Ovaries and germline cysts and their evolution in Dermaptera (Insecta)

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ABSTRACT

We studied the ovary structure and initial stages of oogenesis in 15 representatives of several dermapteran taxa, including the epizoic Arixeniina. In all examined species, the ovaries are meroistic–polytrophic. The ovaries of the basal taxa ('Pygidicranidae', 'Diplatyidae', and Labiduridae) are composed of elongated ovarioles, attached to short lateral oviducts. In these groups, ovarioles contain several (more than 30) ovarian follicles in a linear arrangement. In the Eudermaptera, the ovaries are composed of 1–6 (Spongiphoridae) or 20–40 (Forficulidae, Chelisochidae) short ovarioles (containing 2 ovarian follicles only) that open to strongly elongated lateral oviducts. In all investigated dermapterans, the ovarian follicles are composed of two germline cells only: an oocyte and a polyploid nurse cell that are covered by a simple follicular epithelium. Our studies indicate that despite a rather unique morphology of the ovarian follicles in the examined species, the processes leading to the formation of the oocyte and nurse cell units are significantly different in basal versus derived taxa.

The ovaries of Arixenia esau are composed of 3 short ovarioles attached to a strongly dilated lateral oviduct, 'the uterus', containing developing embryos. Histological analysis suggests that the origin of the oocyte and nurse cell units in this species follows the pattern described in eudermapterans.

The interpretation of our results in an evolutionary context supports the monophyly of the Dermaptera and Eudermaptera, and the inclusion of the Arixeniina and Hemimerina in the latter taxon.

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1. Introduction

The female reproductive system of insects consists of the ovaries and a Y-shaped oviduct, ending in the vagina and genital opening. The ovaries are composed of several elongated elements, termed the ovarioles that open into each branch of the oviduct. The eggs (oocytes) develop during their passage from the tip of the ovariole to the common oviduct. There is a great variation in the structure of the ovariole, being long or short and few or many.

The individual ovariole always consists of three easily recognizable elements: a terminal filament, germarium and vitellarium (see Büning, 1993, 1994; Biliński, 1998 for detailed description of insect ovarioles). Traditionally, two basic categories of insect ovaries and ovarioles are distinguished, the panoistic and meroistic types. In the panoistic ovaries, all germline cells develop into functional, fertilizable oocytes and each ovarian follicle consists of an oocyte plus a monolayer of follicular cells. Hence, all types of RNAs accumulated in the oocyte cytoplasm are synthesized in a transcriptionally active oocyte nucleus (germinal vesicle).

In the meroistic ovarioles, some of the germline cells differentiate into oocytes, while others become nurse cells (trophocytes). Depending on the spatial relations between the oocyte and the nurse cells within the ovariole, two types of meroistic ovaries are usually recognized: polytrophic and telotrophic (see Büning, 1993, 1994; Biliński, 1998 for details). The main function of the nurse cells is the synthesis and subsequent transport of macromolecules and organelles to the oocyte cytoplasm (Büning, 1994; de Cuevas et al., 1997; Matova and Cooley, 2001; Tworzydło and Kisiel, 2010). In the meroistic–polytrophic ovarioles, the germaria are relatively large and contain characteristic cysts (clusters, clones) of sibling germline cells (cystocytes). The cysts arise as a result of a series of mitotic divisions of a founder germline cell, the cystoblast. The number of cells constituting an individual cyst depends directly on the number of mitotic divisions of the cystoblast (Büning, 1994; Biliński, 1998) and follows the $N = 2^n$ rule where N is number of cystocytes and n is number of mitotic divisions. Within each cyst only one cell differentiates into the oocyte, whereas other become the nurse cells. Resulting oocyte–nurse cell complexes are invested with the somatic follicular cells, migrate to the vitellarium and constitute the ovarian follicles. Subsequent growth and development of the follicles can be divided into three, partially overlapping phases: previtellogenesis, vitellogenesis and choriogenesis. During

previtellogenesis various macromolecules and organelles are gradually accumulated in the oocyte cytoplasm (ooplasm). During vitellogenesis the ooplasm becomes loaded with the reserve materials (yolk spheres, lipid droplets). In the last phase (choriogenesis) egg envelopes are secreted on the oocyte surface.

The Dermaptera (earwigs) comprise about 2200 extant species classified usually in 3 'suborders' and 8–11 'families' (see Haas and Kukalová-Peck, 2001; Jarvis et al., 2005 and the Section 4). Recent analyses of the relationships within this taxon employed several morphological character complexes, e.g. articulation and folding pattern of hind wings, the shape and number of locomotory attachment pads, structure of abdomen, as well as molecular data (Haas, 1995; Haas and Kukalová-Peck, 2001; Haas and Gorb, 2004; Haas and Klass, 2003; Jarvis et al., 2005; Klass, 2001; White, 1972). It has been previously shown that the various dermapteran subgroups may significantly differ in both, gross morphology of the ovaries and the processes leading to the formation of germ cell cysts (Büning, 1994; Yamauchi and Yoshitake, 1982; Tworzydło and Biliński, 2008; Tworzydło et al., 2009). The gross morphology of the female reproductive organs have been described for a number of earwig species, e.g. *Anisolabis littorea* (Giles, 1961), *Forficula auricularia* (Fischer, 1853; Brauns, 1912), *Labidura riparia* (Fischer, 1853), *Nala lividipes* (Dufour, 1828), *Arixenia* (Burr and Jordan, 1912; Hagan, 1951), and *Hemimerus* (Deoras, 1941; Heymons, 1912; Hagan, 1951). Despite this, characters derived from ovaries and ovarioles have been used neither to reconstruct dermapteran phylogeny nor the evolution of this organ system within the Dermaptera. In this study, we describe the ovary structure and initial stages of oogenesis in representatives of dermapteran taxa, including the epizoic Arixeniina, compare them with literature data on the Blattodea and Orthoptera as out-groups, and draw some evolutionary conclusions.

