

Yonge
1962

ON THE PRIMITIVE SIGNIFICANCE OF THE
BYSSUS IN THE BIVALVIA AND ITS
EFFECTS IN EVOLUTION

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(Text-figs. 1-6)

No group of animals is better fitted for life in soft substrata than the Bivalvia with complete enclosure of the body in the laterally compressed, hinged shell, insinuating and terminally dilating foot, and most usually with both inhalant and exhalant apertures, i.e. all contacts with the water above, confined to the posterior end. It is initially surprising to find such animals, and often with supreme success, exploiting the possibilities of life on hard, sometimes highly exposed and surf-beaten, substrata. This is due to attachment which may take the form either of cementation by way of the mantle/shell—with which we are not here concerned—or, more commonly and certainly more primitively, of fixation by the secretion of attaching threads by glands of the foot.

Long known to scientific literature, although, as pointed out by van der Feen (1949) the term byssus originates in a mistranslation of Aristotle's Greek by Theodorus Gaza in 1497, this byssal apparatus has been recognized as a highly significant component in the structure of such bivalves, notably the Mediterranean *Pinna* and *Mytilus*. Both its structure and its association with the foot, which is responsible for 'planting' as threads the secreted protein (Brown, 1952), as well described by Field (1922) in *Mytilus edulis* are too well known to need comment. It originates possibly by modification of one of the pedal glands primitively concerned with secretion of mucus and of which there are four groups in the Gastropoda (Graham, 1957).

The purpose of this short paper is to inquire into the status of the byssal apparatus which appears somewhat sporadically in adult Bivalvia although it is certainly more widespread, if not universally present, in the post-larvae. In origin it could either be an adult structure which has been lost in animals no longer needing it, which seems to be the usual if never very explicitly stated view, or else be a post-larval organ concerned with problems encountered on initial settlement of the metamorphosing larva from the plankton. After brief but essential appearance it may then originally have disappeared. Its retention into adult life (with the major effects on habits and often on form which its presence certainly involves) would thus represent persistence of a post-larval character, such bivalves being, in this respect, neotenous.

Only selected items of literature are here quoted. Classification, apart from separation of the Protobranchia as a Subclass (Yonge, 1959) and of the Septibranchia as an Order, is that of Thiele (1935).

Acknowledgements for the preparation of text-figures are made to Miss J. I. Campbell and to the Department of Scientific and Industrial Research for the grant which covers her salary as research assistant.

ROLE OF THE BYSSUS IN POST-LARVAL LIFE

The byssus gland appears with the foot, within the posterior end of which it develops, at the close of planktonic life when the veliger changes into the late veliger or veliaconch (Werner, 1939). Its appearance has been described in animals where it is retained in the adult such as *Mytilus edulis* (Werner, 1939) and other Anisomyaria and *Dreissena* (Meisenheimer, 1901). It has also been described in the post-larvae of many bivalves where it is *not* present in the adult such as *Ostrea edulis* (Erdmann, 1934)*—adult cemented by left valve; *Tivela stultorum* (Fitch, 1950) and *Venerupis pullastra* (Quayle, 1952)—adults burrow horizontally in sand or gravel; *Mya arenaria* (Kellogg, 1899)—adult a deep burrower; *Cultellus pellucidus* (Werner, 1939)—adult a rapid vertical burrower in muddy sand; *Zirphaea crispata* (Werner, 1939)—adult bores into soft rock or clay; *Xylotrypa gouldi* (Sigerfoos, 1907) and *Bankia setacea* (Quayle, 1953)—adults bore into wood; *Pandora inaequalis* (Allen, 1961)—adults free on surface of soft substrate. If the byssus thread of the glochidium is homologous then the larvae of the Unionidae provide further examples.

