence of a small foot. *B. stefanensis* is the only species of the Etheriidae to possess this organ in the adult although it is possible that all etheriids may have a foot in early, uncemented stages of life. Its presence in adult *Bartlettia* provides further evidence that cementation does not occur.

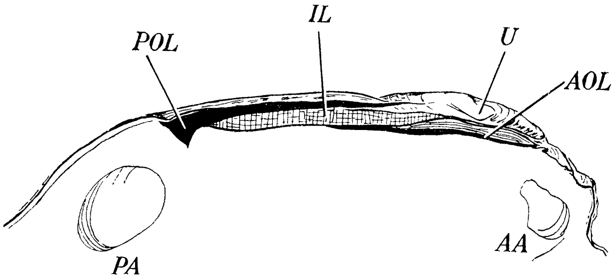

FIGURE 13. *Bartlettia stefanensis*. Dorsal inner surface of left valve showing opisthodetic ligament with anterior outer layer (black) extending under inner ligament layer and this under posterior outer layer which displays typical etheriid transverse 'pinching'. *U*, umbo, other lettering as before. (Magn. × 1.)

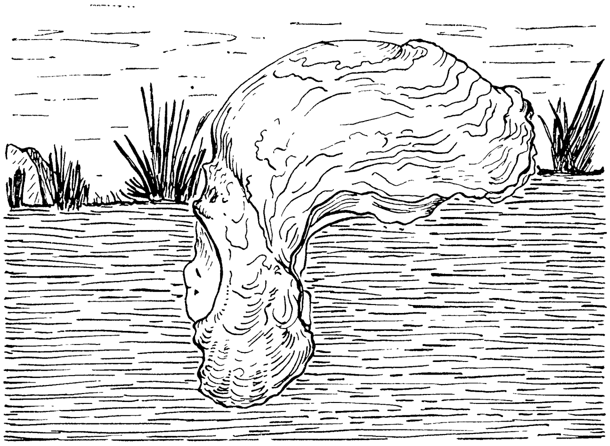

FIGURE 14. *Bartlettia stefanensis*. Animal viewed in natural habitat with anterior extension of shell inserted into irregular crevice in rocky substrate to the shape of which it has conformed with growth. (Magn. × $\frac{3}{4}$.) (From Carcelles 1940.)

Habits and habitat

Carcelles (1940, 1942) is the sole source of information about habits. His initial paper contains a drawing (reproduced in figure 14) showing the animal *in situ* while later (1942), writing of specimens obtained from Arroya Guaza, Paraguay, he states that '*Bartlettia* lives in the water-falls, incrusted in hard rocks ("tosca")'. He adds later that 'The anterior area extends into the water, and the posterior area is hidden between the stones'. He observes of the shell that it is most irregular over this anterior area and is free when young but adherent when adult.

Dealing with this last matter first, the absence of any evidence of cementation in shells up to 34 mm long has already been noted; the eroded older shells give no external evidence of attachment while internally the character of the ligament, with the absence of both bilateral asymmetry and thickening (unlike *Etheria* in these respects), indicates that cementation does not occur. But the animals may become so wedged in crevices between stones or possibly amongst submerged tree roots (as suggested by Anthony (1907)) that the shells become adventitiously attached. This is precisely what is indicated in the original description and drawing (figure 14) of Carcelles. The animal is shown with what is obviously the anterior end (*not* the posterior end as he states in his later paper) embedded within the 'tosca'. Indeed, any penetration posterior end foremost could be contrary to bivalve structure, where the presence posteriorly of both inhalant and exhalant openings involves entry anterior end first in burrowing and boring species. In *Bartlettia*, the inhalant current will be drawn in about the middle of the ventral surface of the posterior region of the shell, the exhalant issuing, as always, just below the posterior adductor. Moreover, the variation in size and the striking irregularity of the anterior extension of the shell appears certainly due to the effects of confinement within restricted cavities, which is responsible for similar irregularities of the shells of marine 'nestlers'.

The course of life in *Bartlettia* is probably somewhat as follows: the young animals with equivalve and largely equilateral shells move about in the turbulent water by means of the foot and are temporarily attached by byssus until a crevice is encountered deep enough to inhibit further movement. More permanent byssal attachment may then be made. Change in the form of the shell with growth would permit the anterior end to penetrate deeper into the crevice, although to a variable extent depending on the size of this, and also conform to its irregularities. The animal would thus be secured and the byssus gland, and possibly to some extent the foot also, could then atrophy. At the same time the posterior end would attain its adult, almost globular, proportions, the two ends being united by the isthmus of the mid-ventral embayment. Unlike the other etheriids, all of which are cemented, *Bartlettia* would thus appear to be a freshwater 'nestler' moving when young into crevices to the restrictions of which the shell must conform, essentially as in marine bivalves of similar habits, e.g. non-boring individuals of *Hiatella* (*Saxicava*) as described by Hunter (1949) and *Petricola carditoides* (Yonge 1958).

Acostaea and *Pseudomulleria*

These two very closely related genera each comprise a single known species, *Acostaea* [*Mulleria*]* *rivoli* (Desh.) and *Pseudomulleria* [*Mulleria*] *dalyi* (Smith). The former is South American, occurring in the basin of the River Magdalena in Columbia, the latter Asiatic, an inhabitant of rivers in Mysore, India. Presumably owing to their wide geographical separation, Anthony (1907) suggested their independent descent from locally occurring

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* The generic name *Mulleria* Férussac, under which these species were originally described, was abandoned as a homonym of *Mulleria* Leach, 1814.

species of the Unionacea, but their great similarity and common possession of features unique amongst the Bivalvia are surely adequate indications of descent from a common, etheriid, ancestor. At the same time, somewhat illogically, Anthony also proposed subgeneric rank for *Pseudomulleria* and was followed in this (although not necessarily in the former contention) by Thiele (1935). But their wide geographical separation fully justifies the elevation to generic rank of *Pseudomulleria* proposed by Pain & Woodward.

