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Original Research

The Centrosomes of Haploid and Diploid Cells Have an Equal Number of Centrioles in the Parasitoid Wasp *Anisopteromalus Calandrae*

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Abstract

Background: The centrosome is the main center of the organization of microtubules (MT) in the cell, the origin for the formation of flagella and cilia, as well as the site of many regulatory intracellular processes. In diploid cells, the centrosome includes two centrioles connected to some additional structures and surrounded by pericentriolar material. **Methods**: The ultrastructure of the cells was studied using transmission electron microscopy on serial ultrathin sections. **Results**: Here, using transmission electron microscopy on a complete series of ultrathin sections of the centrosome region, we studied the relation between the number of centrioles and ploidy in diploid cells of female wasps and haploid cells of male in the parasitoid wasp *Anisopteromalus calandrae* (Hymenoptera). It showed that the haploid cells of the male insect have the same number of centrioles as the diploid cells of the female. **Conclusions**: It can be concluded that there is no strict correlation between the number of chromosome sets (ploidy) and the number of centrioles in haplodiploid insects.

Keywords: insects' ultrastructure; centriole; centrosome; Hymenoptera; haploid somatic cells

1. Introduction

Many subtle details of the centrosome structure and function are well characterized [1,2]; however, some fundamental questions on centrosomal biology remain completely unexplored [2,3]. One such issue is the nature of the appropriate number of centrioles in relation to the cell ploidy, i.e., the number of chromosome sets.

Moreover, in some somatic cells, in which natural spontaneous polyploidization takes place, such as megakaryocytes and hepatocytes, the number of centrioles increases as a multiple of ploidy [4,5].

There are several situations where the correlation between the number of centriolar cylinders and ploidy is disrupted. The most notable is the formation of tens or even hundreds of centriolar cylinders in ciliary epithelial cells [6,7]. The formation of many centriolar cylinders also occurs when the cell recovers after centriole destruction by laser microirradiation [8]. In giant cells of the insect *Chironomus cingulatus* (Diptera) salivary glands with polytene chromosomes, which significantly multiply the ploidy of cells, centrioles are nevertheless completely absent [9].

Of special note is the centriole formation in generative cells, in which they can be completely lost (oocytes) or be presented in an amount greater than chromosomal sets—haploid early spermatids in insects and humans have two centrioles [10–13]. In wasps, in the basal body of a mature sperm, the centriole is replaced by a structure that does not contain microtubules (MT), but retains ninth-order symmetry—a "cogwheel structure" [14,15]. The cogwheel structure consists of nine beak-shaped electron-dense "prongs", which can be located in the insects' centriole wall between triplets or doublets of microtubules. The structure of centrioles in the somatic cells of wasp larvae has been described also, whereby these prongs form the centriole wall without microtubules [15].

In humans, like in most mammals, excluding rodents, one proximal centriole is retained in mature spermatozoa, and the distal centriole is replaced by a funnel-shaped structure consisting of doublets of microtubules [16]. In rodents, both centrioles are reduced in mature sperm [17,18].

Diploidy of somatic cells in adult animals seems to us as "natural" and is perceived as something taken for granted. Actual haploid organisms can be much less resistant to any environmental impacts that could damage the integrity of the genetic material (radiation, chemical mutagens, etc.) [19,20]. In *Habrobracon* wasps, it was directly shown that haploid male larvae and pupae were more ra-

diosensitive than diploid female ones [21]. Therefore, in the course of evolution, the haploid stage of development became as short as possible; although other less highly organized organisms such as dictyostelid slime molds, and some green algae are haploidic in the somatic stage [22].

Such organization of the life cycle with alternating diploid and tetraploid cell ploidy fits so well with the principle of "reasonable sufficiency" that it is difficult to imagine that it could be any other way. The same principle extends to the process of centrioles' "reproduction". Nevertheless, extending this logic to the centrioles' "inheritance" is not entirely correct.

