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The nutritive region in the ovaries of astigmatic mites (Acari: Acaridida)

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Abstract

The astigmatic ovary consists of a nutritive region surrounded by maturing germ cells. Serial semithin-sections and computer-generated 3-D-reconstructions were used to analyse the ovaries of four different astigmatic species (two free-living mites, *Sancassania berlesei* and *Glycyphagus domesticus* as well as two parasitic ones, *Otodectes cynotis* and *Chorioptes bovis*). The nutritive region is always restricted to one end of the ovary: it lies anteriorly in the parasitic species and posteriorly in the free-living species. In one specimen of *G. domesticus*, one ovary had two nutritive regions. The nutritive regions possess only a single nucleus with evenly distributed nucleoli. The nucleus is composed of several multiply interconnected strands. Altogether, the nutritive region and the general architecture of astigmatic ovaries closely resemble telotrophic meroistic ovaries of insects.

Keywords: 3-D-reconstruction, *Sancassania*, *Glycyphagus*, *Otodectes*, *Chorioptes*

Zusammenfassung

Das Ovar astigmater Milben besteht aus einer Nährkammer und einer diese umgebende Randzone mit den wachsenden Keimzellen. Mithilfe von Semidünnschnittserien und computergenerierten 3-D-Rekonstruktionen wurden die Ovarien von vier verschiedenen astigmaten Arten (zwei freilebende, *Sancassania berlesei* und *Glycyphagus domesticus* sowie zwei parasitische Vertreter, *Otodectes cynotis* und *Chorioptes bovis*) untersucht. Die Nährkammer ist immer auf ein Ende des Ovars beschränkt: Sie liegt am anterioren Ende bei den parasitischen Arten, und am posterioren Ende bei den freilebenden Arten. In einem Weibchen von *G. domesticus* wurden in einem Ovar zwei Nährkammern gefunden. Es wird gezeigt, dass die Nährkammer lediglich einen einzigen Zellkern besitzt. Der Kern besteht aus mehreren, mehrfach verbundenen Strängen. Im Ganzen ähnelt die Nährkammer und der grundsätzliche Aufbau der Ovarien astigmater Milben sehr den telotrophen meroistischen Ovarien der Insekten.

1. Introduction

In contrast to all other mites, astigmatic mites have paired ovaries (Alberti & Coons 1999). The overall architecture of the genital tracts of adult astigmatic mites has been the subject of several anatomical investigations (Nalepa 1884, 1885; Nevin 1935, Perepelkina-Christopulo 1940, Hughes 1954, Perron 1954, Rohde & Oemick 1967, Kuo & Nesbitt 1970, Prasse 1970, Vijayambika & John 1975a, Baker & Krantz 1985, Witaliński et al. 1990, Walzl 1992, Witaliński & Walzl 1995, Desch 2001, Lekimme et al. 2005), but only few describe the organisation of the ovary in detail. Some earlier light microscopical investigations (Nalepa 1884, 1885, Perepelkina-Christopulo 1940) and the ultrastructural investigations (Witaliński et al. 1990, Walzl 1992, Desch 2001, Lekimme et al. 2005) have shown that each ovary consists of a so-called central region surrounded by a region of maturing germ cells. The central region is generally considered to be a nutritive area, nourishing the surrounding germ cells via intercellular bridges. Uncertainty remains about the central region, specifically whether it is a syncytial mass (Nalepa 1884, 1885, Perepelkina-Christopulo 1940, Prasse 1968, Walzl 1992) or a multilobulated cell (Witaliński et al. 1990, Desch 2001, Lekimme et al. 2005). Clarifying this ambiguity and fully illustrating the number of nuclei inside the central region requires 3-D reconstructions of the ovaries of different astigmatic mite species.

2. Materials and methods

Four species belonging to three families of astigmatic mites were investigated in this study. *Sancassania berlesei* (Michael, 1903) (Acaridae) and *Glycyphagus domesticus* (de Geer, 1778) (Glycyphagidae) were obtained from long-term stock-cultures in our laboratory. *Chorioptes bovis* (Hering, 1845) (Psoroptidae) was collected from a bull and *Otodectes cynotis* (Hering, 1838) (Psoroptidae) from the ears of a domestic cat from Styria/Austria.