These two species are of exceptional interest. Unquestionably members of the Etheriidae, they may be regarded as representing the culmination of the evolutionary possibilities inherent in the family and already outlined when considering *Etheria*. Even more extensively attached, although also indifferently by either valve, they display a unique form of bilateral asymmetry. While the young shell, to quote Jackson (1890), is 'Anodon-shaped, equivalve and dimyarian', the adult is monomyarian but with the first-formed, symmetrical valves both attached to the under valve of the adult which is always larger than the upper valve (figures 15, 16). The monomyarian condition—the possession of which explains the original classification of these animals with the Ostraeidae by Férussac (1823)—is here attained in a manner altogether distinct from that which has taken place in either the Anisomyaria or the Tridacnidae (Yonge 1953*a*).

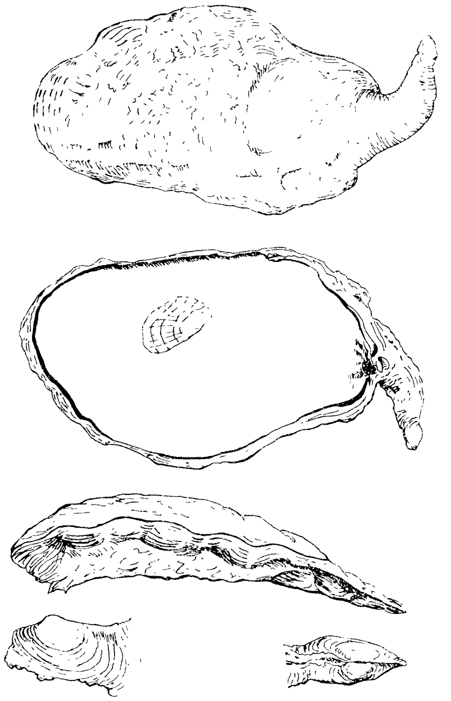


FIGURE 15. *Acostaea rivoli*. Drawings (from Anthony 1907) showing, from above downwards, under and inner surfaces of attached (left) valve, side view of this valve with the upper valve *in situ*, and lateral and dorsal views of the umbonal region in the apical talon. (Magn. upper drawings $\times \frac{1}{2}$, lower $\times 1\frac{1}{2}$.)

Shell

Details of the shell are provided by Smith (1898), Anthony (1907) and by Pain & Woodward (1961) who also give all necessary references to literature. The characteristic feature is the presence of an anterior spur-like projection or 'talon' (Anthony). This structure, which is not comparable in size or formation with the dorsal beak in *E. elliptica* var. *cailliaudi*, appears normally to be retained throughout life in *Acostaea* but to be lost or reduced in *Pseudomulleria*. Certainly in the former it terminates in the paired symmetrical valves of the young bivalve and, where retained, is always attached to the lower valve. The adult valves are round or oval in outline (although much influenced by the substratum to which they are attached), the lower one being usually completely attached apart from the talon. The upper, free valve (figures 15, 16) is both shorter (from hinge to free margin) and shallower. The cavity of the under valve is continued for some distance beneath the ligament into the interior of the talon (figure 16), but usually the great bulk of this, i.e. that lying between the young valves and the early stages of their extension posteriorly, is filled in with shell substance secreted by the general surface of the mantle as this withdraws during growth. To this extent, although only in the very early stages of growth, there is resemblance to the formation of the beak in *E. elliptica* var. *cailliaudi*. The typical condition appears to be that shown in figures 15 and 16, although a range exists. One shell of *Acostaea* bore no trace of a talon while in another, shown in figure 19, this appeared relatively enormous with an internal cavity 30 mm deep and 16 mm wide beneath the ligament. In this case there was evidence that both surfaces of this apparently enlarged talon had been attached (the animal possibly growing in a crevice) so that the shell was unable to twist round into the adult, horizontal condition until relatively late in growth.

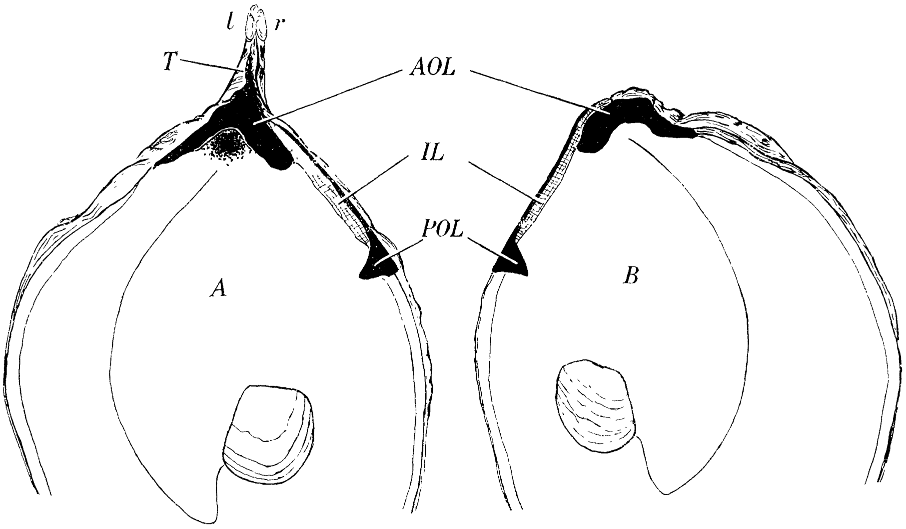


FIGURE 16. *Acostaea rivoli*. Inner surfaces of *A*, under (here right) and *B*, upper (left) valves, showing solitary adductor scar, pallial line and details of ligament with talon (*T*) attached to under valve showing umbones and first formed valves (*l*, *r*) in original position, i.e. vertical to substrate whereas adult valves are horizontal. (Magn. × 1.)

