THE MANY TAILS OF *AKERA BULLATA* MÜLLER 1776 (GASTROPODA: APLYSIOMORPHA)

J. C. A. CRAIK

Scottish Association for Marine Science, Dunstaffnage Marine Laboratory, Oban, Argyll PA37 1QA, U.K.

Abstract *The original description of the opisthobranch gastropod* Akera bullata *mentions a tail-like trailing "pallial filament". Several other early descriptions illustrate this structure, as do a recent field guide and other authoritative works. However, this filament is absent from (at least some) British and Irish populations. In a population in west Scotland there is no such structure, but many individuals have "tails" of two kinds – trails of mucus containing pseudofaeces, or filamentous algae growing on the shell. Using the latter as an example, I tentatively propose that the "pallial filament" of early authors was not a genuine body part but another organism, possibly a hydroid coelenterate, growing on the shell. This needs verification by examination of* Akera *with a filament like that described by early authors. However, there seem to have been no first-hand descriptions of animals with this structure since Tchang-Si (1931).*

Key words Akera bullata, *commensal, algae, filament, mucus, pseudofaeces*

INTRODUCTION

Akera bullata Müller 1776 is an opisthobranch mollusc belonging to the order Aplysiomorpha. Several early accounts of its anatomy describe and illustrate a "pallial filament", a slender extension of the rear edge of the mantle which protrudes behind the shell and appears like a tail at the rear end of the crawling animal. Accounts by other authors state that this structure is absent, at least in certain populations. This article tries to clarify this inconsistency.

Descriptions with and without a "pallial filament"

The pallial filament was first mentioned in the original Latin description of the genus *Acera* by Müller (quoted by Meyer & Möbius, 1865): "*Pallium postice cirrum emittit filiformem contractilem*" ["A contractile filament arises from the rear fringe of the mantle."]. In their own description of the genus, Meyer & Möbius say "At the rear edge of the mantle there is a filament-like appendage". They go on to describe the species *bullata* in more detail and their figs 1–3 (opposite their p. 86) show a crawling *Akera bullata* with a filament trailing behind it. On p. 84 they say that the filament arises from a fissure in the spire of the shell just under the notch of the suture, that it can be extended and withdrawn, that if pressed it contracts in irregular undulations and the basal part is withdrawn, and that broken fragments shorten considerably and shrivel transversely. They illustrate (in fig. 8 opposite p. 86) a 300x magnification of a longitudinal fragment of the filament that shows transverse and longitudinal muscle fibres lying under a finely granular cuticle or epidermis.

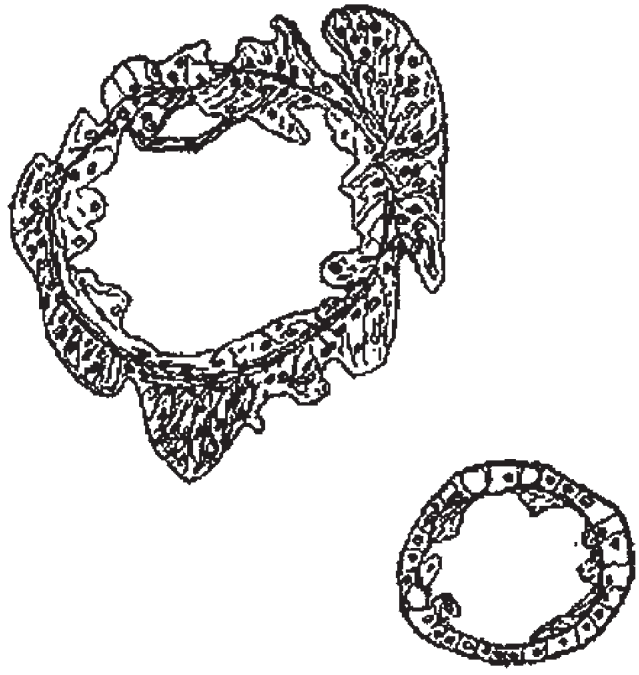

Figure 1 Transverse sections of the filament ("pallial posterior lobe") of *Akera bullata* from the French Mediterranean coast. Upper: near the base. Lower: near the tip. From Tchang-Si (1931: fig. 29; p. 66].

