FOSSIL REMAINS IN KARST AND PALEOCLIMATE

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THE PALEOENVIRONMENTAL SIGNIFICANCE OF SOME LATE PLEISTOCENE (MIDDLE VALDAI) *DIPTERA* PUPARIA (*CALLYPHORIDAE*) FROM THE EMINE BAIR KHOSAR TRAP-CAVE (CHATYRDAG, CRIMEA)

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Introduction

Climate signals from terrestrial records are extracted with a wide range of techniques, some of them based on biological evidence. In this respect, the coleopteran records and chironomid evidence seem to offer great potential (Walker, 2001). Other dipteres (including flies) also became important for palaeoenvironmental and climatic reconstructions. Their remains were found in various Quaternary sediments (especially peat bogs, permafrost, organic silt/sand, etc.), but also, recently, from cave deposits. Fossil or subfossil fly puparia are commonly recorded mainly from archaeological sites (Egyptian mummies, Mexican tomb shafts and various settlement organic sediments) but also from Pleistocene deposits in Western Europe, associated to large mammal bones (Germoupre & Leclercq, 1994). Late Pleistocene fly puparia were described from steppe wisent horn core cavities and woolly rhino skulls in Late Eemian—Weichselian fluviatile deposits in Belgium (Gautier & Schumann, 1973). In North America, fly puparia are also found in Pleistocene open-air sites (Matthews & Telka, 1997) and caves (Bain et al., 1997). The preservation and/or mineralization of such organic remains in caves are linked to particular micro-environments.

Paleontological investigations carried out in caves from the Crimean high mountains (Crimea peninsula, Ukraine), especially on the Chatyrdag karst plateau (985 - 1527 m a.s.l.), revealed some interesting trap-caves containing passive vertebrate mass accumulations (Vremir and Ridush, 2002; Ridush and Vremir, 2004). The most interesting site is the Emine Bair Khosar (EBK) cave, which functioned as a natural trap at least for the last 50.000 years. Eleven paleontological sites were investigated inside this cave, providing over 7.000 identified specimens belonging to more than 40 vertebrate species (mammalian, avian and herpetological materials) as well as human remains. Beside the huge amount of vertebrate fossils (Vremir and Ridush, 2005), the invertebrates are represented by terrestrial snails marked by entrapped species (Helicidae) as well as troglophylic species (mainly Enidae) and insects. For this study, insect remains represented by Diptera (fly) puparia were collected from certain levels of EBK-Bc and EBK-Be2 sites. The preservation state of the organic remains (including fairly well preserved dung and stomachal content remains associated to a complete mammoth skeleton) suggest special taphofaciesal conditions.

Task orientation

The necrobiotic processes include the cause and mechanism of death of an organism as well as the decomposition until the last stage of decay. In vertebrate carcass decomposition, five stages are separated until complete skeletonization, each characterized by particular biochemical and physical transformations (Blanco, 1992). The insects are the first opportunistic organisms which start to recycle the decomposing tissues. The succession of insects from the initial colonization of the carcass until skeletonization is predictable and important for forensic enthomologists to determine the moment of death. Insects feeding directly from carrion are known to arrive within minutes of death, followed by necrophagous/predatory organisms of a wide taxonomic variety. Among the first arriving insects very important are certain flies, especially the Callyphoridae and Sarcophagidae (blow and flesh flies). The development stages of fly larvae are well documented (Kamal, 1958) and forensic enthomologists have shown the effect of various environmental conditions on the rate of maggot development, one of the most important being the air temperature. Because the physical environment directly affects the development cycle of larvae, the comparative base of forensic enthomology linked with additional paleontological, palynological and sedimentological data can be used to determine the paleoclimatic and paleoenvironmental conditions during the carcass accumulation in the EBK trap cave.

From a meroclimatic point of view, the paleontological sites providing autochtonous fossil fly puparia are located at the limit of the entrance and interior facies of the cave, under the influence of seasonal temperature variations. The insect colonization activity could indicate minimal temperature values, according to the tolerance regime of particular taxa. This is the first attempt to determine the meroclimatic conditions in some caves of the Crimean high mountains during the early-middle Valdai cold stage.