The solitary adductor scar is subcentral, remaining adjacent to the posterior end of the ligament. This has the same composition as in the other Etheriidae, as noted by Anthony (1907), although he gives no indication in text or in figures of the extent and disposition of the three layers in the adult. But such information is essential in the interpretation of the change in form leading to monomyarianism. As shown in figure 16, the adult ligament is extensive. The long anterior outer layer (*AOL*) is bent round the base of the talon, so lying above the cavity, with the long inner (*IL*), and the transversely extended outer (*POL*), layers stretching along the margin of the valves posteriorly.

Conditions are closer to *Bartlettia* than to *Etheria*. Although, as in the latter, the ligament layers are thick and indicate, as in other cemented bivalves, ventralward movement of the contained animal, the ligament is opisthodetic with the layers growing under one another from the anterior end back, precisely as in *Bartlettia*.

Animal

Here complete dependence has to be made on the description of *Pseudomulleria dalyi* by Woodward (1898) from whose paper figure 17 has been taken. Fortunately it provides all essential information. It will be simplest to indicate resemblances to, and differences from, *Etheria elliptica*. The mantle lobes have the same solitary point of fusion, there is no foot but here also a small posterior retractor persists as well as the pedal ganglia. The gut has a similar course and runs above the pericardium; similarly plicate ctenidia, with outer demibranch slightly the smaller, run dorso-ventrally (figure 17).

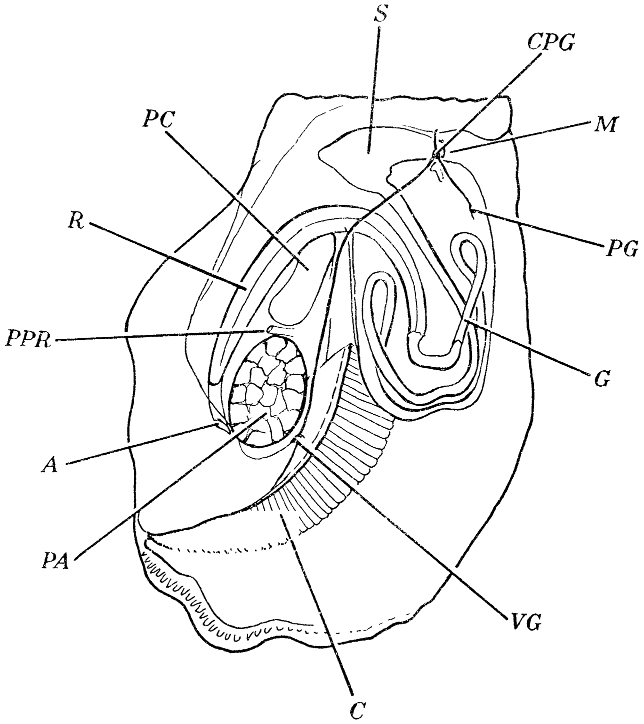


FIGURE 17. *Pseudomulleria dalyi*. Anatomy viewed from right side (after Woodward 1899). (Magn. × *ca.* $1\frac{1}{2}$.) *C*, inner demibranch of left ctenidium. Other lettering as before.

Differences have to do with the loss of the anterior adductor and the accompanying reduction in that end of the animal. Judging from Woodward's figures, the anterior (dorsal) end of the ctenidia is very close to the mouth. The palps (not figured) he describes as leaf-shaped and very small and so in striking contrast with those of *Etheria* (figure 3)—and possibly also with those of *Bartlettia*. The oesophagus is similarly reduced, the mouth (*M*) opening directly into the stomach (*S*). The posterior adductor has moved to some extent ventrally and towards the centre of the valves (figures 15, 16) but does not assume the central position it attains in members of the Anisomyaria such as *Pecten*, and in the Tridacnidae. Nor is the body concentrated around it as in those bivalves. There is apparently no division, at least macroscopically, into 'quick' and 'catch' muscles.

Monomyarian condition

Change in form in the Bivalvia involves the separate entities of enclosed body and enclosing mantle/shell (Yonge 1952, 1953 *a*). Changes in the latter, brought about by alterations in the growth gradients around the margin, modify the disposition but *not* the proportions of the enclosed body. This is the case with *Etheria*. The proportions of the body do not significantly change unless the body is byssally attached when the anterior end may be greatly reduced, with accompanying effects on the mantle/shell, or in these Etheriidae where the mantle/shell becomes attached and growth is exclusively posterior.

The heteromyarian and monomyarian conditions found throughout the Anisomyaria (e.g. *Pinna* and *Mytilus* or *Pecten* and *Ostrea*, respectively), with corresponding reduction in the anterior half of the body, are associated with byssal fixation (later possibly leading to freedom as in many Pectinidae, or to cementation, i.e. attachment by the mantle/shell, as in *Spondylus*, *Hinnites* or *Ostrea*). The totally unrelated type of monomyarianism found in the Tridacnidae is also associated with byssal fixation (Yonge 1953 *a*, *c*). In the Anisomyaria, apart from the Limidae, change from the heteromyarian to the monomyarian condition has been accompanied by change from a vertical to a horizontal posture of the valves and with much consequent bilateral asymmetry. In the Limidae, and in the Tridacnidae, the shell valves remain vertical and the animals are bilaterally symmetrical.

In the Etheriidae monomyarianism is associated with cementation due to direct attachment by the mantle/shell. A probable post-larval stage of temporary byssal fixation, at a period when species of all four genera are certainly bilaterally symmetrical and very probably mobile, could be followed when cementation occurs (i.e. in all but *Bartlettia*) by atrophy of the byssal apparatus and the foot, the pedal ganglia and one or both pedal retractors persisting. Unlike the monomyarian Anisomyaria which always lie on a predetermined side, the monomyarian Etheriidae cement indifferently by either valve. Assumption of this condition also involves late loss of the anterior adductor and also, as will be demonstrated, a possible change *during growth* from an initial vertical to a final horizontal posture.

