Bovine Hypodermosis: Phenology in Europe, Table 9 Comparative phenology (chronobiology) of *Hypoderma* species in some European ecological regions

Species	*Hypoderma lineatum*			*Hypoderma bovis*		
Region	Southwest	Central	East	Southwest	Central	East
L1	April–December	September–March	September–April	November–January	January–May	October–May
L3	October–April	February–May	February–April	December–May	May–July	March–June
Mature larvae	January–April	April–June	March–April	March–May	May–August	April–July
Adults	February–May	May–June	May–July	May–June	May–September	June–September

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Bøving, Adam Giede

Born at Saby, Denmark, on July 31, 1869, Adam Bøving graduated from the University of Copenhagen in 1888. His interests included insect larvae, and those of *Donacia* (Coleoptera: Chrysomelidae) were the subject of his Ph.D. research. Then he was appointed Assistant Curator of Entomology at the Royal Zoological Museum in Copenhagen, and he continued to study beetle larvae. Two years after the death of his first wife, he moved to the United States in 1913 and found employment with the U.S. Department of Agriculture. His work still revolved around beetle larvae, but concentrated on those of economic importance. He took an American wife and citizenship. With F. C. Craighead as coauthor, he published in 1930–1931 in Entomologica Americana, the work "An illustrated synopsis of the principal larval forms of the order Coleoptera." This major work has been much-cited by later authors for the wealth of its informational content; no such comprehensive study appeared in print until the second volume of F. C. Stehr's (1991) Immature Insects. Bøving died in Washington on March 16, 1957. [Note: Bøving (not Boving or Böving) is the correct Danish orthography].

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Brachelytry

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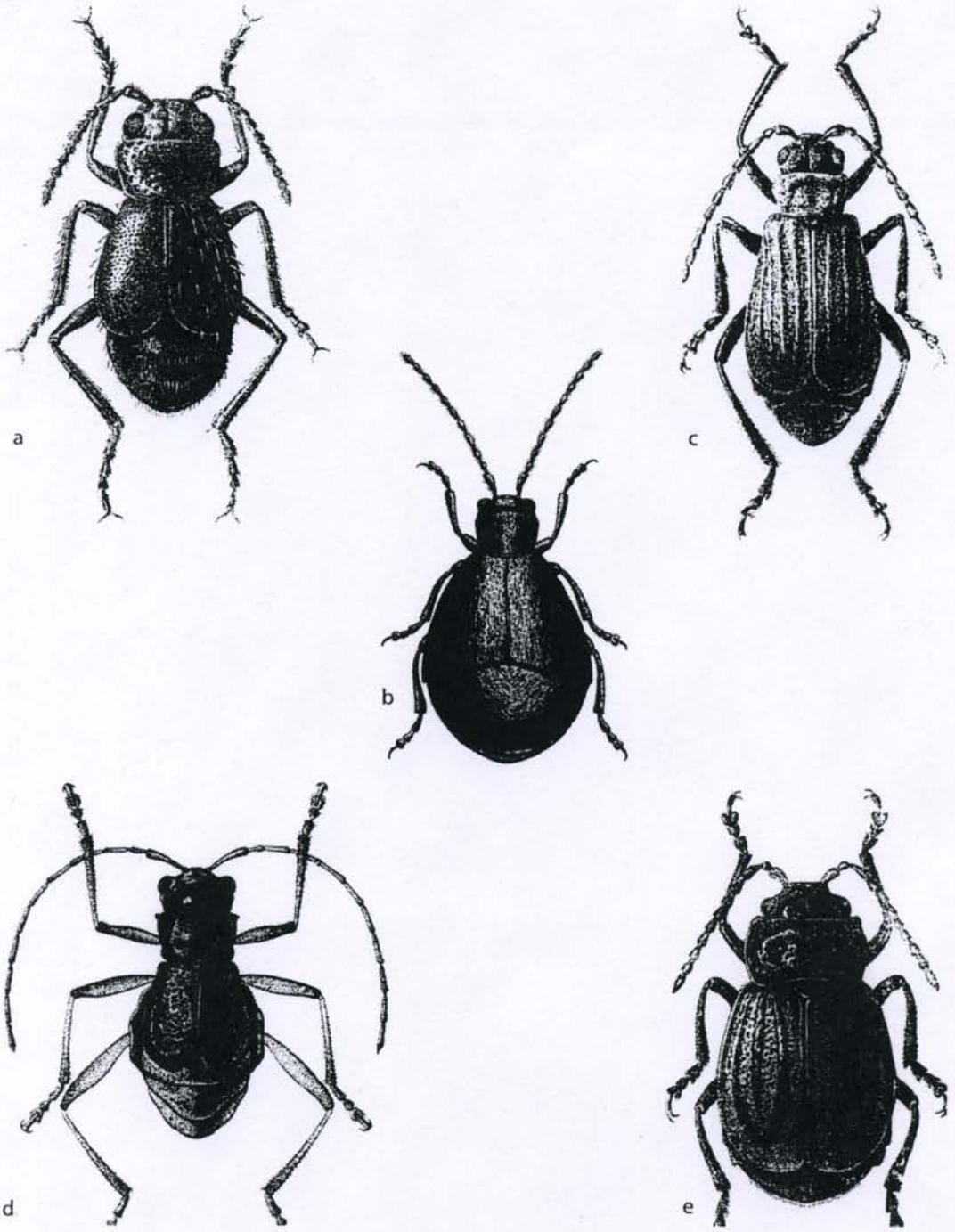
Elytra are characteristic of Coleoptera, and substantial thickening of the first pair of wings (elytra) is uncommon among other orders of insects. The elytra are modified mesothoracic wings, normally rigid and fitting over the abdomen. Brachelytry is the possession of abbreviated wing covers or elytra. Brachelytrous insects are commonly found among the Coleoptera, including

