A REVIEW OF THE FAMILY AGNESIIDAE HUNTSMAN 1912; WITH PARTICULAR REFERENCE TO *AGNESIA GLACIATA* MICHAELSEN, 1898

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Synopsis

Known species of the family Agnesiidae are reviewed and their relationships are clarified. Particular attention has been given to the genus *Agnesia* and the synonymy and distribution of *Agnesia glaciata*. New occurrences are recorded for *Agnesia glaciata* and *Adagnesia opaca*.

Similar modifications of body musculature to operate specialized closing mechanisms are demonstrated in each genus of the family. The development of this protective closing mechanism is associated with the extent to which the test is made brittle and rigid with encrusting sand thus preventing the general contraction of the body as a defence mechanism. The three known genera are closely related and distinguished by branchial sac modifications from *Caenagnesia* through *Adagnesia* to *Agnesia*. *Adagnesia opaca* and *Agnesia glaciata* are the most specialized species. The family appears to be an ancient one and records indicate relict populations of all species.

Introduction

The family Agnesiidae of the Suborder Phlebobranchia contains a limited number of closely related and highly specialized genera. Records of the family are not common, although often large numbers of individuals are taken together.

The following genera are known:

(1) *Caenagnesia* Ärnbäck, 1938, is known only from Antarctica and is represented by two species.

(2) *Agnesia* Huntsman, 1912, is represented by one species from the north Pacific; a second species extends from California to Tierra del Fuego and the Antarctic Peninsula, North Island, New Zealand, South Africa, Moreton Bay, Queensland, and Japan; a third species is known from abyssal depths of the north Atlantic.

(3) *Adagnesia* Kott, 1963, of which 2 species are known, one from a single specimen off Macquarie Island, and one from a limited area of the Australian coast.

In the present work the inter-relationships of species of this family are discussed, especially in regard to the increasing specialization of body musculature.

Family Agnesiidae Huntsman, 1912

Gut on the left side of the branchial sac; internal longitudinal vessels reduced to papillae on the transverse vessels; stigmata spiral; branchial

tentacles arranged in 4 concentric circles; the border of the branchial and atrial apertures produced into 6 and 7 pronounced lobes respectively: muscle bands reduced in length, often considerably.

Throughout the family Agnesiidae there is an increasing reduction in the numbers of papillae on the transverse vessels; reduction in numbers of infundibula; and a reduction in the number of transverse vessels present. The musculature becomes highly specialized and there is a progressive reduction in numbers and length of muscle bands throughout the family.

Despite the specialized nature of body musculature in the Agnesiidae, the homologues of the cionid musculature can be traced. In *Ciona intestinalis,* the most primitive species known, the external layer of musculature is represented by longitudinal bands and the internal layer consists of circular fibres. Only on the siphons, anterior to the tentacular band, does the circular muscle layer become superficial to the longitudinal bands. The internal transverse musculature, present more posteriorly in Agnesiidae, represents the inner layer of circular fibres in *Ciona.* While the anterior and superficial transverse bands represent the continuation of the circular bands which in *Ciona* are confined to the siphons. The inner circular bands associated with the tentacular ring in Agnesiidae are also a vestige of the inner circular layer of *Ciona.* The most significant departure from the cionid condition observed in the musculature of Agnesiidae is the reduction in length and number of longitudinal muscle bands; and the interruption of circular bands to form shorter transverse bands confined to the dorsal and ventral borders of the body. True circular bands are, in Agnesiidae, confined to the siphons. On the rest of the body the circular musculature is interrupted first laterally (*Caenagnesia* spp.) and then also in the median dorsal and ventral lines (*Agnesia* spp. and *Adagnesia* spp.).

The shortened muscle bands of Agnesiidae are associated with increasing rigidity of the test due to encrustation with sand. The body is consequently less contractile and the functions of the muscles become more specialized. In *Caenagnesia bocki, Agnesia glaciata* and *Adagnesia opaca* the shortened muscle bands pull lips or folds of test, which is generally rigid with sand, across the apertures to form a closing mechanism. This undoubtedly serves as a protective device for these non-contractile species existing in a vulnerable sublittoral locality.