The function of the byssus, which often consists of a single thread, is to secure the post-larva while it is undergoing metamorphosis into the adult form which will enable it to exploit the adult habitat. This is primitively a soft substratum for life in which the dimyarian bivalve with its laterally compressed foot is ideally fitted. Such indeed is the habitat of *Tivela stultorum*, *Venerupis pullastra*, *Mya arenaria* and *Cultellus pellucidus* (with the last much the most specialized in form and activity). Where adoption of the final adult habit is slow, as for instance in *Mya arenaria*, the young of which are byssally attached to weeds or stones, the byssus (Fig. 1) is retained for a relatively long time, up to lengths of 7 mm and over (Kellogg, 1899). But where the adult form and habit are highly specialized, byssal attachment, although absolutely essential, is very brief. This is true of the boring pholads and teredinians, e.g. *Zirphaea* and *Bankia* (*Xylotrypa*) (Fig. 2) and also of *Cultellus* (Solenacea) (Fig. 3). In the Ostracidae where the byssus gland produces the cement for post-larval attachment by the left valve, secretion is extremely rapid and cannot be repeated. If detached immediately after settlement the animal cannot

* Many references throughout this article follow specific or generic names. It should be sufficiently evident that these do not refer to original authors of the species or genus concerned.

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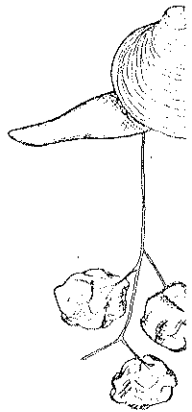


Fig. 1. *Mya arenaria* showing byssus thread attached to sand grains.

Fig. 2. *Bankia* (*Xylotrypa*) showing byssus thread attached to wood, from base of foot, X.

Fig. 3. *Cultellus* showing byssus thread attached to substrate.

re-attach itself: the empty byssus gland atrophies at once (see Yonge (1960) for details and literature).

The retention of the byssus after metamorphosis has been noted in *Mya arenaria* (Fig. 1) where it is absent in the adult. But it retains an important anchoring function while the foot remains large and the animal lives on the surface before gradually assuming the adult habit with enlargement of the siphons, reduction of the foot and assumption of a vertical posture. The byssus also persists in species of *Cardium*, both *C. lamarcki* and *C. exiguum* attaching to algae or hard substrata (Petersen, 1958). In cases where the

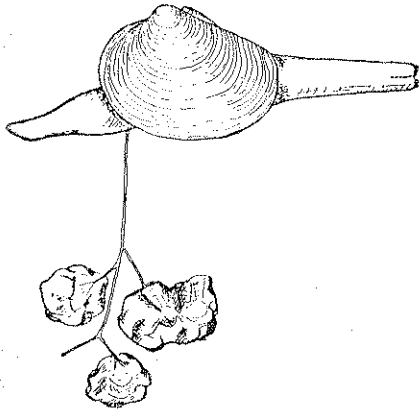


Fig. 1

Fig. 1. *Mya arenaria*, specimen 2.3 mm long, removed from sand and showing attachment of byssus to sand grains. (After Kellogg, 1899.)

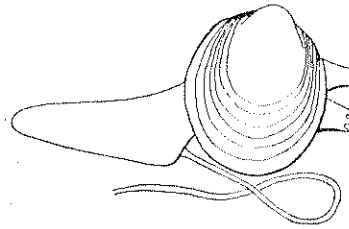


Fig. 2

Fig. 2. *Bankia (Xylotrya) gouldi*, newly attached larva showing byssus thread emerging from base of foot, $\times 74$. (After Sigerfoos, 1907.)

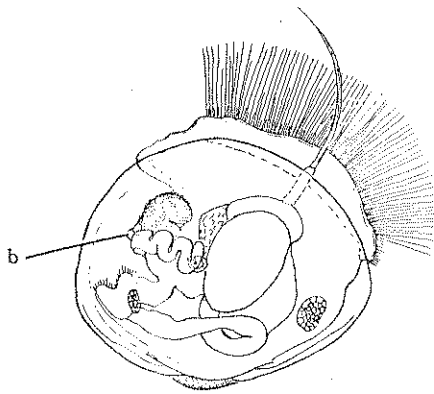


Fig. 3. *Cultellus pellucidus*, late (veliconch) larva showing byssus gland (b), $\times 120$. (After Werner, 1939.)

byssus is retained for permanent attachment of the adult, it serves in early life when the foot is still active as an organ of temporary attachment. By this means, for instance, the young bivalve climbs vertical surfaces. This is the case in *Mytilus edulis* (Field, 1922), in the anomiid *Pododesmus* (*Momia*) *macroschima* (personal observations), in the pearl oyster (Herdman, 1903) and in the young of the totally unrelated *Tridacna crocea* before this begins to bore into rock (Yonge, 1936). The use of the byssal apparatus during this stage of life is undoubtedly very significant.

