POINT-OF-VIEW

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An attempt to reconstruct the natural and cultural history of the granary weevil, *Sitophilus granarius* (Coleoptera: Curculionidae)

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Abstract. It is generally accepted that stored grain insects are food opportunists and, when originally made the transition to man-made storage facilities, came from natural reservoirs like bird or rodent nests. This may not be true for *Sitophilus granarius*. Among all stored-product insects, the granary weevil *S. granarius* is the only species never recorded outside of storage facilities. Anatomical, physiological, and behavioural aspects of recent and hypothetical ancestral species in the genus *Sitophilus* are presented and discussed in terms of adaptation to the anthropogenic storage of grain. Full development inside the host kernel, endosymbioses with bacteria, and the reduction in flight activity to prevent water loss in a dry environment can be regarded as pre-adaptations for the evolution of a full synanthropic grain pest of cosmopolitan distribution. Faunistic, archaeological, and historical evidences of the pest's origin and spread in conjunction with early agriculture are reviewed to support a hypothesis of a co-evolutionary event with the dawn of Neolithic agriculture.

INTRODUCTION

A wide variety of insects can be found in durable stored food products of plant and animal origin. They are generally denoted as stored-product insect pests (Reichmuth et al., 2007). They are food opportunists that possess wide ecological potency for biotic and abiotic parameters. Almost all insect species that can be found in human-stored products can also be found outside of storage facilities, nidicolously in birds nests, anthills, or rodent nests, on ripe seeds and fruit in fields, in layers of leaf litter, under bark, or on carrion (Heselhaus, 1925; Nordberg, 1936; Linsley, 1944; Weidner, 1961; Khare & Agrawal, 1964; Buckland, 1981; Cogburn & Vick, 1981; Crowson, 1981; Wright et al., 1990; Ramirez-Martinez et al., 1994; Levinson & Levinson, 1998a; pers. observ.). Most of stored-product insects can actively cover large distances in the search for suitable food and breeding substrates (Hagstrum et al., 1996), and they only become stored-product insect pests when they occur in mass in or on an artificial accumulation of these substrates. The life-form type "stored-product pest insect" as such thus does not really exist from an ecological viewpoint. One exception to this is the exclusively synanthropic granary weevil, *Sitophilus granarius* L., which appears to be perfectly adapted to the man-made artificial grain storage system and which has up to day not been observed in natural reservoirs.

Sitophilus granarius is of significant economical importance and must be, in comparison to the generally heterophagous stored-product pests which feed on food of many different sources, viewed more as an oligophagous granivore. The granary weevil primarily afflicts grains such as wheat, barley, rye, and oats, as well as triticale, corn, rice, millet, and sometimes manufactured pastas (Dobie & Kilminster, 1978; Schwartz & Burkholder, 1991). The complete development of its larvae – from the egg to the imago – takes place hidden within the interior of the grain kernel. Unlike other stored-product insect pests, the granary weevil cannot fly; its elytra have become fused, the hind wings and the flight muscles have been significantly reduced (Andersen, 1938; Longstaff, 1981). Therefore, *S. granarius* cannot cover large distances on its own, its propagation is tied to the conveyance of infested grain and/or the suitable food substrates. There are no reported findings of this species in open nature. This strong dependence upon and adaptation to grain storage and trading, and the propagation through humans, could be the result of a co-evolutionary process of the domestication of grain and the sedentary settlement of humans in Neolithic agriculture with its intrinsic storage of supplies. In order to evaluate this hypotheses, the putative morphological, physiological, and ethological adaptations and predispositions of *S. granarius* and its predecessors to the grain storage biotope must be observed and reconstructed in comparison to the next recent relatives of the granary weevil.

TAXONOMY OF THE GRANARY WEEVIL AND OTHER SPECIES OF *SITOPHILUS*

The granary weevil is a small black-brown weevil. Its size, which depends primarily on its food supply and the size of the developmental grain (Surtees, 1965), varies between 3.8 and 5.1 mm (including the rostrum). At 25°C and high relative humidity, the developmental period for one generation averages 40 days. Their lifespan ranges between several months to about one year, and the mature weevils also ingest food and cause damage to stored grain. When the young weevil emerges from the kernel, it does not yet have the characteristic black-brown colouring, but is reddish brown, which is why they are called "red" and later "black" granary weevils in some regions.