2. Materials and methods

The ovaries of the investigated species (see Table 1) were fixed, dehydrated and embedded according to standard protocols (see Tworzydło and Biliński, 2008). In brief, the ovaries were dissected from adult females and (a) fixed either in 100% ethanol or 2.5% glutaraldehyde, post-fixed in 4% formaldehyde in PBS, dehydrated in series of ethanol and embedded in Histocryl (Agar Scientific Ltd, Stansted, Essex, UK) (*Cranopygia*, *Diplatys*, *Labidura*, *Nala*, *Marava*, *Irdex*), or (b) fixed in 1% glutaraldehyde, post-fixed in 2% osmium

Table 1
Species examined.

Systematic Position	Species	Author	Location
Forficulina			
'Diplatyidae'	*Diplatys flavicollis*	Shiraki (1907)	Japan
'Pygidicranidae'	*Cranopygia ophthalmica*	Dohrn (1863)	Australia
Anisolabididae	*Euborellia plebeja*	Dohrn (1863)	Taiwan
Labiduridae	*Labidura riparia*	Pallas (1773)	Germany
	Nala lividipes	Dufour (1828)	Turkey
Eudermaptera			
Forficulidae	*Forficula auricularia*	Linnaeus (1758)	Poland
	Chelidurella acanthopygia	Géné (1832)	Poland
	Cosmiella bilobata	Brindle (1973)	Kenya
	Doru lineare	Eschscholtz (1822)	Bolivia
	Opisthocosmia silvestris	Moreira (1930)	Bolivia
	Eparchus forcipatus	de Haan (1842)	Malaysia
Chelisochidae	*Proreus ludekingi*	Dohrn (1865)	Malaysia
Spongiphoridae	*Marava* sp.		Malaysia
	Irdex sp.		Malaysia
Arixeniina			
	Arixenia esau	Jordan (1909)	Malaysia

tetraoxide, dehydrated in ethanol and embedded in Epon 812 (Fullam Int., Latham, NY, USA) (*Chelidurella*, *Cosmiella*, *Doru*, *Eparchus*, *Euborellia*, *Forficula*, *Opistocosmia*, *Proreus* and *Arixenia*).

Semithin (0.7 μm) Histocryl or Epon sections were stained with 1% methylene blue in 1% borax, and examined under a Leica DMR microscope (Heidelberg, Germany).

Numerous morphological studies have shown that in both out-groups, the Blattodea and Orthoptera, the ovaries are composed of a few (less than 10), long panoistic ovarioles (see Štys and Biliński, 1990; Büning, 1993, 1994 for a review). As a rule, the ovarioles consist of several ovarian follicles, and are attached to shortened lateral oviducts. The description of the ovaries of the Hemimerina is based on the classical studies of Heymons (1912) and Hagan (1951). According to these authors, the ovaries of *Hemimerus* are composed of a few relatively short meroistic–polytrophic ovarioles that house, in the vitellaria, two ovarian follicles only. The "ovarian" characters are mapped onto the phylogenetic tree based on Jarvis et al. (2005). The low number of new characters prevented us from conducting a new phylogenetic analysis.