It should be noted that only one centriole appears initially in a diploid cell during the formation of *de novo* (i.e., not on pre-existing old centrioles) centrioles in the early development of mice. Only later, the typical ratio between cellular ploidy and the number of centrioles is formed [23,24].

The insect order Hymenoptera, which includes wasps, ants, and bees, is characterized by a mode of reproduction called haplodiploidy, whereby unfertilized eggs develop into haploid males and fertilized eggs develop into diploid females [25,26]. Since all the cells of the male are haploid, during the process of meiosis, one spermatocyte produces not four, as in diploid organisms, but two spermatids, due to the so-called abortive meiotic division, as was previously described in the bees *Apis mellifera L.* [27]. Our study of spermatogenesis in the wasp *Cotesia congregata* showed that the early spermatid has two centrioles [15]. During spermiogenesis, one of the centrioles forms a flagellum, and the second migrates to the central zone of the syncytium through cytoplasmic bridges and thus is not retained in the spermatozoon [15]. A similar observation was made for the wasp *Nasonia vitripennis*, closely related to *Anisopteromalus calandrae* [28]. Thus, during spermiogenesis, parasitoid wasps are characterized by a later removal of the second centriole. For somatic cells of haploid males, the structure of the centrosome has not been previously studied.

In this study, we analyzed the structure and number of centrioles present in somatic haploid male cells of the parasitoid wasp *Anisopteromalus calandrae* (Hymenoptera, Pteromalidae) to answer the question of a link between the cell ploidy and the number of centriolar cylinders.

2. Materials and Methods

2.1 Insects' Development

Male pupae were obtained from egg laying of virgin *Anisopteromalus calandrae* females on their host *Callosobruchus maculatus* (Coleoptera, Bruchidae), which is a pest in leguminous seed stocks. Female pupae were obtained from fertilized females; the sex of the insect is visible at the pupal stage. The parasitoid wasp develops outside of its host, allowing the observation of the whole development. Standard laboratory breeding occurred at 27 °C. Insects were collected at the surface of their host and fixed for electron microscopy.

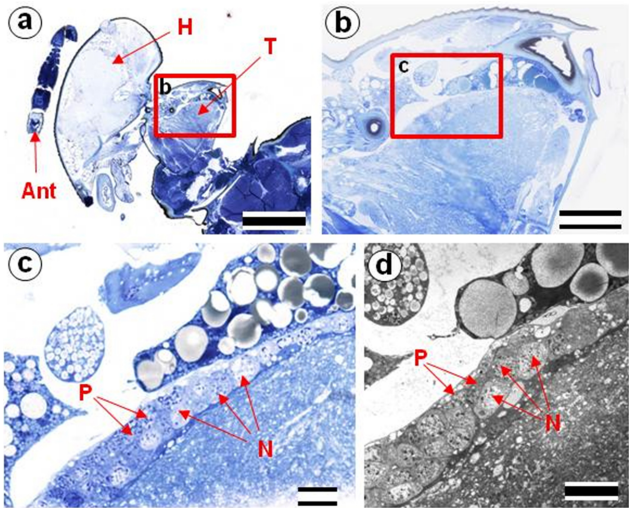

Fig. 1. Location and morphology of the cells of the dorsal part of the prothoracic ganglion of the female *Anisopteromalus calandrae*. (a) Semi-thin section through the head and thoracic region of the wasp at low magnification. (b) Semi-thin section of the thoracic region. (c) Semi-thin section of a section of the thoracic region with cells of the prothoracic ganglion. (d) One of the ultra-thin sections after the semi-thin section shown in the previous photo with cells of the prothoracic ganglion. Ant, antenna of wasp; H, head of wasp; N, nucleus of neurons; P, perineural cells; T, thorax of wasp. Scale bar: (a)—200 µm; (b)—50 µm; (c,d)—10 µm.