Sitophilus granarius was initially scientifically described by Linnaeus (1758) as *Curculio granarius.* Linnaeus (l.c.) also described the so-called "red granary weevil" as *Curculio* (later *Attelabus* or *Apion*) *frumentarius*, which was regarded in the literature as a separate species into the late 19th century. The generic name *Curculio*, originally comprising most of the weevils including the granary weevil, was later used for naming the entire group of snout beetles, or weevils (the current superfamily Curculionoidea), and of true weevils (the current family Curculionidae), whereas the generic name *Curculio* gradually became more restricted. Already Müller (1774) states that …"The Latin name *Curculio*, etymologically derived from Gurgulio (meaning throat) by some, has since been denoted only to the species that prefer to devour seeds and kernels in a devastating manner…" (translation into English of Volume 1, part 5, p. 210 of the German translation of the 12th Latin edition of the "Systema Naturae").

In 1798, De Clairville & Schellenberg established the genus *Calendra* (spelled with "e" in the original text) or *Calandra* (spelled with "a" in the illustration caption) and classified the granary weevil, among others, within this genus. This apparent printing error was often discussed subsequently (Cotton, 1924; Müller, 1927; Andersen, 1938). The fact that the spelling "*Calandra*" finally won out is only of historical relevance, as the term "*Sitophilus*," which was introduced in 1838 by Schoenherr, was declared for the genus in 1959 by the International Commission on Zoological Nomenclature (Riley & Melville, 1959). The rice weevil, *Sitophilus oryzae*, a stored-grain pest, which was described as *Curculio oryza* by Linnaeus in 1763 and was collected in a rice shipment from Surinam (name amended by Riley & Melville in 1959), is also included in this genus, as is the maize weevil, *Sitophilus zeamais*, which was collected in corn samples from Cayenne and described by Motschulsky in 1855. Due to the very great morphological similarity between the rice and maize weevils, they have often been mistaken for one another in the past, or not considered to be different species but rather different races. To add to the confusion, the presumably smaller race of the rice weevil, which corresponds to what today is called the rice weevil (*Sitophilus oryzae*), was called *Calandra sasakii,* and the presumably larger race was called *Calandra oryzae,* which corresponds to what today is considered to be the maize weevil (*Sitophilus zeamais*) (Kiritani, 1959; Kuschel, 1961; Frey, 1962). Both species can rightly be considered to be "twin species" or "sibling species" to reflect their extreme similarity but not necessarily their phylogenetic relationship as sister species (Birch, 1944; Hidayat et al., 1996). A certain morphological differentiation between the two species is only possible according to the shape and size of the genitalia (Frey, 1962; Khan & Musgrave, 1968).

Delobel & Grenier (1993) augmented the last revision of the genus *Sitophilus* by Csiki of 1936 and recognised fourteen species. In addition to the three above-named species and the tamarind weevil (*Sitophilus linearis),* which was described as *Rhynchophorus linearis* by Herbst in 1797 found in tamarind seeds from the West Indies, these are as follows: *S. conicollis* Marshall, *S. cribrosus* Pascoe, *S. erosa* Marshall, *S. glandium* Marshall, the unverified species *S. gotschii* Hochstetter, *S. quadrinotatus* Wiedemann, *S. rugicollis* Casey, *S. rugosus* Thunberg, *S. sculpturatus* Gyllenhal (synonymous with *S. shoreae* Marshall) and *S. vateriae* Marshall. The species described by Zherikhin (2000), †*Sitophilus punctatissimus*, is only documented by a fossil. The holotype originated from rocks from the Rhône Alps near Andance in Ardèche (France) and is dated in the Lower Miocene.

REGION OF ORIGIN AND DISSEMINATION OF THE *SITOPHILUS* SPECIES

Due to their economic impact worldwide as stored-product pests, as well as to that fact that they are an easily bred object for study, the written records are exceptionally numerous for at least those *Sitophilus* species that cause damage to stored grains. The granary weevil primarily causes economic damage in the Mediterranean area, in Middle Europe, in the temperate climates in Asia and North America, and in Australia. In contrast, the rice and maize weevils are often found in the warm and humid lowlands and tropical areas. The ecological potential of the rice weevil also allows it to appear in part in more moderate climates (Longstaff, 1981). The dissemination of *S. linearis* is closely related to its appearance in its host and forage plant, the tamarind (*Tamarindus indica*, Caesalpiniaceae). The tamarind, also called the Indian date, is either of Oriental or African origin and was introduced into the Neotropics by the Spaniards after the discovery of the New World. With it came the *S. linearis*, as well (Cotton, 1920). As far as is known, the tamarind weevil naturally only breeds on the mature seeds of the *T. indica*.