Tchang-Si (1931 p. 66) says: "The posterior pallial lobe, which is very wide and long in *Bulla*,

Contact author : clive.craik@sams.ac.uk

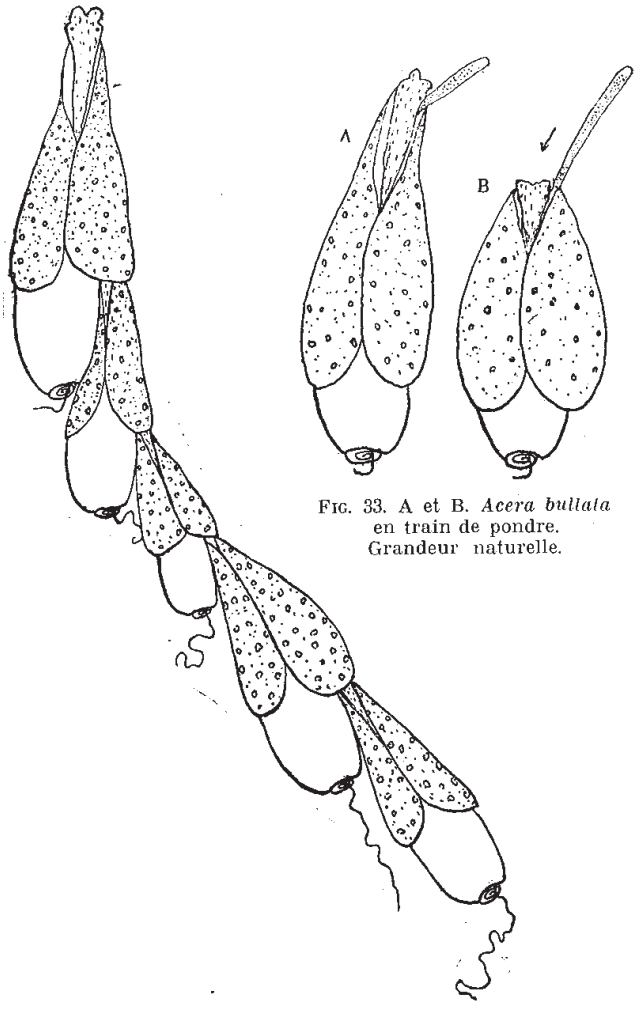

Fig. 33. A et B. *Acera bullata* en train de pondre. Grandeur naturelle.

Figure 2 A mating chain of five *Akera* and (above) two *Akera* laying eggs. Note the narrow width, and the individual variation in length, of the posterior filaments. From Tchang-Si (1931: figs 32 and 33; p. 70).

and particularly in *Haminea*, occurs in *Akera* in the form of a flagellum. This flagellum is very slender, almost as long as rest of the body, and is often broken off and incomplete; sometimes it is hidden in the spire of the shell and . . . (if broken) . . . it regenerates very slowly. That is why Legendre did not see it in specimens collected at Concarneau (France). But if one searches behind the anus, on the posterior extremity of the mantle, one always finds a piece of flagellum of variable length. The diameter of the flagellum varies along its length, its base being much thicker than its distal end; it is hollow and its walls are made of glandular cells." One of Tchang-Si's drawings, shown here as Fig. 1, shows the pallial filament to be a hollow tube with a wall of two layers, each one cell thick – effectively an ectoderm and an endoderm. The magnification cited implies that the filament's base and tip are respectively about 0.3 and 0.1 mm thick.

Tchang-Si also gives a drawing of five *Akera* mating in a near-linear chain, shown here as Fig. 2. Each animal has a thin tail. The tail lengths vary considerably between individuals, presumably because of breakages caused by their fragile nature.