2.2 Transmission Electron Microscopy

All samples were fixed through incubation for 48 h in a mixture of 2% paraformaldehyde and 2% glutaraldehyde in 0.1 M cacodylate buffer (pH 7.4) with 0.1 M sucrose. Samples were then post-fixed by incubating for 1 h in 2% osmium tetroxide in 0.1 M cacodylate buffer (Electron Microscopy Science, Hatfield, PA) with 0.1 M sucrose.

Samples were washed in 0.1 M cacodylate buffer (10 min) and water (3 × 10 min), dehydrated in a graded series of ethanol solutions (50% for 2 × 10 min, 70% for 3 × 15 min, 90% for 3 × 20 min, 100% for 3 × 20 min) and propylene oxide (100% for 3 × 20 min), and embedded in Epon resin (Sigma), which was allowed to polymerize (24 h at 37 °C, 48 h at 60 °C). Semi-thin sections (500 nm thick) were cut with a "Leica Ultracut UCT" ultramicrotome, stained with toluidine blue for 30 s at 60 °C, washed with distilled water for 5 s, 100% ethanol for 10 s, and again with distilled water for 20 s. Later, they were dried at 60 °C and embedded in Epon resin that was allowed to polymerize for 48 h at 60 °C. These sections were used for the cor-

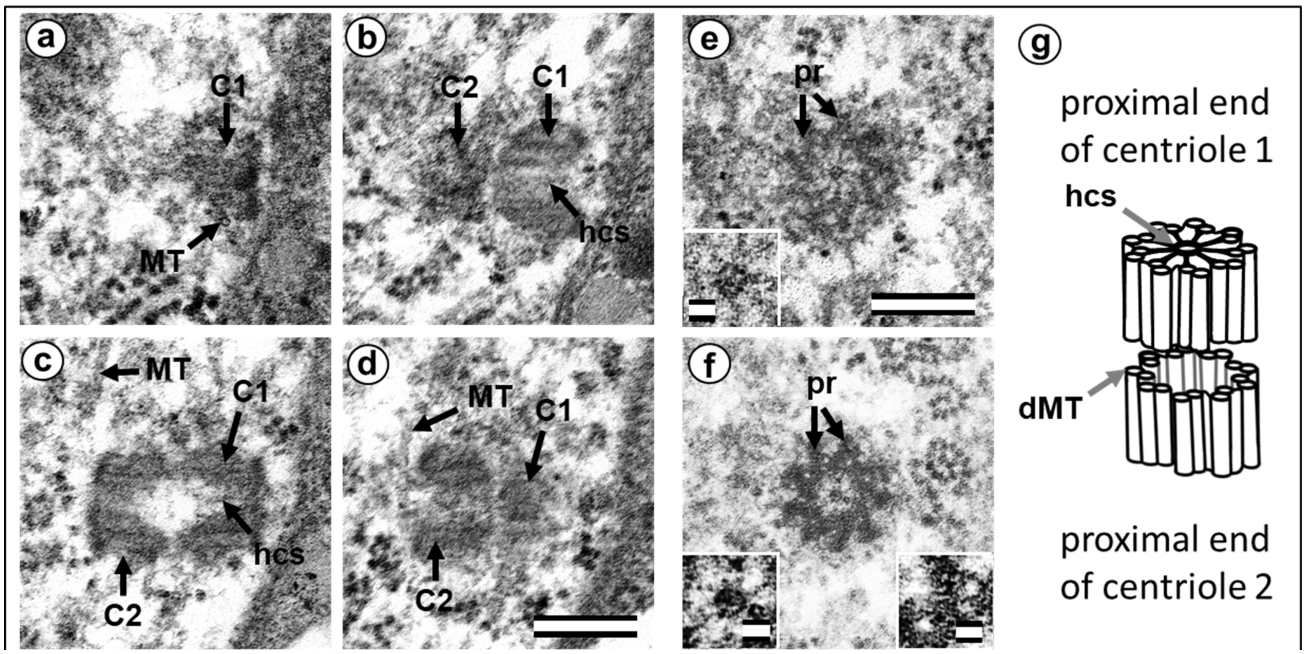

Fig. 2. Centrosome structure of the *Anisopteromalus calandrae* female cells. (a–d) Four consecutive serial sections of the centrosome of a neuron of the dorsal part of the prothoracic ganglion in the longitudinal direction. (e,f) Two consecutive serial sections of the centriole of the perineural cell of the dorsal part of the prothoracic ganglion in the perpendicular direction. (g) Schematic diagram of the centrosome structure. It should be noted that the direction of twist of microtubules (MT) doublets in centrioles 1 and 2 is opposite, since centriole 1 is shown from the proximal end, and centriole 2 from the distal end; prongs of cogwheel structure and the ligaments between the two centrioles are not shown in the diagram. C1, centriole 1; C2, centriole 2; dMT, MT doublets of the centriole wall; hcs, hub of cartwheel structure in the internal lumen of centriole; MT, cytoplasmic MTs; pr, prongs of cogwheel structure. Insertion in (e)—cartwheel structure at high magnification; left insertion in (f)—cartwheel structure at high magnification; right insertion in (f)—centriole wall at high magnification with doublets of MT. Scale bar for (a–f) is 200 nm, for insertions 20 nm.