3. Results

3.1. Germaria and early stages of oogenesis in 'Diplatyidae', 'Pygidicranidae', Anisolabididae and Labiduridae

This type of the ovary is characteristic for taxa considered basal in dermapteran evolution, the 'Diplatyidae', 'Pygidicranidae', Anisolabididae and Labiduridae and has been first described by Yamauchi and Yoshitake (1982) in the representative of the Anisolabididae, *Anisolabis maritima*, and therefore will be referred to as "Anisolabis" type. Our comparative studies have shown that in all basal taxa ovaries are composed of 5 elongated ovarioles of the meroistic–polytrophic type (Fig. 1A). The germaria are relatively long and comprise several germ cell cysts in subsequent developmental stages (Fig. 2C–F) and small somatic, i.e. prefollicular cells. Analysis of the serial sections has shown that in the anterior part of the germarium cysts composed of 2, 4, and 8 cells reside (Fig. 2C). The cystocytes are small and morphologically identical. They comprise relatively large, spherical nuclei with well-defined chromatin aggregations (Fig. 2C). The posterior region of the germarium is filled with several 2-cell cysts surrounded by somatic cells or their extensions (Fig. 2D–F). The "posterior" cysts always consist of 2 morphologically distinct cells: the pro-oocyte and pro-nurse cell (Fig. 2D–F). The neighboring cysts are arranged irregularly, and often their antero-posterior axis is not parallel to the antero-posterior axis of the ovariole (Fig. 2D). The vitellaria are strongly elongated and contain up to 30 sequentially larger ovarian follicles (Fig. 1A). All the follicles comprise an oocyte and a single nurse cell. Interpretation of the above results clearly indicates that in *A. maritima* (Yamauchi and Yoshitake, 1982), *Tagalina burri* (Büning, personal communication) and *L. riparia* (this study) the process of germline cysts generation is unique and much more complicated than in eudermapterans (see below). In these species the cystoblasts apparently divide 3 times generating 8-cell cysts. These cysts split secondarily into four, 