

They are in entirely different categories, as I have shown<sup>2-4,9</sup>. One should not (and here I also think of electron microscopists) apply conclusions drawn from observations on spirillums and vibrios to the flagella of typhoid, *Proteus* and *subtilis* bacteria. In this letter I shall try to confine myself to a discussion of the latter bacteria. Weibull also mentions Fleming's experiments on penicillin-poisoned *Proteus* bacteria. I have repeated these experiments and made a film of them and find them inconclusive. I think these grotesque movements are more readily explained by bodily contortions. If flagella could perform in this way, they would require an elaborate system of co-ordination, something like a central nervous system.

Weibull agrees with Reichert's interpretation of the mechanical function of flagella. I have often pointed out<sup>2-4,6,7,10-12</sup> that Reichert never saw normal flagella functioning, at least not in typhoid and *Proteus* and suchlike bacteria. He himself states that he could only make their flagella visible with his darkground technique by suspending them in a colloidal solution. He imagined that the colloid just retarded motion and had an effect on refraction; but in reality, as I have repeatedly shown, it became adsorbed on the bodies and flagella, just like *H*-serum. What Reichert studied were live artefacts. Weibull's own *Proteus* flagella, coming from an agar medium and therefore growing in a colloidal medium, during growth are also covered with a sheath of agar. Weibull evidently does not know of and under-rates *sunlight* darkground microscopy. It is only with *sunlight* darkground microscopy that I succeeded in making *naked* flagella and tails properly visible in broth or water<sup>2,11-14</sup>. By this technique, one can see the naked thin tail split into numbers of very thin flagella; this is entirely different from the picture on which Reichert and Weibull have worked.

With this *sunlight* darkground method<sup>15</sup> I have made further observations on the function of normal, that is, not artificially thickened, tails and their constituent flagella. There is the sudden reverse, the semi-somersault, the possibility of shaking off flagella by mechanical means after which swimming goes on undisturbed, the curious fact that the same bacterium will produce magnificent tails in one broth and none in another while motility is identical in both, and the definite spiral movement and shape of bacterial bodies (sometimes hidden by their high speed and then made visible by slow-motion filming). These studies, extending over twenty years, make it impossible for me to regard flagella as motor organs<sup>2-16</sup>.

As a result of X-ray diffraction analysis of his flagella from *Proteus* and *subtilis* bacteria, Weibull places their proteins in the fibrous protein group, which comprises keratin and myosin. Chemical analysis gave him a low cystine and a high lysine content. This would fit in much better with myosin than with keratin. But chemical analysis of flagella from typhoid bacteria undertaken in my Department showed high cystine and low lysine content<sup>17</sup>. This would place flagella in the keratin group. I find it difficult not to consider that perhaps we are all analysing our respective nutrient media and not so much the flagella.

Weibull says the source of energy of flagella is obscure. This is not the only obscurity. Supporters of the motor theory of bacterial flagella do not commit themselves readily as to the origin of flagella.

If they start in the protoplasm they must pierce the cell wall. In the case of peritrichous bacteria such as *Proteus*, this would mean dozens of holes. When are the new holes made, before or after cell division? After piercing the wall, the flagella must bend at right angles, run along the cell wall in close apposition, and at the end of the bacterium they must twist round one another to form a tail, which performs spiral movement. The mechanical implications of such an arrangement are extraordinary, and sudden reverses and semi-somersaults must cause awkward complications. If, on the other hand, the flagella arise outside the cell wall and yet are active motor organs, it follows that bacteria must have live active protoplasm both outside and inside the cell wall. These two masses of protoplasm evidently cannot directly communicate with one another and this creates an entirely novel situation in biology. The mechanical implications here are too formidable. My theory at least does away with difficulties of this kind. I do not claim that it is the last word on bacterial motility.

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<sup>1</sup> Weibull, C., *Nature*, **167**, 511 (1951).

<sup>2</sup> Pijper, A., *J. Path. Bact.*, **58**, 325 (1946).

<sup>3</sup> Pijper, A., *J. Bact.*, **57**, 110 (1949).

<sup>4</sup> Pijper, A., and Nunn, A. J., *J. Roy. Micr. Soc.*, **69**, 138 (1949).

<sup>5</sup> Pijper, A., in "The Nature of the Bacterial Surface" (Blackwell, Oxford, 1949).

<sup>6</sup> Pijper, A., *Schw. Z. Pathol. u. Bakt.*, **12**, 681 (1949).

<sup>7</sup> Pijper, A., *J. Path. Bact.*, **47**, 1 (1938).

<sup>8</sup> Pijper, A., *J. Bact.*, **42**, 395 (1941).

<sup>9</sup> Pijper, A., *Science*, **109**, 379 (1949).

<sup>10</sup> Pijper, A., *Z. Bakt., I. Orig.*, **118**, 113 (1930).

<sup>11</sup> Pijper, A., *Z. Bakt., I. Orig.*, **123**, 195 (1931-32).

<sup>12</sup> Pijper, A., *J. Biol. Phot. Assoc.*, **8**, 158 (1940).

<sup>13</sup> Pijper, A., a motion picture of bacterial shape and motility (Pretoria, Wallachs, 1947).

<sup>14</sup> Pijper, A., *Nature*, **161**, 200 (1948).

<sup>15</sup> Pijper, A., *S. Afr. J. Sci.*, **46**, 296 (1950).

<sup>16</sup> Pijper, A., *J. Bact.*, **53**, 257 (1947).

<sup>17</sup> Unpublished observations.

As any reader of Pijper's many works on bacterial flagella will soon discover, his opinions on this subject have changed considerably during the years. In the work from 1947, cited by me, bacterial flagella are described as "lifeless mucous twirls" or "polysaccharide twirls".

That the flagella of *Proteus vulgaris* are not mucous twirls or polysaccharide twirls is clear from chemical analyses and from X-ray investigations. It should suffice to mention their nitrogen content (16 per cent), and the near absence of carbohydrate (less than 0.2 per cent). From this it follows also that the *Proteus flagella*, prepared by me, are obviously not covered by a sheath of agar, as Pijper says.

As to the question of their role as motor organs, an excellent review of the different opinions on this matter is found in ref. 3. I am still convinced that the experiments of Ørskow, Kauffmann, Kingma Boltjes, Fleming, and others, carried out by independent methods, show that they are active motor organs.

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<sup>1</sup> Weibull, C., *Biochim. Biophys. Acta*, **3**, 379 (1949).

<sup>2</sup> Astbury, W. T., and Weibull, C., *Nature*, **163**, 280 (1949).

<sup>3</sup> "The Nature of the Bacterial Surface" (Blackwell, Oxford, 1949).