These early accounts of *Akera* with a tail-like filament appear to be the basis of later illustrations or descriptions, some written in a manner suggesting that, while the authors were familiar with *Akera*, they had not themselves encountered a tail-like filament. They often state or imply both possibilities. Thus Jeffreys (1867: vol. 4; pl. VIII) shows a crawling *Akera bullata* without any filament, but his text (p. 429) states that the mantle forms "at the rear a cylindrical or thread-shaped process which occupies a slit at the front of the spire when the animal is at rest". Likewise, Forbes & Hanley (1853: vol. 3; p. 527) illustrate *Akera* with no filament but they write: "According to Lovén, a long slender filiform process of the mantle is lodged in the canal of the spire".

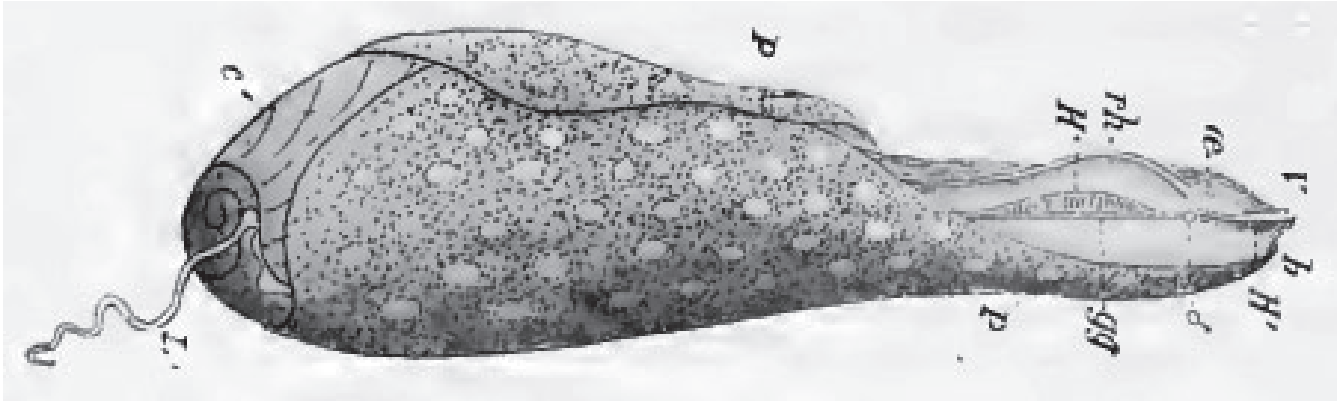

Figure 3 *Akera* from the Atlantic coast of France, with filament as illustrated by Guiart (1901: fig. 69, p. 118).

Figure 4 *Akera* with filament, as illustrated by Barrett & Yonge (1958: pl. 18; p. 141]

Other authors facing this dilemma show inconsistencies or surprising omissions. Guiart (1901) gives four drawings of *A. bullata*, all with a pallial filament. Three are diagrammatic but one, shown here as Fig. 3, is realistic and shows a filament about 38% of the length of the rest of the body. Despite legends to these drawings describing the filament as the "posterior pallial lobe", Guiart does not mention the structure anywhere in his text.

Later, in a widely-used and excellent Field Guide, Barrett & Yonge (1958) illustrate a filament about three-quarters as long as the rest of the body, shown here as Fig. 4.

In contrast, in a brief synoptic classification, Thompson & Brown (1976) show a more stubby "posterior mantle tentacle" that is only about one-tenth as long as the rest of the body, shown here as Fig. 5.

In a more scholarly work of reference, Thompson (1976) recognises these inconsistencies and gives drawings of *Akera* both with and without a pallial filament. He cites three works in support of the former: Jeffreys (1867); Tchang-Si (1931); and Meyer & Möbius (1865). The relevant parts of all three are given above. In Thompson's drawing (shown here as Fig. 6) the filament length is about 76% of the rest of the body and its thickness varies from about 0.9 mm at the base to 0.5 mm at the tip, some three to five times thicker than shown by Tchang-Si (1931).