2-cell clusters that are invested with somatic follicular cells and constitute ovarian follicles. Surprisingly, despite the processes leading to the formation of germline cysts in "Forficula" (see below) and "Anisolabis" ovarian types are strikingly different, the resulting functional units of the ovary (i.e. the ovarian follicles) are morphologically almost identical (compare Fig. 3A–D and E, F). In the vast majority of investigated species representing basal taxa the nurse cell nuclei are highly ramified and surrounded by a deeply folded envelope (Fig. 3E and F), and the follicular epithelium diversifies into 3 subpopulations: (cuboidal follicular cells surrounding the oocyte, stretched cells covering the nurse cell
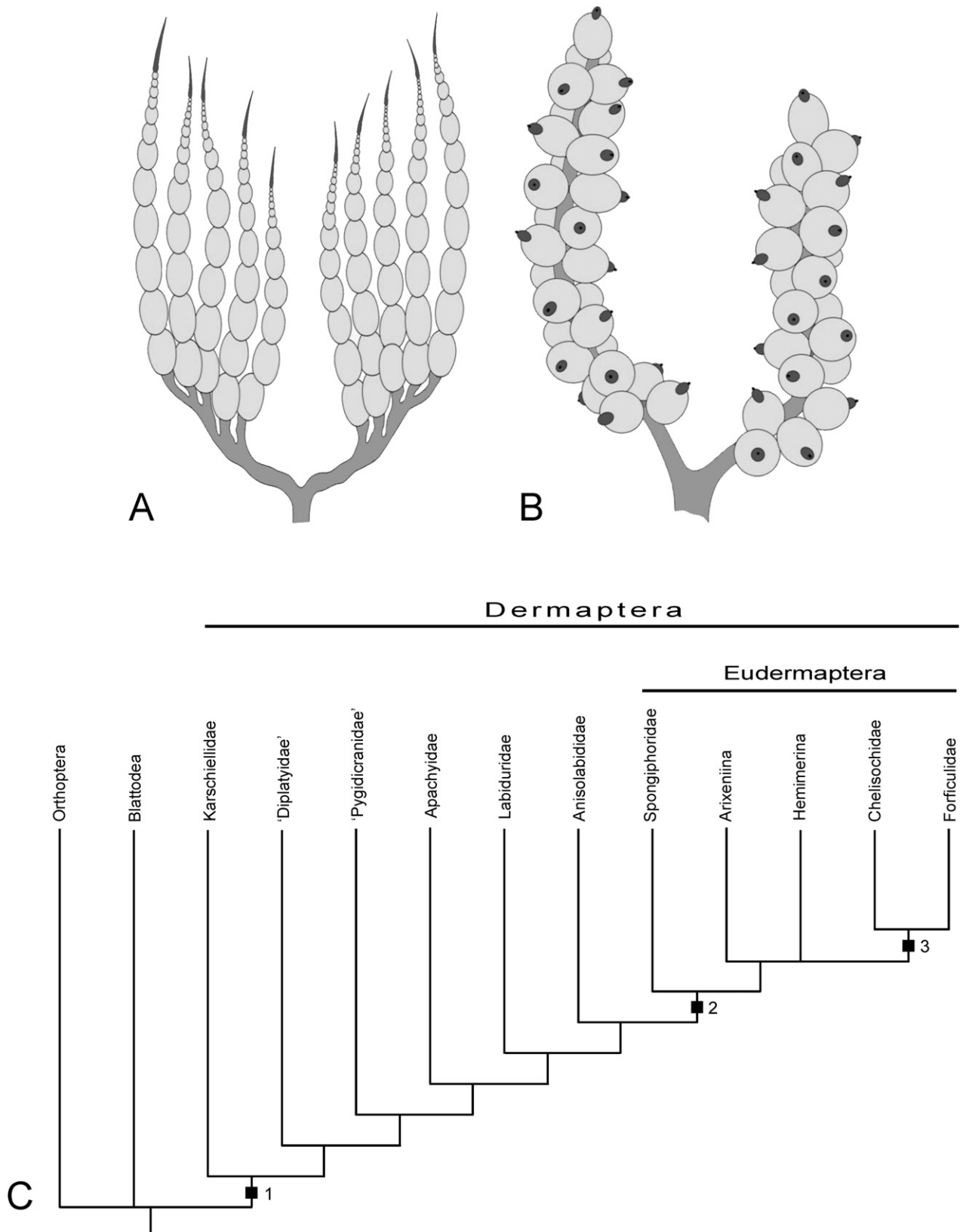
Fig. 1. Morphology of the ovaries in the basal taxa (the "Anisolabis" type, A), and the Eudermaptera (the "Forficula" type, B). Note the differences in number and length of ovarioles (light grey), length of lateral oviducts (grey), and the size of the germaria (dark grey). (C) Phylogenetic hypothesis for the relationships within the Dermaptera based on Jarvis et al. (2005). In contrast to the original, the Spongiphoridae are considered monophyletic, the Karschiellidae and 'Diplatyidae' (based on Haas and Kukalová-Peck, 2001), as well as the Arixeniina (this study) have been added. The Orthoptera and Blattodea possess a few panoistic ovarioles attached to short lateral oviducts (suggested plesiomorphic character state). Node 1: Meroistic ovary of the "Anisolabis" type (few and long ovarioles, many follicles in the vitellaria, and a secondary division of 8-cell germline cysts) as an autapomorphy of the Dermaptera. Node 2: ovary with a few and short ovarioles attached to elongated lateral oviducts, and reduced number of mitotic divisions of a cystoblast, as a synapomorphy of the Eudermaptera including the Arixeniina and Hemimerina. The inclusion of the latter group was already suggested by Jarvis et al. (2005). Node 3: ovary of the "Forficula" type, with numerous, short ovarioles, as a synapomorphy for the Chelisochidae and Forficulidae.