Site description

EBK, the largest cave in the area, is a good example of multiphase karst system with a total length of 1460 m and a depth of -125 m. Morphological data and its presumed development stages were discussed by Dubliansky et al. (1987) and Vremir & Ridush (2005). The collapse pit entrance (7-8 m diameter, 13.3 m deep) is located on the northern edge of the Chatyrdag plateau (990 m a.s.l.) and was opened by erosional processes. The present day meroclimatic regime inside EBK cave (according to the Onyx Tour database), varies trough the whole year, summer (July) mean temperatures measured at Museum chamber and Middle Bair passage (close to the fossiliferous sites) are 5.5 – 6.2ºC.

EBK-Bc site represents an ascendant passage and a small room located at the depth of -41 to -37 m and somewhat below the main debris-cone. Hundreds of pupal remains were recovered by screenwashing from units EBK-Bc2b and EBK-Bc3. The mineralised (calcium phosphate) pupal cases were more or less dismembered. Even if the majority of pupal remains are rather fragmented, there is no doubt on their autochtony. EBK-Be2 site is located 25 m from the end of the main passage, 15 m under EBK-Bc at the depth of -53 m. The 25 complete puparia found in emerged stage were collected from around a disarticulated saiga antelope skeleton. Generally, the preservation is linked to very high organic matter content of the sediment in the entrance facies of this peculiar cave type, providing a rather good preservational microenvironment.

Species identification

The puparium of flies (Figure 1) is composed of the outer skin of the 3rd instar stage larvae, retaining many characteristics important for species identification. Larvae of most Callyphorid species are scavengers of carrion and dung and most likely constitute the majority of the maggots found in such material, however very few Pleistocene fossil species have been identified. From both sites, the pupal cases were found in emerged stage (empty). Most pupal remains from the Bc site are fragmented and difficult to reconstruct, but the general morphology, structure, size and colour are characteristic to Calypterate (Smith, 1931). The pupae from Be2 site are better preserved mainly because of the depositional setting and collecting technique. The puparia belong most likely to the Callyphoridae (obviously a cold and shade tolerant species). Size differences could be influenced by environmental factors (especially low temperature), carcass size and decomposition stage. The EBK pupae (5-7 mm in Be2 site, less than 6 mm in Bc site) are significantly smaller than those of P. terranovae and the majority of Sarcophagidae. Until we obtain a more precise taxonomic identification, we must note that certain differences exist between the development stages of various species, but in low temperature conditions (especially under 10oC), the larva- and/or oviposition rate and development trend decrease significantly and show statistically quite similar values in all common species (Ames & Turner, 2003).

Entomo-etological analogies and comparison

In order to define and evaluate the climatic and/or environmental signals potentially extracted from the fly-puparia materials, the most important analogies are listed following forensic-entomological studies (see also Figure 2).