the Carabidae, Staphylinidae, Cerambycidae, Histeridae, Meloidae and Chrysomelidae. It seems most common among Galerucinae and is unusual among Alticinae. Both subfamilies are closely related, as part of the Trichostomata. Alticinae, Galerucinae (both Chrysomelidae) and Bruchidae sometimes show only an exposed pygidium, with only a small shortening of the elytra. Some beetle families are exclusively brachelytral, as is the Lymexylidae, but they fly very well, as do most of the myrmecomorphic Cerambycidae. Brachelytry should not be confused with physogastry (the swelling of the abdomen to an unusual degree due to the hypertrophy of fat bodies, ovaries or both), which can result in a similar appearance. In that case, the abdomen is so big that it is protruding over the end of the elytra. Physogastry is common among certain Chrysomelinae (*Gastrophysa*) and Galerucinae (*Agelastica*) (both Chrysomelidae). Brachelytry occurs also in Dermaptera and Gryllidae.

Pseudophysogastry (artificial swelling of the abdomen) is also common among cavernicolous or termitophilous beetles. In many Meloidae (*Meloe*), the elytra appear to fit badly, as among physogastric beetles. The elytra overlap but the beetle is apterous already as a pupa, as in *Timarcha*. This means a long history of apterism. In certain cases, brachelytry can be seen as a consequence of apterism, but many macroelytrous (normal) beetles are alternatively brachyapterous or apterous (*Chrysolina banksi*), or totally and permanently apterous (*Timarcha*). Often, in that case, the elytra are fused. They are never fused among brachelytrous beetles.

A set of mutations is surely at the origin of brachelytry, but macroelytrous and brachelytrous individuals do not occur in the same species. Brachyeletry is found mostly among mountainous or desert frequenting species or genera, but also among parasitic species. It seems absent from *arctic* species, which would seem to benefit from protection on the abdomen, though apterism or brachypterism there remains frequent. Brachelytry is also frequently linked with brachy-or apterism, though some brachelytrous beetles maintain complete wings and fly very well. Brachelytry is a very old, derived character (Fig. 59). There are a number of beetle families where the elytra become truncated, with the apical part of the abdomen uncovered, including Hydroscaphidae, Histeroidea, Staphylinidae, Nitidulidae, Inopeplidae, etc. In all these groups, the elytra completely cover the folded wings. In some others, such as the myrmecomorph Cerambycidae and the Lymexylidae, the wings are left free without any protection. The adaptive significance of this feature is not well understood. Among the Staphylinidae, the main adaptive advantage of abbreviated elytra seems to be a greater flexibility in the abdominal region, but that does not explain the truncated elytra of Histeridae. Many beetles with truncate elytra and with wings completely covered live on the ground, and are saprophagous. But there are always exceptions; among the Histeridae, for instance, some genera have the elytra entirely covering the abdomen. In the Staphylinidae, usually there are at least four abdominal segments exposed, sometimes six. There are, however, some Staphylinidae with the elytra not truncate.