Morton & Holme (1955) give excellent drawings and photographs of *Akera* from Plymouth. These show no filament but, inconsistently, the description states "A long white filament, forming a grooved tentacle produced from the pallial

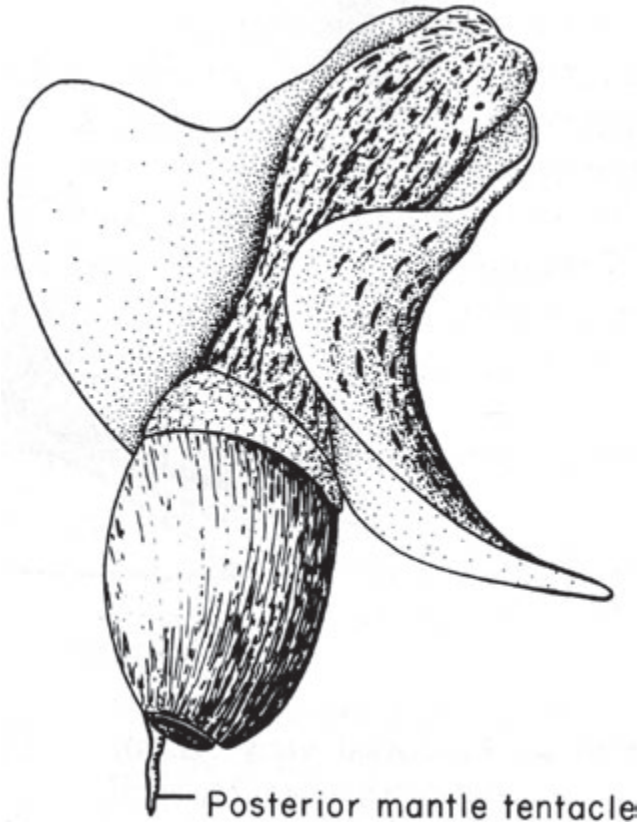

Figure 5 *Akera* with filament (tentacle), as illustrated by Thompson & Brown (1976: fig. 11b; p. 30).

margin, trails behind". Thompson & Seaward (1989) make it clear that there is no posterior pallial tentacle on *Akera* from the Fleet Pond, Dorset. In their Abstract they describe *Akera* from Lough Ine in south-west Ireland as having an "elongated posterior tentacle". Inconsistently, however, in the text this structure is not mentioned for Lough Ine specimens, nor does it appear in the drawing

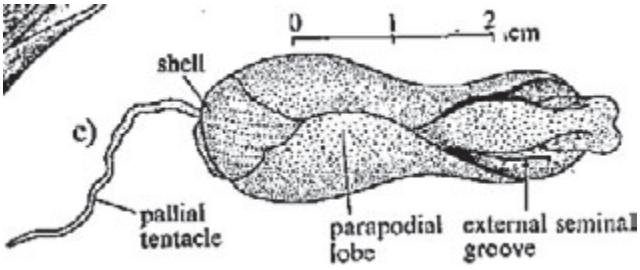

Figure 6 *Akera* as illustrated by Thompson (1976: fig. 66c; p. 130).

of one of these in their fig. 5B. Rather, the text states that Lough Ine specimens have a "short posterior pallial siphon", shown in the drawing as a short siphon barely projecting from the rear end of the body. This siphon is possessed by all *Akera* (see Fig. 7 below) and is nothing like the long pallial filament illustrated by others. Similarly Morton (1972), in a detailed account of the pallial organs of this species, mentions the pallial filament or tentacle briefly thus: ". . . the aperture (of the posterior pallial siphon) . . . is guarded by the pallial tentacle . . .". Yet Morton does not describe or illustrate this tentacle, or mention it again. In particular, its point of attachment is not given. This omission is surprising in an account that describes and illustrates all the neighbouring structures with beautiful precision.

All of these inconsistencies suggest that authors were familiar with *Akera* without a filament but had never seen any with this structure. Some may have felt obliged to repeat the descriptions of those who had.