PRESENCE OF THE BYSSUS IN ADULT BIVALVIA

The widespread but also very sporadic appearance of the byssal apparatus in adult Bivalvia is indicated in the following brief survey of its presence.

Subclass PROTOBRANCHIA

Drew (1899, 1901) has described the presence of an apparently functional byssus in the very modified larvae of *Yoldia* and *Nucula*. The gland persists as a small, functionless organ in the adult

Subclass LAMELLIBRANCHIA

Order Taxodonta Superfamily Arcacea

Massive byssus in those attached to rock although absent in tropical 'cockles', e.g. *Arca senilis* (Yonge, 1955a) and in similarly burrowing *Glycymeris*, etc.

Order Anisomyaria Superfamily Mytilacea

Highly developed; employed in connexion with mechanical boring in *Botula*, present though reduced in chemically boring *Lithophaga* (Yonge, 1955b)

Pteriacea

Typically present, e.g. in *Pteria*, *Pedalion*, *Foramulina*, *Malleus* and highly developed in association with life in a soft substratum in the Pinnidae (Yonge, 1953a); absent in *Crenatula*, *Vulsella*

Pectinacea

Characteristically present, e.g. *Semipecten*, *Pedum* and some species of *Pecten* and *Chlamys*; absent in cemented Dimyidae, Plicatulinae, Spondylinae and in mobile Amussiinae and *Pecten* and *Chlamys* spp. Limidae, some byssally attached, others free although retaining byssus for nest formation (e.g. *Lima hians*)

Anomiacea

Highly developed calcified byssus with great modification of under valve in *Anomia* and allied genera; for temporary attachment only in mobile *Enigmonia* (Yonge, 1957); absent in *Placenta* (*Placuna*)

Ostreacea

Absent in adult (all cemented)

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in early	Order Eulamellibranchia	
By this	Suborder Schizodonta	
is the	Superfamily Trigonacea	Small byssus gland in adult (Thiele, 1935)
(<i>Momia</i>)	Unionacea	<i>Absent in adult</i> (all burrowers except Etheriidae, * Yonge, 1961)
903) and	Suborder Heterodonta	
is to bore	Superfamily Astartacea	
stage of	Carditacea	Small byssus gland in adult Gland forming few attaching threads in those living on hard substratum, e.g. <i>Glans</i>
	Sphaeriacea	Small gland forming fine threads
	Isocardiacea	Gland forming fine threads in <i>Kelliella</i> (Clausen, 1958); gland present in <i>Isocardia</i> (Owen, 1953)
	Cyprinacea	<i>Absent in adult</i> (all burrowers)
paratus in	Cyamiacea	Byssus gland in adult, with attaching thread in <i>Turtonia</i> (Oldfield, 1955)
ance.	Gaimardiacea	Byssus gland in adult (Thiele, 1935)
	Dreissenacea	Byssus highly developed
	Lucinacea	<i>Absent in adult</i> (all burrowers) (Allen, 1958)
byssus	Erycinacea	All with fine byssal attachment both free-living, e.g. <i>Galeomma</i> , <i>Lasaca</i> , <i>Kellia</i> , and for semi- permanent attachment in numerous com- mensal genera, e.g. <i>Montacuta</i> (Oldfield, 1955, 1961)
small,		
	Chamacea	<i>Absent in adult</i> (permanently cemented except <i>Echinochama</i>)
rock ab-	Cardiacea	Small byssus in some Cardiidae: massive byssus in boring species of <i>Tridacna</i>
e.g. <i>Arca</i>	Veneracea	Usually absent in adult; occurs in a few species which 'nestle' in rock crevices, e.g. <i>Venerupis</i> <i>saxatilis</i> , possibly in <i>Petricola</i> spp.
ly bur-	Mactracea	<i>Absent in adult</i> (all burrowers)
	Tellinacea	<i>Absent in adult</i> (all burrowers)
union with	Suborder Adaptedonta	
at though	Superfamily Solenacea	<i>Absent in adult</i> (all burrowers)
<i>Lithophaga</i>	Saxicavacea	Present in 'nestling' individuals or species of <i>Hiatella</i> , absent in those which bore (Hunter, 1949); absent in deep-burrowing <i>Panope</i> , <i>Panomys</i> , <i>Cyrtodaria</i>
<i>Pedalion</i> ,	Myacea	Present in Aloididae, e.g. <i>Aloidis</i> (<i>Corbula</i>) <i>gibba</i> (Yonge, 1946) also in some Myidae, e.g. <i>Sphenia binghami</i> (Yonge, 1951), absent in true burrowers, e.g. <i>Mya</i> , <i>Cryptomya</i> , etc.
veloped in	Gastrochaenacea	Small gland in adult, <i>Rocellaria</i> (<i>Gastrochaena</i>) <i>cuneiformis</i> with byssus attached to anterior end of boring (Purchon, 1954)
stratum in	Adesmacea	<i>Absent in adult</i> (all rock or wood borers)
absent in	Suborder Anomalodesmata	
	Superfamily Pandoracea	Well-developed byssus in some Lyonsiidae, e.g. <i>Entodesma</i> (Yonge, 1952); otherwise probably absent
<i>Limipectan</i> ,	Clavagellacea	<i>Absent in adult</i> (tube-dwelling <i>Clavagella</i> and <i>Brechites</i>)
<i>ecten</i> and		
Dimyidae,	Order Septibranchia	<i>Absent in adult</i> (all burrowers)
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7); absent		