There are also cases where the elytra are abbreviated and do not completely cover the folded wings. In *Atractocerus* (Lymexylonidae), the elytra are very reduced and don't cover the wings. There are also some myrmecomorphic Cerambycidae, some Cantharidae (*Malthinus* and *Malthodes*), the male of Stylopidae, and several Rhipiphoridae, which are more-or-less brachelytrous, with exposed wings. In male Stylopidae, the elytra are peculiarly modified to form balancing organs, like the halters of Diptera. Often those beetles are free-living and floricolous. This elytral reduction is increased among some endogeous Staphylinidae (Leptotyphlinae and Osoriinae), where the elytra are reduced to two contiguous scales, covering only the posterior thoracic segments and the first abdominal segment. A similar situation is found among a Moroccan *Staphylotroglops* (Cantharidae). The



Brachelytry, Figure 59 Somes cases of brachelytry (a) *Nyctiphantus nocturnus* (Semenov). Russia. Transcaspia; (b) *Marseulia dilativentris* (Reiche). Israel; (c) *Theone octocostata* (Weise). Tibet; (d) *Parageina andrewesi* (Jacoby). India; (e) *Galeruca barovskyi* Jacobson. Tibet (after Jolivet P (2005) Brachelytry among Chrysomelidae. Lambilionea 105(3):371–384).

reduction of the elytra can also be done laterally, revealing the sides of the abdomen (some Cetonidae) or be disjunct on the back (Oedemeridae). There are also cases where only the females are apterous and brachelytrous, as with *Metacycla* in Central America (Chrysomelidae: Galerucinae). Also, the elytra are completely absent in the females of glow-worms (Lampyridae), Drilidae and some Scarabeidae (*Pachypus candidae*) (Fig. 60).

Among the parasites, apterism can be linked with shortening of the elytra among the females (*Silphopsyllus*), or even among both sexes (*Platypsyllus*) (both Leiodidae). We find also a total disappearance of elytra among females of *Pachypus* (Dynastidae), *Thylodrias*, and *Rhipidius* (Rhipiphoridae).

