

## On the Shape of the Golgi Bodies in Invertebrate Eggs.

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IN a recent paper<sup>1</sup> Professor Gatenby mentions that at the Second International Cytological Congress held at Cambridge several scientists expressed grave doubts about the existence of the Golgi apparatus as a permanent cell component. Though I have not come across any recent paper expressing such doubts, the attempt of Dr. Gatenby in trying to establish the presence of the Golgi apparatus once again in his paper reflects that even after 38 years after its discovery there exists a body of scientists which does not believe in its existence. After a perusal of the papers of Strangeways and Canti,<sup>2</sup> Walker and Allen,<sup>3</sup> Tennent, Gardiner and Smith<sup>4</sup>, I have been attempting to analyse the probable reasons for this disbelief. Ever since the discovery of the apparatus there has been a lack of unanimity of opinion even on major questions. The points in dispute have varied from time to time. Golgi and his pupils believed that the apparatus should necessarily have a reticular structure. This was shown to be an error by Weigl who with his co-workers demonstrated that in invertebrates the apparatus has the form of discrete bodies. Gatenby and Bowen demonstrated the duplex structure in invertebrates and Bowen after a wide search came to the conclusion that there is no representative of the idiosome of the discrete bodies in relation with the network. Parat and his collaborators from vital staining experiments came to the conclusion that the Golgi apparatus as seen after silver and osmic technique was

an artifact and that the real Golgi apparatus was the neutral red staining vesicles or bodies to which the name 'Vacuome' was applied. Thus so many unsolved problems have arisen that grave doubts have been engendered in the minds of some scientists. The best course to adopt in the circumstances is to attempt to fill up the gaps in the existing knowledge regarding the apparatus. I believe that uncertainty about the following points has been responsible for the scepticism expressed. (1) Is there any relation between the various shapes of the apparatus found in invertebrates and is there any possibility of deriving one from the other? (2) Is the network found in vertebrate somatic cells derived from the discrete bodies of invertebrates and, if so, what is the fate of the chromophobic or idiosomic region? (3) What is the function of the Golgi apparatus in all types of cells? (4) Is there any relation between the Golgi apparatus and the Vacuome? Unless these problems are solved there will exist cause for scepticism.

In this communication I shall try to deal with one of the questions raised and analyse the various shapes of the Golgi apparatus described in the eggs of various invertebrate animals and attempt to interpret these shapes in the light of a common basic procedure. Cytologists working on the phenomena of oogenesis have ignored many of the suggestions of the students in other branches of the study, especially that of Bowen.<sup>5</sup> This lack of a clearer understanding of the shape of the Golgi apparatus in oogenesis is reflected even in reviews on the subject. Hence, I shall attempt to put all the available facts into a connected whole taking into consideration the already

<sup>1</sup> Gatenby, J. B., *Quart. Journ. Micr. Sci.*, 1936, **78**, 387-397.

<sup>2</sup> Strangeways, T. S. P., and Canti, R. G., *Quart. Journ. Micr. Sci.*, 1927, **71**, 1-14.

<sup>3</sup> Walker, C. E., and Allen, M., *Proc. Roy. Soc. London, (B)*, 1927, **101**, 468-483.

<sup>4</sup> Tennent, D. H., Gardiner, M. S., and Smith, D. E., *Carnegie Instn. Wash. Pubn.*, 1931, **27**, No. 413.

<sup>5</sup> Bowen, R. H., *Quart. Journ. Micr. Sci.*, 1926, **70**, 75-113, 193-217, 395-451.



established knowledge in spermatogenesis and secretory phenomena.

In the earliest oocytes of some animals the Golgi apparatus is said to occur as a mass without any differentiation into an osmiophilic region and an idiosome. In some other early oocytes as well as in growing ones the apparatus has been described in a variety of ways. Granular, vesicular and batonette shapes are commonly referred to. In the ring and batonette shapes differentiation into chromophilic and chromophobic regions have been observed. The question arises whether all these could be derived from the Golgi mass without any differentiation into osmiophilic and osmiophobic regions or whether the shape is fixed. Curiously enough Nath<sup>6</sup> and Harvey<sup>7</sup> seem to consider that the shape is fixed. Nath in the earliest oocytes of scorpions<sup>8</sup> described "a few clearly-defined curved rods lying on one side of the nucleus". But in *Culex*,<sup>9</sup> *Dysdercus*,<sup>10</sup> *Periplaneta*<sup>11</sup> and *Pheretima* he describes vesicles and especially in *Pheretima* he attempts to interpret the various other shapes that he observed as caused by improper fixations and optical sections. In a recent paper<sup>12</sup> he mentions that the Golgi apparatus is polymorphic, but I have not been able to make out whether that applies to oogenesis also.