The significant points which emerge from this far from exhaustive survey may be summarized by dividing the Bivalvia into the following six groups:

- (1) Byssus highly developed in the adult (either now or in ancestral history) so that it has had a major effect on the form of the animal: Anisomyaria (heteromyarian or monomyarian); Dreissenacea (heteromyarian); Tridacnidae (monomyarian); *Sphemia* (heteromyarian); *Entodesma* (heteromyarian).
- (2) Byssus highly developed in some genera but without influencing antero-posterior symmetry (remain isomyarian), or else absent: Arcacea.
- (3) Byssus small, of one or few threads usually, but of great functional significance because the animals, although they can be mobile, are normally attached to a firm surface which may be that of another animal, i.e. influencing habits but not form: Erycinacea, Sphaeriacea, some Carditacea, and Cardiidae.

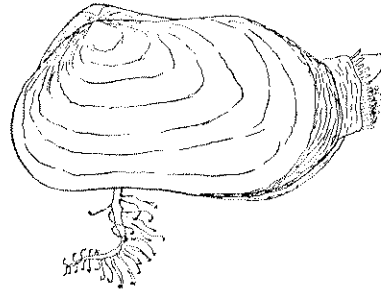


Fig. 4. *Sphemia binghami*, siphons fully extended in life showing byssus, $\times 8$.
(From Yonge, 1951.)

(4) Small byssal apparatus functional in scattered genera or species in association with the habit of 'nestling' in rock crevices (sometimes leading to boring): some Veneracea; some Saxicavacea; Gastrochaenacea. Or with attachment to stones or gravel: *Turtonia* (dubiously Cyamiacea); some Myacea, e.g. *Aloidis* and *Sphemia* (Fig. 4); some Isocardiacea (*Kelliella*).

(5) Small byssal apparatus dubiously functional: Protobranchia; Trigonacea; Astartacea; Gaimardiacea and Isocardiacea.

(6) Byssal apparatus apparently absent in adult: Unionacea; Cyprinacea; Lucinacea; Chamacea; Mactracea; Tellinacea; Solenacea; Adesmacea; Pandoracea (less Lyonsiidae); Clavagellacea; Septibranchia.