The subfamily Rhodosomatinae of the family Corellidae, also of the suborder Phlebobranchia, contains monotypic *Rhodosoma turcicum* (Savigny), the only species outside the present family which exhibits a similar closing mechanism protecting the apertures. In *Rhodosoma* this is less symmetrical but more conspicuous than in the Agnesiidae and a fold involving the body wall and test is developed only on the right side of the apertures to form a lid. This is operated by the transverse muscle bands at the base of the siphons, particularly those across the mid line between the apertures, which extend out into the fold (Kott 1952). The mechanism is similar in Agnesiidae where the circular muscles surrounding the base of the siphons are interrupted laterally and operate across the dorsal midline from the base of the test fold on either side of the apertures. The mechanism appears to develop independently in each genus of the family. Closing lips are formed in *Caenagnesia bocki* and are present but not so well developed in *Adagnesia antarctica* which appears to have been derived from *Caenagnesia.* In *Adagnesia opaca* the closing mechanism achieves its greatest development and in *Agnesia,* a genus which probably evolved from a primitive *Adagnesia*

sp. a gradual specialization of musculature to operate closing lips is observed within a single species, *Agnesia glaciata,* where, in its most specialized form, it closely resembles the mechanism found in *Adagnesia opaca.*

Genus Caenagnesia Arnbäck, 1938

Traces of longitudinal vessels remain as bifid papillae on the transverse vessels of the branchial sac. Dorsal lamina retains the primitive condition of a plain edged membrane. Primary transverse vessels bearing papillae are present between each row of infundibula. Branchial papillae are more numerous than the number of infundibula in each row and more than a single papilla corresponds to each infundibulum. There are at least 12 primary transverse vessels present.

Caenagnesia schmitti Kott

(Text Fig. 1)

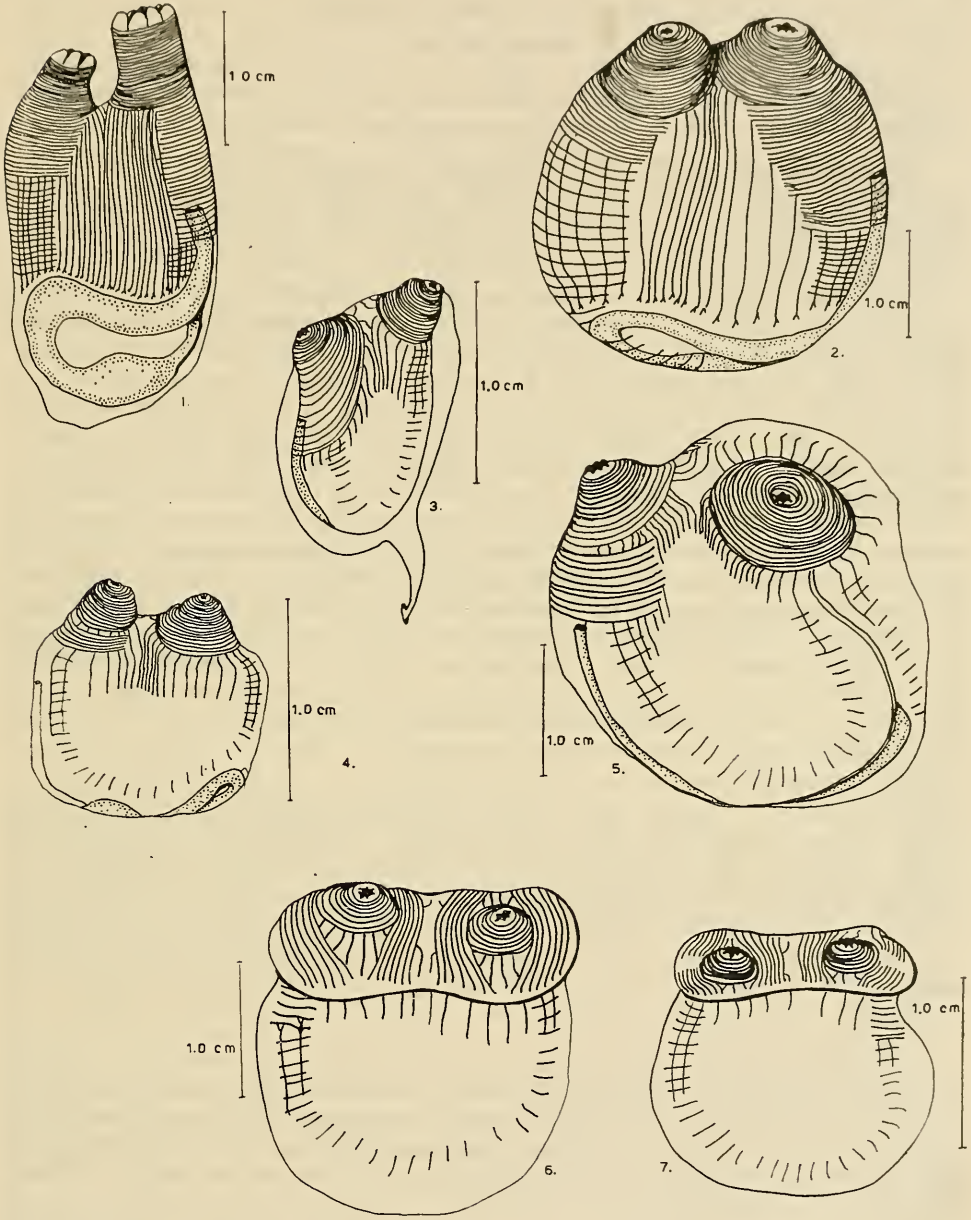
Caenagnesia schmitti Kott, 1969, p. 94.