Harvey, on the other hand, considers that there can only be one form of Golgi apparatus in invertebrates and that resembling the dictyosomes. He had previously described in the oogenesis of *Ciona intestinalis*<sup>13</sup> the Golgi apparatus occurring as "argentophil vesicles and irregular masses" but in a recent paper he has ignored his previous results. The reason for such a procedure becomes apparent when he remarks, while criticising Nath's work, that "there can be no connecting link between these vesicles

and the net-like Golgi apparatus characteristic of vertebrate cells which is the fundamental absolute to which all questions of the form of Golgi apparatus must ultimately be referred". Thus the very existence of the other shapes recorded are questioned. In this he does not attempt to interpret or refer to similar shapes observed by other workers in spermatogenesis and secretory cells of both vertebrates and invertebrates.

That hollow spheres have an existence could be made out from the fact that the main reason of Hirschler<sup>14</sup> for postulating an "apparatinhalt" was that in the case of hollow Golgi spheres the central contents could not possibly be the same as the external cytoplasm. Hirschler had described the Golgi apparatus in the eggs of *Ciona intestinalis* as having ring and half-ring shapes. Gatenby<sup>15</sup> records in some Lepidoptera batonettes becoming converted into rings. Beams and Goldsmith<sup>16</sup> in the salivary gland cells of *Chironomus* present photomicrographic evidence of ring and half-ring shapes occurring side by side. Finally, Bowen's<sup>17</sup> figures of the acroblast and the Golgi remnant in *Euschistus euschistoides* show that in the case of the dictyosome shaped like a U, sections in some particular planes produce rings as the Golgi body necessarily has three dimensions.

It is quite possible as my experience has shown,<sup>18,19</sup> that in some eggs the shape is fixed throughout oogenesis. But that fact alone does not entitle one to define the shape of the Golgi bodies as fixed in all types of eggs. Variations in the shapes of the network—like Golgi apparatus of vertebrate somatic cells led Bowen<sup>20</sup> to conclude that the Golgi apparatus may assume any shape, the reticulum or network being only one expression of its protean appearance. How different is this conception from that of Nath and Harvey!

The Golgi apparatus of secretory cells and spermatocytes is in no way different from

<sup>6</sup> Nath, V., *Quart. Journ. Micr. Sci.*, 1930, **73**, 477-507.

<sup>7</sup> Harvey, L. A., *Proc. Roy. Soc. London*, (B), 1931, **107**, 414-441-455.

<sup>8</sup> Nath, V., *Proc. Roy. Soc. London*, (B), 1925, **98**, 44-58.

<sup>9</sup> Nath, V., *Zeit. zellf. mikr. Anat.*, 1929, **8**, 655-690.

<sup>10</sup> Bhandari, K. G., and Nath, V., *Zeit. zellf. mikr. Anat.*, 1930, **10**, 604-624.

<sup>11</sup> Nath, V., and Mohan, P., *J. Morph.*, 1929, **48**, 253-279.

<sup>12</sup> Nath, V., *Quart. Journ. Micr. Sci.*, 1933, **76**, 129-143.

<sup>13</sup> Harvey, L. A., *Proc. Roy. Soc. London*, (B), 1927, **101**, 136-162.

<sup>14</sup> Hirschler, J., *Arch. mikr. Anat.*, 1918, **91**, 140-182.

<sup>15</sup> Gatenby, J. B., *Quart. Journ. Micr. Sci.*, 1917, **62**, 407-465.

<sup>16</sup> Beams, H. W., and Goldsmith, J. B., *J. Morph.*, 1930, **50**, 497-517.