Females of each species were fixed in modified Karnovsky's fluid (Hayat 1986) in sodium-cacodylate buffer. To ensure a better infiltration of the fixative and the resin, the gnathosomata of *G. domesticus*, *C. bovis* and *O. cynotis* specimens were removed in the fixative using sharpened tungsten needles; in *S. berlesei*, however, the ovaries were dissected. After rinsing in buffer, specimens were postfixated with osmium tetroxide and dehydrated either with acidified 2,2-dimethoxypropane (Muller & Jacks 1975, Pernstich et al. 2003) or a graded alcohol series. Dehydrated specimens were embedded in Spurr's resin (Spurr 1969) and sectioned serially (1 or 2 μm) with a Histo Jumbo diamond knife (Blumer et al. 2002) on a Reichert Ultramicrotome. After staining according to Richardson et al. (1960) the sections were analysed and photographed digitally on a Nikon Eclipse E800 light microscope with a DS5M-U1 camera. 3-D reconstruction was carried out with the reconstruction software Amira 3.1 (www.tgs.com) after contrast enhancement and converting the microphotographs into greyscales using Photoshop CS2. After alignment of the image stack, the central region, the nuclear parts of the central region, the oocytes and the oocyte nuclei were labelled in the original section plane. To optimise the reconstruction quality, they were also labelled in the virtual section planes (see Handschuh et al., in press, for details). A surface of the labelled structure was created, reduced in size and smoothed; snapshots of the reconstructions were then taken with the Amira software.

3. Results

The ovaries of the analysed astigmatic mites lie in the posterior part of the opisthosoma. In the free-living *G. domesticus* and *S. berlesei* they lie more terminally, at the end of the opisthosoma, as opposed to the parasitic species *C. bovis* and *O. cynotis*, where the ovaries are located more anteriorly. Medially, the ovaries of all species butt against the hindgut and, laterally in *G. domesticus* and *S. berlesei*, against the oviducts. In the parasitic *C. bovis* and *O. cynotis*, they are not constricted by another organ and extend into the haemocoel cavity.

In *G. domesticus* the closely adjoining, egg-bearing oviducts give the ovaries an irregular shape, i.e. elongated in the anterior-posterior axis but constricted by the eggs in the oviducts and therefore indented concavely on their lateral sides (Fig. 1a, b).

In contrast, the ovaries of *C. bovis* and *O. cynotis* are ovoid to ellipsoid (Figs 1c, d). The shape of the *S. berlesei* ovary was not determined because only the central region was reconstructed. The sizes of the ovaries vary, depending on the number of oocytes they contain. The two reconstructed ovaries of *G. domesticus* were 170 µm long, 140 µm wide and 100 µm high (left ovary), and 160 µm long, 130 µm wide and 110 µm high (right ovary). The corresponding values in the smaller *C. bovis* and *O. cynotis* ovaries were 40 µm, 40 µm and 30 µm and 50 µm, 50 µm and 40 µm.

The nutritive regions of all ovaries are never located 'centrally': they occupy the anterior part of the ovaries in the psoroptid mites (Figs 1c, d) and the posterior end in *G. domesticus* (Fig. 1a). The two investigated ovaries of *G. domesticus* had different numbers of nutritive regions – the left ovary with one at the posterior end (Fig. 1a) and the right ovary with two separate regions, one at the posterior end and a second one at the anterior end (Fig. 1b).

Although this investigation did not reconstruct the exact position of the ovary inside the body of *S. berlesei*, its nutritive region is clearly adjacent to the surrounding ovarian epithelium and not central inside the ovary (Fig. 2a).