Specimens examined.—U.S. National Museum: South Shetlands, "Eltanin", St. 428, 662–1120 m; coll. W. Schmitt, St. 66/63, 62 m. Victoria Land, S. W. Robertson Bay, 400 m (Holotype USNM 11968). (Single specimens from each station.)

Remarks.—The body is cylindrical, the test is thin and the body wall highly contractile. The apertures are on short cylindrical siphons which are furrowed along their length. The longitudinal muscle bands are especially numerous (about 50 on each side) and extend the whole length of the body on the right and as far as the gut loop on the left. Contraction of these muscles tends to draw the gut loop up along the branchial sac; however, in relaxed specimens the gut loop appears to lie behind the branchial sac reminiscent of the situation in *Ciona intestinalis.* Circular muscles are present around the siphons, external to the longitudinal muscles and numerous fine circular bands are present internally, associated with the 4 circles of branchial tentacles. Ventrally a superficial layer of transverse muscles is present anteriorly and is continuous across the endostyle. About 5 of the most posterior bands of this series overlap, in the middle of the body, with an inner transverse series present posteriorly on either side of the endostyle but not continuous across it. Dorsally a similar series of superficial transverse muscles is continuous across the dorsal line in the anterior two thirds of the body. These overlap with approximately the 5 most anterior bands of an inner transverse series which are interrupted across the dorsal line. The anterior superficial transverse bands, continuous across the dorsal surface, extend across the distal part of the rectum; while the inner and more posterior bands, interrupted across the dorsal surface, allow for some expansion of the stomach and proximal part of the rectum. Ventral transverse muscles are longer than the dorsal bands and neither extend across the sides of the body. In the branchial sac the number of rows of infundibula (60) and the number of infundibula in each row (25) are especially numerous for species of this family. The number of papillae on the transverse vessels are also numerous, with especially long biramous arms. There is a simple dorsal lamina as in *Ciona intestinalis* and other families of Phlebobranchia.

Occurrence.—Antarctica, probably circum-antarctic continent 74 m to 1000 m (Kott 1969).

Discussion.—The shape of the body, the furrowed external siphons, the thin test and the large numbers and length of the longitudinal muscles are unspecialized and reminiscent of *Ciona intestinalis*. The branchial sac also shows primitive affinities, as the number of rows of stigmata and the number



Text-figure 1–7 (Semi-diagrammatic showing body musculature) 1. *Caenagnesia schmitti* (Relay Bay, Antarctica). 2. *Caenagnesia bocki* (South Shetlands, Antarctica). 3. *Agnesia septentrionalis* (St. Georges Sound, Probilof Is.). 4. *Agnesia glaciata* (Corona del Mar, California). 5. *Agnesia glaciata* (South Shetlands, Antarctica). 6. *Agnesia glaciata* (Antarctic Peninsular, Antarctica). 7. *Agnesia glaciata* (Moreton Bay, Queensland).

of papillae per row is reduced in more specialized forms; and the retention of long biramous arms on the papillae suggests that the reduction of the longitudinal vessels has not proceeded as far as in other species with smaller papillae.

Caenagnesia bocki Ärnbäck

(Text Fig. 2)

Caenagnesia bocki Ärnbäck, 1938, p. 41. Van Name 1945, p. 202. Millar 1960, p. 94. Kott 1969, p. 96. *Agnesia complicata* Kott 1954, p. 151.

Specimens examined.—U.S. National Museum: Weddell Sea, "West Wind", St. 4, 796 m; "Edisto", St. TR6, 394 m; South Shetlands, coll. W. Schmitt, St. 9/63, 57 m; "Eltanin", St. 437, 267–311 m. Australian Museum: BANZARE Collection: Enderby Land, 220 m. (Single specimens.)