<sup>17</sup> Bowen, R. H., *Biol. Bull.*, 1920, **39**, 316-359.

<sup>18</sup> Subramaniam, M. K., *Proc. Ind. Acad. Sci.*, 1934, **1**, 6, 291-316.

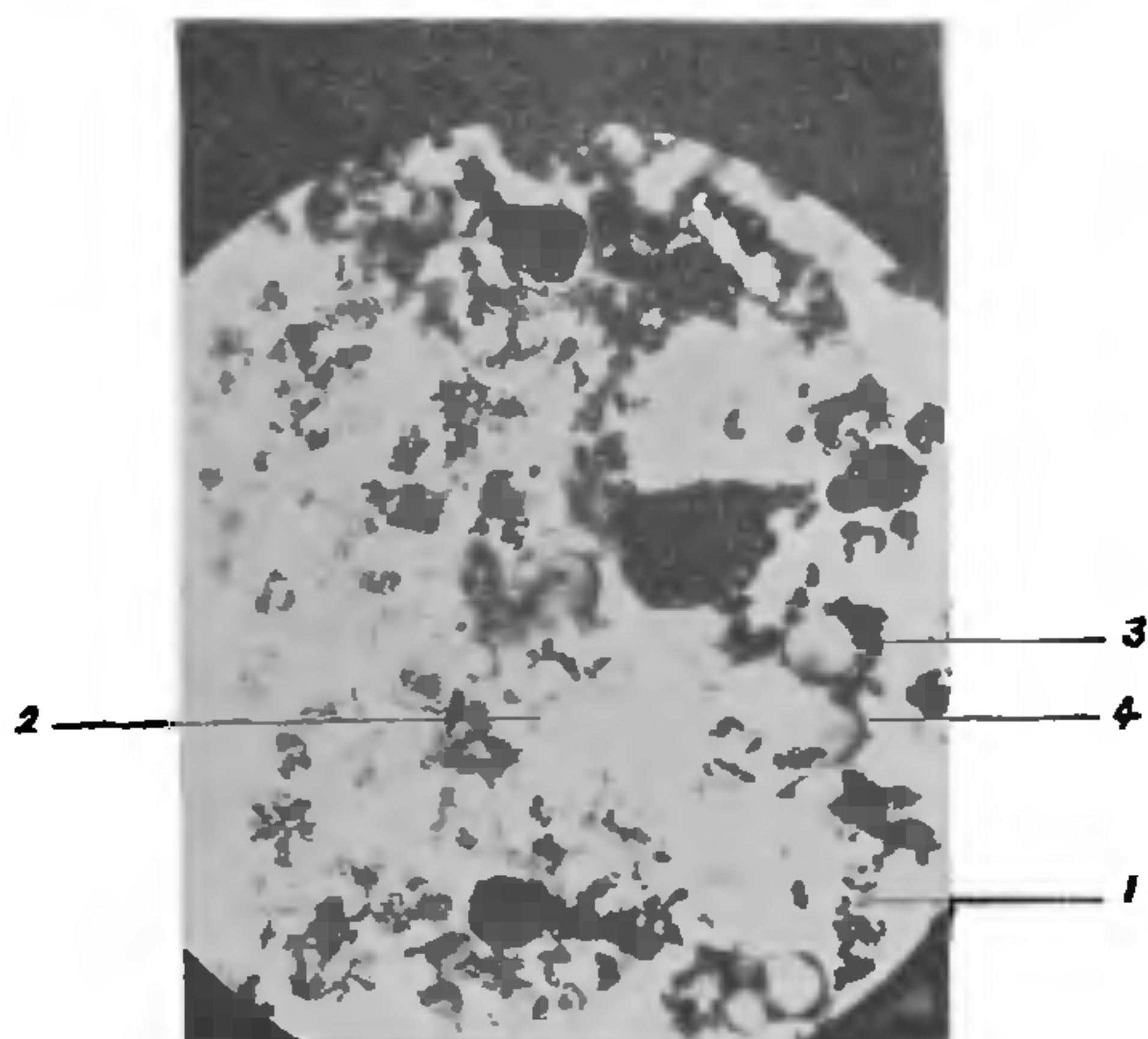
<sup>19</sup> Subramaniam, M. K., and Gopala Aiyar, R., *Proc. Ind. Acad. Sci.*, 1936, **3**, 3, 175-195.