rect preparation of the analysis zone during the ultrastructural study. The serial ultrathin sections (70 nm thick) were cut with a "Leica Ultracut UCT" ultramicrotome (Leica Microsysteme GmbH, Wien, Austria), placed on electron microscopy nickel one-slot grids (EMS2010-Ni, Electron Microscopy Science, Hatfield, PA, USA) coated with Formvar film, and stained with 5% water solution of uranyl acetate (20 min) and lead citrate (5 min). The sections were observed at 100 kV with a JEM1011 transmission electron microscope (JEOL, Tokyo, Japan) connected to a Gatan digital camera operated on Digital Micrograph software (GMS 3, Pleasanton, CA, USA) for image acquisition and analysis.

3. Results

3.1 Centrioles in Diploid Female Somatic Cells of Anisopteromalus Calandrae

The structure of the centrosome in somatic cells of female *Anisopteromalus calandrae* has been studied in 17 neurons and perineural cells of the dorsal part of the prothoracic ganglion (Fig. 1). Two centrioles of about 200 nm in diameter and about 170 nm long were found in each cell (Fig. 2). These centrioles were connected with their distal ends, their mutual orientation was collinear (Fig. 2c). Thus, the microtubules of their walls were parallel to each other, but had opposite polarity; this orientation is usually called antiparallel.

There was always a clearly visible gap between the hub of cartwheel structure (structure based on nine dimers of the SASS6 protein laterally connected to each other—identified in the early stages of procentriole growth and later triplets (doublets) of centriole microtubules grow at the ends of each ray of cartwheel [29–32]) in the lumen of the two centrioles (Fig. 2c). On transverse sections, the centriole had canonical nine-beam symmetry (Fig. 2e,f). The bases of prongs of the cogwheel structure [33] lay at the ends of the spokes of the cartwheel structure (Fig. 2e). In cross-section, nine doublets of MTs were seen between the prongs of the cogwheel structure (Fig. 2f, right insertion).

3.2 Centrioles in Haploid Somatic Cells of Anisopteromalus Calandrae Pupae

The study of epithelial cells in *Anisopteromalus calandrae* male pupae revealed the presence of four centriolar cylinders—two mother centrioles and two procentrioles (Fig. 3). From the morphology of the centrosome, it can be concluded that the cell is in the S-phase of the cell cycle