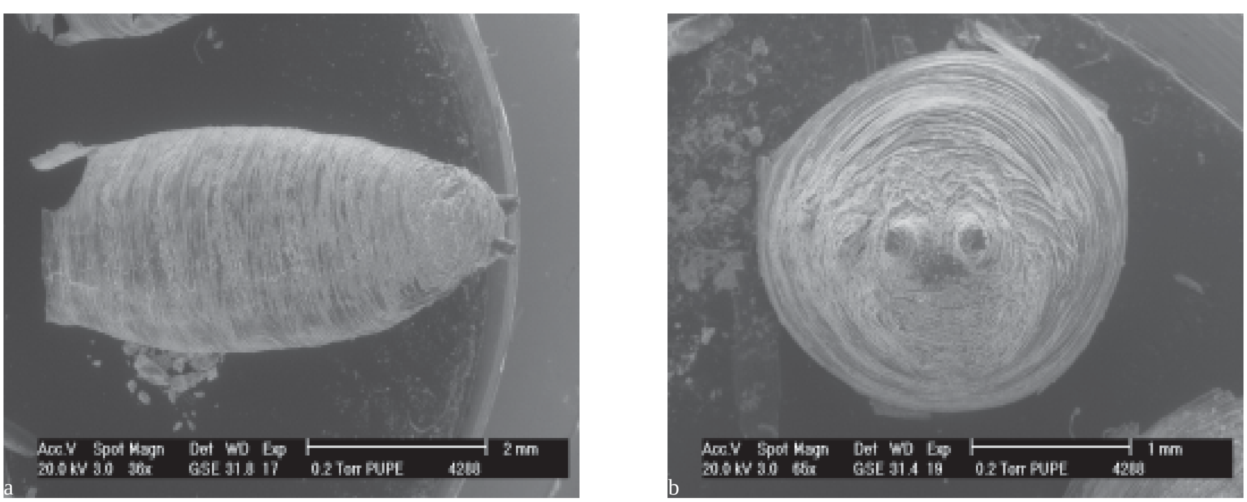

Figure 1. Puparia of blow-flies (Callyphoridae) from EBK cave (Chatyrdag, Crimea): a - puparia in emerged stage in lateral view; b - same in caudal view, showing the pair of cylindrical processes.

Nocturnal behavior

Blowflies are inactive at night, oviposition being expected only during the day. A substantially reduced oviposition rate at night or in a cave entrance facies (30%) may be obtained only due to the attraction of new food sources. A decomposing carcass will attract certain species (especially Callyphoridae) however the low temperature will substantially influence the structure, oviposition and larvae development rate of the invading species. In EBK-Be2 and possibly in EBK-Bc, monospecific colonization is registered. The distribution and number of puparia - dispersal index (which not necessarely indicate the number of initially developing maggots), is quite low in EBK Be2 and rather high in EBK Bc, comparing to the size of colonized carcasses. The high dispersal index could indicate a temperature regime warm enough (over 5-6ºC) to permit the successful development of a large number of pupae.

Sheltering

The larvae number decreases proportionally to the decomposition stage. Callyphores are more suitable than Sarcophages to colonise and oviposit in shade and sheltered settings as well as caves, even in low temperature regimes.

Oviposition

The females of blow and flesh flies deposit eggs or larvae mainly in and around the natural orifices of the carcass. Adult Callyphores oviposit, and some species are known to lay their eggs only outdoor (cave environment excluded). The initial species structure and colonisation of carrion depends by the enviromental conditions and carcass size (Davies, 1999). A larger size carcass in open land is rapidly colonized by different species producing full sized individuals (the size of carcass could eliminate the competition). In a cave, even in large size carcasses, the limitative environment will directly influence the oviposition procedure, the maggot-cluster size and their development trend, so that undersized larvae could occur.

Development

The larvae (1st instar) feed rapidly and shed their skins (2nd instar). Feeding and growing rate accelerate and the outer skin develops completely (3rd instar larvae) before migrating from the food source to pupate. After roughly two weeks (in normal temperature conditions) an immature adult fly emerges from the rigid pupal case. The development rate of the larvae varies significantly due to temperature variations (Kamal, 1958; Anderson, 2000. The developmental sensitivity and increased mortality of pupating larvae to low temperature is explained by the pupae increased metabolic demands due to extensive tissue remodeling (Myaskowiak & Doums, 2002).

Migration

Fully developed larvae (3rd instar) normaly migrate away from the carcass in order to find a suitable site to the prepupal and pupal stages. The distance varies depending on the substrate (burrowing) and/or presence of shelters, puparia frequently being reported from below or around the carcass. In EBK the empty pupal cases were found closely around and under the carcasses. In the Bc site it is difficult to determine a precise distribution, however they were commonly found around and under large herbivore skeletons in several units. This could idicate that carcass accumulation and their colonisation was a common and foregoing process and certainly not an isolated event.

Temperature as influencing factor

Low temperature has been reported to stop insect development under 4ºC and even if oviposition takes place, the larvae cannot fully grow. Diapause and quiescence are the main physiological responses to low temperature condition (Myskowiak & Doums, 2002). Diapause is a period during which growth and development of the insect is suspended, while quiescence is a drop in insect metabolism in response to a drop in temperature and only stops development for a short time, having effect on biometry as well. Only the rigid pupal case (puparium) could be fosilized, thus the larve must have reached the 3rd instar stage prior to temperature decrease.