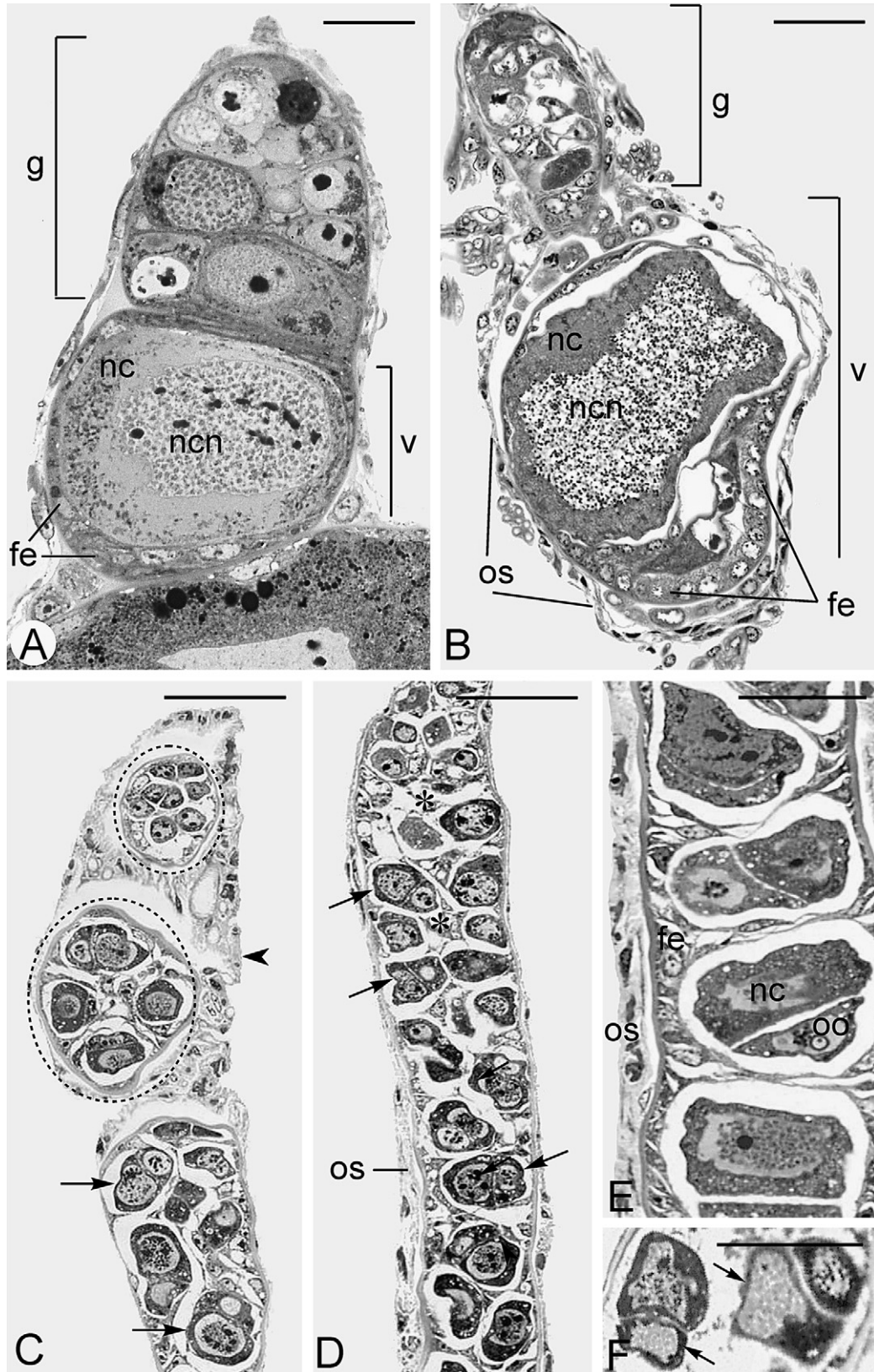
Fig. 2. The apical part of the ovariole in the Eudermaptera (A, B), and in the basal dermapterans (C–F). Note that in *Opisthocosmia silvestris* (Forficulidae) (A) and *Proreus ludekingi* (Chelisochidae) (B) the germaria (g) are relatively short, and filled with cystoblasts and 2-cell germline cysts. The vitellaria (v) are short and composed of two ovarian follicles only. In the representatives of the basal group, Labiduridae, *Labidura riparia* (C–E), and *Nala lividipes* (F), the germaria are relatively long and comprise germline cysts in various developmental stages. 8- and 4-cell cysts are encircled (C); 2-cell cysts (arrows in C, D and F) are surrounded by somatic cells or their extensions (asterisks). (E) The contact zone between germarium and vitellarium. Note young ovarian follicles composed of an oocyte (oo) and a nurse cell (nc) covered with follicular epithelium (fe); nurse cell nucleus (ncn), ovariole sheath (os). Scale bars: 25 μm in (A–D), 40 μm in (E) and 45 μm in (F).
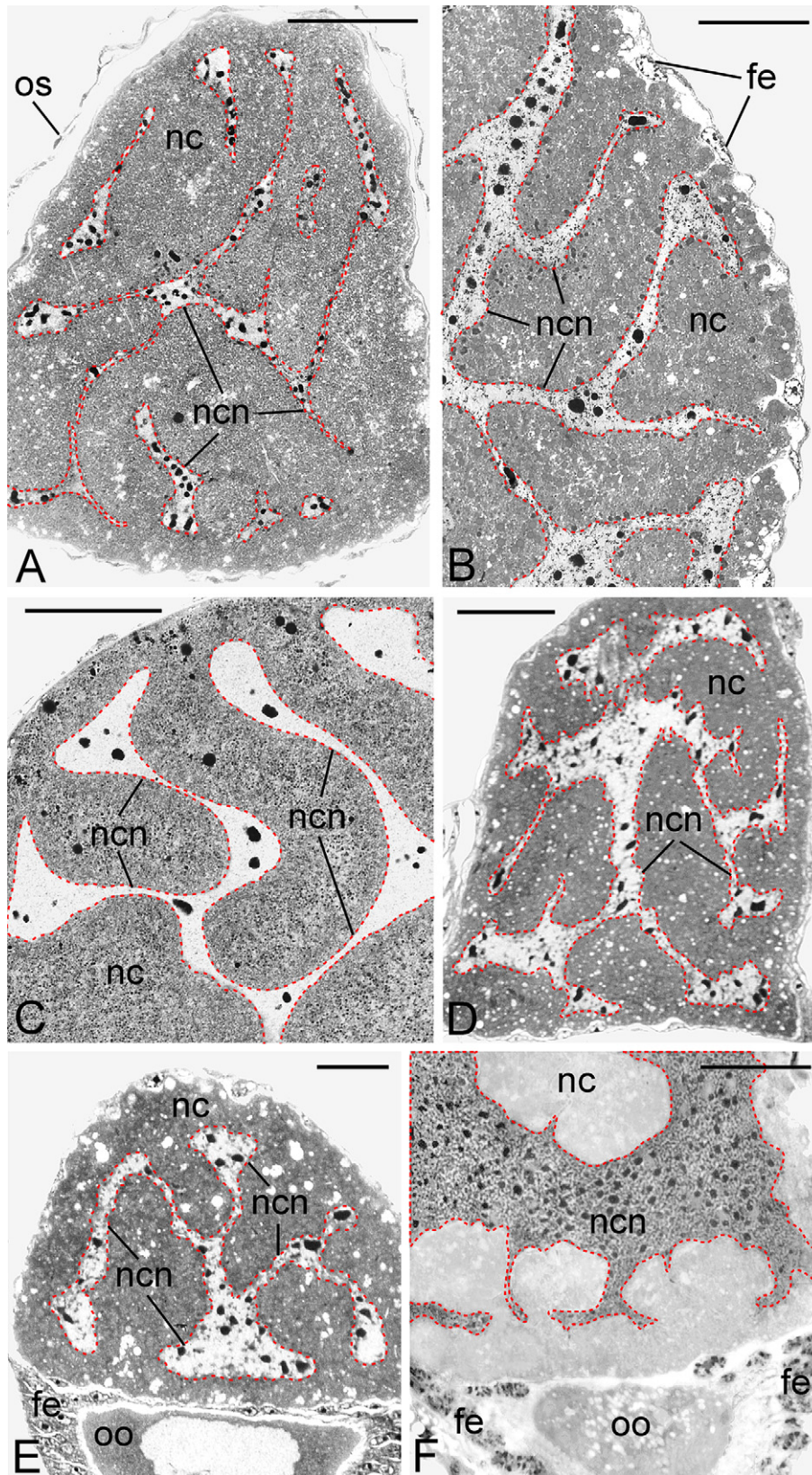
Fig. 3. Morpohology of nurse cells (nc) in derived (A–D) and basal (E, F) groups. (A) *Cosmiella bilobata* (Forficulidae), (B) *Forficula auricularia* (Forficulidae), (C) *O. silvestris* (Forficulidae), (D) *Eparchus forcipatus* (Forficulidae), (E) *L. riparia* (Labiduridae), and (F) *N. lividipes* (Labiduridae). Note that in all species nurse cell nuclei (ncn) are 'amoeboidal', and surrounded by highly folded envelope (red dotted outline); oocyte (oo), follicular epithelium (fe). Scale bars: 20 μm in (A–F).
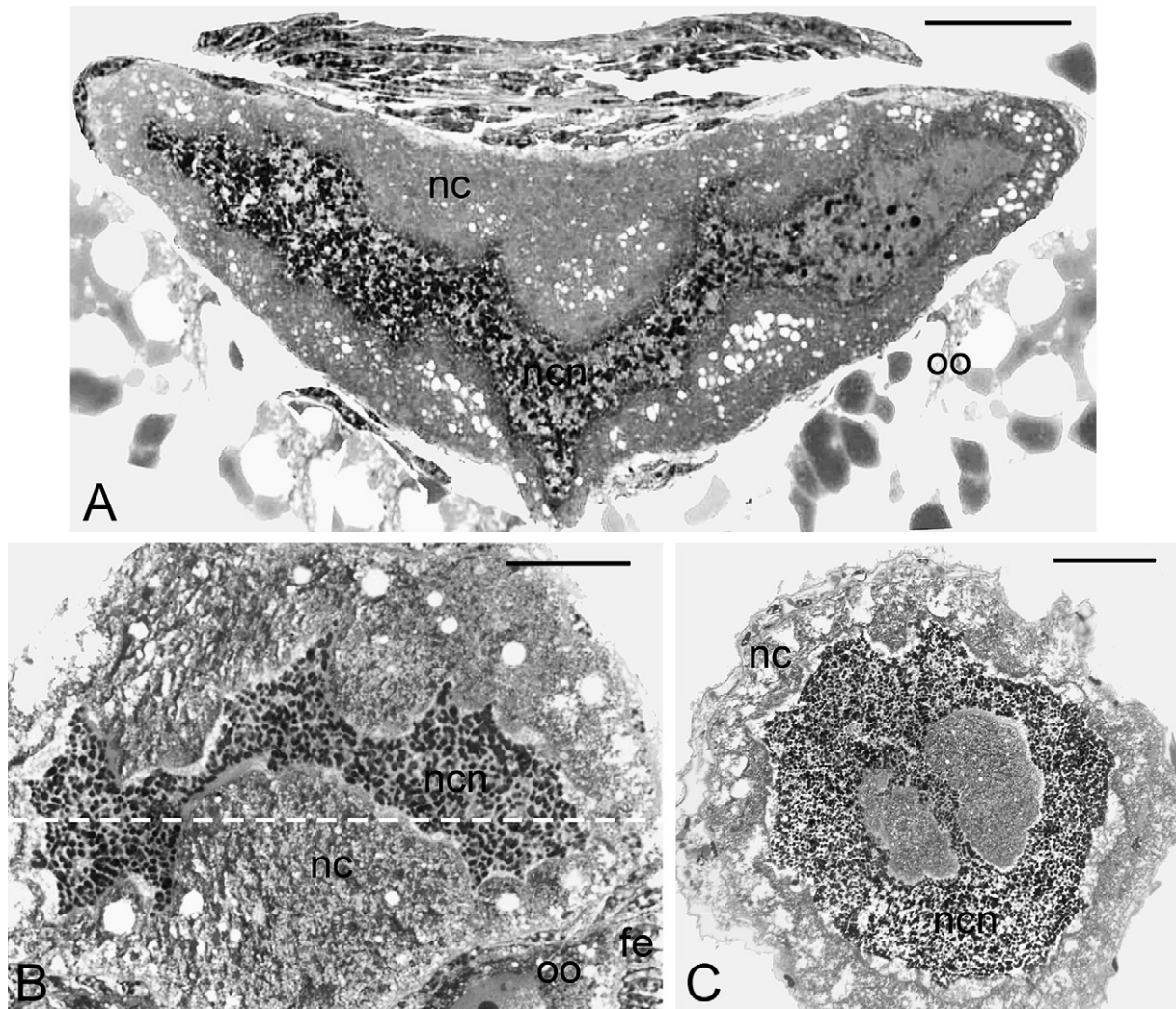
Fig. 4. Morphology of nurse cells (nc) in representatives of the most basal dermapterans: (A) *Cranopygia ophthalmica* ('Pygidicranidae'), (B, C) *Diplatys flavicollis* ('Diplatyidae'). The nurse cell nuclei (ncn) have more regular shape; (A, B) longitudinal sections; white dashed line in (B) indicates the 'level' shown in transverse section (C); oocyte (oo), follicular epithelim (fe). Scale bars: 30 μm in (A–C).