Remarks.—The species is dorso-ventrally flattened and the almost sessile apertures are fairly close together on the upper surface. Folds of test are formed along each side of the apertures into which the body wall projects. These folds may meet along the median line, thus covering and protecting the apertures. The test is firm and transparent and is sometimes brittle with sand. Due to the dorso-ventral flattening of the body the gut appears to lie across the posterior surface only slightly to the left. The longitudinal muscles are numerous (about 20) on each side. They extend the whole length of the body on the right but only to the gut loop on the left. There are circular muscles on the siphons external to the longitudinal muscle. Internally there are about 11 circular muscles associated with the 4 circles of tentacles. In a continuous series with the external circular siphonal muscle bands there are transverse bands across the dorsal border of the body in the anterior two thirds. Similar transverse muscles are present in the anterior one third of the body ventrally. The most anterior of these transverse muscle bands are inserted into the body wall at the base of the protective folds of test. Overlapping with the external transverse muscles there is a layer of internal transverse musculature across the dorsal border on the inner surface of the proximal part of the gut loop; and across the endostyle ventrally. More diffuse musculature across the posterior end of the body is gathered into bands which are inserted into the area enclosed by the pole of the gut loop where they are obscured by gonad lobes. All transverse muscles are interrupted across the sides of the body. The protective closing mechanism operates by the contraction of the external transverse muscle bands anteriorly which pull the lips together; meanwhile the siphonal musculature closes the apertures.

The branchial sac in this species is reduced from the condition found in *C. schmitti*. There are primarily 12 rows of 13 to 14 spiral infundibula. With growth the number of rows multiplies and a specimen of 30 mm (Kott 1954) has 24 rows of about 17 spirals. Biramous papillae with long arms are present on the transverse vessels between each row of infundibula. There are about 3 corresponding to each spiral.

Occurrence.—South Shetlands, Antarctic Peninsula (Ärnbäck 1938, Millar 1960, Kott 1969); South Georgia (Millar 1960); Weddell Sea (Kott 1969); Enderby Land (Kott 1954); at 57–800 m.

Discussion.—This species is distinguished from *C. schmitti* especially by the reduced numbers of branchial papillae, transverse vessels and infundibula.

and by the protective lips which cover the apertures. The reduced number and length of longitudinal muscle bands and the reduction in number of internal circular muscles associated with the tentacular sphincter is probably related to the development of a closing mechanism associated with the loss of a flexible body. The internal muscle bands are continuous posteriorly and dorsally across the mesial surface of the gut loop beneath the retropharyngeal groove that extends from the oesophageal opening at the base of the dorsal lamina to the posterior end of the endostyle. In Aplousobranchia the musculature of the body wall extends outside the gut loop, generally to the posterior end of the body. It has been suggested (see Kott 1969, p. 190) that the position of the gut loop on the side of the branchial sac could have resulted from a backwards extension of the branchial sac to the right or left of the gut loop. The muscle bands would, in this case remain outside the gut loop. The presence of the internal transverse muscle bands on the mesial surface of the gut loop in the present species suggests that, at least in this family, the gut has been drawn up on the left side of the branchial sac by relative shortening of the longitudinal muscle bands, leaving the inner transverse muscles across the posterior end of the body.

Genus Agnesia Michaelsen, 1898

Simple undivided flat triangular papillae present on transverse vessels. Dorsal lamina absent. Area of flat unperforated membrane crossed by primary transverse vessels present along mid dorsal line of branchial sac. Enlarged triangular papillae on the primary transverse vessels to the left of the dorsal line may correspond to dorsal languets. The number of infundibula present in each row always exceeds the number of papillae present on the transverse vessels. Four primary transverse vessels present (crossing the mid dorsal line).

Agnesia septentrionalis Huntsman

(Text Fig. 3)

Agnesia septentrionalis Huntsman, 1912, p. 118; 1912*a*, p. 106. Van Name, 1945, p. 200. *Agnesia beringia* Ritter, 1913, p. 493.

Specimens examined.—U.S. National Museum (Cat. No. 10633): coll. G. W. Hanna, St. George Island, Alaska (5 specimens). American Museum of Natural History (Cat. No. 1896): coll. G. Hanna, St. Georges Sound, Pribilof Islands, 74 m (3 specimens).