In an earlier consideration of the monomyarian condition (Yonge 1953 *a*), reference to the Etheriidae was brief. Interpretation could only follow that of Anthony (1907) who gave no information, in text or figures, about the disposition of the ligament in adult *Acostaea* and who figured young and adult shells as lying in the same plane (figures 15, 18). He concluded that the loss of the anterior adductor was due to exclusively posterior growth, with accompanying cementation, of the initially equilateral shell. Attachment of the talon to the under valve he attributed to a discontinuity in shell growth due to loss of the anterior adductor and the assumption by the enlarged posterior adductor of entire responsibility for closure of the valves. Figures 18 (taken from his paper) illustrates his views.

If these are correct then in figure 18 the ligament should extend along the upper surface of the shell in line with the umbones between which it originates. This is certainly the case in the byssally attached Pinnidae where growth is also entirely in a posterior direction and where the ligament, with a long secondary extension of posterior fusion layer, stretches the entire length of the greatly extended dorsal surface (Yonge 1953 *b*). The small anterior adductor is retained although the anterior end of the valves, with the umbones, is lost during growth. But, as shown in figures 16 and 19, the ligament in *Acostaea* actually stretches around the base of the talon and so along the line where the functional upper valve is shown by Anthony (figure 18, *S*) as severing contact with the first-formed regions of that valve. No such break takes place. Major bilateral asymmetry has occurred during growth due to a change in the disposition of the mantle margins which secrete the anterior region of the valves and the anterior outer ligament layer (figure 16, *AOL*). These swing round as indicated in figure 20.

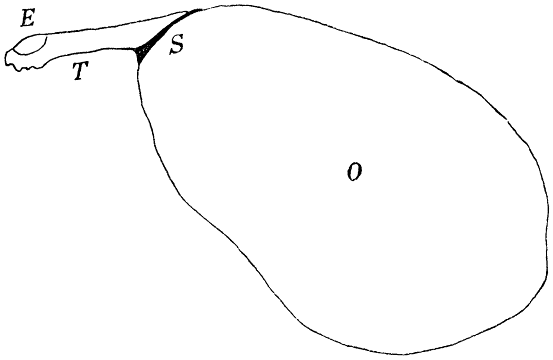


FIGURE 18. *Acostaea rivoli.* Diagrammatic figure taken from Anthony (1907) showing his interpretation of structure, i.e. with early valve (*E*) and talon (*T*) in same plane as adult valves and with thick line (*S*) representing break in continuity (not ligament) between talon and upper or opercular valve (*O*).

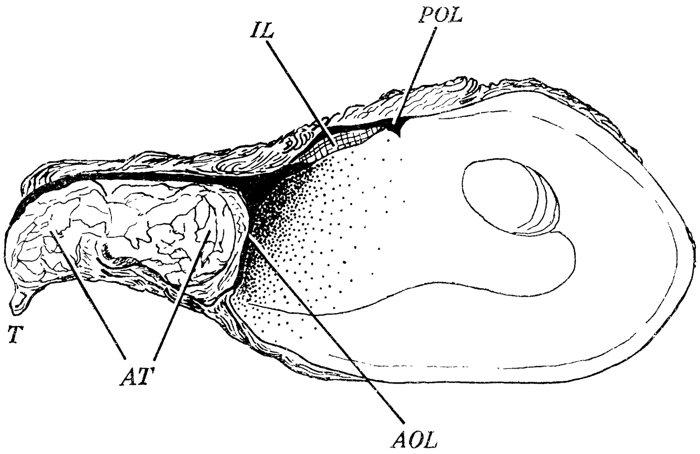


FIGURE 19. *Acostaea rivoli.* Attached (right) valve of a specimen in which *both* valves apparently initially cemented, with consequent late 'metamorphosis' into adult asymmetry. (Magn. × 1.) Lettering as before.

The arrangement of the ligament demonstrates this conclusively. In certain shells of *Acostaea*, e.g. that shown in figure 16, the first-formed valves are vertically disposed and the change to the horizontal posture of the adult—due to the increasing bilateral asymmetry of the mantle—can be traced along the talon. In other shells, such as that illustrated by Anthony (figure 15) no such change is apparent. This is also the case with the under valve shown in figure 19 which possesses what appears to be a greatly enlarged talon. However, in this case the upper as well as the lower surface of this region was clearly cemented in life (figure 19, *AT*). Hence delay in 'metamorphosis' to the adult condition, i.e. in the onset of bilateral asymmetry, can reasonably be attributed to settlement between closely opposed surfaces and consequent initial cementation by *both* valves. Adult asymmetry cannot apparently appear until only *one* valve is so attached (or one is free). The somewhat enlarged talon shown in figure 15 may be similarly explained.