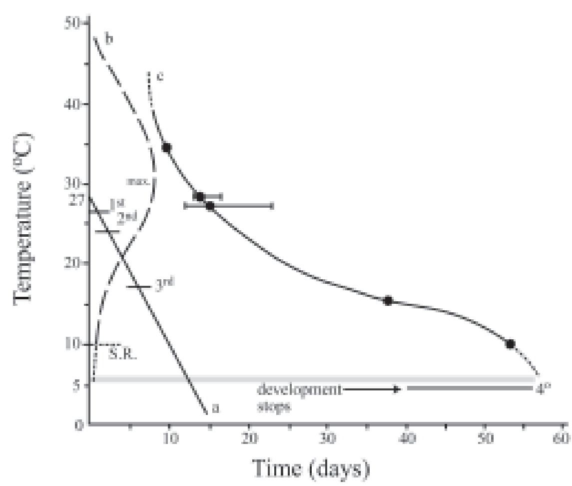

Figure 2. General trend of maggot development in common callyphorid and sarcophagid species according to temperature (data compiled according to Anderson (2000), Kamal (1958) and Smith (1931)): a = instar stages 1 - 3 in days at 27ºC and 50% humidity (pupal stage over 14 days); b = general trend of oviposition (maximum at 35ºC, insignificat below 10ºC); c = development speed of larvae (significant decrease below 10ºC, disruption at 4ºC). S.R. – significant reduction of oviposition and development speed. Gray bar represents mean July temperature (2004-2006) in EBK cave.

Other palaeoenvironmental indicators

Pollen unit 2 is characterised by an open landscape (with *Artemisia*) followed by a more forested environment dominated by *Pinus* (unit 3). Malacofauna consists of terrestrial snails, represented by xerophytic species with temperate affinities. *Helix albescens* is regarded as entrapped specimens, however some Enidae are shade-demanding but characteristic of dry-ground open habitat, retreating in caves during winter and forming huge colonies. Their winter survival requires temperatures over 4°C. Herpetofauna is represented by lizards and snakes, some of them warmth-demanding. The presence of Colubridae within unit 3 could indicate the proximity of a forested environment. Avifauna - most specimens belong to juvenile mountain chough *(Pyrrhocorax graculus*) and rock dove (*Columba livia*), quite frequent in European alpine karst , representing rests of pray associated to the peregrine falcon (*Falco peregrinus*) identified within unit 2. The sky lark (*Alauda arvensis)* is also typical for open landscapes, but the the field fare (*Turdus pilaris*) and eagle owl (*Bubo bubo*) in unit 3 are linked more to wooded areas, even if the owl prefers hunting in open landscapes. Theriofauna - the herbivores are represented mainly by steppe species (*Bison priscus*; *Saiga tatarica/borealis*; *Equus hemionus*; *E. cf. latipes*) within unit 2, including also arctic elements (*Mammuthus primigenius*, *Coelodonta antiquitatis*). Unit 3 is dominated by cervids, indicating wooded areas. The carnivores are represented mainly by the steppe fox (*Vulpes corsac*) and wolf (*Canis lupus*) and the steppe polecat (*Mustela eversmanni*), indicating an open landscape. The abundance of saiga antelope and steppe fox all year long year indicate mild winters and very low snow accummulation. The arctic elements (especially mammoth and wooly rhino of unit 2) are probably linked to winter migration events.

Discussion and conclusions

From a chrono-stratigraphic perspective based on the faunal assemblages and ^{14}C AMS ages, the bone accumulation belongs to the early-middle Valdai cold stage (~ 40 Kyr. BP). The whole EBK-Bc section indicates a warming episode, from cold steppe (Bc2 a) to warmer dry steppe (Bc2 b - Bc3 a), preceded by a cold phase (Bc1 part). The upper unit (Bc3) indicates transition to a more forested (*Pinus* - dominated) and wet environment in the vicinity (Vremir and Ridush, 2005). This is most probably a warming episode within the OIS3 correlable with the lower Vitachev soil complex (Ukraine) and upper Moershoofd (The Netherlands), respectively Krasnaya Gorka (NW Russia) warm phases.