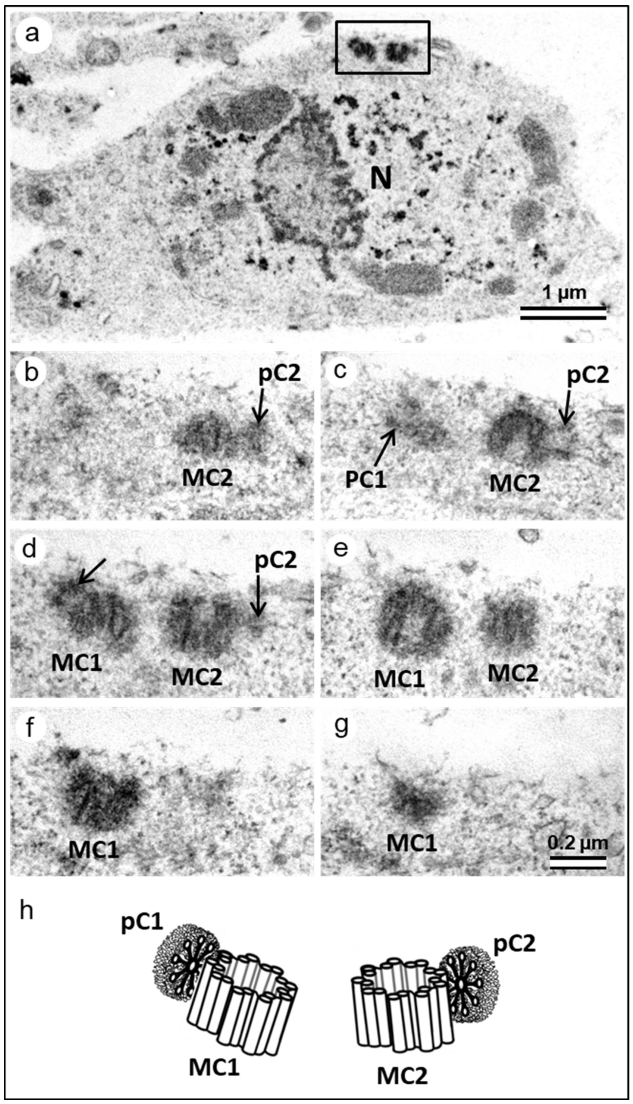

Fig. 3. Centrosome structure of the interphase stage of epithelial somatic cells in *Anisopteromalus calandrae* male pupa. (a) Overall view of the cell at low magnification. (b–g) Six consecutive ultrathin sections through the centrosome region. (h) Schematic diagram of the structure of a centrosome, in which both mother centrioles are shown from the distal end, so the cartwheel structure is not visible; it should be noted that the diameter of procentrioles at this stage is much smaller than that of the mother centrioles, so these procentrioles walls are shown here with MT singlets rather than with doublets; prongs of cogwheel structure are not shown in the diagram. MC1 and MC2, two mother centrioles 1 and 2; PC1 and PC2, two procentrioles; N, nucleus. Scale bar: 1 µm for (a), 0.2 µm for (b–g).