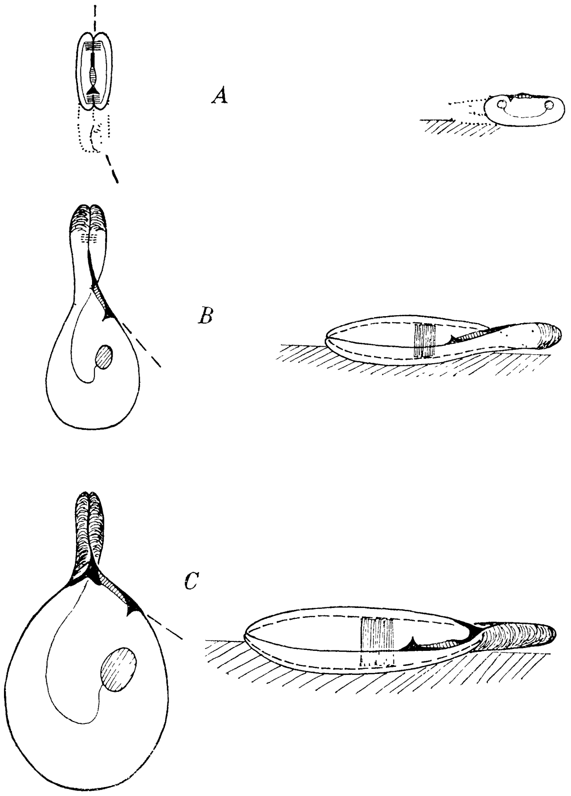


Figure 20. Diagrammatic representation of stages in growth after fixation to substrate in *Acostaea* or *Pseudomulleria*. Left, viewed from above (anterior end uppermost); right, viewed from right side (anterior end to right). *A*, initial stage in attachment, young dimyarian bivalve growing posteriorly (indicated by dotted lines) with one valve (here the right) becoming cemented; *B*, suggested intermediate stage with mantle withdrawing from anterior region and interior of talon becoming filled in, posterior regions of valves horizontally disposed, anterior adductor dubiously persisting, posterior adductor enlarged and subcentral; *C*, final condition with upper (left) valve now separated from talon owing to twisting from vertical to horizontal posture with consequent turning of anterior end of ligament at right angles, interior of talon almost completely filled in. Adductors and three regions of ligament indicated conventionally throughout, broken lines indicate successive changes in direction of ligament.

The process of growth in *Acostaea* (and also presumably in *Pseudomulleria* where the talon is lost) and which involves, at any rate where there is only one surface of attachment, a twisting of the valves through an angle of 90°, is indicated semi-diagrammatically in figure 20 which represents fixation by the right valve (as in the shell shown in figure 16). Starting with an equivalve and almost equilateral shell which is vertically disposed (and very possibly byssally attached) and about 1 mm long, further growth is confined to the posterior end. This is clearly indicated in figure 15. Initial attachment to the substratum by the mantle/shell has taken place when the animal turned with the right valve undermost (figure 20*A*). Shell subsequently secreted by the right mantle margin becomes cemented to the substratum presumably by the agency of the periostracum which is the outermost layer. Continued asymmetrical growth brings about a gradual twisting, an unusual form of torsion, in the course of which the left, free, valve comes to lie above, instead of lateral to, the right valve now increasingly widely cemented to the substratum (figure 20*B*). This process involves movement of the ligament—transversely extended posterior outer layer 'foremost'—from its original position in the mid-line to one now topographically on the right (as viewed in the left series of figures). This, of course, represents a change in position of the mid-dorsal line. As the mantle lobes spread out more widely and horizontally, their anterior extremities are withdrawn while continuing to secrete shell. Thus the interior of the talon fills up.

The final stages in this process involve more complete withdrawal from the anterior of the talon with fusion of the two valves by continued shell secretion and loss of the anterior adductor. But this must be accompanied, *pari passu*, with separation of the upper valve from the talon. This is indeed the inevitable final outcome of this twisting movement which now brings the mid-dorsal line (represented in figure 20 by a broken line that extends posteriorly from the ligament) to a position almost at right angles to its original one. This change is due to assumption of a horizontal posture accompanied by, and finally (20*C*) accentuated by, an increasing tendency for the mantle/shell to round off around the solitary adductor. The posterior extension of the ligament and the manner in which its anterior end swings round are well shown in figure 16 where connexion of the latter with the ligamental region in the talon is apparent. The final bilateral asymmetry comes about as a result of withdrawal of the left mantle lobe (the right lobe continues to penetrate the interior of the talon). Indeed the whole process of growth and change in posture and form must be considered in relation to the growth and secretory activities of the two mantle lobes. The separation of these, which represents the essential feature in the evolution of the Bivalvia, opened prospects of bilateral asymmetry which have been widely exploited in this Class.

The monomyarian bivalve finally produced bears unmistakable evidence of its mode of origin. This becomes apparent (figure 21) when conditions in the Anisomyaria, taking a byssally attached species of the Pectinidae (*C*) as an example, and in the Tridacnidae (*E*) are compared with those in *Acostaea* and *Pseudomullaria* (*G*). For each a precursory condition is shown, represented respectively by *Mytilus* (*B*), *Cardium* (*D*) and *Bartlettia* (*F*), together with the original conditions in an unmodified equilateral isomyarian, exemplified by *Glycymeris* (*A*).

The body and the mantle/shell in the Mollusca represent distinct entities with different growth axes. In the Bivalvia, comparison between the bodies of different species can be made by suitable distortion of rectangular, and between their shells only of radial, coordinates (Yonge 1952, 1953*a*, 1955). Changes in form can most conveniently be followed by reference to the antero-posterior and median axes of the body and to the hinge and demarcation lines of the mantle/shell. The two first run between mouth and anus and from the middle of the mantle isthmus (mid-dorsal point) through the base of the foot or visceral mass to the middle of the end of the foot, or tip of the visceral mass if the foot has been lost. This median axis divides the body into anterior and posterior regions, the first of which is denoted by oblique lines in figure 21, and which are approximately equal in an isomyarian (figure 21 *A*).