Brief (100–1000 years) and sharp climate oscillations mark OIS3 (57-24 Kyr BP) in the Greenland GISP2 and GRIP ice cores. The NW European pollen records display a number of warm intervals, such as Moershoofd (49–41 Kyr BP), Hengelo (39–36 Kyr BP) and Denekamp (32–28 Kyr BP). Similar oscillations, that might correspond to events in the North of the Alps, have been identified in Southern Europe (Van Andel & Tzedakis, 1996). As the fine structure of OIS3 still needs chronological improvements, the precise correlation with East European climatic oscillations is still problematic. Pedostratigraphical and palinological studies in Dniper valley in central Ukraine indicate a series of climatic and environmental variations during this interval (Rousseau et al., 2001). The succession of loess and soil complexes suggests rapid vegetational changes during the early and middle Valdai, especially in the interval of Pryluky and Vitachev soil complexes (70–27 kyr BP). According to Gerasimenko (2004), the Vitachev phase (50-27 Kyr BP: ^{14}C and ESR dating) in Ukraine was characterised by the spreading of brown forest soils. Several soil horizons divided by loess are recognised, belonging to vt1 and vt2 stages. During the substages vt1b1 (approx. 44-50 Kyr BP, correlated to Moershoofd) and vt1b2 (approx. 39-44 Kyr BC, correlated to Hengelo), the Crimean foothills were characterised by forest-steppe. A cooling event (vt1b1/b2, correlated to Hasselo) is marked by loess formation, interbedded between the vt1b1 and vt1b2 soil horizons; the decrease of deciduous species and extension of steppe characterized the Crimean plain.

According to Van Andel & Tsedakis (1996), a brief interstadial event, about as warm as today, which seems to have followed a previous phase somewhat drier and colder than present, has occurred in NW Europe approximately 43 to 41 Kyr BP. The warmth ended suddenly, with a switch to an extreme cold phase (probably correlable to H4 Heinrich event). The sparse datings on the Vitachev soil complex, as well as the lack of comprehensive pollen diagrams and the few radiocarbon ages from the EBK section, cannot precisely indicate if the whole Bc sequence includes the equivalents of upper Moershoofd and Hengelo warm phases (49–36 kyr BP), or is restricted to a single warming event. The palynologic and paleofaunistic data show a gradual warming (from unit Bc 2a to Bc 3) which may be contemporaneous with a Mousterian butchery-site from Western Crimean lowlands (39.8 +/- 5 kyr BP; Patou-Mathis & Chabai, 2003). The paleoecological context, pollen and faunal assemblage indicate a mild period (a transition from steppe to forest-steppe), similar to that registered in EBK cave.

Taking account of the present day geomorphologic features of the area (steppic plains and dry grassy or forrested hills in the N, high mountains reaching 1540 m a.s.l., and plateaus with abrupt, forested or rocky slopes to the Black Sea coast in the S), a huge variety of environments and biotopes are represented. The temperature variations over the mountains from North (plains) to South (sea coast) are remarkable, with winter gradients of +/- 10°C. The main reason of such differences is represented by the proximity of the Black Sea and the warm Anatolian current (from the E), and by the chain of the Yayla mountains, protecting the Southern coast from Northern cold winds. Even if we consider the no-analog palaeoenvironments of the Late Pleistocene, and especially the status of the Black Sea basin, the Crimea certainly had a complex environmental and local-climatic structure and particular biomes. The sea (or a brackish lake) probably functioned as a natural thermostat, keeping temperatures higher in Southern Crimea than to the North in the Ukrainean plain. Crimea functioned as a refuge even for relict mediterranean species. This particular geomorphologic situation could explain why this mid-Valdaian warming event could eventually be more pronounced here (even in higher altitude) than in other regions of Central and East Europe.

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