The largest of these groups is the last with eleven superfamilies or the equivalent. This would support a general conclusion that the byssal apparatus was not originally universally present in adult bivalves to be subsequently lost in certain superfamilies or genera and retained in others. The same conclusion may be drawn from group 4 where, in the extremely large superfamily Veneracea, the byssal apparatus occurs in only a few adults. In the Saxicavacea it occurs in only some species of one genus out of four; in the Myacea in perhaps two genera out of eight. The great majority of members of these

superfamilies byssus occurs true of group of any size, is to epifaunal myarian form epifaunal life

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Major ad the members even where t earlier, a by *Bankia* (Ad in various Ve (Tellinacea) presence of Adesmacea, undoubtedly presence of

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superfamilies are burrowers and, with the exception of *Aloidis* (*Corbula*) a byssus occurs only in those that are attached to rock or stones. This is equally true of group 2. In general, wherever a functional byssal apparatus, at any rate of any size, is present this is obviously related to change in habit from infaunal to epifaunal life. In the one obvious exception, the Pinnidae, the heteromyarian form indicates that the animals must have experienced a period of epifaunal life (see below).

A small byssus can be concerned not only with attachment to a hard substratum consisting of rock, stones or the surface of another animal, as in group 3; it may also be present in burrowers. These include *Aloidis* which, after slow burrowing, finally anchors itself semi-permanently in muddy gravel (Yonge, 1946), and *Kelliella miliaris* which lives at some depth in muddy sand (Clausen, 1958), i.e. members respectively of the Myacea, and Isocardiacea. The presence of a small byssal apparatus in a variety of other burrowers (group 5) may indicate that these animals also can attach themselves temporarily to the soft substrate they inhabit, precisely as do young *Mya arenaria* (Fig. 1). In other words the presence of a byssal apparatus in some burrowing adults may reasonably be regarded as the retention of a structure which was advantageous to young, as distinct from post-larval, animals.

Major additional evidence would be provided if it were known whether all the members of group 6 possessed a byssus in the post-larva. Unfortunately even where the veliger is known, the late larva is usually unknown. As reported earlier, a byssus has been observed in *Cultellus* (Solénacea), in *Zirphaea* and *Bankia* (Adesmacea), in *Pandora* (Pandoracea), in the Ostreaeidae and also in various Veneracea where there is no byssus in the adult. In *Macoma balthica* (Tellinacea) although Werner (1939) could not determine with certainty the presence of a byssus he thought it unlikely to be absent. It could, as in Adesmacea, appear for a short, although critical, period. However, it would undoubtedly strengthen the argument here advanced if the universal early presence of a byssus in the Bivalvia could be demonstrated.

EFFECT OF THE BYSSUS ON ADULT FORM

In the post-larva the small byssus is an essential agent of stability during metamorphosis; in the young motile bivalve it permits fixation for shorter or longer periods, in the adult Erycinacea (as the major example of group 3) it is the means of prolonged attachment in free-living genera like *Kellia* and *Gulowma* and in commensals such as *Devonia* and *Montacuta*, although in the latter there is a much larger byssus in *M. substriata* which is permanently attached to the anal spines of *Spatangus purpureus* than there is in *Montacuta ferruginosa* which is attached to those of *Echinocardium cordatum* only in early life (Oldfield, 1961). But the byssus never secures these animals against

powerful water movements such as tidal currents or waves. When the byssus is so employed it has become a massive structure and a major influence on form. We are now considering the bivalves in groups 1 and 2.

In the Arcacea (group 2) the hypertrophied byssus extends along much of the ventral surface holding the animal so firmly that it is most difficult to dislodge. The effect on form is relatively slight, little more than a flattening of the ventral surface so that the shell becomes roughly rectangular in contrast, as shown in Fig. 5, to the rounded shell of the superficially burrowing tropical 'cockles' such as *Arca (Senilia) senilis* (Yonge, 1955a). The retention of an anterior inhalant current in the attached species of *Arca* allows ample water to enter the mantle cavity (see arrows in Fig. 5) and this probably explains why the Arcacea have remained isomyarian and more or less equilateral.

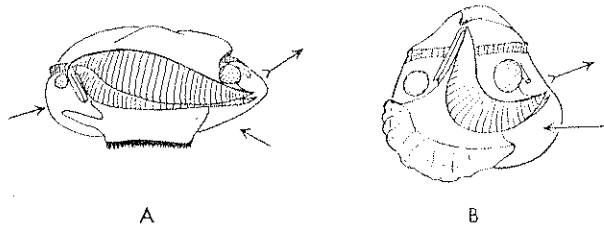


Fig. 5. A, *Arca tetragona*, B, *Arca (Senilia) senilis*, former with massive byssal attachment, shell flattened ventrally and with anterior as well as posterior inhalant current (plain arrows); latter with enlarged foot for burrowing, rounded shell and with only posterior inhalant current.

