

ON THE OCCURRENCE OF MID-GUT CAECA, AND
ORGANS OF SYMBIONT TRANSMISSION, IN
LEAF-BEETLES (COLEOPTERA: CHRYSOMELIDAE)

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ABSTRACT

The presence of paired unbranched pouches opening into the vagina is recorded in all of 31 species of Eumolpinae (23 reported here for the first time) studied. Paired 2-, 3-, or 4-branched vaginal pouches are recorded here from 8 species of Cassidinae additional to the 8 species in which they were recorded by Stammer (1936), Donia (1958), and Kasap (1975), also for 5 species of Hispinae in addition to the 3 in which they were found by previous authors. Many-branched paired vaginal pouches are reported here from all of 9 species of Sagrinae studied. Simple vaginal pouches are here recorded also for *Aulacoscelis* and the disteniid *Cheloderus*. Absence of such pouches, reported by Stammer in 2 species of Cassidinae, and by Donia (1958) and Kasap (1975) in 1 species of Hispinae, was found by us in 2 further species of Hispinae. Such organs have not been found in any species, studied by us or by others, of Bruchinae, Donaciinae, Criocerinae, Orsodacninae, Megalopodinae, Zeugophorinae, Chrysomelinae, Megascelinae, Camptosomata, Synetinae, Galerucinae, or Halticinae.

Anterior and posterior mid-gut caeca have been found in the adult alimentary canal in all of 31 species of Eumolpinae studied by us or by others, and in all 3 species of larvae of the group so far studied. In adult Hispinae, anterior mid-gut caeca have been found by us in those species dissected which have vaginal pouches but not in those lacking them; we have no data on the larval alimentary canal in this group. Those adult Cassidinae so far studied which have anterior mid-gut caeca also have vaginal pouches, and Stammer (1936) found that in *Cassida*, larval mid-gut caeca were found only in species possessing them in the adult. In Sagrinae and Donaciinae, anterior mid-gut caeca have been found in the larvae only.

The possible adaptive significance of these findings is discussed.

MATERIALS AND METHODS

Specimens collected from northern India (1976-1978) and the Glasgow area (1980) were dissected under a stereobinocular microscope. The internal reproductive organs and the alimentary canals (both males and females) were taken out as a whole to investigate the presence and number of gut caeca and the vaginal pouches. The presence or absence of small, thin, and tubular caeca just above the anterior insertion of the Malpighian tubules was also studied. Many species from the Bishop Collections of the Glasgow University and 4 species (i.e., *Aulacoscelis melanocera*; *Hoplionota padia*; *Hemisphaerota cyanea*; and *Immatidium fasciatum*) from the British Museum, London, were utilised for the present study. The alimentary canal and its gut caeca and the vaginal pouches of the dry specimens (both males and females) were investigated by softening them first in hot water and then potashing in warm dilute KOH solution (approximately 1%) for 5-10 minutes. Dissections of many adults and two larvae, each of *Typophorus viridicyaneus*, *Megalopus jacobyi*, and *Cassida rubiginosa* and of several other subfamilies (from Dr. R. A. Crowson's personal

collections) were made to confirm the presence of gut caeca. The figures were drawn with a squared eye piece.

OBSERVATIONS

Subfamily Sagrinae: (Figs. 1–8)

Kasap (1975) recorded a 4-branched structure opening to the common oviduct in a female of *Sagra congoana*. We discovered a pair of 6–8 branched vaginal pouches, one on either side of the common oviduct and opening to it by a wide tubular stem, in the same species. The pouches are 4-branched in *S. senegalensis*, 5 in *S. amethystina*, 6 in *S. femorata*, 15 in *S. adonis*, 16 in *S. jansoni*, and more than 20 in *S. stevensi*. In *S. jansoni*, the stem of each pouch is bifurcated, bearing 8 branches on each. The branches tend to be in pairs in most of the species studied except *S. stevensi* where they are set in a radial fashion. In *Megamerus kingi*, each pouch has 4 lobes arising from a common base as in Fig. 1.

Subfamily Cassidinae: (Figs. 9–15)

Dufour (1825), Stammer (1936), and Donia (1958) recorded a pair of 3-branched vaginal pouches in the females of *Cassida viridis* and Spett and Lewitt (1926) in *C. murrea*. Stammer, also, recorded a pair of 4-branched pouches in *C. rubiginosa* and *C. vibex*; a pair of 2-branched ones in *C. nobilis*; and neither pouches nor symbionts in *C. nebulosa* and *C. flaveola*. The adult classification of Spaeth and Reitter (1926) and the larval one of Steinhausen (1950) both place the last 2 species closer to each other than to any of the known symbiont-containing species. Our observations also confirm the absence of pouches in the two species mentioned by Stammer. In addition, we record 4-branched pouches in *Oocassida cruenta*, a pair of 3-branched ones with two branches forming a ring in *Lacoptera nepalensis*, and 2-branched ones in *Cassida enervis*, *C. syrta*, *Oocassida pudibunda*, and *Glyphocassis trilineata* (Figs. 9–15).