Very little is known about the biology of additional species of *Sitophilus. S. glandium*, *S. rugicollis*, *S. rugosus*, *S. sculpturatus* and *S. vateriae* breed on the seeds of *Quercus incana*, *Q. leucotrochophora*, *Q. floribunda* and *Q. dilatata,* as well as on the seeds of trees in the Dipterocarpaceae and Fabaceae families in temperate to subtropical mixed forests of the Orientalis, from the southwest and south sides of the Himalayas all the way to the Indian subcontinent (Marshall, 1920, 1940; Weidner, 1983; Kaushal et al., 1993; Nardon et al., 2002). As far as is known in the breeding biology, all species of *Sitophilus* develop from egg to pupa inside the kernel of their host plants. The female deposits the eggs with her ovipositor in an oblong hole in the kernel, which she prebores with her mouthparts. Then the egg cavity is sealed with a clear and sticky secretion. For *S. linearis* and *S. glandium*, it is known that the host kernel can hold multiple eggs (Cotton, 1920; Kaushal et al., 1993). With only a few exceptions, for the stored grain pest species *S. granarius*, *S. oryzae* and *S. zeamais,* each kernel only hosts one egg. During the larval period of the beetle, the kernel is completely hollowed out. Once the adult beetle emerges from the pupa, it remains for a short time inside the kernel until it has bored its way to the outside.

While both the rice and maize weevils have been observed feeding on stored grain, as well as on ripe fruit and mature grain in fields (Kirk, 1965 cited in Grenier et al., 1994a; Taylor, 1971; Fleurat-Lessard, pers. commun. 2009), this behaviour – as previously mentioned – has never been observed for the granary weevil. Interestingly, the stored-product pest weevils not only can be found on grains, but can also, under laboratory conditions, successfully breed on acorns and chestnuts (Zacher, 1931; Howe, 1965; Delobel & Grenier, 1993). The later hold also true for *S. linearis* (Cotton, 1920). The breeding and the propagation of non-stored-product pest species of *Sitophilus* on grains, on the other hand, are not, or only limitedly, possible (Cotton, 1920; Delobel & Grenier, 1993; Nardon et al., 2002). For the species *S. conicollis*, *S. cribrosus*, *S. erosa*, *S. gotschii*, and *S. quadrinotatus*, which are also native to the Orientalis, there is insufficient knowledge about their host plants (Delobel & Grenier, 1993).

In conclusion, the extant *Sitophilus* species can be considered to be endemic to the forested areas of the Oriental Region. The stored-grain pest species *S. granarius*, *S. oryzae*, and *S. zeamais*, whose worldwide propagation is the result of the global grain trade, and *S. linearis*, whose pantropic incidence can also be traced to the human trading of its host plant, are with great likelihood also of Oriental origin (Buckland, 1981; Weidner, 1983). Supporting this, the western to middle Orientalis is considered to be the area of origin of the tamarind and most of the agricultural grain crops. The area of origin of the grains that were cultivated early on by humans, especially the distichous barley crop *Hordeum distichum*, wild einkorn *Triticum monococcum*, and emmer wheat *Triticum dicoccum*, lies in the Fertile Crescent in the Middle East (Flannery, 1973; Hammer et al., 1997; Fesq-Martin, 2000; Murphy, 2007).

PREDISPOSITION FOR UTILISING STORED GRAINS

How the facultative transition to grain kernels as the breeding and nutritive substrate for one or more species of *Sitophilus* came to be may never be explicable in detail. However, one important prerequisite for this transition was the possession of endosymbiotic bacteria, so-called SOPE (Sitophilus oryzae primary endosymbionts), which were first characterised for *S. oryzae,* later for S. *granarius* and *S. zeamais,* and more recently also for *S. rugicollis* (Mansour, 1930; Nardon, 1971; Nardon & Grenier, 1988; Heddi et al., 2001; Nardon et al., 2002). These gram-negative bacteria of the gamma 3-proteobacteria group exist freely in the cytoplasms of adult beetles, are passed onto future generations via the oocyte by a complex transmission during oogenesis (Nardon, 2006), and are found in the larva in the bacteriomes (mycetomes) at the junction between the stomodeum and the midgut. They play a decisive interactive role with the host for the effective and efficient metabolism of nutrients (Heddi & Nardon, 2005). There are clear indications of gene interactions between bacterial and host genomes including gene transfer (Shen et al., 2005; Anselme et al., 2008; Gil et al., 2008), and that the symbiotes are directly involved in the metabolism and catabolism of the beetles (Heddi et al., 1991, 1993, 2001, 2005). SOPE-free laboratory strains of the stored-grain pest species of *Sitophilus* display extreme delays in larval development on grain without additional nutrients (Lum & Baker, 1973) and for adult rice and maize weevils, the loss of the ability to fly (Grenier et al., 1994a). By possessing endosymbiotes, the respective species of *Sitophilus* have been and still are relatively independent of the quality of the existent variety of nutrient and breeding substrates. This was an important predisposition in order to be able to develop on grain, which, although rich in starch, still provides very one-sided nourishment. *Sitophilus linearis,* which lives on tamarind, does not have any symbiotes (Nardon et al., 2002; Lefèvre et al., 2004). Development on grain without additional nutrients is thus not possible for this species (Delobel & Grenier, 1993).