Some Examples Among Chrysomelidae

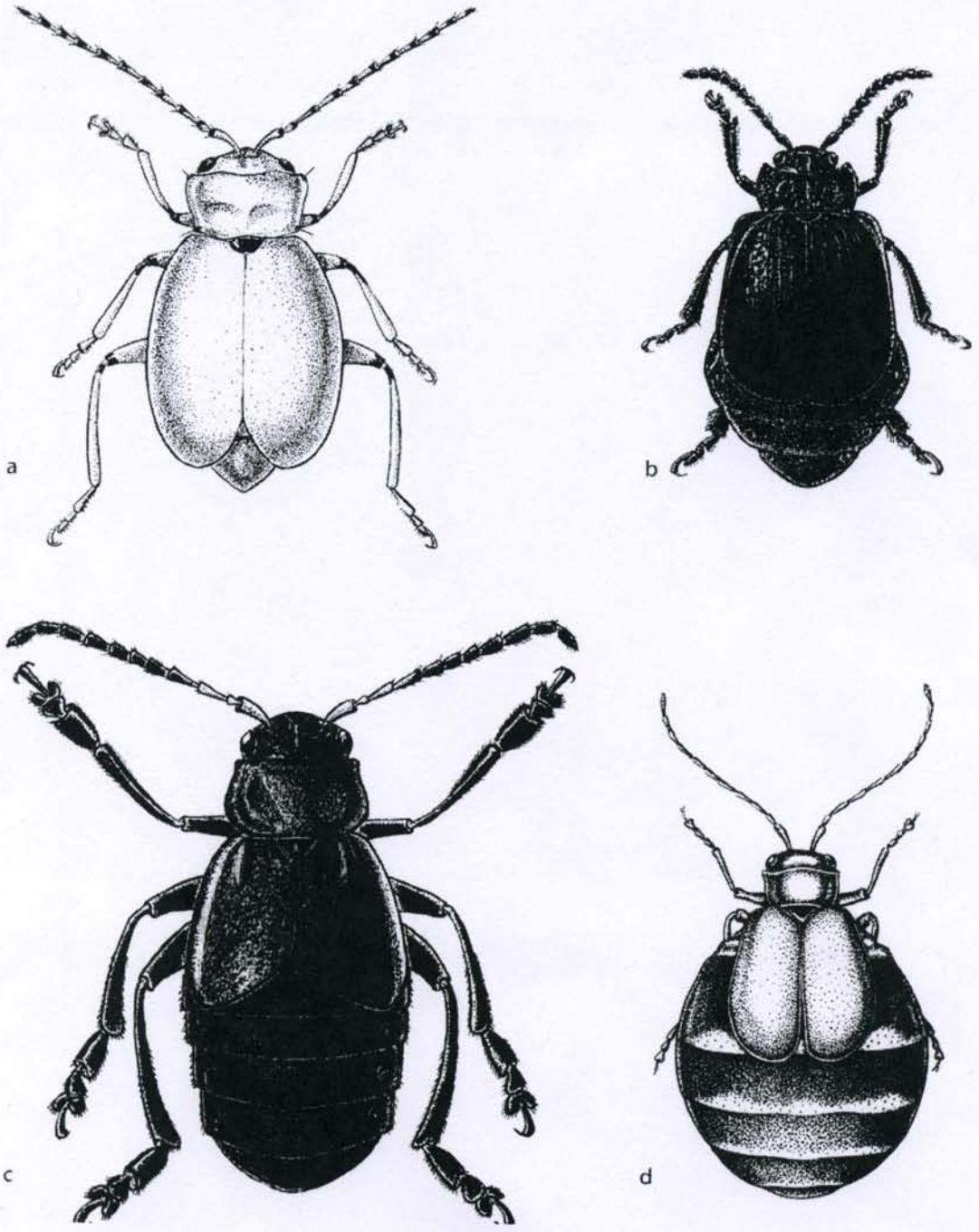
Brachypterism or apterism is common among Chrysomelidae, whereas brachelytry seems limited to Galerucinae and a very few Alticinae. As far as we know, macro-brachypterism seems to be transmitted in Mendelian fashion, when both morphologies are present. Brachelytrism is a derived character, but mixed forms do not exist.

Brachelytrous leaf beetles, which are generally apterous, are evidently devoid of a subelytral cavity, which exists among many apterous Chrysomelinae and Tenebrionidae. Probably, this lack of isolation against cold in mountains or heat and UV in deserts is compensated by other means, such as stronger sclerotizaton of the upper abdomen (tergites).

Brachelytry among Galerucinae is distributed in the Mediterranean region (*Arima marginata*, *Galeruca monticola*, *Marseulia dilativentris*); in mountains or steppe areas of Siberian, Indian and Chinese mountains (*Theone octocostata*, *Galeruca barovskyi*, *Paregeina andrewesi*, *Geinula antennata*); in Australian desert areas, where apterous beetles are common (*Rupilia ruficollis*); in the Ethiopian and East African mountainous areas (*Mahutia alluaudi*); in the Mexican and Central America dry tropics (*Metacycla caeruleipennis*); and in the highlands of South America (*Metalepta tuberculata*). Between 60 and 100 galerucine species in the whole world display brachelytry. Strangely, brachelytrous forms are extremely rare in South Africa and probably absent from Madagascar. Some live in India and Malaysia, but generally are linked with mountains. The genus *Galeruca*, which is essentially palaearctic, has numerous species (nearly 70 taxa) from Western Europe to Siberia, China, and Japan, and normally is macroelytrous and macropterous. However, it displays brachelytrism, joined with brachypterism or apterism, at higher altitudes. It can occur, as *Chrysolina*, above 5300 m in China, Himalayas and Tibet and many of those highland frequenting species are brachelytrous and all apterous. Very few real brachelytrous Alticinae can be quoted: *Hespera brachelytra* from the Yunnan mountains, *Sjoestedtina fordi*, *S. montivaga* from mountains in eastern African, though there may be more.