The majority of such massively attached bivalves (group 1) which include members of widely scattered superfamilies, are fundamentally influenced in form. As discussed elsewhere (Yonge, 1952a, 1953b), the unattached bivalve alters in form largely as a result of changes in the growth gradients around the mantle margin. Such changes, as from an equilateral shell such as *Glycymeris* to a razor shell such as *Solen*, cause a change in the disposition but *not* in the proportions of the enclosed body. But where the animal (considered phylogenetically) is firmly secured to the substratum by a mid-ventral byssus then the proportions of the body may be altered in relation to this fixed point. In theory either end could be enlarged at the expense of the other. In practice, because the anterior inhalant current has been lost, reduction of the posterior end would reduce water circulation within the mantle cavity and could have no survival value. But enlargement of that end has precisely the opposite effect, both increasing and also raising further above the substrate the inhalant opening. This has the obvious advantages displayed in the Mytilacea (Fig. 6A), amongst the most numerous and successful of bivalves, and in the Dreissenacea, and is also apparent in *Entodesma* (Pandoracea: Lyonsiidae) (Yonge, 1952b) and *Sphenia* (Fig. 4) (Myacae) (Yonge, 1951). The effects on the mantle/shell of this change in the proportions of the body include enlarge-

ment of the myarianism families.

Fig. 6. Effect by ventral surface attached (with phaga, isomye in shell growth enlargement. Inhalant current from initial h

In the Pectinacea, byssal attac

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ment of the posterior, and reduction of the anterior, adductor, i.e. heteromyarianism, which has been attained independently in these four superfamilies.

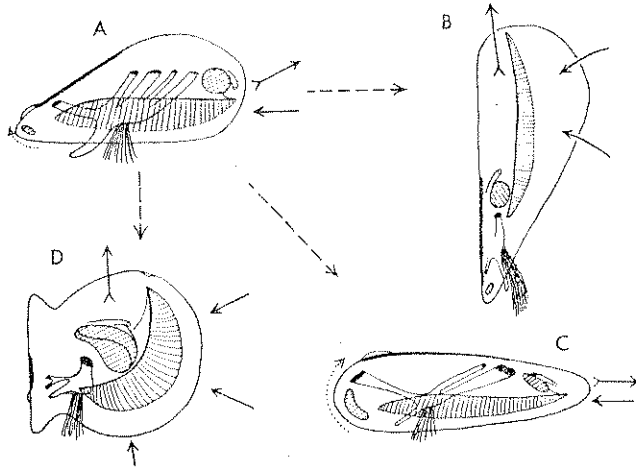


Fig. 6. Effect of byssal attachment within Anisomyaria. A, *Mytilus*, heteromyarian, attached to ventral surface with posterior end of body and mantle/shell enlarged; B, *Pinna*, vertically attached (within soft substrata) and posterior end of mantle/shell much enlarged; C, *Lithophaga*, isomyarian condition regained owing to greater development of tangential component in shell growth (cf. dotted arrows in A and C); D, *Pinctada*, monomyarian, showing further enlargement of posterior region and re-organization of body around the posterior adductor. Incurrent current indicated by solid arrows, exhalant current by feathered arrows, evolution from initial heteromyarian condition by broken arrows.

In the Anisomyaria (comprising the superfamilies Mytilacea, Pteriacea, Pinnacea, Anomiacea and Ostreacea) certain further consequences of massive byssal attachment appear, namely

(1) In the Pinnidae (Pteriacea) there has been a return to the original infaunal habitat, this involving a vertical posture (Fig. 6B), anterior end down, attachment by a massive byssus to stones some distance below the surface and a variety of major modifications (Yonge, 1953a). But the heteromyarian form could only have been initially assumed during a period of epifaunal attachment.

(2) In some Mytilidae a further development of the tangential component in shell growth counteracts the heteromyarian effect causing reorganization with the shell elongated and secondarily isomyarian (Fig. 6C). This occurs in the rock-boring *Botula* and *Lithophaga* and is an essential pre-requisite for their habit of life (Yonge, 1955b).