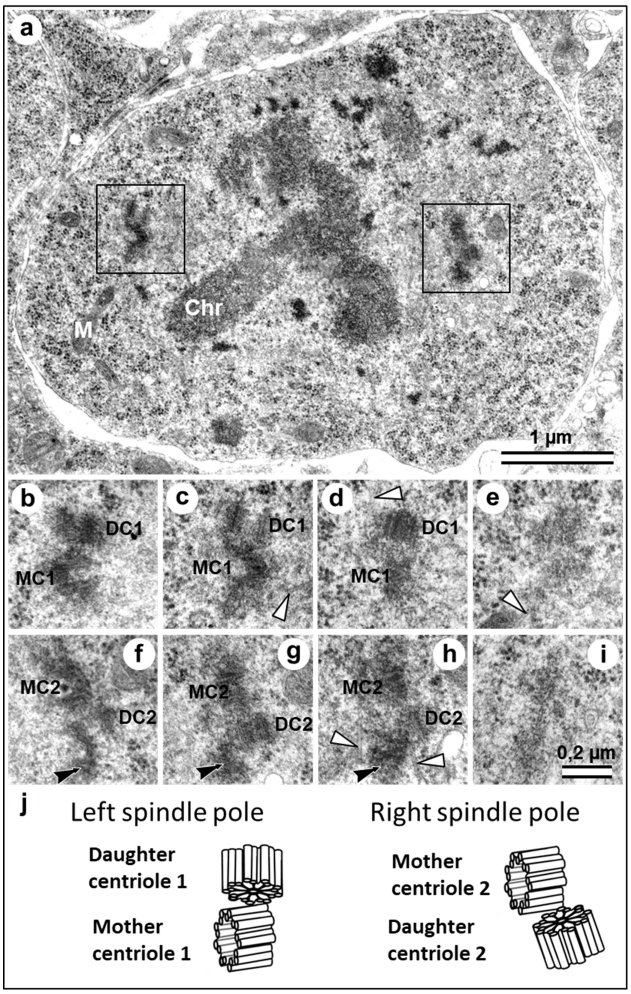

Fig. 4. Centrosome structure in the mitotic cell of *Anisopteromalus calandrae* male pupa spermatocytes. The cell is in the prometaphase of mitosis. (a) Overall view of the cell at low magnification. (b–e) Four consecutive ultrathin sections through the left pole. (f–i) Four consecutive ultrathin sections through the right pole. (j) Schematic diagram of the structure of centrioles at the spindle poles, where both mother centrioles are shown from the distal end, so the cartwheel structure is not visible; prongs of cogwheel structure are not shown in the diagram. Chr, chromosome; M, mitochondrion; MC1 and DC1, mother and daughter centrioles of the left spindle pole; MC2 and DC2, mother and daughter centrioles of the right spindle pole. White arrowheads show MTs of the spindle and black arrows show dense, spherical aggregates near the right mitotic pole. Scale bar: 1 µm for (a), 0.2 µm for (b–i).

and, therefore, has a genome in the course from haploid to diploid state. Thus, in the haploid somatic cells, there was twice the number of centrioles/ploidy ratio observed in all diploid cells.

The study of mitotic spermatocytes in pupae, which are transitorily diploid before mitosis in terms of chromosome sets, showed the presence of two centrioles in each of the poles of the mitotic spindles (Fig. 4).

Centrioles in each mitotic spindle pole formed diplosomes, the length of all four centrioles was near 170 nm, and the diameter was near 215 nm. Dense, spherical aggregates were also found in the mitotic poles, near the centrioles (Fig. 4f–h, black arrows).

4. Discussion

Like most Hymenoptera, *Anisopteromalus calandrae* wasps are characterized by the diploid–haploid type of sex inheritance. All females of these insects develop from fertilized eggs and all their somatic cells are diploid, while males develop from unfertilized eggs and all their somatic cells are haploid [34–36]. Unlike vertebrate centrioles, their centriole wall contains doublets rather than triplets of microtubules, as was also previously described in *Drosophila* [37,38] and *Caenorhabditis elegans* [39,40]. The structure of centrosomes and the number of centrioles were studied in detail in the cells of diploid females and haploid males of the parasitoid wasp *Anisopteromalus calandrae*.

The "end-to-end" orientation of two centrioles in the cell, which we found in the diploid neurons, was first described in fungi [41]; later, the same authors showed that this orientation comes from an unusual mechanism of centriole duplication in this organism [42]. Turner [43] first showed that the "hub" of the cartwheel structure appeared to be continuous between the two centrioles. A detailed electron microscope study by Moser and Kreitner [44] revealed centrosomes of a similar structure in the plants *Anthoceros laevis* (Notothyladaceae) and *Marchantia polymorpha* (Marchantiaceae). At the same time, it was shown that microtubule triplets in two centrioles are twisted in opposite directions—the authors made a three-dimensional reconstruction of such a centrosome [44].

In contrast, in the centrosomes of the females of *Anisopteromalus calandrae* studied in this work, the central "hub" of the cartwheel structure from one centriole was not a continuation of this structure of another centriole—there was always a break in this structure in the central part. This can be explained by the difference in the stage of the cell cycle in different models. In neurons, centrosomes are not in the cell cycle; therefore, in this case, the second centriole is not new-synthesized, and the observed gap could be a consequence of the destruction of the integrity of the "hub" of the cartwheel structure over time. Centrioles oriented "end-to-end" were found in the *Drosophila* eye on the apical surface of photoreceptor cells [45].