The size and shape of the nutritive region differ among the analysed species. In *G. domesticus* (Figs 1a, 2b, 3d) and *O. cynotis* (Figs 1d, 2c, 4d) the region is an irregular, flattened ellipsoid, whereas in *S. berlesei* (Figs 2a, 3a) and *C. bovis* (Figs 1c, 2d, 4a) it has a convex side bulged into the surrounding ovarian epithelium and a concave side facing the maturing oocytes.

The concave side of the nutritive regions of the latter species shows several protrusions (Figs 1c, 3a). These protrusions represent additional attachment sites for oocytes connected with the nutritive region.

In all species investigated, the lumen of the intercellular bridges that connect the growing oocytes with the nutritive region is filled with intensively stainable material (Fig. 2a – d).

In *G. domesticus* the oocytes are distributed dorso-ventrally within the ovary, mainly concentrated ventrally but also extending to the lateral side; a few are also located in the anterior region (Fig. 1a).

In contrast to the parasitic species, *G. domesticus* and *S. berlesei* had several more mature oocytes that were larger (Figs 1a, b, 2a). In *O. cynotis* and *C. bovis*, however, only three to four oocytes mature at one time; the remaining immature oocytes form a tight girdle at the base of the nutritive region (Fig. 1d). The spherical to ellipsoid nucleus fills most of the immature oocytes, leaving only a thin rim of cytoplasm (Figs 2a – c). The size increase during maturation is mostly due to plasma increase, though the nucleus enlarges as well. In *O. cynotis* one mature oocyte is as large, if not larger, than the nutritive region (Fig. 1d).