<sup>20</sup> Bowen, R. H., *Anat. Rec.*, 1926, **32**, 151-193.



A portion of *Clibanarius* egg showing the various stages mentioned in text.

Nassonov  $\times 1,800$

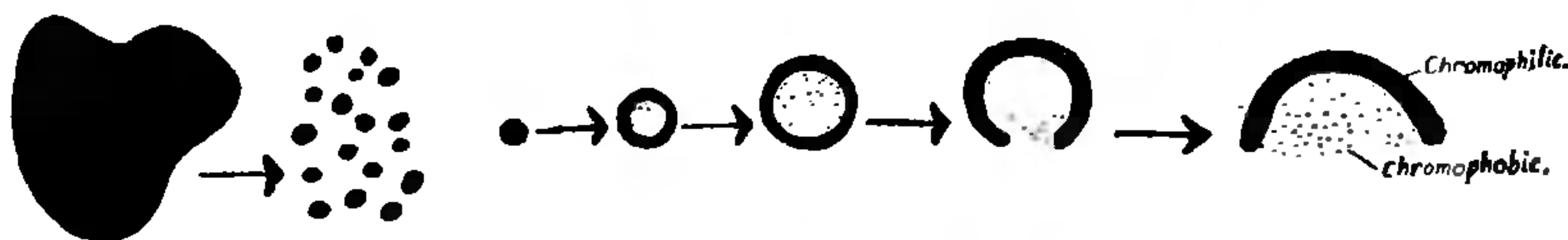


1. Golgi grain. 2. Golgi vesicle. 3. Rupture of vesicle. 4. Batonette.

that I have found between a mass and a typical batonette.

In the eggs of *Clibanarius*<sup>21</sup> and *Stomopneustes*<sup>22</sup> granules, vesicles and batonettes occur side by side at certain stages. But from their order of appearance and from the fact that no case of a *de novo* origin has ever been noted by me or others and also from the occurrence of distinct and unmistakable intermediate stages, I believe it will be interesting if all the stages could be demonstrated in a single photomicrograph and thus the position cleared, in regard to the inter-relationship of the various shapes at the same time.

My own conception of the batonette formation is this. The Golgi mass occurring in the earliest oocyte breaks up into a number of granules in which, as in the mass itself, there is no chromophobic component. These granules when they enlarge into vesicles become differentiated into osmiophilic and osmiophobic regions. Rupture of the vesicles takes place resulting in the formation of a



*Golgi mass*  $\rightarrow$  *Grains*  $\rightarrow$  *Vesicles*  $\rightarrow$  *Rupture of vesicle*  $\rightarrow$  *Batonette*.

those found in the various other tissues of the body because it is the Golgi bodies in the eggs which give rise by division and distribution to the Golgi apparatus of all the cells in the body. Hence we are faced with the question how the Golgi bodies having the same origin can be assigned different shapes in different cells. Either the diversity of shape should be accepted or a *de novo* origin of the Golgi apparatus in different cells should be proved. The latter possibility being negligible the only recourse will be to accept the former one. If the diversity of shape is accepted, naturally there should be intermediate stages between the Golgi mass, granules, vesicle, batonette and the network. Leaving the origin of the network for a later communication I shall consider here the nature of the intermediate stages

batonette in which the idiosome is in relation with the cytoplasm. In the photomicrograph and the accompanying text-figure my conclusions are given in a pictographic manner.

It is true that such a regular series of stages leading from the Golgi mass to a typical batonette is of rare occurrence and hence extreme caution is necessary in coming to conclusions. It seems that the more one learns about the shape or function of the Golgi bodies, the more evident does it become that its shape or function at first described in many patterns is gradually resolved into numberless variations of a single basic procedure.

<sup>21</sup> Subramaniam, M. K., *Journ. Roy. Micr. Soc.*, 1935, 12-27.

<sup>22</sup> Subramaniam, M. K., and Gopala Aiyar, R., *Zeit. Zell. mikr. Anat.*, 1936, 24, 4, 576-584.