Numerous curculionids successfully breed in hard-shelled seeds of Dipterocarpaceae, *Quercus*-species, as well as on the fruits of other plant groups (Lyal & Curran, 2000, 2003). Several members of this seed-breeding guild, however, mandatorily leave the host as larva and pupate in the leaf litter or in the upper soil layer. This is the case for: *Curculio sikkimensis* Hell., which breeds in acorns in the Himalayas; *Curculio nucum* L., the acorn beetle in Middle Europe, and *Conotrachelus retentus* (Say), which breeds in the seeds of the black walnut (*Juglans nigra*) in North America (Kaushal et al., 1993; Stamps & Linit, 2002), to name just a few. Other species pupate within parts of their food plant and do not leave them until they are adult beetles. The fact that all species of *Sitophilus*, for which the developmental cycles are known, complete the entire larval development inside the food plant kernel, was certainly another decisive predisposition for utilising grain kernels as hosts – at times before the onset of the human storing of grains, when non-human organisms such as birds and rodents were collecting grain and depositing it at safe places for future consumption. Moving from those “stored” seeds to the upper soil layers for pupation might have posed a difficulty, especially since animal derived “food storage” is usually up in trees or buried deep in the ground. (Levinson & Levinson, 1998a, 1999).

The facultative development of *Sitophilus* species in grain and/or their natural wild forms is thus comprehensible before the domestication and stockpiling by humans in the Neolithic period. The infestation of anthropogenic stored grain must have taken place in the area near the mountainous forests of southwest Asia, or where people stored grain together for instance with acorns collected from the mountainous forests (Weidner, 1983). In addition to the large river water oases and floodwater farming of the Jordan, Euphrates, Tigris, and Indus rivers, which are considered to be the areas of origin of Neolithic agriculture (Sherratt, 2007; Willcox, 2007), early forms of farming also existed away from the river valleys in upper-lying mountainous areas. These were forms of rain-fed farming, such as the 7th or 8th millennium B.C. farming on the Chemchemal plains of Iraqi Kurdistan and the slopes of the Zagros mountains in what is today Iran, or along the Kithar range in central Pakistani Baluchistan from the 7th millennium B.C., where there was a flowing transition between hunting, gathering, and the farming of wild einkorn, emmer, and barley (Jankuhn, 1969; Jarrige & Meadow, 1980; Kajale, 1991; Charles, 2007). It is important to consider, that for the early period of Neolithic farming continuous storing of grain is very unlikely, because good evidences point to oscillations among various production modes with the storing of wild cereals forming only one component in the spectrum of gathering and hunting resources before the classical combination of cereal cultivation, domestic life-stock-keeping and village life came about (Flannery, 1973; Charvát, 1999; Weisdorf, 2005; Murphy, 2007; Sherratt, 2007). This also results in discontinuous availability of the nutrient and breeding substrates for pests in early anthropogenic storages. Purely synanthropic populations of *Sitophilus* species in stored grain were thus unlikely at that time. It is more likely that a high level of gene flow among beetles in stored grains and in natural habitats (reservoirs) existed during that period. It is also known, that stored-grain pest weevils are able to survive many months in moderate temperatures without food. Therefore an opportune breeding biology and adaptation to variable food resources must have already existed in the *Sitophilus*-group. Their potential natural food plants, the Dipterocarpaceae species and the species of the *Quercus*-group, in their original habitat also have seeds that ripen in irregular intervals (Janzen, 1974 cited from Lyal & Curran, 2000).