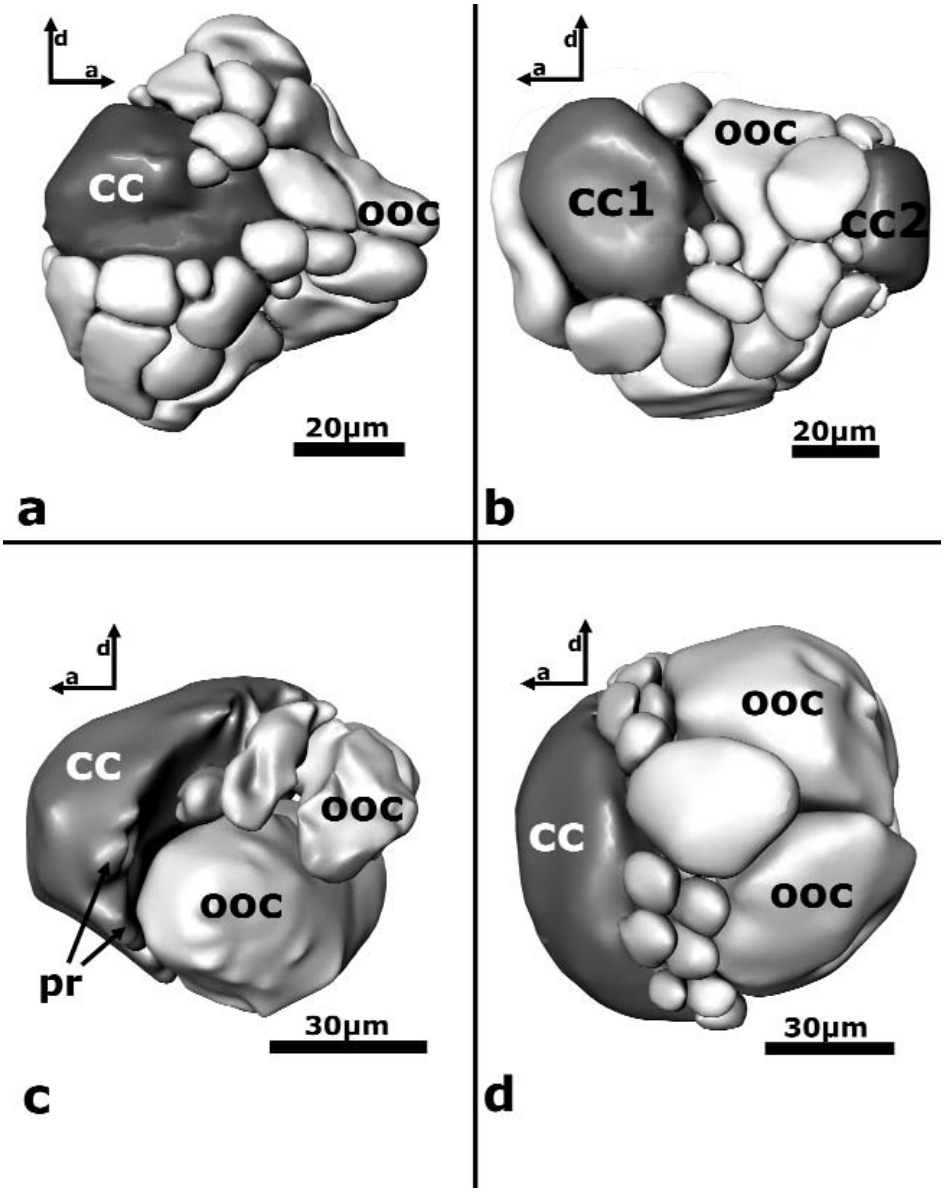

Fig. 1 3-D reconstructions of: a & b: *G. domesticus*, a: left ovary; b: right ovary; c: *C. bovis* (immature oocytes not reconstructed due to their small size); d: *O. cynotis* (The surrounding, adjacent ovarian epithelium is not reconstructed). The arrows point to the anterior (a) and dorsal (d) direction of the specimen. cc: nutritive cell; cc1; nutritive cell 1; cc2: nutritive cell 2; ooc; oocyte.