Remarks.—Rounded oval body from 0·5 to 1·5 cm long, usually supported by a delicate short stalk from the posterior end of the body. The stalk may be 1 cm long on a specimen of 0·8 cm but is generally much shorter than this. The test is thin and glassy, with few hairs and adherent sand grains. The apertures protrude on short rounded siphons, the branchial aperture anterior, and the atrial aperture antero-dorsal. There are 4 rows of equally long and closely placed branchial tentacles and posterior to these, at the base of the siphon, a ring of about 6 circular muscles which may coalesce into a single wide band in the rim of the tentacular velum. About 30 longitudinal muscle bands radiate from each siphon for only a very short distance. Externally each siphon has about 22 circular muscle bands. On the atrial siphon these extend well down the dorsal surface to cross the rectum. Short transverse muscle bands are arranged in single series on either side of the dorsal and ventral median lines, beneath the longitudinal muscles, and, especially on the dorsal surface, these extend anteriorly beneath

the circular siphonal musculature. In this species the branchial sac is well developed. There are 4 primary transverse vessels, bearing large flattened tongue-like papillae. Between successive primary transverse vessels 4 rows of 22 infundibula develop from double rows of 11 primary spirals. Secondary transverse vessels develop about 7 papillae corresponding to those on the primary vessels. Intermediate transverse vessels of a third order separating the double rows of infundibula between the primary and secondary vessels also develop papillae but these are generally incomplete. Each infundibulum develops a maximum of 4 to 5 coils.

Occurrence.—Bering Sea (Ritter 1913); British Columbia (Huntsman 1912, 1912*a*); Alaska, Pribilof Islands (Ritter 1913); at 27 to 78 m.

Discussion.—Differences between this species and *A. glaciata* involve the development of the body musculature which is less complex in the present species and the siphonal muscles in particular are not modified to operate a special closing mechanism. Apertures close by simple sphincter muscles around the siphons and these circular muscles are never interrupted. Similarly the branchial tentacles are more conspicuous in the present species and the inner circular muscles at the base of the branchial siphon associated with a velum are better developed. Development of the branchial sac depends, in the present species, on a proliferation of primary infundibula. In *A. glaciata* growth is accompanied by increase in the number of coils of each infundibulum.

Agnesia glaciata Michaelsen

(Text Figs 4–7)

Agnesia glaciata Michaelsen, 1898, p. 370; Van Name, 1945, p. 200; 1900, p. 76; 1907, p. 75; Millar, 1960, p. 92; Kott 1969, p. 97. *Agnesia krausei* Michaelsen 1912, p. 181. *Agnesia capensis* Millar 1955, p. 191. *Agnesia himeboja* Oka 1915, p. 1. *Agnesia sabulosa* Oka 1929, p. 152. *Agnesia septentrionalis;* Van Name, 1945, p. 201, Part (specimens from Newport Harbour, Southern California).

Specimens examined.—U.S. National Museum: Antarctic Peninsula, coll. W. Schmitt, St. 27/63, 75 m; 66/63, 74–92 m (single specimens); South Shetlands, coll. W. Schmitt, St. 64/63, 86 m (2 specimens). American Museum of Natural History (catalogue Nos. 1570, 1571, 1572, identified as *A. septentrionalis* by Van Name 1945): coll. MacGinitie; Corona del Mar California. Queensland Museum (Registration No. G5214): coll. W. Stephenson, Moreton Bay, Queensland 27°14′50″S, 153°18′00″E, 23 m; 27°16′20″S 153°20′50″E, 24 m (numerous specimens on muddy sand).

Remarks.—Mature specimens vary in size from less than 1·0 cm in diameter to 4 cm long. They are generally more or less rectangular and contracted specimens may be dorso-ventrally or laterally flattened. Both siphons are sessile and are present on the anterior surface. Variations in morphological characters occur in association with increasing size or increasing rigidity of test due to sand encrustation. Without sand the test is thin and semitransparent and may have fine hairs especially from the posterior end.

In large specimens from the South Shetlands (coll. W. Schmitt, 3 to 4 cm long) the test is free of sand and is very delicate posteriorly while the anterior half of the body is thickened, except for an area immediately surrounding the siphons. On contraction, the anterior thickened portion of the test forms a protective dome over the dorso-ventrally contracted body

and the siphons are drawn down into, and are protected by, the surrounding thicker test. Smaller specimens from California (Newport Harbour coll. MacGinitie, 1·0 cm) and from Patagonia (*A. krausei* Michaelsen 1898, 0·9 cm) have the test thickened in a similar way although there is some sand adhering. Contraction causes a withdrawal of the apertures which are protected by the sandy ridge of thickened test surrounding them. Specimens from Moreton Bay (1·5 cm), from Tierra del Fuego (Michaelsen 1898, 1·8 cm) and the specimen from the Antarctic Peninsula (Kott 1969, 2 cm) are heavily encrusted with sand causing the test to be rigid. Here the area of test surrounding the apertures is extended into a fold involving the body wall. On contraction the body is laterally flattened and the fold, especially from the right side, closes over the apertures.