Seeds and dry plant matter contain very little water. One could describe the organisms that live off of them as being euryhygric and xeropotent. If necessary, they can gain some water through the catabolism of the carbohydrates in their food and/or create aggregations that influence the microclimate through respiratory transpiration. These adaptations can be found in numerous stored-grain pests (Levinson & Levinson, 1978; Plarre & Burkholder, 2003), including the granivorous *Sitophilus* species. Anthropogenic grain storage, especially in mild climatic zones or in subalpine to alpine regions of the subtropics, are marked by stable dry conditions. The granary weevil, which is unable to fly, is considerably more tolerant against desiccation than *S. oryzae* (Robinson, 1926). The reduction of respiratory water loss to a minimum, e.g. by forgoing any activities that require gas metabolism and the respective longer closing time of the spiracles, can counteract desiccation and can be considered to be a selective advantage in dry environments such as the desert (Chown, 2002) or grain stockpiles. With respect to the basal metabolism, the oxygen demand for flying insects is 10 to 100 times higher, which requires an increase in breathing gases through the spiracles, which are completely open during flight (Lehmann, 2002). Numerous species of beetles that exist in the desert have coadunated elytra, which permit the development of a subelytral chamber around the abdominal spiracles that is nearly saturated with water vapour (Duncan & Byrne, 2002). A small slit-opening for gas exchange above at the posterior end of the elytra functions as a physical spiracle and minimises the water loss through respiration (Lehmann, 2003). In the granary weevil, the abdominal spiracles are also covered by the coadunated elytra. Kiritani (1959, 1965) reported that adult rice weevils although physically capable show only very limited flying activity. The limitations in flight behaviour in *S. oryzae* to the reduction of the flight ability in *S. granarius* could thus reflect a trend in adaptation to extremely dry locations.

In conclusion, full development inside the host kernel, endosymbioses with bacteria, and the reduction in flight activity to prevent water loss in a dry environment can be regarded as pre-adaptations to successfully survive as a synanthropic grain pest. It is conceivable that an isolated population of the stem form of the granary weevil evolved in a prehistoric stockpile possibly in the subalpine region of the western Himalayas into a strain with a high tolerance to dryness that became unable to fly. Coadunated elytra also provide greater protection against mechanical stress (Crowson, 1981), which undoubtedly exists in grain stored by humans. This, however, also means that the propagation and the search for breeding grounds must have become more difficult, unless alternative means of propagation had become about. Had there not been at least some local trading of grain, or possibly only of the seeds, in prehistoric times, the spread of the founder-population would not have been possible and this “experiment of nature” would have failed. But under conditions of storing and sharing of seeds and the increasing multi-seasonal usage of storage areas, the opportunity for dissemination by transmission was created.

EVIDENCE OF PROTOHISTORICAL PROPAGATION

After being transferred over to human stored products, namely cereal grains, the propagation of the *Sitophilus* species *S. oryzae*, *S. zeamais*, and *S. granarius* appears to be closely tied to Neolithic agriculture. It has been possible to experimentally reproduce the beetles’ development in ancient forms of grain cultures such as einkorn (*Triticum monococcum*), emmer (*T. dicoccum*), durum (*T. durum*) and spelt (*T. spelta*) wheat (Trematerra et al., 1996). Today’s mid-sized form of the stored-grain pest species of *Sitophilus* is the result of the increasing size of the kernels of cultured grain. In choice experiments, it was possible to observe the ability of the *S. granarius* to differentiate between larger and smaller wheat kernels and to prefer the first for laying its eggs (Ewer, 1945). In the other direction, through artificial selection and by supplying them exclusively with smaller kernels, it was also possible to breed “dwarf forms” of the granary weevil (Saleh, 1990).

For the continued propagation of the pests as a result of the spreading of their hosts, the following three paths were possible (Weidner, 1983): a south-eastern path via the Indian subcontinent to East Asia; a south-western path via Mesopotamia to Egypt; and a northern route through the Transcaspian region in southern Russia to the Danube River.

In a pre-Christian illustrated encyclopaedia from China, the "Erh-ya", one finds reference to a small black worm that eats rice kernels from the inside, the "Ku-shih-ch'iang-yao" (Bodenheimer, 1928). The corresponding illustration depicted several beetles in nature. This could be a depiction of the rice weevil, however the characteristic rostrum of the weevil cannot be discerned. The oldest archaeological *S. oryzae* specimen from East Asia was found in an approx. 2100-year-old Han dynasty tomb near Ma-wang-tui in subtropical China (Chu & Wang, 1975).