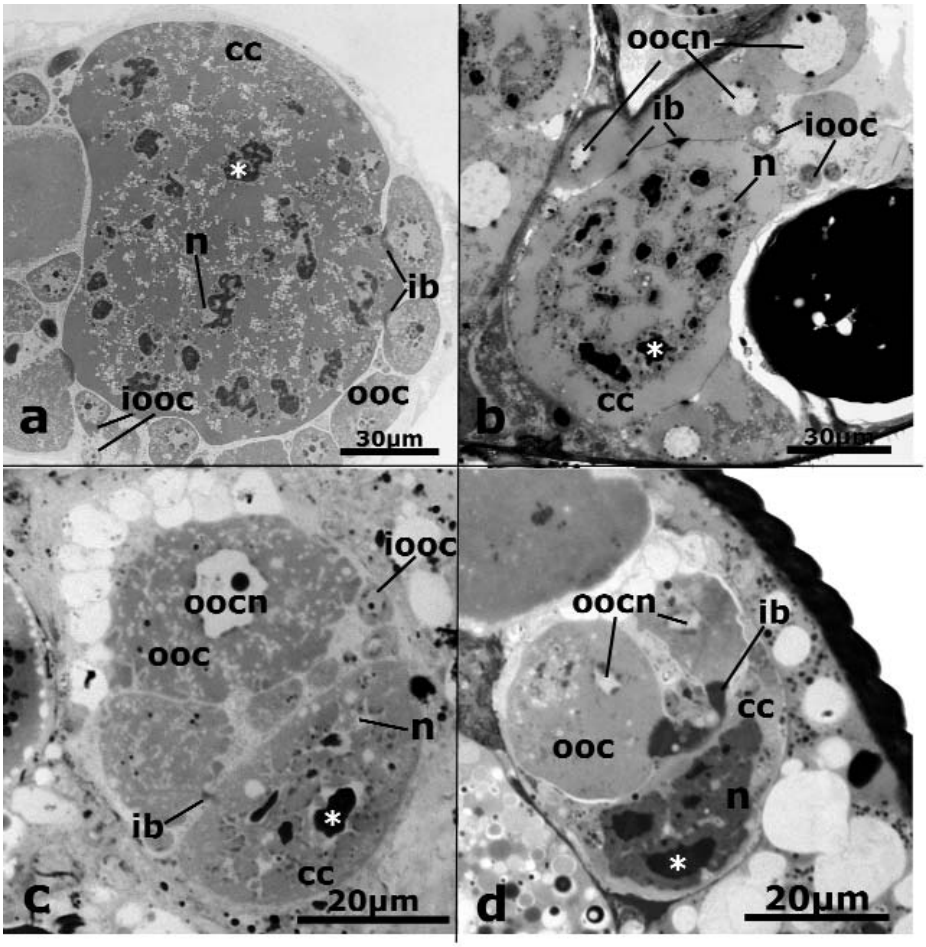

Fig. 2 Semithin sections of the ovary of: a: *S. berlesei*; b: *G. domesticus*; c: *O. cynotis*; d: *C. bovis*. cc: nutritive cell; ib: intercellular bridge; iooc: immature oocyte; n: nucleus; ooc: oocyte; oocn: oocyte nucleus; asterisks mark the nucleolus-material inside the nucleus.

In all investigated species the nuclear area of the nutritive region represents a single entity which fills almost the whole cavity of the nutritive region (Figs 2a – d; 3a, d; 4a, d). The largest extensions in the reconstructed nuclei were 35 µm, 27 µm, 18 µm in *C. bovis*, and 40 µm, 31 µm, 20 µm in *O. cynotis*. In *G. domesticus* the values were 80 µm, 60 µm, 44 µm and in *S. berlesei* 130 µm, 90 µm, 65 µm.

The surface of the nucleus is not smooth but perforated. In *G. domesticus* it has several blindly ending, spiny processes (Fig. 3d), in *O. cynotis* it is very spiny and indented (Fig. 4d), and in *C. bovis* it has a hilly surface (Fig. 4a).