The body musculature basically consists of about 20 superficial circular muscles around the branchial siphon and usually more associated with the atrial siphon. The basal muscles on the atrial siphon are not continuous around the anterior side of the siphon. These are referred to as posterior atrial muscles and they extend well down the dorsal surface. There is only a single circular band associated with the tentacular velum. From each side of the siphons longitudinal bands radiate not more than half-way down the body. There are more longitudinal bands from the branchial than from the atrial siphons. The proximal 8 to 10 circular bands around each aperture have fibres joining the longitudinal bands; and the posterior atrial muscles also have some fibres joining the distal extent of the longitudinal muscles.

In specimens from California there are about 20 circular bands around the branchial siphon; about 15 circular bands around the atrial siphon; and 6 posterior atrial bands. There are 14 longitudinal bands from each side of the branchial siphon and 8 from each side of the atrial siphon. In the specimens from the South Shetlands there are 18 longitudinal bands from either side of the branchial aperture; 15 from either side of the atrial aperture and 6 to 15 posterior atrial bands. The circular bands vary from 20 to 50 on both siphons. Where a protective fold of test is developed (specimens from Moreton Bay) the anterior 8 circular muscles of the branchial and atrial siphons remain unmodified and remain associated with the proximal extent of the longitudinal bands. However the next 4 to 7 circular bands break up into fibres dorsally, ventrally and on both sides of each siphon in the fold of the body wall associated with the test fold. These bands are not associated with the longitudinal bands. Posteriorly to these, a further 10 muscle bands on either side of the dorsal line are homologous with the posterior atrial bands in other specimens and some fibres branch into the longitudinal bands: 5 similar bands on either side of the ventral line represent modified circular bands from the base of the branchial siphon and are also associated with the longitudinal bands. In these specimens there are 11 longitudinal bands on either side of the branchial siphon and 6 longitudinal bands on either side of the atrial siphon. In the larger specimen from the Antarctic Peninsula 12 circular bands remain uninterrupted around the apertures and the next 7 circular muscles are associated with the protective folds and break into fibres on each side of the apertures. In this specimen these muscles are continuous across the dorsal and ventral surfaces. This is a more posterior group of muscles than those associated with the fold in the Moreton Bay specimens and only 5 short bands remain posterior to the folds, on either side of the dorsal line and associated with the longitudinal bands. In this specimen there are 25 longitudinal bands per side.

The data given above indicate that, with an increase in size of the body, there is an increase in the number of longitudinal muscle bands and the numbers of bands associated with the siphons. There is also considerable variation in the relative numbers of bands utilized for different functions. The longitudinal muscles are never involved with the fold or ridge surrounding the apertures and their function appears to be to draw the apertures down into the body and to dorso-ventrally flatten the body. They are consequently longer when the test is less rigid. The uninterrupted circular bands act as siphonal sphincters. However, when the protective fold is developed, it is the circular bands from the middle of the siphons which, together with a varying number of posterior atrial muscles, break into fibres and operate the protective folds of test. The number of circular bands which remain entire in the anterior extent of the siphon affects the number of posterior atrial muscles which become involved with the closing mechanism and seems to depend on the extent to which the siphons are developed. Consequently, in the large specimen from the Antarctic Peninsula where 12 muscle bands operate as a sphincter, the posterior atrial bands contribute to the operation of the closing mechanism leaving only a few of these below the folds. In the Moreton Bay specimens 8 muscle bands operate as a sphincter, the remainder of the circular siphonal muscles are modified to operate the closing mechanism, and the posterior atrial muscles, interrupted across the dorsal line, all remain behind the protective fold and probably contribute to the lateral flattening of the body. Unmodified posterior atrial bands, inserted into the body wall where it is associated with the thicker test around the siphons, probably draw the atrial siphon towards the branchial siphon and draw the test in more closely around both siphons.

In addition to the muscle bands described above short muscle bands deep to the longitudinal bands are continuous around the dorsal and ventral borders of both sides of the body. These muscles tend to flatten the body.

The dorsal tubercle is a simple slit and there is a tongue-like evagination of the body wall projecting from the region of the dorsal gland. The branchial sac has 6 double rows of 11 infundibula. Transverse vessels between each double row bear triangular papillae which are enlarged to the left of dorsal line. These transverse vessels are continuous over the dorsal membrane. A dorsal lamina is not formed. Only in the specimen from the Antarctic Peninsula are papillae developed also on the intermediate transverse vessels. The latter do not cross the dorsal line. Stigmata form 8 to 10 spirals. These are often interrupted in the vertical or horizontal axis and are crossed by radial vessels.