Although conditions should have been optimal for *Sitophilus*, there are no reported findings of grain weevils from Mesopotamia. In Egypt, well-eaten barley kernels as well as fragments of granary weevils were discovered in a chamber tomb under the pyramid from the 6th dynasty (approx. 2300 B.C.) near Saqqarah, as well as in stables in Amarna from the 18th dynasty (mid-14th century B.C.) (Solomon, 1965; Levinson & Levinson, 1985, 1994; Panagiotakopulu, 1999). Already before the early Bronze Age, there was intensive trading occurring between Mesopotamia and the "wreath-mound" cities in the northern part of what is today Syria, as well as in the harbour towns along the Mediterranean Sea and the Persian Gulf, where, in recent excavations, large areas for grain storage have been discovered (Buckland, 1981; Bretschneider, 1999; Knapp, 1991 cited in Panagiotakopulu, 2000). It is more than likely that granary weevils also existed in antique Mesopotamia. One indication of this can be found on the 14th cuneiform tablet of the series "HAR-RA=HUBULLU", which depicts a bilingual tabular lexicon of Sumerian characters (as were in use in approx. 2300 B.C.) and Akkadian words. The series of tablets originated from the 6th to 9th century B.C. and includes numerous names of domesticated and wild animals, as well as of insects, including pests (vermin) for humans and those in their vicinity. The symbol 261 "uh še.kú" (Sumerian) is "ri-'-a-šu" (Akkadian) and is interpreted as being a grain-eating vermin or granary weevil (Landsberger, 1934). From sediment from the 9th, 8th, and 7th centuries B.C. from Tel Arad and Atlit-Yam in today's Israel, additional findings of granary weevils are known (Hopf & Zachariae, 1971; Panagiotakopulu, 2000; Kislev et al., 2004). Egypt and Palestine served as the breadbasket of the Roman Empire (Rickman, 1980), and with its expansion and the provisioning of the legions with grain, the granary weevil would have also made its way into Europe. There are numerous findings of *S. granarius* associated with pre-Roman and Roman archaeological sites in the south-eastern European-Mediterranean region, in Herkulaneum at Vesuvius, at camps of the Roman legions such as Novaesium (today's Neuss on the Lower Rhine), and in England from the 1st and 2nd century A.D., where grain heavily infested with granary weevil larvae, pupae, and adults were found (Schimitschek, 1975; Buckland, 1981, 1990). This proves that *S. granarius* was already widespread in Europe at least during Roman times.

The oldest carbonised granary weevil remains found in Europe, together with carbonised einkorn, emmer, and barley kernels, are dated at 4935–4800 B.C. and come from a village from the Neolithic period (Linearbandkeramik) near today's Göttingen, Germany (Büchner & Wolf, 1997). It is also possible that there was a pre-Roman introduction of the granary weevil as a result of the expansion of farming via the Mediterranean to south-west Europe and via the Rhone valley northwards from around 6000 to 5000 B.C.; or it might have been introduced with the spread of barley across Greece and/or the Transcaspian region, southern Russia, and along the Danube River (Jankuhn, 1969; Weidner, 1983; Zimmermann, 2002; Colledge & Conolly, 2007; Gyulai, 2007; Marinova, 2007; Monah, 2007; Valamoti & Kotsakis, 2007). This is supported through archaeological findings of the pest weevil from villages from the Neolithic to Bronze Age periods from sites near Servia in Macedonia, from Knossos on Crete, from Akrotiri on Santorini, and from Yevpatoria (antique Eupatoria) on the western coast of the Crimean peninsula (Antipina et al., 1991 cited in Zherikhin 2000; Panagiotakopulu & Buckland, 1991; Panagiotakopulu, 2001).

In historical writings from the Greek antiquities, such as in Aristophanes and Theophrastus, stored-product pests, primarily those that bore into wheat kernels, are referred to as "kis" (Keller, 1913; Beavis, 1988). Aristotle does not explicitly mention post harvest grain insects in his compendium about animals at his time (Sundevall, 1863; Aubert & Wimmer, 1886). In the agricultural and nature writings by Cato, Varro, Columella, Plinius Secundus, and Palladius from the Roman antiquities, *Sitophilus* spp. is called "curculio", and note is made that they can be combated using olive fruit water, "amurca" (Wittstein, 1881; Ahrens, 1976; Flach, 1990; Schönberger, 2000). Bodenheimer (1928) and Weidner (1983) rightfully clarified, however, that "curculio" probably also referred to the larvae of the *Nemapogon* moth species, which also develop on the inside of grain kernels. "Curculio" stood in general for parasite, guzzler or gormandizer, as in a comedy by Plautus (2nd century B.C.), which was titled "Curculio" and dealt with a parasite of human society (Andersen, 1938; Bryk, 1954).