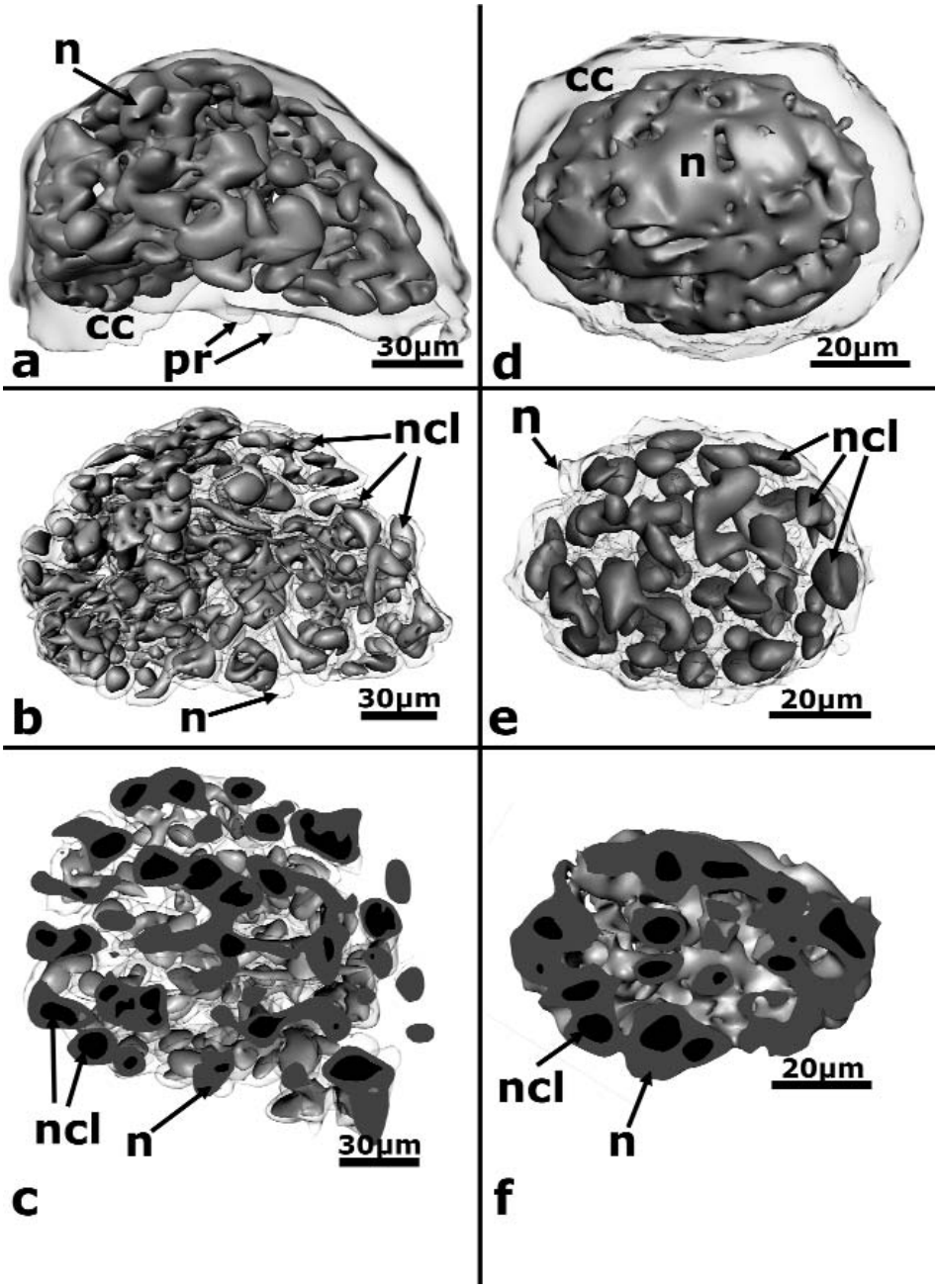

Fig. 3 3-D reconstructions of the ovary's nutritive cell in the free-living *S. berlesei* (a – c) and *G. domesticus* (d – f). cc: nutritive cell; n: nucleus; ncl: nucleoli; pr: protrusions. Nutritive cell transparent, nucleus shaded (a & d); nucleus transparent, nucleoli shaded (b &e); Cuts through the nucleus of the central cell (c & f).

