sequence data.

How are we to explain this clear discrepancy in apparent phylogenetic origin of cnidarian 5*S* and 18*S* rRNA sequences? The 18*S* sequences presumably should be more reliable indicators of organismic phylogenetic relationships, on the basis of a much greater number of nucleotides. However, as Field *et al.* emphasize, extreme differences in rates of nucleotide substitutions can obscure phylogenetic origins. There is no suggestion that the 5*S* rRNA cnidarian sequences diverged at a notably faster or slower rate than did the mean metazoan sequence (*7*). Figure 2 in the 18*S* analysis (*1*) indicates unusually short branches for the two cnidarian sequences relative to their presumed time of divergence (*8*). However, it is not clear how this might result in a major error in branching assignment for the cnidarian sequences. Typically there are many 18*S* and 5*S* rRNA genes in metazoans, as well as in other eukaryotes. Thus, the possibility presents itself that a relic minor 18*S* rRNA genotype was carried in the early metazoan lineage and became dominant in the cnidarian lineage. Alternatively, we might propose that the smaller 5*S* rRNA sequences of protocnidarian and protometazoan lineages converged. This would seem a fortuitous chance event. Could selection have been involved? Could lateral gene transfer between protocnidarian and protometazoan lineages or protocnidarian and protistan lineages have occurred? Until the apparent discrepancy between the 5*S* and 18*S* rRNA sequence analyses is resolved by data from other molecules or perhaps by a more illuminating phylogenetic analysis methodology, the significance of the finding that the 18*S* rRNA sequence data do not support a common phylogenetic origin of Cnidaria with other metazoans should be treated with caution.

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We read with interest the article by Katharine G. Field *et al.* (*1*). The authors constructed a phylogeny based on the comparison of the 18*S* ribosomal RNA sequence of a number of organisms. Particularly interesting is the conclusion that metazoans arose twice and independently from an early protistan ancestor. Cnidarians are inferred to have arisen from a branch that gave rise to fungi, ciliates, and plants, whereas the rest of the animals are said to have arisen from a separate branch. However, a number of other cellular, subcellular, and molecular characteristics that cnidarians share with other metazoans, but not with plants, fungi, or ciliates, render this conclusion unlikely.

Nervous systems composed of neurons are unique to animals. The nervous system of cnidarians, while not as complex as that of other metazoans, is made up of cells that are easily identifiable as neurons. In hydra, they have the typical morphology of interneurons or sensory cells (*2*). The ultrastructure of the chemical synapses formed by these neurons with other neurons and with the muscle processes of epithelio-muscular cells is similar to those found in many other animals (*3, 4*). The sensory cilium-stereociliary complex formed in sensory cells is also similar to that seen in vertebrate hair cells (*4*). The neurons express neuropeptides found in many metazoans [see, for example, (*5*)]. Additionally, a neuropeptide originally identified in hydra (*6*) is expressed in the nervous tissue of several mammals [see, for example, (*7*)].

Cnidarians have several subcellular structures with complex organization in common with other animals. As is typical of invertebrates, the occluding junctions between epithelial cells of, for example, hydra and Polyorchis, are septate junctions (*8, 9*). The ultrastructure of these junctions is identical to that in many invertebrates, as is their occurrence in circumferential bands around the apical ends of the epithelial cells.

Epithelial cells are also connected to one another by gap junctions that have the same ultrastructural features observed in many animals [see, for example, (*8, 9*)]. Further, they appear to have a similar function. Small fluorescent dyes (for example, Lucifer yellow), but not large ones (for example, fluoresceinated dextran) will pass from one epithelial cell to the next (*10*), which is typical of gap junction–mediated cell-to-cell communication. An antibody raised against rat liver gap junction protein recognizes a protein in hydra with the same molecular weight as that of the gap junction protein in many species of animals (*10*). When introduced into cells, the antibody specifically interrupts communication between epithelial cells (*10*). In hydra (*11*) and other cnidarians (*8, 12*), gap junctions have been observed between neurons and between neurons and muscle processes of the epithelial cells.

Even though there are no separate muscle cells in cnidarians, epithelial cells contain muscle processes in which the contractile elements are arranged in a manner identical to that in other metazoans. The circumferential swimming muscles of many medusae have the appearance of typical striated muscle found in other animals. The myofibrils exhibit the usual arrangement of sarcomeres with A-bands, I-bands, and Z-lines [see, for example, (*12, 13*)]. In hydra, the myofibrils of the epitheliomuscular cells have an arrangement similar to that of smooth muscle (*14*).

In addition to the molecules mentioned above that cnidarians share with other metazoans, two more are associated with animals but not with other organisms. Between the two epithelia of every cnidarian is a mesoglea, a basement membrane. The mesoglea of several cnidarians has been shown to contain collagen [see, for example, (*15*)]. Further, in the two instances where it has been analyzed, the number of glycosylated hydroxylysine residues is high, as is typical of collagens found in basement membranes (*15, 16*). Finally, it has been shown that all metazoans including cnidarians contain a tyrosine kinase that is immunoprecipitable by pp60$^{\mathrm{src}}$ antibodies (*17, 18*). Such a kinase is absent from all plants and unicellular organisms, including ciliates, examined (*17*). Recently, the *src* gene of hydra has been sequenced and found to have 65% homology with the *src* gene of chickens at the amino acid level (*19*).

Because the Cnidaria share these many characteristics with other metazoans, but not with fungi, ciliates, and plants, it is difficult to accept the proposed biphyletic origin of the cnidarians and the rest of the animals. The amount of convergent evolution that would have been required to explain the shared characteristics seems improbable. Thus, we feel the preponderance of the evidence indicates that it is more likely that the Cnidaria arose with the other metazoans, as is traditionally described.

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similar to the human protein (*6*). In addition, there are some striking molecular differences between cnidarians and other animals, including the structure of mitochondrial DNA. This is a very conservative feature in animal phyla, where it exists as a small circular genome. On the other hand, in hydra and other cnidarians the mitochondrial DNA is present as a linear DNA genome (*7*), as it is in ciliates and some other protists (*8*).

It is clear from our data that Cnidaria are very distant from other animals. We do not, however, argue forcefully for Cnidaria having an independent origin from other animals. The inferences drawn from the bootstrap analysis of 18*S* rRNA sequences discussed above indicate that these organisms should be placed either on a separate branch from true metazoans or very deep within the metazoan branch. We believe that the issue remains to be resolved. Although all of the data, both molecular and nonmolecular, taken together may agree best with a deep origin of Cnidaria within the metazoan clade (as a sister group to the Bilateria), the independent origin of Cnidaria is a possibility that must still be considered and further investigated by accumulation of additional sequence data, not only for rRNAs.

The inference of deep phylogenies from molecular sequence data is a new and exciting endeavor. The 18*S* rRNA sequence data have allowed us to address some important problems in metazoan phylogeny and to define the first large-scale molecular-based phylogenetic tree for this group. We have provided concrete answers to some major questions; we have revealed some major rapid radiations; and we have explored the strengths and limitations of using rRNA sequence data for resolving relationships among animal phyla. These results will hardly be the last word, but they both provide more focused questions and outline a new approach to systematics.

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