A similar orientation of centrioles was also later described in mammals for calf thymocyte centrosomes both on isolated centrosomes and in centrosomes of fixed whole cells [46]. The capacity of calf thymus centrosomes to nucleate MTs *in vitro* from purified tubulin was two to four times less than for centrosomes obtained from KE 37 cells (human lymphoblasts cell line) with the classical mutual orientation of centrioles, in which the proximal end of the daughter centriole is directed towards the surface of the mother centriole [46].

It has also been shown that, unlike centrioles isolated from other calf cell types or from other animals, these centrosomes are also unable to induce parthenogenetic development when injected into unfertilized amphibian eggs [47]. These results allowed us to conclude that this orientation of centrioles in the centrosome is a characteristic of functionally inactive centrioles. In our experiments, this orientation was found in all 17 neurons and perineural cells of wasps that we studied, which are terminally differentiated cells. In addition, only single microtubules were associated with centrosomes in neurons. Thus, centrosomes in cells of females with an "end-to-end" orientation of two centrioles were inactive. In *Drosophila*, a similar mutual orientation of the two centrioles was also previously found in terminally differentiated cells [45]. In contrast, in the haploid cells of the hypodermis of male *A. calandrae*, the centrioles were not end-to-end oriented. In the process of duplication in these cells, new procentrioles were formed not at the end of the mother centriole, but near its lateral surface, as described for most of the studied objects [2,48]. In mitotic cells, the two centrioles were located at each of the poles.

These data show that the inheritance patterns of centrosomes and DNA hereditary material are not directly interdependent, but are two mechanisms that have developed relatively independently in the course of the evolution of organisms. Previous hypotheses about a direct correlation between the number of centrioles in a cell and the number of chromosomal sets were based on the analysis of polyploid cells [4,5]. In contrast to the normal cell cycle, during polyploidization, doubling of the amount of DNA and centrioles occurs without cytotomy. As a result, the normal number of copies of the genome and centrioles changes in parallel and multiples—up to four in tetraploid cells, up to eight in octoploid cells, and so on [4,5]. At the same time, during the formation of the mitotic spindle, in each of its poles, a multiple number of centrioles is also normally located.

Since in normal haploid somatic and generative cells of Hymenoptera male insects, we found the number of centrioles, both in the interphase and in the poles of the mitotic spindle, identical to their number in the diploid cells of the females of these insects, this is a direct evidence of the absence of a direct correlation between centrioles quantity and cell ploidy.

5. Conclusions

Although the processes of DNA replication and centriole duplication are closely related and have apparently similar mechanisms [49–51], an identical number of centrioles identified in haploid cells of males *Anisopteromalus calandrae* and diploid somatic cells of females showed that the coincidence of the number of centrioles and the genome ploidy in diploid organisms is not necessarily interdependent.

Availability of Data and Materials

All data points generated or analyzed during this study are included in this article and there are no further underlying data necessary to reproduce the results.

Author Contributions

RU and CB designed the research study. RU, SWMON, AG, MP, SYC, CB performed the research. RU, SWMON, AG, MP, SYC, CB analyzed the data. RU, CB wrote the manuscript. All authors contributed to editorial changes in the manuscript. All authors read and approved the final manuscript. All authors have participated sufficiently in the work to take public responsibility for appropriate portions of the content and agreed to be accountable for all aspects of the work in ensuring that questions related to its accuracy or integrity.

Ethics Approval and Consent to Participate

Not applicable.

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Conflict of Interest

The authors declare no conflict of interest. Dr. Rustem Uzbekov is a guest editor of the journal. Given his role as guest editor, Rustem Uzbekov was not involved in the review of this article and does not have access to information relevant to its review. Full responsibility for the editorial process for this article has been delegated to Amancio Carnero Moya.

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