In scripts from the Middle Ages and more recent history, references are often made to vermin in close proximity to humans and descriptions of means to combat them. A definitive classification of the species is not possible, however, due to various trivial denotations and mix-ups (Bodenheimer, 1928; Weidner, 1988). In the year 1630, a drawing of a weevil, drawn with the assistance of a microscope, was created by Francesco Stelluti, which can be identified beyond doubt as *Sitophilus granarius*, though not due to its proportions, but rather to distinct morphological characteristics (Bryk, 1954). Antony van Leeuwenhoeck used experiments with granary weevils (or rice weevils) to disprove the theory of spontaneous generation at the beginning of the 18th century (Bodenheimer, 1928). Since the mid-eighteenth century, the granary weevil appears to have been generally widespread in Middle Europe (Müller, 1927; Weidner, 1983). Due to the worldwide cultivation of grain and its trade, the stored-product pest species of *Sitophilus* ultimately became cosmopolitan.

ANNOTATIONS ON THE PHYLOGENESIS OF *SITOPHILUS*

A phylogenetic analysis to clarify the relationships between the various species of *Sitophilus* has not yet been carried out explicitly. *Sitophilus oryzae* and *S. zeamais* are almost morphologically indistinguishable from one another, yet are clearly isolated in their reproduction and ecology, as hybridisation and competition experiments by Birch (1944, 1954) and Floyd & Newsom (1959) have shown. *Sitophilus rugicollis*, which is very similar to the rice and maize weevils at least eidonomically, also must be considered to be part of this "twin or sibling species" complex (see above). The other *Sitophilus* species demonstrate greater morphological differences.

The larval development of curculionids in general on and specifically in plant seeds certainly has developed independently multiple times (Zwölfer, 1975; Morris, 1976; Crowson, 1981). Nonetheless, the complete development within the host kernel might be apomorphic for the clade *Sitophilus*.

The very high level of genetic resemblance of the SOPE suggests a unique evolutionary occurrence of the endosymbiosis (Heddi et al., 2001; Lefèvre et al., 2004; Conord et al., 2008), which would mean that *S. granarius*, *S. oryzae*, *S. rugicollis*, *S. zeamais* and possibly *S. vateriae* might be traceable to one original species, common only to them which became infected by the stem form of the SOPE.

During mating, male rice, maize, and granary weevils rub their rostrums more or less continually on the pronotums of the female (Wojcik, 1969; Holloway & Smith, 1987; Walgenbach & Burkholder, 1987). According to Wojcik (1969), this behaviour is not found for any other species of Curculionidae. Cotton (1924), who has described in detail the mating biology of *S. linearis,* does not mention this behaviour either. As has already been stated, not much is known about the other species of *Sitophilus*; nonetheless, these mating-behavioural components could possibly be apomorphous for the stored-product pest species of *Sitophilu*s.

Serological studies with antigens (McLaurin & Downe, 1966), analyses of the amylase-isozymes (Baker, 1987) and esterase activities (Beiras & Petitpierre, 1981; Grenier et al., 1994b), as well as of the mitochondrial DNA for specific markers (Hidayat et al., 1996; Peng et al., 2002), and a comparison of the epicuticular hydrocarbons (Nelson et al., 1984) confirm the similarities of these three species, with the *S. oryzae* and *S. zeamais* being more similar to each other than either to *S. granarius*. As these studies were conducted for the biochemical identification of the species, no outgroup comparisons were made in these studies. They therefore can not be analysed for the clarification of relationships.

The pheromone biology also demonstrates strong correlations between the rice and maize weevils (Walgenbach et al., 1983). The main component of the aggregation attractants – "sitophinone" – produced by male rice and maize weevils has demonstrated interspecific effectivity in the laboratory, where the female granary weevil also reacted positively to the male rice or maize weevils, while the male granary weevil differentiated between the male rice and maize weevils, only reacting to the latter. The "sitophilate" of the granary weevil, on the other hand, had a very species-specific effect.