and the follicular cells migrating between the oocyte and the nurse cells), as it is the case in the Eudermaptera (see below). Only in the two most basal taxa available ('Diplatyidae' and 'Pygidicranidae') the morphology of ovarian follicles is slightly different. Analysis of serial sections has revealed that in *Diplatys flavicollis* and *Cranopygia ophthalmica* the nurse cell nuclei, even during later stages of oogenesis, have a more "regular" shape of a hollowed or partly hollowed hemisphere (Fig. 4).

3.2. Germaria and early stages of oogenesis in Eudermaptera

The ovaries of representatives of the Eudermapteran taxa, the Forficulidae, Chelisochidae and Spongiphoridae, are morphologically strikingly similar. They will be referred to here as the ovaries of the "Forficula" type. The ovaries of the investigated species are elongated and composed of 1–6 (Spongiphoridae: *Irdex* sp. and *Marava* sp.) or 20–40 (Forficulidae: *Chelidurella*, *Cosmiella*, *Doru*, *Eparchus*, *Forficula*, *Opisthocosmia*; Chelisochidae: *Proreus*) short meroistic–polytrophic ovarioles attached to long lateral oviducts by the ovariole stalks (Fig. 1B). The terminal filament is composed of 4–6 small disc-shaped somatic cells that are oriented perpendicularly to the long axis of the ovariole (Tworzydło et al., 2010).

The germarium comprises germline stem cells that are located at the tip of each germarium and are surrounded by specialized somatic "niche" cells (for further datails see Tworzydło et al., 2010). The remaining part of the germarium is filled with cystoblasts, and germ cell cysts in various stages of development (Fig. 2A and B). All the cysts consist of two cells, pro-oocyte and pro-nurse cell, only (Fig. 2A and B). This observation indicates that in advanced dermapterans, the cystoblast divides only once (see Section 1). The vitellarium is relatively short and comprises two ovarian follicles. Each follicle consists of an oocyte and a single, highly polyploid nurse cell that are surrounded by somatic follicular cells (Fig. 2A and B). During subsequent stages of development, the oocytes gradually grow and accumulate the reserve materials. As a result of that process, late vitellogenic oocytes are tightly filled with lipid droplets and yolk spheres. The nurse cells of "derived" species are large and contain amoeboidal (ramified) nuclei surrounded by deeply folded envelope (Fig. 3A–D). A detailed description of the morphogenesis of nurse cell nuclei has been published by Tworzydło and Biliński (2008). The follicular cells covering the early previtellogenic ovarian follicles form a continuous epithelium that during later stages of oogenesis becomes diversified into three subpopulations: (1) cuboidal follicular cells surrounding the oocyte,
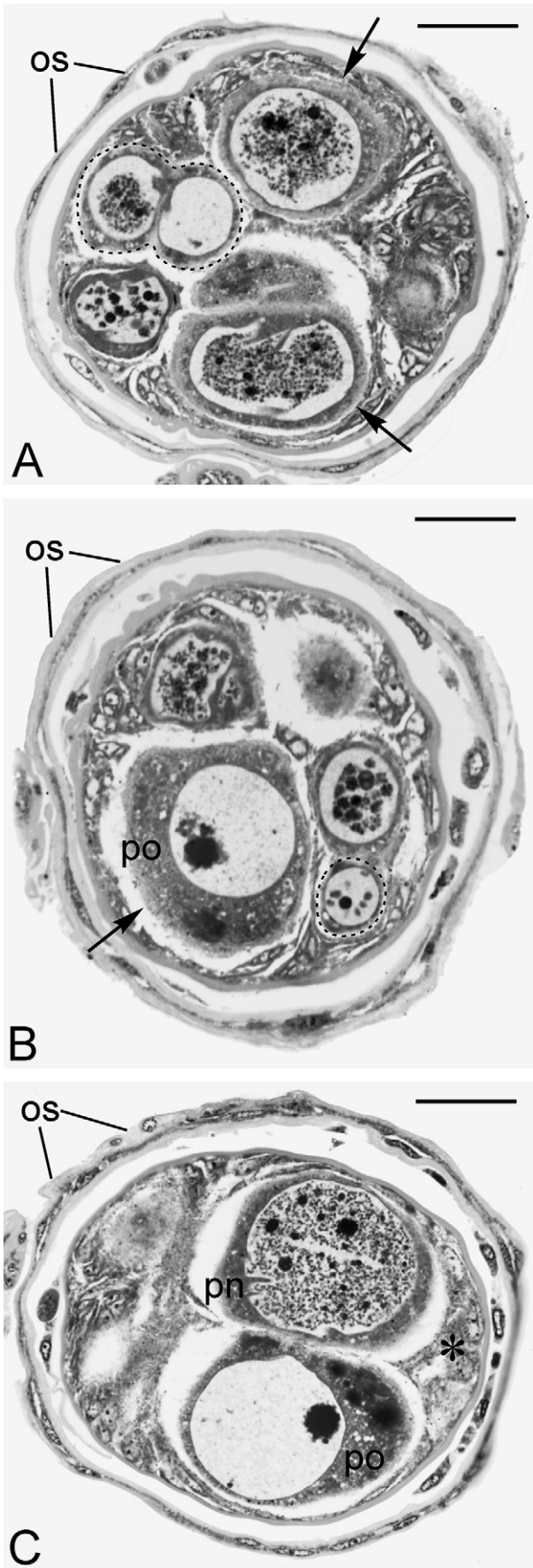
(2) small, stretched cells covering the nurse cell and (3) the follicular cells migrating between the oocyte and the nurse cells (for further details see Tworzydło and Biliński, 2008).

