Myriapoda–Hexapoda assemblage' and to give a name, the Uniramia, to this group[7]. The component taxa are united on their basic arthropodan features; their particular type of jaws, and their limbs lacking any trace of true outer ramus. The jointed limbs of myriapods and hexapods could, arguably, have been derived from lobopodial limbs essentially resembling those of the extant Onychophora, and these limbs could have been derived from limbs of metamerically segmented worms with a haemocoel which, along with the muscles, worked the uniramous limbs. As long ago as 1940, Tiegs[8,9] emphasised the unity of these three taxa and Anderson[10] has shown in detail the common ontogenetic theme which exists throughout the Uniramia and contrasts absolutely with that pervading the entire crustacean group. Further, crustecean ontogeny could not have been derived from that of any known annelidan group. In contrast, the uniramian ontogeny might have been derived from that of some yolky-egged annelid or annelid-like worm which possessed a haemocoel and lobopodia, but not coelomate parapodia.

There is no justification on the basis of Golgi phenomena for the restriction of the term Uniramia to the Myriapoda and Hexapoda alone, nor for the exclusion from the arthropods of any animal on one character alone. That the Onychophora are thoroughly arthropodan is shown by their cuticle[11,12], which contains protein and chitin, but not collagen, in contrast to annelids; by the presence of an ecdysial cycle as in other arthropods[13], the cuticle being shed in one piece, as in no other invertebrates on Locke and Huie's list[1]; and by the general anatomy of the Onychophora, which tallies with that of other uniramian taxa. We do not know the significance of onychophoran Golgi phenomena nor of its association with unstriated muscle, but this one feature is no acceptable reason to disrupt the Uniramia or exclude the Onychophora from the arthropods.

Thus, without further consideration of the several other arthropodan taxa, it is clear that the Uniramia and Crustacea each represent well defined arthropodan taxa, which could not have originated from common annelidan ancestry, and that their cuticles must have evolved in parallel.

The exoskeleton of all arthropods has the same mechanical functions in providing unstretchable cuticles, sclerites and arthrodial membranes concerned with trunk movements and muscle insertions. The requirements of other invertebrates are different. The cuticles of the various arthropodan taxa are not identical, although protein and fine-fibre systems form the basis of most sclerites. There is thus no reason that the general manner of formation of arthropod cuticle may not have evolved more than once; nor is there any sound evidence against the unity of

the Uniramia or against a polyphyletic concept of arthropodan evolution.

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Are viroids negative-strand viruses?

IN their paper detailing the complete sequence of 359 bases in potato spindle tuber viroid (PSTV) RNA, Gross *et al.*[1] considered, as have other workers[2], that the circular single-stranded molecule is unlikely to function as a messenger RNA. The possibility that PSTV RNA might be a non-coding strand rather than a positive (coding) strand may have been overlooked.

I have examined the base sequence complementary to that established by Gross *et al.*[1]. Four possible initiation triplets (all GUG) and six possible strong termination triplets could result in four polypeptides containing 108, 79, 43 or 28 amino acids, of which the two larger (with molecular weights (MWs) 11,300 and 8,500) are the more interesting. The longest of these sequences begins with a GUG at positions 134–136 and teminates at a double UAG at positions 99–104 (Fig. 1). The GUG is preceded by a well-placed potential ribosome recognition sequence as indicated in Fig. 1. The second potential polypeptide is in a different reading frame and begins with a GUG at residues 177–179. It is preceded by an unbroken sequence of 14 purines, and teminates in an UAG at residues 55–57. The amino acid composition of the small polypeptide is unremarkable except for a high content of phenylalanine (10%), but the larger polypeptide has a content of arginine (11%) and lysine (5%) that would give it histone-like properties.

Two experimental observations would fit with the view that one or both of these polypeptides are produced by viroids. First, there is evidence for an RNA strand complementary to citrus exocortis viroid (CEV) RNA in infected tissues[3]; CEV is fairly closely related to PSTV[2]. Some of the hybridisable RNA was in the nuclear fraction but more was in the soluble cytoplasmic fraction, where it might have possessed a messenger function.

Second, an increase in amount (and in radioactive labelling) of two polypeptide bands in polyacrylamide gels was found in CEV-infected plants[4]. MWs assigned to the two polypeptides were 18,000 and 15,000. I have recalculated these MWs as 13,200 and 10,400, using as internal markers the large and small subunits of ribulose-1′,5′-diphosphatecarboxylase (MWs 54,000 and 12,000). The larger of the CEV-induced polypeptides was located preferentially in the histone fraction, the smaller was in the non-histone fraction[4]. This partitioning fits with the amino acid composition of the two polypeptide components that could be derived from the negative strand.
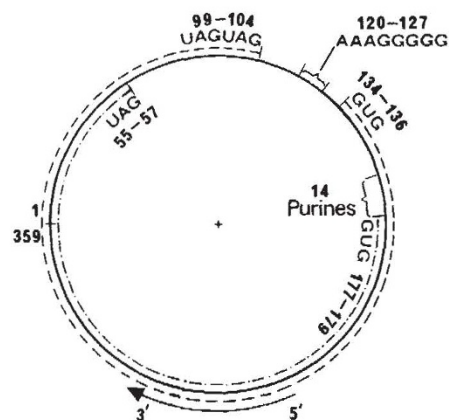

Fig. 1 Model of a PSTV RNA strand complementary to the viroid strand sequenced by Gross *et al.*[1]. The heavy line represents the circular RNA. The numbers 1 and 359 indicate the same start position as that used by Gross *et al.*, but because the strand represented here is antiparallel to the viroid strand, the position of base 1 in this diagram is equivalent to that of base 359 in the viroid sequence. Dashed line, polypeptide of MW 11,300; dotted-dashed line, polypeptide of MW 8,500.

In the light of the above evidence I suggest that viroids may be very small negative-strand viruses with the following properties. (1) They use secondary structure rather than a protein coat for protection of the genome; (2) they use a host polymerase to make a complementary RNA strand; and (3) this strand serves as a template for progeny viroid particles and as message for one or two viroid proteins. This hypothesis can be tested by a search in PSTV-infected tissues for one or two viroid-induced polypeptides of the predicted size and composition.

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