In conclusion, the opinion that because to their closer resemblance *S. oryzae* and *S. zeamais* are more closely related – so to say sister species – has never been renounced. Their similarities could, however, be symplesiomorphic characteristics. During a molecular-biological study of 26 species of Dyrophthorinae, which included 5 *Sitophilus* species (*S. granarius*, *S. linearis*, *S. oryzae*, *S. vateriae*, and *S. zeamais*), the DNA sections of three genes (cytochrome oxidase I, elongation factor 1-alpha, and 28S) were studied with a phylogentic analysis with the inclusion of outgroup taxa (O'Meara, 2001). The dendrograms, which were created based on the three studied gene sections through the use of parsimony criteria with various computer-supported comparative methods, consistently postulate the monophyly among the studied *Sitophilus* species. Within this group, however, no definitive clarification of the relationships could be demonstrated. The dendrogram based on the combined analysis of the three gene sections suggests the following, yet little substantiated, relationship between the studied *Sitophilus* species: *S. linearis* + (*S. vateriae* + [(*S. oryzae* + (*S. granarius* + *S. zeamais*)]). Thus, among the stored-product pest species *S. granarius* and *S. zeamais* form a sister taxon to *S. oryzae*.

Alternatively, it is possible that the sister species of the granary weevil is the rice weevil, which is supported through an independent comparative cytochrome oxidase I amino acid sequences analysis (Conord et al., 2008). Furthermore, as already mentioned above, rice weevils demonstrate a very minimal affinity for flying. This behaviour could have already been present in the stem species of *S. granarius* and *S. oryzae,* so that the granary weevil's later inability to fly could have already had a behavioural predisposition. Both would then form the sister taxon to the maize weevil.

Not considered in the discussion above are the possibilities that a sister species of *S. granarius* has become extinct or is as yet undetected and therefore not described in morphology, ethology and genetics. The consequence of either possibility would be that the separation of the descent-lineages which led to the recent grain pests of *Sitophilus* must have occurred much earlier in time.

OVERALL CONCLUSION

It is generally excepted that the primary origin of stored grain insects is the nidicolous fauna in birds or rodent nests or similar habitats. On first view, the only difference between animal derived stores of seeds and human ones is one of scale, so that the transition is not that surprising. However, differences are more pronounced than they may appear. Anthropogenic storage systems are permanently manipulated by man in terms of conservation. Ecological processes like natural successions are limited in these artificial systems. On the contrary, man creates conditions in which biological metabolic processes are prevented or at least minimized in order to guarantee long term use of stored goods. Protecting stored grain by any means is most likely as old as Neolithic storage itself and indubitably documented from historical sites (Flannery, 1973; Panagiotakopulu et al., 1995; Levinson & Levinson, 1998b; Panagiotakopulu, 2000).

As anthropogenic storage systems differ from natural reservoirs it must be assumed that this new environment with its new ecological valences was immediately utilized after its creation, by either euryoecious species or by species with existing predispositions. Consequently new ecological niches were formed, possibly leading to speciation. Early storage facilities were probably patchily distributed in dispersed settlements and populations of the stem form of *S. granarius* and its sister species, may it be *S. zeamais* or *S. oryzae*, could have made the transition to the new habitat, possibly several times. At one such time a population must have become separated from wild habitats. Consequently, autapomorphic characteristics evolved that caused reproductive isolation.

The time line from the early Neolithic period may appear to be too short for such an evolutionary event. However, the transition to a new environment with only little interspecific competition for this new anthropogenic habitat in the beginning, together with a strong selective unidirectional influence by man could have favoured this process. Additionally favourable are small populations of only a few individuals, which have made the transition, with high reproductive capacity of several generations per year, enhancing survival of advantageous mutations. The transition could have occurred repetitively and independently in time and space with long periods of separation between founder-populations and wild populations, which enhances the overall probability of a successful transfer. All these circumstances have shown to drive likelihoods of speciation events in new habitats (Osche, 1973; Whitlock, 1997; Sudhaus, 2004; Templeton, 2008).

This scenario may have not been the general pathway for stored product insects in general, but for the granary weevil, because this species has not been found away from synanthropic situations. Even if its natural habitat has vanished over the millennia, due to possible climate change (Kislev et al., 2004; Willcox, 2007) or extensive use and destruction of wood-lands by man (Meiggs, 1982; Sherratt, 2007), one would expect, if the weevil, as it appears today, may have made the move from “stores” of some rodents to those of man at one time, it should be able to also return to those of rodents, at least occasionally in its current distribution range. This has not happened.

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