3.3. Late oogenesis

Subsequent stages of oogenesis in earwigs, i.e. vitellogenesis and formation of egg coverings on the oocyte surface have not been studied in detail. However, our observations indicate that they follow the same scenario in both described ovarian types.

3.4. Ovaries of A. esau

Our preliminary studies have shown that each ovary of this viviparous species is composed of 3 short ovarioles attached to a strongly dilated lateral oviduct. The oviduct contains developing embryos, and therefore might be regarded as the uterus. The ovarioles are meroistic—polytrophic and consist of a terminal filament, germarium and vitellarium. The germaria contain only 2-cell cysts of germline cells (Fig. 5A). Surprisingly, the growth of neighboring cysts is not synchronous. These observations indicate that in *Arixenia*, the neighboring cysts are formed independently, i.e. from different cystoblasts, as it was described in the Eudermaptera (Tworzydło et al., 2009). In the posterior part of the germarium, cysts differentiate and become invested with somatic follicular cells (Fig. 5B and C). Resulting ovarian follicles contain, besides the oocytes, the single nurse cells only (Fig. 5C). The vitellaria of *Arixenia* are relatively short and contain two ovarian follicles. All the above data suggest that the formation of germline cysts and the subsequent development of the ovarian follicles in *Arixenia* follow the pattern described in Eudermapteran species.

4. Discussion

Numerous comparative studies carried out on a wide range of insect groups indicate that the structure of the ovaries and ovarioles, i.e. the type of the ovariole, the number of mitotic divisions of the cystoblast or the number of the nurse cells in the ovarian follicle, are relatively stable characters on the 'family' or higher systematic level (Štys and Biliński, 1990). Our results based on histological data showed that,

1. Basal dermapterans ('Diplatyidae', 'Pygidicranidae', Anisolabididae and Labiduridae) are characterized by:
   - Short lateral oviducts.
   - Elongated ovarioles with several (more than 30) ovarian follicles in the vitellaria.
   - Low number (5) of ovarioles per ovary.
   - Secondary division of the 8-cell germline cysts into 4, 2 cell clusters (Yamauchi and Yoshitake, 1982; Büning, personal communication; this study).
2. The Eudermaptera and Arixeniina share 3 important characteristics:
   - Elongation of the lateral oviducts, transformed in the Arixeniina into dilated uteri.
   - Shortened ovarioles with a few ovarian follicles (2) in the vitellaria.

Fig. 5. The apical part of the ovariole of *Arixenia esau* (Arixeniina). (A, B) The anterior region of the germarium; germline cells forming 2-cell cysts are encircled. Note that relatively young cysts are located next to already differentiated ones (arrows). (C) The posterior part of the germarium. Note differentiated germline cyst composed of a pro-oocyte (po) and a pro-nurse cell (pn); follicular cells (asterisk), ovariole sheath (os). Scale bars: 45 μm in (A–C).

- Reduced number of mitotic divisions of a cystoblast to 1, which leads to the formation of ovarian cysts composed of 2 cells only.
3. The Forficulidae and Chelisochidae share:
   - High number of short ovarioles per ovary.

The process of secondary divisions of the germline cysts is unique and has never been reported in any other insects with meroistic–polytrophic ovaries. It might be compared only with the secondary division of the germline cysts into individual oocytes as described in some vertebrates (mammals, frogs and fish; Pepling and Spradling, 1998; Kloc et al., 2004, 2008; Marlow and Mullins, 2008), pycnogonids (Miyazaki and Biliński, 2006), and insects with secondary panoistic ovaries (Pritsch and Büning, 1989; Gottanka and Büning, 1990). The out-group comparison (the Blattodea and Orthoptera; see Štys and Biliński, 1990; Büning, 1993, 1994 for a review) and character distribution on the phylogenetic tree, suggest that the ovaries of the "Anisolabis" type (few and long ovarioles attached to short lateral oviducts) represent an autapomorphy of the Dermaptera as a whole, which then evolved into the situation described for the Eudermaptera and Arixeniina (see below). We do not consider this character as a potential autapomorphy for the basal Dermaptera, since none of the previous phylogenetic analyses indicates their (even weakly supported) monophyly. In this context, it is parsimonious to assume that the secondary division of the 8-cell germline cyst represents an autapomorphy of dermapterans, transformed later, during evolution, to the state (2-cell germline cyst) found in the Eudermaptera. Moreover, short oviducts and a low number of long ovarioles, being present in both out-groups, suggest a plesimorphic situation.