Occurrence.—Antarctic Peninsula, South Shetlands (Kott 1969); Tierra del Fuego (Michaelsen 1898); Patagonian Shelf (Michaelsen 1912, Millar 1960); California (Van Name 1945); New Zealand (Millar 1960); South Africa (Millar 1955, 1960); Moreton Bay, Queensland (New records); Japan (Oka 1915, 1929); at 23 and 115 m.

Discussion.—The tremendous variation in the disposition of the body wall musculature together with the widely dispersed records suggests that more than a single species is involved here. It is apparent however that the muscles are disposed merely in response to the degree of rigidity of the test. Where a heavy sand incrustation prohibits contraction of the anterior test around the withdrawn siphons the test instead folds over the siphons and the muscle bands break up into fibres in the folds. The numbers of muscle bands which are modified to effect the various contractions required of the body wall are immensely varied and the most posterior circular bands may

either be involved in the protective fold or may remain superficial to the longitudinal bands posterior to the fold. This may depend to some extent on the size of the fold; or on the relative size of the body; or the development of the siphons.

In younger specimens (*A. capensis* Millar, *A. himeboja* Oka, *A. sabulosa* Oka, *A. krausei* Michaelsen), the apertures remain in the primitive position, the branchial aperture anteriorly and the atrial aperture antero-dorsally and the ridge of test protecting them has not developed. The interrupted muscles bands behind the atrial siphon, the number of coils in each fundibulum, the number of infundibula and transverse vessels and the single muscle band in the tentacular velum all indicate that these specimens do fall within the range of variation of the species.

The species is distinguished from *Agnesia septentrionalis* by the larger number of spirals in each infundibulum; by the fact that at least some circular muscles are not completely continuous around the siphons; and by single muscle band associated with the tentacular velum.

Agnesia depressa Millar

Agnesia depressa Millar, 1955*a*, p. 1.

Remarks.—Millar's specimens (4) ranged from 0·8 to 1·1 cm in greatest diameter and this species resembles other *Agnesia* spp. in the presence of hair like processes from the test and in the numbers and arrangement of transverse vessels and infundibula. The species is distinguished only by the reduction of the branchial papillae and is apparently closely related to *Agnesia glaciata.*

Occurrence.—Swedish Deep-sea Expedition Sta. 371; N 24°12′, W 63°23′ to N 24°28′, W 63°18′; 5850 to 5860 m (Millar 1955*a*).

Discussion.—It is remarkable that a species from this depth shows so little deviation from other species. Apart from the longer test hairs it demonstrates none of the usual modifications, especially of the branchial sac, which are usually associated with abyssal species.

Genus Adagnesia Kott, 1963

Bifid papillae on the transverse vessels. Dorsal lamina absent. Area of flat unperforated membrane crossed by primary transverse vessels present along mid-dorsal line of branchial sac. Enlarged triangular papillae on the primary transverse vessels to the left of the dorsal line may correspond to dorsal languets. The number of infundibula always exceeds the numbers of branchial papillae in each row. Always more than 4 primary transverse vessels present.

Adagnesia antarctica Kott

Adagnesia antarctica Kott, 1969, p. 99.

Specimen examined.—U.S. National Museum: West of Macquarie Island, "Eltanin", St. 1418, 86–101 m. (Holtype U.S.N.M. 11966.)

Remarks.—The single available specimen is rounded and 1·5 cm in diameter. The test is thin but brittle and encrusted with sand. The apertures are surrounded by a rim of thickened test around the upper surface. There are about 20 circular muscles around each siphon and 35 longitudinal muscles on each side of the body extending only a short distance from the base of the siphons. Short transverse muscle bands are present in rows around the dorsal and ventral borders on either side of the body. In the branchial

sac there are 7 double rows of spiral infundibula separated by 6 primary transverse vessels. Biramous papillae with long arms are present on the primary transverse vessels but there is never more than one of these papillae corresponding to each spiral and often there are fewer. Along the dorsal line a large single languet develops from each primary transverse vessel, as in *Agnesia*.

Occurrence.—Only the holotype from west of Macquarie Island is known.

Discussion.—The species is distinguished from *Caenagnesia* spp. by reduction in the numbers and length of longitudinal muscle bands, a reduction in the length of transverse bands and their interruption over the mid line, and a reduction in the numbers of circular siphonal muscle bands; a reduction in the numbers of primary transverse vessels, infundibula and branchial papillae; the loss of the dorsal lamina and the presence of enlarged dorsal languets on the primary transverse vessels on the dorsal line. In the condition of the dorsal lamina and numbers of infundibula in each row, the species resembles *Agnesia* spp. However, other reductions in the branchial sac and body musculature in the latter genus are greater than in *Adagnesia antarctica* which retains the biramous branchial papillae of *Caenagnesia* and may be considered phylogenetically intermediate between *Caenagnesia* and *Agnesia*.