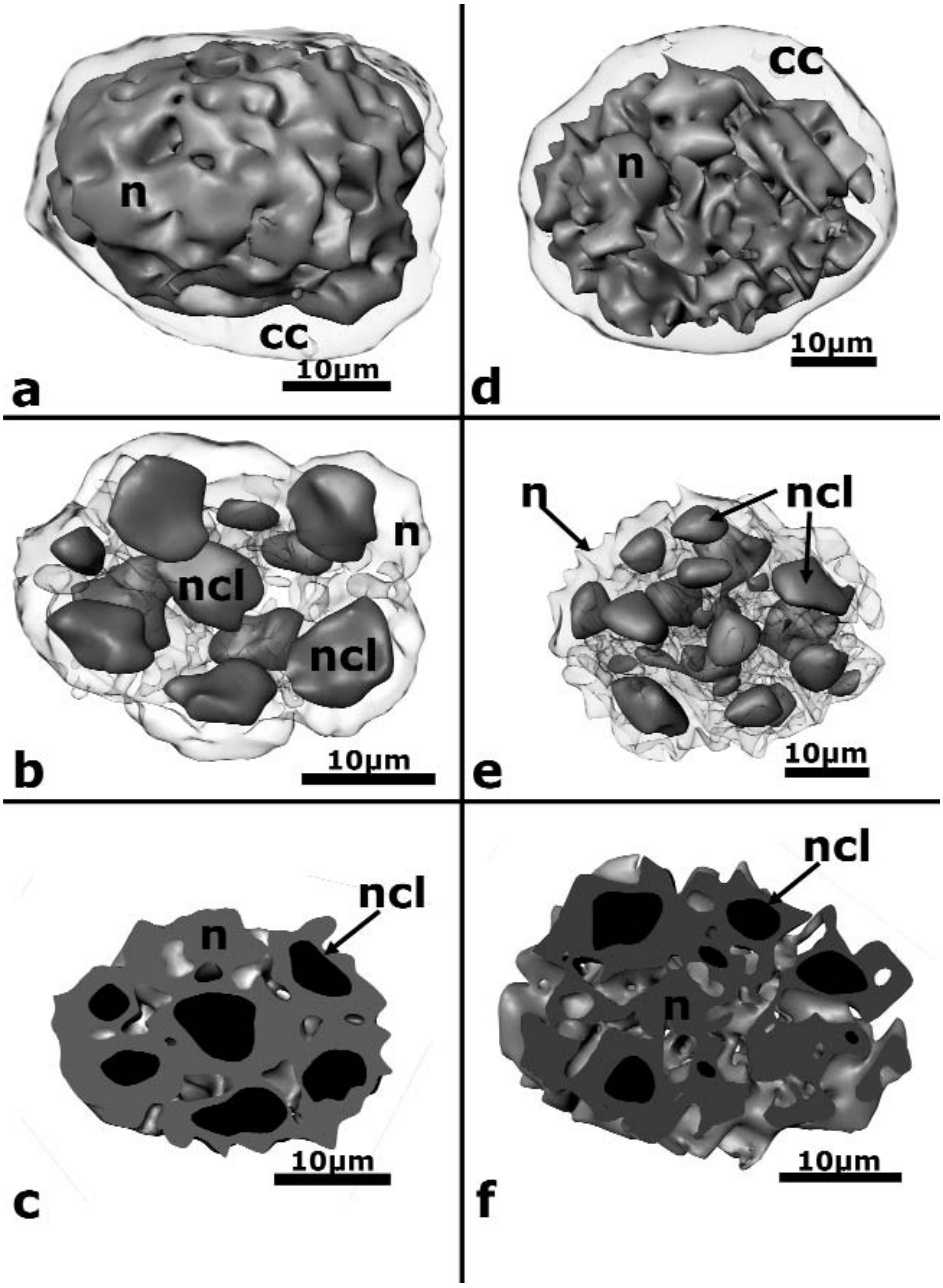

Fig. 4 3-D reconstructions of the ovary's nutritive cell in the parasitic *C. bovis* (a – c) and *O. cynotis* (d – f). Nutritive cell transparent, nucleus shaded (a & d); nucleus transparent, nucleoli shaded (b & e); Cuts through the nucleus of the central cell (c & f). cc: nutritive cell; n: nucleus; ncl: nucleoli.

The whole nucleus has a complicated shape with an enormous outer surface of the nuclear membrane. It possesses holes and channels of cytoplasm which separate the nuclear strands resembling a Swiss cheese or a bath sponge. In *S. berlesei* the nuclear strands are loosely arranged, leaving a much wider space between the separated strands than in the other species (Figs 2a; 3a, c). The nuclei of the other investigated species are much more compact, that of *C. bovis* being the most compact (Figs 2d; 4a, c). The nuclear strands in the nucleus of *O. cynotis* are conspicuously thin (Figs 2c; 4d, f).

The nuclear strands are filled with intensively staining nucleoli (Figs 2a – d asterisk) that are more or less evenly distributed within the strands (Figs 3b, e; 4b, e). The shape of these nucleoli varies, i.e. spherical, ellipsoid or elongated, sometimes lobulated and interconnected (Figs 3b, e; 4b, e). In *S. berlesei* there are 138, in *G. domesticus* 62, in *O. cynotis* 30 and in *C. bovis* 12 discernible elements.

4. Discussion

In astigmatic mites, ovary position and structure are influenced by the location of the receptaculum junction and the oviduct origins. Computer-generated 3-D-reconstructions enabled us to illustrate the 3-dimensional shapes of the ovaries and the position of the nutritive cell within the ovary of four species. In both parasitic species, *O. cynotis* and *C. bovis*, the oviducts originate at the ventro-posterior side of the ovary, as in *P. ovis* (Lekimme et al. 2005) but opposed to *S. scabiei* (Witaliński & Walzl 1995, Desch 2001). This region is entirely filled with growing oocytes and the nutritive cell lies at the anterior border of the ovary, as in *S. scabiei* (Desch 2001) and *P. ovis* (Lekimme et al. 2005). The origin of the oviduct at the posterior end of the ovary is also decisive that the ovaries are not terminally located in the opisthosoma. Contrary to the parasitic species, in all analysed free-living species (see Rohde & Oemick 1967, Kuo & Nesbitt 1970, Prasse 1970, Baker & Krantz 1985, Witaliński et al. 1990, this study) the oviducts originate at the anterior border of the ovary and the nutritive cell is located posteriorly.