(3) By a further stage in the process, usually involving bilateral asymmetry with assumption of a horizontal posture (except in the Limidae), the anterior adductor is lost and the animal, with both mantle/shell and body re-organized around the hypertrophied posterior adductor, becomes monomyarian (Fig. 6D).

The processes involved and the further consequences that ensue, such as cementation (i.e. attachment by the mantle/shell) or freedom with or without the capacity for jet propulsion (e.g. Pectinidae and *Placenta* (*Placuna*) respectively) are fully discussed elsewhere (Yonge, 1953 *b*).

It might be noted that the retention of the filibranch ctenidium in all Anisomyria apart from the Ostreacea (in which there are many other distinctive features such as attachment by the left valve and incubation of larvae in the *inhalant* chamber) may well be associated with byssal attachment. Although the filibranch ctenidium is clearly less efficient than the much more compact eulamellibranch ctenidium, this will be of no more than minor disadvantage if the animals are epifaunal and so live in relatively clear water. Change to the heteromyarian or monomyarian condition occurred after the evolution of the eulamellibranch ctenidium in the Dreissenacea, Tridacnidae and other groups where this change has taken place.

Just as heteromyarianism in different superfamilies can be attributed to a common factor of massive byssal attachment, so can monomyarianism in four superfamilies of the Anisomyria (all but the Mytilacea) and in the Tridacnidae (Cardiacea). Although the mode of change and the final effect (wide exposure to light of the hypertrophied siphonal tissues containing zooxanthellae) are very different in the Tridacnidae (Yonge, 1936, 1953 *b, c*) yet the change could not have occurred if the body had not been byssally attached. Only in the unionid Etheriidae is the monomyarian condition attained as a result of cementation (Yonge, 1961).

Thus to byssal attachment may be attributed some of the most characteristic and often the most successful of bivalves such as the mussels (Mytilacea), pearl oysters and fan shells (Pteriacea), scallops (Pectinacea), saddle oysters (Anomiacea), edible oysters (Ostreacea), zebra mussels (Dreissenacea), boring and giant clams (Tridacnidae). All are either attached to a hard substratum by a massive byssus or, as in the infaunal Pinnidae and the motile scallops, have been modified in form owing to former attachment. While the view could presumably be upheld that a byssal apparatus primitively present in the adult could have been responsible for these far-reaching changes in form and habit, the opposing view now appears inherently the more probable. This would imply retention of the byssus from the post-larva to the young stages and then to the adults which were first modified in habit (as in group 3). But where the byssus became more massive and attachment against adverse environmental factors more sustained, the animals became increasingly modified in form with subsequent unpredictable consequences leading both to cementation and to high motility. The threads find an additional function in the Mytilidae and the Limidae where they are used for nest construction in certain species of *Musculus* (*Modiolaria*) and *Lima*.

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SUMMARY

The byssal apparatus appears during post-larval life when its secretion permits brief attachment during metamorphosis when the animal assumes the form which fits it for life in the adult habitat.

The byssus persists for continued temporary attachment in animals which may lose it in adult life, e.g. *Mya arenaria*, or in which it becomes an organ of permanent fixation, e.g. *Mytilus edulis*, *Pododesmus macroschisma* and *Tridacna crocea*.

The appearance of a byssal apparatus in adult Bivalvia is briefly reviewed; it is absent in eleven major groups most of them burrowers in habit.

A small but functionally very important byssus is present in certain groups, notably the Erycinacea. It influences habit but not form. A massive byssus, capable of maintaining the animal against powerful water movements, occurs in the Arcacea and Anisomyaria and in various eulamellibranch superfamilies. It has little effect on form in the Arcacea (where an inhalant current persists) but throughout the Anisomyaria and in the Dreissenacea and the Tridacnidae and in scattered members of other groups it influences form by first reduction and then loss of the anterior adductor, the animals changing from an isomyarian to a heteromyarian and then to a monomyarian condition. Further effects of these changes involve cementation and also motility. Early appearance of the byssus in adult Arcacea and Anisomyaria may explain the persistence of the filibranch ctenidium.

It is concluded that the presence of a byssal apparatus in the adult represents the persistence of a post-larval organ, i.e. that the animals possessing it are in this respect neotenus or paedomorphic.

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