There is no doubt that both Meyer & Möbius and Tchang-Si saw *Akera* with an attached filament. Although the two studies involved different geographical regions, namely Kiel Bay in the west Baltic and the coast of Provence in the French Mediterranean, the similar descriptions imply the same or a similar structure. The longitudinal fragment of the filament described by Meyer & Möbius usefully complements the transverse section shown by Tchang-Si. However, there are several reasons for questioning the belief that this filament was a genuine body part. First, Meyer & Möbius stated that the filament could be extended and withdrawn. No other author has suggested this. Few, if any, molluscs possess slender filaments that can be projected from the mantle edge or from a site close to the shell spire in this way. Its thin, fragile nature and its projectibility are so unlike the posterior pallial lobes of *Haminea* and *Bulla* that the homology implied by Tchang-Si seems unlikely. Second, molluscs have poor regenerative abilities (Balinsky, 1965). Thus Tchang-Si's assertion that *Akera* can regrow its pallial filament needs examination. Third, it is difficult to think of any molluscan tissue or organ that possesses a simple diploblastic structure like Tchang-Si's drawing (Fig. 1). The molluscan body plan is triploblastic (ectoderm, mesoderm, and endoderm, each usually more than one cell thick). Fourth, it is unlikely that one species would exist in two forms, one with and one without a fragile mantle filament of no known function.

Other kinds of trailing filaments

The population of *A. bullata* in a seawater pond near Oban in west Scotland (Craik, 2012) lack a posterior pallial filament, like those at Plymouth and at the Fleet. However, it is common to see swimming and crawling animals with trailing filaments of two kinds, sometimes both types on one individual. *Akera* shown in the following photographs were all from the Oban pond.

The first of these are mucus strands coming from the posterior pallial siphon. The anus lies just inside the tip of this siphon, which projects

Figure 7 Swimming *Akera* with a loosely attached pseudofaecal filament of mucus containing yellow solid, coming from the posterior pallial siphon (dark colour). Such filaments usually detach from the animal soon after it begins to swim, and always when it is touched or caught in a net. The large, brown-edged structure left of the siphon is the shell. 4 April 2010

slightly at the animal's rear end (Morton, 1972). The colourless mucus originates further forward in the mantle cavity, from the gill, but the trailing strands often contain faecal matter as well as pseudofaeces (fine sediment swept into and out of the mantle cavity by the strong ciliary current). Such filaments vary in colour and consistency depending on the substrate on which *Akera* has been feeding and crawling (Figs 7 & 13).

Freshly-collected *Akera* crawling on the bottom of a white bucket can be seen to discharge short lengths of faecal or pseudofaecal filament from the pallial siphon every few minutes. These often remain attached, sometimes for many lengthening movements, so that a filament may consist of successive faecal pellets separated by intervening transparent mucus (Fig. 8).

These faecal or pseudofaecal strands that have yet to break away from the pallial siphon are mentioned here to emphasise the confusing variety of filaments that may be seen trailing behind *Akera* when it crawls or swims.

The second kind of "tail" found on *Akera* at Oban are small macro-algae of various colours growing on the shell spire. The spire is flat and faces backwards at the rear end of crawling *Akera*. The algae may be single filaments, tufts of many filaments, or ribbons, blades, or oval leaf-like structures (Figs 9–12). Similar structures have been described by Sykes (1905) on *Akera* from Ballynakill Harbour, Co. Galway, on the west coast of Ireland. He wrote: "The exposed part of the shell is not infrequently (at least in summer) adorned with a plume of alga – *Enteromorpha* or the like – having something of the appearance of a tail."

Figure 8 Strand of mucus containing faecal pellets trailing from the pallial siphon of *Akera* crawling out of water. April 2010

Figure 9 *Akera* swimming in a bucket. One has a tuft of filamentous green algae growing on its shell. 3 April 2010

Figure 10 . One *Akera* shell without and two shells with dry algal filament attached to spires, from specimens frozen in April 2010. Lowest shell is 20 mm long.

