in *Acaenoplax* is unknown, suggesting that *Acaenoplax* is a (semi-)sessile organism with an anchoring or opercular structure.

Solenogastres and Polyplacophora are ciliary gliders. In contrast, the ventral surface of *Acaenoplax* shows features of a muscularly creeping animal, which are typically found in contracted polychaetes. These features include transverse furrows and a shallow mid-ventral groove that marks the course of the ventral nervous system.

As many polychaete families have highly plastic morphology[6,7], the characteristics of *Acaenoplax* fit well within this frame. A ventral, cuticular shield that shows co-marginal accretion is present in the Sternaspidae[7] (Fig. 1a); dorsal plates, referred to as elythra, formed by the parapodia and often bearing papillae, are diagnostic for the Aphroditidae[7]. For analogous dorsally fused parapodia, see *Chaetopterus variopedatus* (Chaetopteridae; Fig. 1b) and representatives of the Chrysopetalidae, Euphrosinidae and Spintheridae[7]. *Chaetozone* (Cirratulidae; Fig. 1c) has almost completely annular parapodial structures[7,8]. These analogies may be no better than those with molluscs, but they are also no worse. Interpreting *Acaenoplax hayae* as a highly specialized polychaete thus avoids most of the uncertainties involved in assuming that it is a mollusc.

The polychaete characteristics of *Acaenoplax hayae* in its original description are: serially (segmentally) arranged parapodial appendages with chaetae; cuticle-covered, transversally wrinkled ventral surface with a longitudinal groove, here interpreted as a clear indication of a closed dermo-muscular tube (*Hautmuskelschlauch*) and transversal musculature, with the midventrally positioned nervous system; dorsal, cuticular plates resembling elythra; modified parapodia adapted for mobility and anchoring in a tube (as in Flabelligeridae, for example); and a terminal 'opercular' structure (Sedentaria).

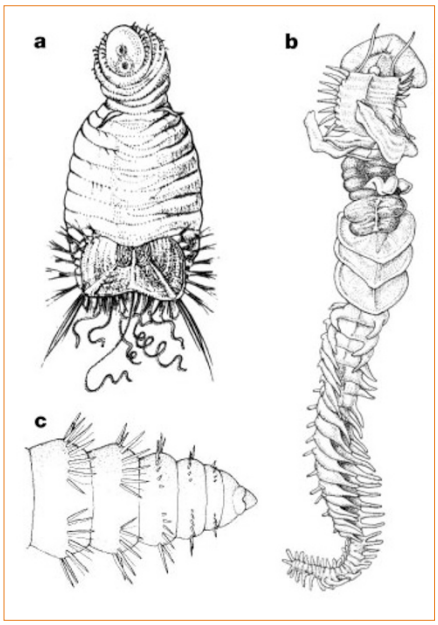

Figure 1 Polychaete examples of *Acaenoplax* characteristics. **a,** *Sternaspis scutata* (Sternaspidae), with ventro-posterior shield showing co-marginal accretion[9]. **b,** *Chaetopterus variopedatus* (Chaetopteridae), with dorsally fused notopodia[9]. **c,** *Chaetozone setosa* (Cirratulidae), with near-annular parapodia[7].

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Sutton et al. *reply* — Steiner and Salvini-Plawen claim that *Acaenoplax* cannot be a mollusc because it would sit uneasily within the caudofoveates, solenogastres or polyplacophorans; however, the fossil record frequently reveals character combinations that have not survived to Recent times[1]. Although *Acaenoplax* displays a mosaic of molluscan characters that does not accord with any single modern group, this does not necessarily eliminate it from the phylum as a whole.

Aragonitic valves that grow by marginal accretion are highly characteristic of molluscs and were undoubtedly present in *Acaenoplax*. Valves of the closely related genera *Arctoplax*, *Heloplax* and *Enetoplax* occur in coeval deposits on Götland[2]. These are preserved in a manner that is identical to that of co-occurring molluscan shells of original aragonitic composition (such as the valves of polyplacophorans)[2,3] and display clear co-marginal growth lines. The composition of the spines of *Acaenoplax* is less certain, but they were rigid and sharp (see Fig. 2d in ref. 4) and hence were probably biomineralized, and those that arise from the cuticle are preserved in the same manner as those that project from valves. Our use of the term 'cuticular' was intended to refer to the occurrence of the spicules on the cuticle, rather than to their composition.

The groove on the ventral surface is the one feature of *Acaenoplax* that appears to be more polychaete-like than molluscan, although this morphology is typically associated with errant rather than sedentary polychaetes. The other proposed polychaete characters are problematic. Although there is clearly a serial structure in *Acaenoplax*, there are no external signs of segmentation. Indeed, the overlap between subsequent 'lobe chevrons' is incompatible with true segmentation. The lobes and ridges of *Acaenoplax* are difficult to homologize with parapodial structures, as there are up to eight pairs of lobes per ridge. As spines arise from lobes, ridges and the cuticle (see Fig. 2d in ref. 4), they cannot be homologous with chaetae, which arise only from parapodia[5].

Acaenoplax has multiple projections that emerge from a cavity at its larger termination. These features are very hard to homologize with polychaete posterior structures, so if *Acaenoplax* is a polychaete, then this termination must represent the anterior. Many sedentary polychaetes do have an anterior (prostomial) cavity from which feeding tentacles emerge[5]. There is, however, no evidence that the projections could extend significantly from the cavity and, with this anterior–posterior polarity, the spine array faces forwards, which is unlikely on functional grounds. By contrast, interpreting this termination as an aplacophoran-like mantle cavity containing gills is compatible with both the observed mobility of the projections and the direction of the spines.

Several *Acaenoplax* structures (such as lobes, ridges and the postero–ventral plate) lack convincing polychaete or molluscan homologues, and hence are considered to be autapomorphic and phylogenetically uninformative. Nonetheless, this leaves four molluscan characters (polyplacophoran-like aragonitic scleritome, spicules arising from cuticle and probably composed of aragonite, serial rather than segmented structure, and posterior cavity with projections) arrayed against one polychaete-like character (the ventral surface). We consider that the balance of evidence places *Acaenoplax* firmly within the Mollusca rather than in the Polychaeta.

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