Turning to the mantle/shell, the hinge line follows the line of the ligament. The demarcation line represents the projection on to the flat surface of the sagittal plane of a line, starting at the umbo, which joins the points of greatest inflation on the curved surface of the shell, i.e. where the ratio of transverse to radial component in shell growth is greatest (Owen 1953*a*). This line divides the mantle/shell into anterior and posterior *territories* (Yonge 1955) which initially, although by no means after subsequent evolutionary processes,

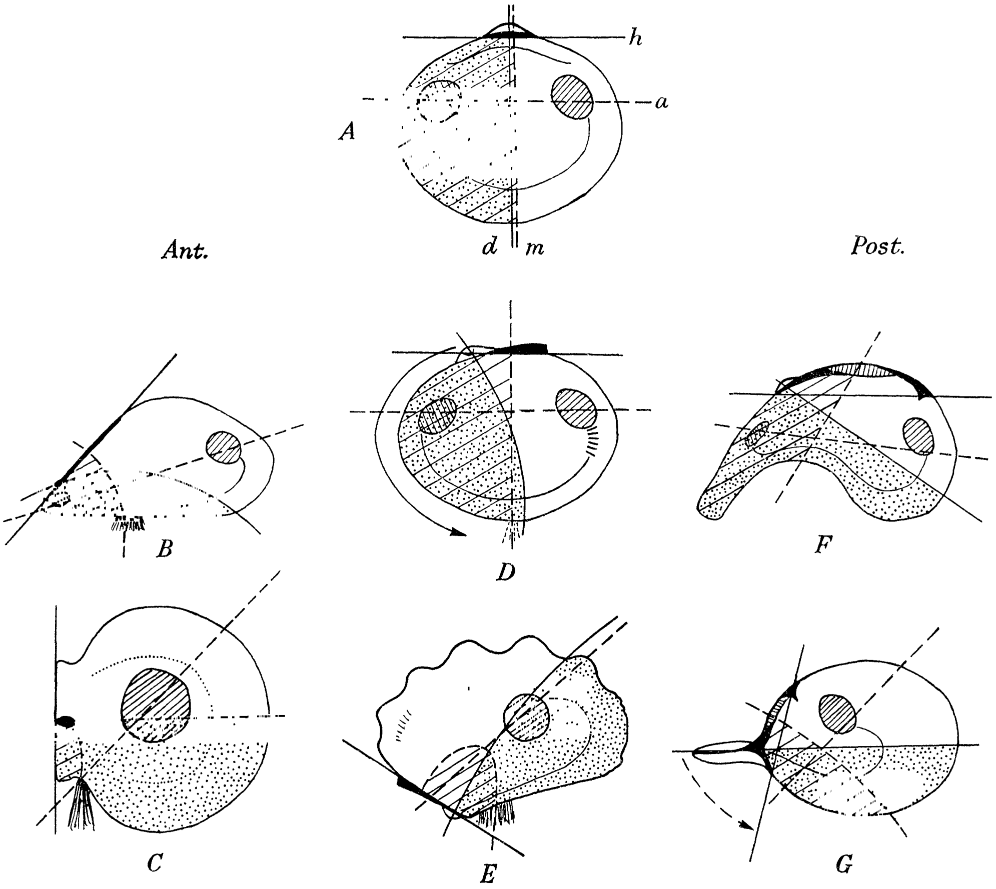


Figure 21. Diagrams indicating the different ways in which the monomyarian condition has been attained in the Anisomyaria (*C*), Tridacnidae (*E*) and Etheriidae (*G*). Adductors and pallial line shown;s econdary pallial line in *Pecten* dotted. *A*, *Glycymeris* (equivalve, equilateral isomyarian); *B*, *Mytilus* (heteromyarian, Anisomyaria); *C*, *Pecten* (monomyarian, Anisomyaria); *D*, *Cardium* (isomyarian, Cardiacea) with arrow indicating rotation of mantle/shell in relation to byssally attached body, leading to *E*, *Tridacna* (monomyarian, Cardiacea), extent of siphonal muscles shown by parallel lines; *F*, *Bartlettia* (heteromyarian, Etheriidae); *G*, *Acostaea* (monomyarian, Etheriidae), broken arrow indicating movement of anterior end of hinge line which accompanies change from vertical to horizontal posture of valves. Byssus shown in *B*, *C*, *E*; assumed present in *D* and during subsequent rotation leading to *E*; postulated during early stages in *F*, but monomyarianism in *G* result of cementation (i.e. attachment by mantle/shell). *a*, *m*, anterior-posterior and median axes of body (broken lines); *h*, *d*, hinge, and demarcation lines of mantle/shell (unbroken lines). Anterior region of animal denoted by oblique lines, anterior territory of mantle/shell by stippling.

conform to the anterior and posterior regions of the body (cf. obliquely lined and stippled areas in figure 21). The two axes, *a* and *m*, are denoted in figure 21 by broken lines, and the hinge and demarcation lines, *h* and *d*, by entire lines. It will be noted that in the unmodified isomyarian (*A*), *a* and *h* are parallel and *m* and *d* effectively coincide.

With regard to the monomyarians, the major features to be noted are:

(1) In the Anisomyaria (*C*), monomyarianism is a consequence of byssal fixation, the mid-ventral region of the body remaining a fixed point; increasing reduction of the anterior part of the body with accompanying effects on the mantle/shell leading to reduction (*B*) and then loss (*C*) of the anterior adductor. Change to a horizontal posture occurs between *B* and *C*. The body finally becomes reorganized round the now centrally placed adductor with the demarcation line coming again to divide the mantle/shell into equal anterior and posterior territories (cf. stippled areas in *B* and *C*) and also coming to represent the *effective*, although not the morphological, 'median axis'. A secondary pallial line (shown dotted) now encircles the adductor, the original line of muscle attachment being restricted to an area immediately anterior to the adductor (Yonge 1953*a*).

(2) In the Tridacnidae (*E*), allied to the Cardiidae (*D*) (the two families constituting the Cardiacea), monomyarianism comes about as a result of an essentially rotating movement of the umbones and hinge in the longitudinal vertical plane through almost 180° in relation to the body which here also is byssally attached, and may be presumed to have been so throughout the period when this change took place. This rotation, indicated by the arrow in *D*, is due to great hypertrophy of the siphonal tissues with consequent additional accommodation for the symbiotic zooxanthellae found in all species of the Tridacnidae (Yonge 1936, 1953*a*, *c*). The anterior part of the body is reduced as in (1) but by different means; the anterior territory is not so greatly reduced. Pallial attachments are retained with the area occupied by the siphonal retractors greatly extended and carried forward above the dorsal surface of the body. The adductor, sub-centrally placed, thus has pallial attachments extending in *both* directions (*E*).