Both Jeffreys, and Forbes & Hanley, cite a close relationship between the pallial filament and the spire of the shell. Inspection of dried shells of affected *Akera* from Oban showed that the algae were always growing on the shell, attached close to or on the spire (Fig. 10). They were not detached algal fragments that had become entangled in the whorls or spire. In some examples, a larger area of shell close to the point of attachment

Figure 11 Live *Akera* with various kinds of green algae growing on shells. 11 August 2011.

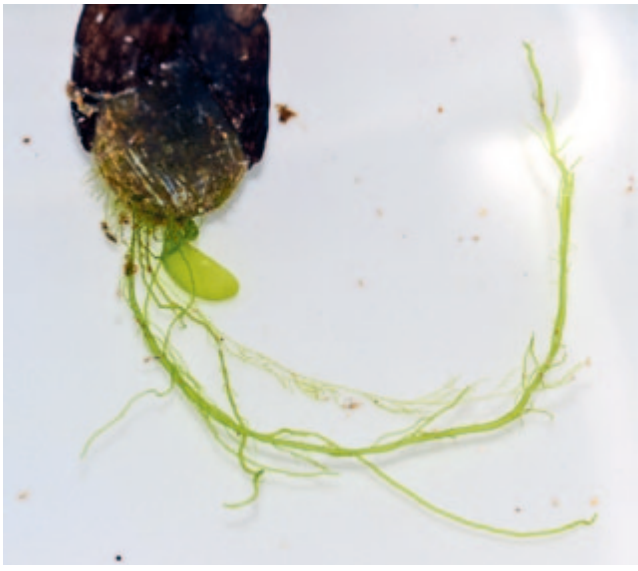

Figure 12 A living *Akera* with various green algae and smaller organisms, possibly stalked ciliates, growing on its shell.

Figure 13 A live *Akera* trailing faeces containing sand (centre). Another large mass of faecal sand is at right. April 2010.

was discoloured and roughened compared with unaffected shells, perhaps the result of disease or aborted attachments of other algae. In live *Akera* examined by naked eye during weighing of individual animals, the following proportions had algae growing on the shell: 9/42 in April 2010, 15/113 in July 2011, 18/113 in July 2011 and 8/96 in August 2011. Understandably, such algae were less frequent in the winter months or in samples of younger *Akera*.

Possible explanation of the "pallial filament"

The filaments described by Tchang-Si and by Meyer & Möbius were clearly not algae, since no pigment was mentioned. However, if filamentous algae can grow on the shell in such a high proportion of individuals, other sessile filamentous organisms might do the same under different conditions or in other geographical areas. Thompson (1976: 112–113) illustrates epizoitic stalked ciliates growing commensally on the shell of another opisthobranch, *Retusa obtusa*.

The two unicellular layers in Tchang-Si's drawing (Fig. 1) strongly suggest the epidermis and gastrodermis of a hydroid coelenterate. The epidermis of hydroids contains musculo-epithelial cells which can be striated in appearance (Hyman, 1940) and can contract both longitudinally and transversely. This could explain the striated structure, writhing movements and contractions described by Meyer & Möbius. The "cuticle" lying above the muscle cells would then have been the non-cellular tubular coenosarc or perisarc that encloses and protects the stems of hydrozoans (Barnes, 1980). Regrowth of broken filaments described by Tchang-Si is consistent with the high regenerative ability of coelenterates (Balinsky, 1965). Abrasion caused by being dragged over the sand-silt favoured by *Akera* might explain the absence of well-developed polyps, although the protruding mass of cells at one point of the circumference in Fig. 1 is suggestive of one such deformed entity. Another possibility, less plausible, is that the filaments were sessile annelids or other worms. These would have muscular structure and serpentine movement, but are less likely to show two simple layers of cells.

In summary, pictures and descriptions of *Akera bullata* with a tail-like "pallial filament" are shown in standard works of reference but the nature of this structure should be reconsidered.

The filament regarded as part of the mantle by early authors, including Müller in his original description of the species, might have been a commensal epizoitic animal attached to the shell. Investigation of specimens with well-attached, non-algal "tails" is needed to resolve this question. However, there appear to have been no first-hand accounts of *Akera* with this structure since Tchang-Si (1931).

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