Adagnesia opaca Kott

Adagnesia opaca Kott, 1963, p. 76.

Specimens examined.—Queensland Museum (Reg. No. G4907): coll. W. Stephenson *et al.*, Moreton Bay, Queensland (numerous specimens). Australian Museum: coll. J. MacIntyre, 16.6.65, 140 m, off Cronulla, N.S.W. (fragments only).

Remarks.—This is a particularly large species (3 to 4 cm diameter) and represents the most highly specialized genus of the family in regard to its closing mechanism. The test is thin and completely rigid and brittle with sand. On both sides of the apertures folds of test form lips so shaped that the excurrent aperture is directed upwards and the incurrent aperture is directed downwards toward the substrate on which the animal lies. The body musculature is correspondingly specialized and bears a relationship to that of *Agnesia glaciata*. Only a limited number of circular muscle bands are present around the siphons, superficial to short radiating longitudinal bands which extend no further than the base of the siphons. Both anterior and posterior to the circular muscles of both siphons, there are very strong transverse bands extending across the dorsal line from the base of the protective folds of test. Their contraction draws these folds together. The general body musculature is reduced to very short muscle bands around the anterior, dorsal, posterior and ventral borders of both sides of the body. These short bands along the dorso-lateral border are arranged in parallel to the long axis of the body and may represent the remnants of the distal portions of longitudinal bands which radiate from the siphons. The remaining short muscle bands which appear to be deeper in the body wall than those along the dorsal border, are probably homologues of similar muscles in *Agnesia glaciata* and represent the remnants of the inner circular body musculature. About 30 transverse vessels, each supporting about 32 bifid papillae, alternate with single rows of about 60 infundibula. However, although there are triangular languets on each transverse vessel to the left of the dorsal line large languets alternate with small languets suggesting that those transverse vessels bearing the latter have developed later as a

result of proliferation of the branchial sac. In the posterior part of the branchial sac this proliferation can be observed occurring and single infundibula tend to subdivide into two to increase the number of spirals in each row and then further subdivision occurs to increase the number of rows of infundibula so that 4 spirals, arranged in a square, result from the subdivision of a single spiral infundibulum. In association with the highly developed closing mechanism the gonoducts are directed anteriorly and the species is probably viviparous.

Occurrence.—Moreton Bay, Queensland (Kott 1963); off Cronulla, N.S.W., 140 m (New Record).

Discussion.—The reduction of body musculature has proceeded beyond the condition found in *Adagnesia antarctica* and indeed, beyond the degree of reduction and specialization of this musculature known in *Agnesia* spp. However the condition of the dorsal lamina and branchial papillae, and the numbers of branchial papillae in relation to the numbers of infundibula in each row establish its relationship to *Adagnesia antarctica* from which it has diverged by modifications of the musculature to operate a highly specialized closing mechanism, by the secondary development of numerous transverse vessels in the branchial sac and proliferation of the numbers of infundibula in each row and by a corresponding increase in the numbers of branchial papillae on the transverse vessels. The similarity of the branchial sac of this species to that of *Caenagnesia* spp. is due to this proliferation of infundibula and transverse vessels together with the retention of biramous branchial papillae. However the reduced number of branchial papillae associated with each infundibulum in the present species together with the condition of the dorsal lamina clearly distinguish the species from *Caenagnesia*. The large numbers of infundibula in the branchial sac is a secondary development perhaps related to the large size characteristic of individuals of this species.

Zoogeography

The widely dispersed records of *Agnesia glaciata* suggest that this represents an ancient species with a well established cosmopolitan distribution, and that today records of this species from the Pacific, Antarctic and Indian Oceans may represent relict populations now isolated. The occurrence of 2 species of the family exclusively in the Antarctic also probably represent relict populations now isolated by the submergence of land or submarine bridges. Despite the fact that it is the phylogenetically primitive genus *Caenagnesia* which is today endemic in the Antarctic it is not thought possible for the family to have developed there and to have then radiated northwards as far as northern boreal waters. If this had occurred one would not expect, in isolated areas, so very few species. It is the wide distribution and morphological homogeneity of *Agnesia glaciata* which suggests that the species (and the family) was well established a long time ago and persists today as a highly successful relict form.

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