Flightlessness and brachelytry generally occur in both sexes. *Metacycla* is an exception, with only the female brachelytrous and apterous. Flightlessness is favoured in females because it allows greater allocation of resources to egg production (physogastry); however, flight seems retained in males because it increases the probability of finding a mate. Many brachelytrous species walk on the ground and are relatively polyphagous, like *Arima* in Europe, *Galeruca* in China, *Marseulia* in Middle East, *Metalepta* on the Peruvian plateau, or *Rupilia* in Australia. *Metacycla* occurs in Mexico on *Ambrosia ambrosioides*, a small plant (Asteraceae). In this species, the beetle does not walk on the ground, but the male is flying and active, searching for females. The female, black in the collections, is red and pink in some species when alive and probably is an aposematic color.

A review of the brachelytrous Chrysomelidae (Galerucinae and Alticinae) has been made by Pierre Jolivet, but due to the numerous galerucine genera



Brachelytry, Figure 60 Some additional cases of brachelytry (a) *Galeruca littoralis* (Fabricius). South of France. Pygidium prominent. Winged; (b) *Galeruca monticola* Kiesenwetter. France: Pyrenean mountains. Apterous; (c) *Arima marginata* (Fabricius). South of France. Apterous; (d) *Metacycla marginata* Chapuis. Female. Mexico. Apterous; (after Jolivet P (2005) Brachelytry among Chrysomelidae. Lambilionea 105(3):371–384).

affected, the list is not complete. The phenomenon is more frequent among mountain, steppe or desert-inhabiting genera and species, mostly in the tropics, but it also exists in temperate areas. Life on the edge has its constraints, but such mutants not only survived, but have persisted for a very long time. Other families like Staphylinidae seem more consistent; only in the Arctic, where many apterous or brachypterous species occur, brachelytry is absent. Apparently it can be maintained only under hot or relatively temperate climates. Brachelytry seems ancient and linked to harsh environmental conditions. It is known that wing atrophy helps the female in producing more eggs. That must also be the same for brachelytry. There are many cases where only the female is brachelytrous. We must distinguish between elytra fully developed or truncate (brachelytry), but there are degrees between relictual scales (some Staphylinidae) and relative shortening of the elytra. However, very rarely the elytra disappeared completely. Often scales persist. Among Bruchidae, Alticinae, many Galerucinae, very often the end of the abdomen is apparent, but it is not a case of brachelytry.

Certainly the shortening of elytra helps the mobility of the abdomen among the Staphylinidae. Among the Histeridae, the function for truncated elytra is less clear, but among saprophagous beetles the wings are always covered. This may be a necessity in a dirty and humid environment. In the case of Cerambycidae, mimetism with ants could be responsible, but among floricolous groups the wings can remain free. In many cases, the reason for brachypterism is not clearly understood. The case of the *Metacycla* species (Galerucinae) is unique, having physogastric, brachelytrous, apterous females and, macroelytrous, probably flying males. In some species of this genus, the drawings (yellow bands) of the elytra are printed over the upper side of the abdomen. In most cases of brachyletry, the upper abdomen is strongly sclerotized to replace the absence of protection by the lost elytra.

Brachelytry does not seem to be analogous between the various families of beetles. It has appeared independently, for instance, among Staphylinidae and Histeridae. Wing folding also is different in both families. When the beetles are on their back, the staphylinids use their abdomen to recover and attain their footing, whereas histerids use their elytral stump. For Degallier (pers. comm.), histerid elytra are shortened organs, whereas for staphylinids the elytra could be vestigial in relation to an elongated abdomen. There seems not to be any synapomorphy between the two groups.

Often, brachelytry or apterism are connected with a reduced metasternum and various morphological and anatomical correlations (timarchisation of Rüschkamp, 1927). Among ground Chrysomelidae and others, reflex bleeding, hoemocoelous toxicity, thanatosis, aposematism, extra-sclerotization of the abdominal tergites help in protection against predators for those wingless and relatively unprotected beetles. Most of those beetles are black, as in *Timarcha*, but some are brilliantly colored. Black for a ground insect can be aposematic on grasses. A set of mutations should have produced these conditions, and apterism and brachelytry are generally associated with the many usual morphological conditions.

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