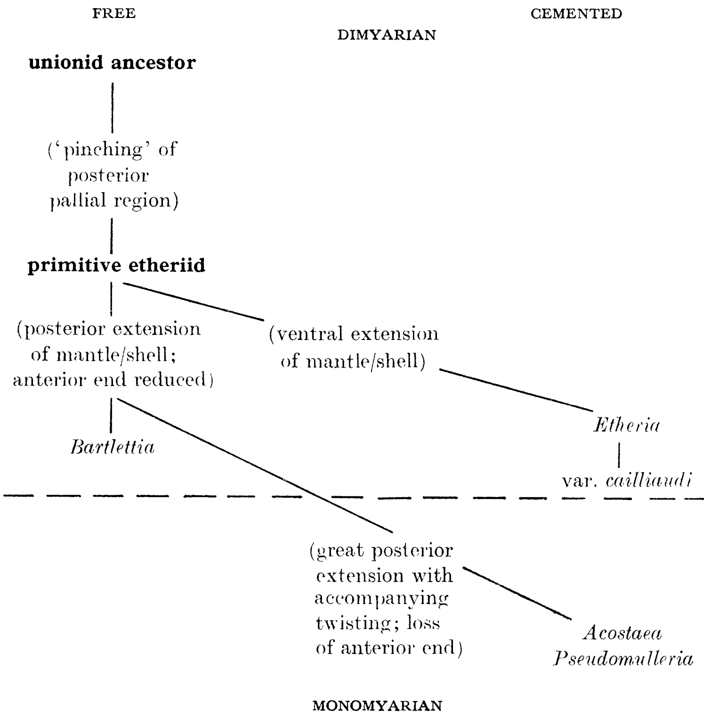
(3) In the monomyarian Etheriidae (*G*), the posterior elongation already noted in *Bartlettia* (*F*) is carried further with an accompanying change from a vertical posture, possibly byssally attached, to a horizontal posture with cementation, i.e. initially as in *Etheria*. But here, with growth, the young dimyarian becomes monomyarian, a process which involves movement of the hinge line through an angle approaching 90° and reduction of the anterior end in a manner different from either (1) or (2). The posterior adductor enlarges and becomes somewhat subcentral but remains at the posterior end of a conspicuous pallial line that stretches anteriorly, unlike either (1) or (2). As in (1), although to a somewhat less extent, there is reorganization of the body around the adductor (a process foreshadowed by conditions in the dimyarian *Etheria*) with the demarcation line again dividing the mantle/shell into not dissimilar anterior and posterior territories.

Discussion

Evolution of the Etheriidae

The superfamily Unionacea (Thiele 1935) comprises the two great families of the Unionidae and the Mutelidae (together known as the Naiades and containing over a hundred genera) together with the monogeneric Margaritanidae and the Etheriidae with four genera. All inhabit fresh waters and species of the Unionacea occur in all continents. The great bulk of them are adapted for life within the varying grades of bottom material, i.e. gravel, sand or mud, found in rivers and lakes. They are typically equivalve but inequilateral with the oval shell extended posteriorly, the ligament being correspondingly opisthodetic. Without a byssus in the adult, they are incapable (unlike the similarly freshwater *Dreissena*) of attachment. Their most striking adaptive powers concern development where incubation within the gills, sometimes with the shell dilated to provide additional space for the marsupia, is followed by liberation of the highly modified glochidial larvae in the Unionidae and of the lasidial or haustorial larvae in the Mutelidae. These are temporarily parasitic on fish, a habit which enables them both to feed and maintain themselves in what are often moving waters with inconstant supplies of fine phytoplankton.

TABLE 1. EVOLUTION WITHIN THE ETHERIIDAE



The Etheriidae may be assumed to have a similar life history but they are strikingly different in form and habit from the other Unionacea. In basic characteristics of both body and mantle/shell they are unquestionably unionid. The unique features which have enabled them to colonize new environments by attachment to hard substrata in turbulent waters are associated with changes in the mantle/shell. An initial 'pinching' of the posterior pallial region has immediate effects on the form of the posterior outer ligament and on the outline of the shell, with the secondary effects on the body discussed above when describing the structure of *Etheria*.

In this way the primitive etheriid may be presumed to have come into being. As indicated in table 1, further evolution then took divergent paths. In the direction taken by *Etheria* the shell assumed an elliptical shape with the long axis approximately dorso-ventral and consequent effects on the form of the adductors and the disposition of major regions of the body. A horizontal posture doubtless preceded actual cementation—this matter is discussed below—subsequent growth being made possible by the ventralward extension of the body within the shell due to continual secretion by the mantle isthmus and adjacent dorsal pallial surfaces which is developed to such a remarkable extent in *E. elliptica* var. *cailliaudi*.

The other direction taken within the Etheriidae involved great posterior extension of the mantle/shell, with undergrowth of the three ligament layers from anterior end backwards, i.e. an accentuated opisthodetic ligament. The anterior regions of mantle/shell and body were reduced, *Bartlettia* being heteromyarian. But there is no evidence that cementation occurs, attachment in the environment of rushing water being apparently by a unique mode of anterior insertion into crevices. Where cementation does take place it is clearly preceded in ontogeny by assumption of a horizontal posture and involves even greater posterior extension which is accompanied by great bilateral asymmetry which results in loss of the anterior adductor leading to the unique form of monomyarianism found in *Acostaea* and *Pseudomulleria*. The withdrawal posteriorly of the anterior end of the ctenidia found in *Etheria* and due to the pallial 'pinching' provides in advance one of the conditions associated with monomyarianism, namely close connexion between the ctendia and the posterior adductor.

The remarkable powers of adaptive radiation exhibited in this small family are indicated in table 1. The constituent genera are isomyarian, heteromyarian or monomyarian; cementation has been acquired independently in association with ventral and with posterior extention of the mantle/shell. But all species are highly adapted for life in turbulent waters.