We have additionally shown that the number of ovarioles attached to the lateral oviduct in higher dermapterans is variable and attains from 1 to 6 (Spongiphoridae and Arixeniina) to more than 20 (Forficulidae and Chelisochidae). This supports two earlier findings. First, the monophyly of the Eudermaptera, and second, a sister-group relationship between the Chelisochidae and Forficulidae. The latter hypothesis has been suggested by Jarvis et al. (2005) but not by the morphology based analyses of Haas and Kukalová-Peck (2001). Our results suggest that the number of the ovarioles per ovary was low in the last common ancestor of the Eudermaptera, and is still in the Spongiphoridae, and was significantly increased in the common ancestor of the Forficulidae and Chelisochidae.

The Dermaptera are traditionally divided into three separate 'suborders', the Hemimerina, Arixeniina and Forficulina (see e.g. Popham, 1985; Haas and Kukalová-Peck, 2001). This division is based on their external morphology, distribution and, in particular, on their extremely different life histories. Whereas the monophyly of each epizoic lineage (the Hemimerina and Arixeniina) is well established, their relationship to the Forficulina is still controversial. The Forficulina, comprising all but approximately 40 species, are 'typical earwigs', i.e. free-living, feeding on plants or insects, oviparous and equipped with strong forceps, while the Hemimerina (not available for this study) are highly modified (e.g. Haas and Gorb, 2004) living on Gambian Rats (Cricetomys) in Africa. They feed on fungi and skin scales and are unable to survive without their hosts. As a consequence, viviparity significantly increases chances that the nymph finds the proper host. Klass (2001) studied some internal abdominal characters of Hemimerus (exoskeleton, musculature, nervous system) and suggested to nest Hemimerus within the Forficulina. The recent study of Jarvis et al. (2005) based on the molecular and morphological evidence indicated that the Hemimerina are not a sister-group to the remaining Dermaptera (i.e. the Forficulina), and should be placed as a sister-group to the Forficulidae + Chelisochidae. Interestingly, the structure of the ovary, i.e. few and short ovarioles, attached to an elongated lateral oviduct (Heymons, 1912; Hagan, 1951), supports this placement. Although the female reproductive system and ovaries of Hemimerus certainly need further studies (especially at a cytological level), and a placement of the Hemimerina as a sister-group of any of the Eudermapteran taxa (including the Arixeniina) is not strongly supported, the concept of a separate 'suborder' should be abandoned. The Arixeniina are also epizoic but live in a looser association with their major hosts, free-tailed bats (Molosiidae) in the caves in Malaysia, Indonesia and Philippines. Again, viviparity evolved to provide nymphs with an immediate contact to the preferred hosts. Phylogenetic relationships and taxonomical position of the Arixeniina remain unclear, mainly because this group was excluded from all recent phylogenetic analyses (Haas, 1995; Haas and Kukalová-Peck, 2001; Jarvis et al., 2005) due to the unavailability of material. Despite differences and autapomorphies, which are not relevant to decide on their placement within the Dermaptera, the shared characters of the ovaries (elongated oviducts, few and short ovarioles with low number of follicles) support the inclusion of the Arixeniina into the Eudermaptera. However, a placement of this taxon as a sister-group of any of the three Eudermapteran taxa, the Chelisochidae, Forficulidae or Spongiphoridae is not strongly supported. It is interesting to note here, that in two representatives of the Spongiphoridae, i.e. Marava arachidis (Yersin, 1860) (see Herter, 1943), and Chaetospania borneensis (Dubrony, 1879) (see Kočárek, 2009) the (ovo-)viviparity has also been reported. In our opinion, however, because the above spongiphorid species are not closely related, the viviparity observed in certain spongiphorids, as well as in arixenids and hemimerids, represent examples of a convergent evolution.

Unfortunately, we were unable to study 3 important Dermapteran taxa: the Karschiellidae, Apachyidae and Hemimerina. The Karschiellidae, an African taxon, is considered the most basal amongst recent Dermaptera (Haas and Kukalová-Peck, 2001; was not available in Jarvis et al., 2005). However, the males clearly possess highly derived genitalia and nothing is reported on the ovary structure. The Apachyidae are found in the hot–wet tropical areas of Africa, Asia and Australia, and are characterized by an extremely flattened body, which enables them to penetrate under bark. They might be most closely related to Labidurids or Anisolabids, and it would be interesting to study the effects of the extreme flatness on the ovary structure. It should be added here, that according to Klass (2001) the Apachyidae are related to the Hemimerina. This hypothesis has been based on the morphology of the abdomen. However, no further evidence has been brought forward to support or reject it. Jarvis et al. (2005) consider the Hemimerina as the sister-group of Forficulidae + Chelisochidae and Apachyidae close to 'Pygidicranidae' and Labiduridae.

Our studies have confirmed the earlier suggestions that characters derived from the ovary can be successfully used for the evolutionary reconstruction, at the 'family' or higher level. We have found no indication for lower (e.g. genus) level resolution. A key obstacle in evolutionary and phylogentic research in the Dermaptera is the unclear monophyly of some 'families', e.g. 'Pygidicranidae', Spongiphoridae, and Anisolabididae (see Haas and Kukalová-Peck, 2001; Jarvis et al., 2005, for further details). For better understanding of the relationships between dermapteran subtaxa, this issue should be re-investigated.

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