Without more thorough studies on its formation, the nutritive cell of the adult ovary cannot be declared as a syncytial structure as proposed by Nalepa (1884) for *Tyrophagus longior*, Nalepa (1885) for *C. lactis*, Perepelkina-Christopulo (1940) for *Acarus siro* or by Walzl (1992) for *Dermatophagoides farinae* and *D. pteronyssinus*, nor is the nucleus of the cell multilobular (Witaliński et al. 1990, Desch 2001, Lekimme et al. 2005). In fact, the term ramified nucleus is more appropriate because the nucleus has an interconnected plexus rather than a single centre that branches off multiple lobules.

No obvious size differences exist between the inner and outer parts of the nucleus as claimed by Nalepa (1884, 1885) and Perepelkina-Christopulo (1940) for the nuclei of the central syncytium of *T. longior*, *C. lactis* and *A. siro*. The question remains whether the nutritive cell represents several fused cells as proposed by Nalepa (1884, 1885) and Perepelkina-Christopulo (1940). The evenly distributed nucleoli might result from a fusion of several germ cells in a previous ontogenetic stage (not yet analysed three-dimensionally). In females of the gamasid *V. jacobsoni* (= *Varroa destructor*), the unpaired ovaries have a nutritive, so-called ‘lyrate organ’. This organ is syncytial, but the nuclei inside are interconnected by thin peripheral branches as soon as more advanced oocytes (stage 2 and 3 oocytes), or possibly even earlier oocytes (stage 1 oocytes), occur (Alberti & Zeck-Kapp 1986).

The same might hold true in astigmatic mites: this would represent an analogous development of a nutritive structure, similar to telotrophic meroistic ovaries in insects (Alberti & Zeck-Kapp 1986, Büning 1994). As Alberti & Zeck-Kapp already noted for *V. jacobsoni*, in telotrophic insect ovaries the nutritive tissue is always restricted to one part of the ovary, as was the case in our analysed astigmatic mites (even in the 'aberrant' ovary of *G. domesticus* with two nutritive cells, they are restricted to the ovarian border). The many nucleoli in the nuclei of astigmatic mite nutritive cells are clearly a sign of RNA expression, which is essential for the nourishment of developing germ cells. The nutritive cells of astigmatic mites have a high metabolic activity. Accordingly, the shape and general appearance of the cell and its nucleus are probably highly alterable. In order to analyse the changes within the cell and to clarify the seemingly analogous construction to telotrophic ovaries of insects, all postembryonic stages and age-determined adult females (freshly hatched, non-copulated, copulated, etc.) of one species would have to be investigated.

In particular, more focus should be placed on the ovaries of the rarely investigated postembryonic stages (Proto-, Tritonymph) (Nalepa 1884, 1885, Perepelkina-Christopulo 1940, Heinemann & Hughes 1969, 1970, Vijayambika & John 1975 a, b; 1976 a, b). Oocyte development in astigmatic mites continues to be enigmatic.

Especially the free-living species produce large amounts of eggs (*S. berlesei* females produce over 1000 eggs during their lifetime – unpublished data) and the question remains how oocytes are regenerated. Two alternative explanations are under discussion. Nalepa (1884, 1885) and Perepelkina-Christopulo (1940) regard the central cell (termed 'Keimlager' by these authors) as the source for further oocytes, while Heinemann & Hughes (1969, 1970) and Prasse (1968) claim oogonial mitoses for production for further oocytes.

Although the present investigation was not designed to elucidate this problem, we have found several indications supporting the former argument, i.e. that oocytes are created by the central cell. Further studies will yield more clarity on this problem.

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