Cementation

Attachment to a hard substratum by the mantle/shell occurs in a variety of unrelated groups of the Bivalvia. It appears always to have been preceded by assumption of a horizontal posture, actual cementation being presumably due to the formation of an initially fluid periostracal secretion, although the precise process has never been observed. Cementation is commonest in monomyarian Anisomyaria where it occurs in *Dimya*, *Plicatula*, *Spondylus*, *Hinnites* and throughout the Ostreidae. As fully discussed elsewhere (Yonge 1953*a*), the initial horizontal posture came about as a result of earlier byssal fixation, i.e. attachment by the body. Cementation is by the right valve in all except the Ostreidae. As originally noted by Jackson (1890), it occurs at the following stages in the life history:

(1) At the end of the prodissoconch stage, probably in *Dimya* (little known) and certainly in *Plicatula* and the Ostreidae. Initial cementation in the last named is by way of secretion from the briefly functional byssal gland. In these animals the foot is reduced to a vestige or is lost.

(2) At the end of post-larval life, in *Spondylus*, as evidenced by the presence of a byssal notch in the post-larval shell. The foot is retained and assists in cleansing the mantle cavity.

(3) At a relatively late stage in growth after the animal has been byssally attached and also been able to swim. Thus *Hinnites multirugosus* does not become cemented until between 2·2 and 4·2 cm in dorso-ventral diameter (Yonge 1951). Apart from attachment, *Hinnites* is a typical scallop.

The three genera of the Chamacea are all cemented, *Chama* by the left valve and *Pseudochama* and *Echinochama* (the latter only briefly attached during post-larval life) by the right valve. These animals are dimyarian and retain the foot. Nothing is known about the time of settlement, probably early post-larval, and unlike cemented members of the Anisomyaria and of the Pandoracea (see below) there are no related free-living bivalves to indicate the probable earlier habit of life. Cementation is here intimately associated with exceptional development of the tangential component in shell growth, a matter which forms the subject of a forthcoming paper.

The Pandoracea contain two dimyarian cemented genera, *Myochama* and *Chamostrea*, both attached by the right valve although at what stage is unknown. The related *Myadora* and *Pandora*—the latter a widely distributed genus with many species—are also inequivalve, the right valve being convex and the left valve flat. Both inhabit sand, lying on the surface like *Pecten*, the rounded right valve undermost, as described by Allen (1954) for *Pandora inaequivalvis*. The origin of this bilateral asymmetry in these free-living genera is unknown but once established it opens the way to cementation.

The Etheriidae become cemented relatively late, although certainly earlier than in *Hinnites*. But they differ from all other cemented Bivalvia because they begin post-larval life as bilaterally symmetrical animals with presumably a vertical posture and, in view of the turbulent waters in which they settle, probably attached by byssus threads. Only after they assume a horizontal posture do they become cemented either by the entire under valve in *Etheria* or by the posterior prolongation of this valve in *Acostaea* and *Pseudomulleria*. This involves bilateral asymmetry with loss of the foot. The monomyarian condition in this family is also to be attributed to cementation.

The Etheriidae are also unique in their capacity to attach indifferently by right or left valve; in the Chamacea where attachment is by either valve this only applies to the superfamily as a whole; individuals of any particular species invariably attach by the same valve. This ability to attach by either valve is the more remarkable when it is realized how great is the resultant bilateral asymmetry. Probably in no living Bivalvia is this greater than in *Etheria elliptica* var. *cailliaudi* (see figure 9) or in *Acostaea* (see figure 16). It is probably associated with the late assumption of cementation by bivalves which, unlike *Hinnites*, are initially bilaterally symmetrical.

The mantle/shell in the Etheriidae is revealed as capable of profound modification—with consequent effects on the enclosed body—during the life-time of the individual. In their early bilaterally symmetrical, unionid, form followed by late assumption of a horizontal posture and then cementation, the Etheriidae (excepting apparently *Bartlettia*) appear quite literally to recapitulate in the life history of each individual the evolutionary history of the species. This conclusion might be reinforced did we know more about post-larval development and early growth in all species of this unusually interesting family.

Age and distribution

The remarkably scattered distribution of the four genera of the Etheriidae—in tropical South America, Africa and India—with the two most closely allied genera, *Acostaea* and *Pseudomulleria*, the most widely separated, would indicate an old group. But this gets no support from palaeontology. Whereas the Unionidae first appear in the Triassic and the

Mutelidae in the Cretaceous, there appears to be no evidence for the existence of the Etheriidae earlier than the Pleistocene. Although certainly a derived group, yet their remarkable form with the high degree of adaptation it confers for life in turbulent waters would seem to demand a long period of evolutionary development. Perhaps the answer to this is provided by the fact that these striking structural features appear during growth, and have not been pushed back into the early post-larva. A striking contrast is provided by the Teredinidae where change to the highly specialized adult form and habit occurs during a rapid and complex metamorphosis which takes place almost immediately after the veliger larva settles on wood.

However, even though the Etheriidae do represent a relatively late offshoot from the Unionidae, it is difficult to believe that they could be so widely and discontinuously distributed if they only originated in the Pleistocene. Anthony (1907) suggested independent evolution for *Acostaea* and *Pseudomulleria*, implying polyphyletic origin for the group, a view strongly supported by Prashad (1931). But basic structure (especially in the two monomyarians) appears much too similar for this to have occurred. It is just possible that knowledge of the larval and subsequent life history might alter this conclusion. There is also the possibility that the habitat of often rushing water may have prevented the Etheriidae from being preserved in fossil form; this could certainly not have occurred *in situ* and by the time shells reached areas of permanent sedimentation they might be so broken up as to be unrecognizable.

We are left with a group of bivalves unique in the degree to which form becomes modified, not following metamorphosis but, after initial assumption of bilateral symmetry, during growth to the adult.

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