described (for example Roth and Nierhaus, *J. molec. Biol.*, in the press). But in contrast to the 30S particle, the 50S cannot be split into two well-defined halves, despite the fact that the 23S RNA is readily cleavable into an 18S and a 13S RNA (for example Allet and Spahr, *Eur. J. Biochem.*, **19**, 250; 1971). The finding by neutron scattering that the centres of mass of protein and RNA are widely separated in the 50S particle as opposed to the 30S could explain this difference (Moore, Engelman and Schoenborn, *Proc. natn. Acad. Sci. U.S.A.*, **71**, 172; 1974).

It has been known for some time that the 30S proteins interact with one another during *in vitro* reconstitution from protein and RNA in a very specific manner. These interactions have been incorporated into an 'assembly map' (see Held, Mizushima and Nomura, *J. biol. Chem.*, **248**, 5720; 1974, for the latest version). Although these interactions need not necessarily be a direct reflection of the protein neighbourhoods within the 30S particle, there has been striking agreement between those proteins which are found together in cross-linked pairs or ribonucleoprotein fragments and those which are related in the assembly map. It seems reasonable therefore to conclude that most if not all of the assembly interactions are indeed direct reflections of the ribosomal topography. The question of whether all the proteins in the complete particle have substantial contact with the RNA has yet to be settled, and it has been suggested that it may be more appropriate to think of the assembly interactions as being between regions of ribonucleoprotein as opposed to simply interactions between proteins (Kurland, *J. supramolec. Struct.*, **2**, 178; 1974).

There is of course as yet no corresponding assembly map of the 50S particle, since a successful total reconstitution of the *E. coli* 50S particle has only recently been achieved (Nierhaus and Dohme, *Proc. natn. Acad. Sci. U.S.A.*, **71**, 4713; 1974). Some assembly interactions have however been determined, using protein-deficient core particles as the starting point (Highland and Howard, *J. biol. Chem.*, **250**, 831; 1975).

Differential reactivity to chemical reagents has been used by many workers as a probe of ribosomal topography, the assumption being that those proteins which are most exposed on the ribosome surface will react most strongly with a particular protein reagent. Among the methods used have been digestion with trypsin, or reaction with kethoxal, various aldehydes and N-ethyl maleimide. Interpretation of the results of such experiments is however rather complex, since exposure or lack of exposure of a particular reactive group is not necessarily a reflection of the protein topography in the wider sense. A reactive group on a protein could be shielded by RNA, or by the tertiary structure of the protein itself. Further, it is not easy to predict how far a chemical reagent can penetrate into the ribosome, and it is therefore not surprising that the degree of agreement between the various results is not very high. A good summary of the recent data can be found in a paper by Benkov and Delihas (*Biochem. biophys. Res. Commun.*, **60**, 901; 1974). At present, data from reactivity towards very large reagents are more easy to interpret, and two methods are noteworthy in this context. The first of these is measurement of the accessibilty to protein-specific antibodies (for example Stöffler *et al.*, *Molec. gen. Genet.*, **127**, 89; 1973), and the second is the iodination of ribosomal proteins catalysed by lactoperoxidase, of which a recent example is the work of Litman and Cantor (*Biochemistry*, **13**, 512; 1974). The general conclusion from all these methods is that all 30S proteins have some accessible groups on the ribosome surface, whereas the 50S proteins are not so readily accessible.

Several groups have attempted to coordinate the available data into three-dimensional models of the protein arrangement of the 30S particle. In all these models, the proteins have been represented as spheres, and the authors have been careful to point out that the arrangements are only schematic, and serve mainly as a means of testing the self-consistency of the various data. A technique has, however, recently been developed which casts doubt on the whole validity of even this crude type of model building: the direct visualisation of the proteins by electron microscopy of complexes formed between ribosomal sub-particles and protein-specific immunoglobulins. This technique has become possible since both sub-particles have a readily recognisable shape in the electron microscope. Thus, if the ribosome is treated with a single protein-specific antibody, a ribosome–antibody–ribosome complex is formed, with the Fab arm of the antibody attached to a point on the ribosome surface. Several proteins have been localised on the surface of both sub-particles by this method (for example Tischendorf, Zeichhardt and Stöffler, *Molec. gen. Genet.*, **134**, 187; 1974), but the most important feature of the results is that while some proteins show a single surface binding site for their cognate antibodies, others seem to have multiple binding sites over a wide area of the surface, for example protein S4 (Lake, Pendergast, Kahan and Nomura, *Proc. natn. Acad. Sci. U.S.A.*, **71**, 4688; 1974). This indicates that the conformation of the proteins within the ribosomal particle is variable, and can be highly extended, which, as implied at the beginning of this article, alters the whole conception of the ribosomal topography, and rather changes the interpretation which must be made of many other data (such as the protein cross-linking results). In this context it should, however, be borne in mind that the overall dimensions of the 30S particle as measured by electron microscopy differ significantly from those estimated by low angle X-ray scattering in solution (Hill and Fessenden, *J. molec. Biol.*, **90**, 719; 1974).

In conclusion, the topography problem is still obviously some way from complete solution, but it is encouraging that the techniques in current use are by no means exhausted; further rapid progress can therefore be expected.

Devonian arthrodires

from B. G. Gardiner

A. RITCHIE'S article (see this issue of *Nature*, page 569) on Devonian arthrodires is a painstakingly compiled record of the distribution of the genus *Groenlandaspis*. He has shown that—like some other arthrodires (including *Bothriolepis*, *Holonema*) — *Groenlandaspis* is found in Devonian deposits all over the world and pleasingly has confirmed that the poorly known *Coccosteus disjectus* from Ireland and Bristol is yet another species of *Groenlandaspis*.

The distribution of *Groenlandaspis* will certainly excite palaeogeographic interest, but it is dangerous to jump to hasty conclusions about continental drift from such evidence and Ritchie's caution is amply justified. As yet there is no articulated theory to enable us to deal with the zoogeography of Devonian fishes and so the significance of their distribution, which has been a puzzle for many years, remains an enigma. For most groups of fishes this will only be resolved when we have a clear picture of the configuration of the continents in the Devonian. But in the case of arthrodires, an entirely fossil group, an even more critical component is missing. For them we lack an acceptable phylogeny, a vital factor because palaeozoogeography can only make sense as the evolution of organisms in space and time.