Subfamily Hispinæ: (Figs. 16–17)

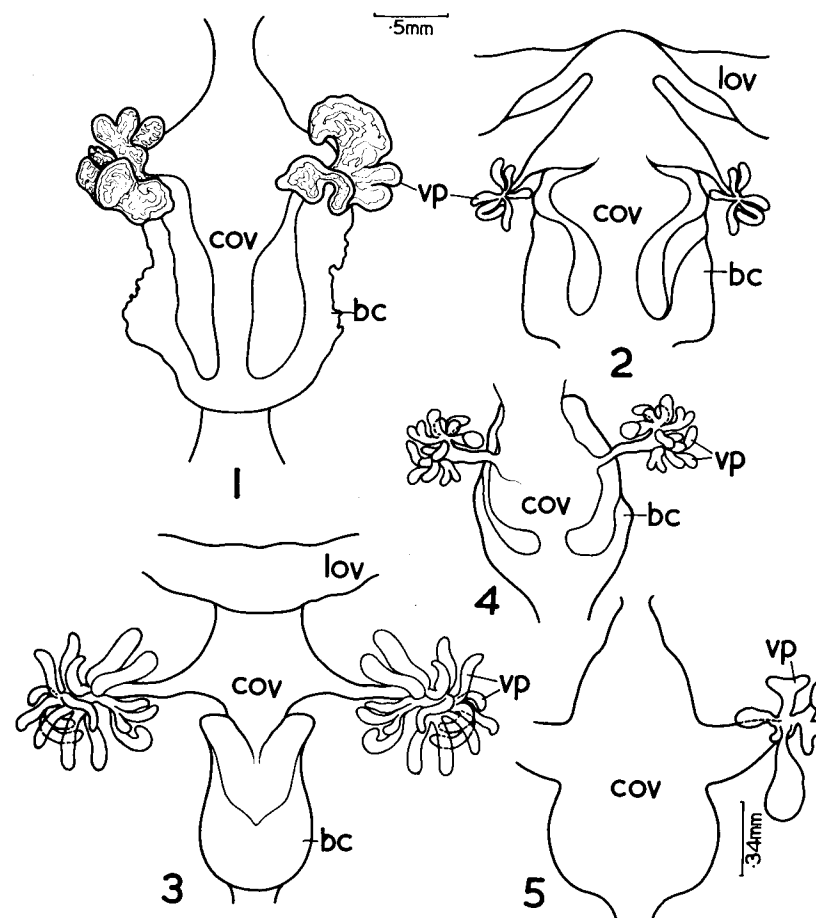
Taylor (1937) recorded a pair of 5-branched pouches in the females of *Promecotheca reichei* and Kasap (1975) 3-branched ones in *Aproidea balyi*. We found 5-branched pouches in *Dactylispa peregrina* and *Platypria erinaceus* (Figs. 16–17). The branches are much convoluted and interlocked forming a globular mass on either side of the vagina. The pouches are lacking in *Asamangulia cuspidata*, *Rhadinosa laghua*, *R. reticulata*, and *Hispa testacea* (Donia 1958; Kasap 1975).

Subfamily Aulacoscelinae: (Fig. 33)

We found one sac-like vaginal pouch on either side of the vagina close to the base of the bursa copulatrix in *Aulacoscelis melanocera*. The pouches are broad and round at base and taper towards the upper end.

Subfamily Eumolpinae: (Figs. 18–30)

Stammer (1936) described a pair of vaginal pouches in the adult females of *Bromius obscurus* and stated that these pouches transmit symbionts to the next

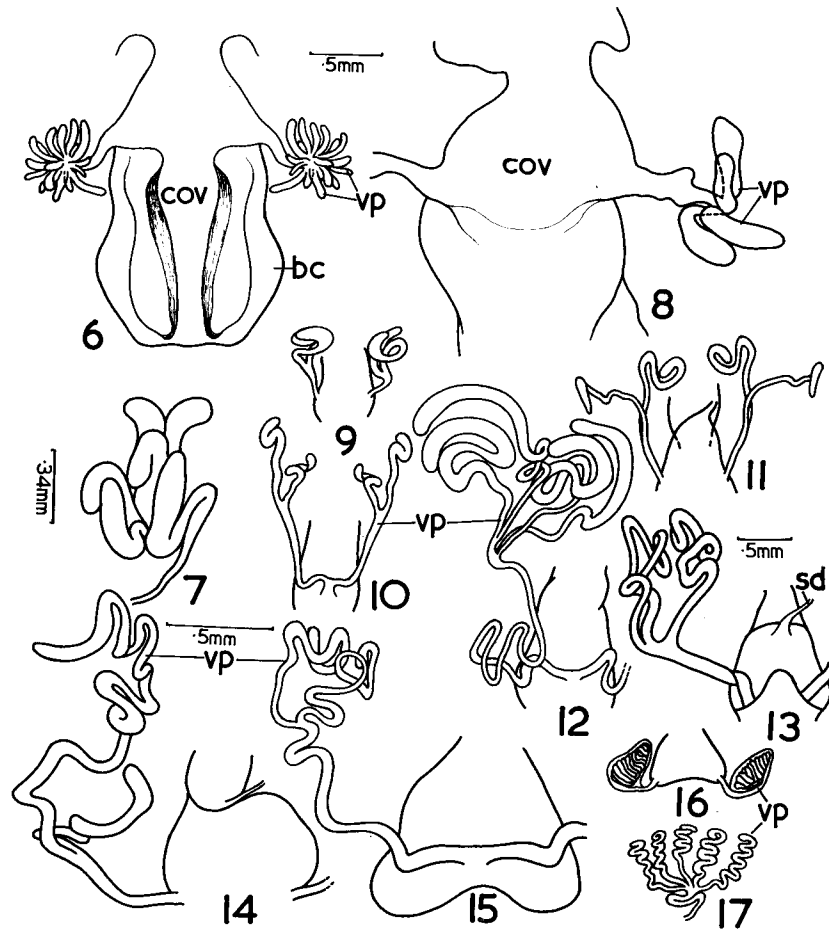


Figs. 1–5. Vaginal pouches of:

- 1, *Megamerus kingi* McLeay
- 2, *Sagra femorata* Drury
- 3, *Sagra adonis* Lac.
- 4, *Sagra jansoni* Baly
- 5, *Sagra amethystina* Guér.

List of Abbreviations Used

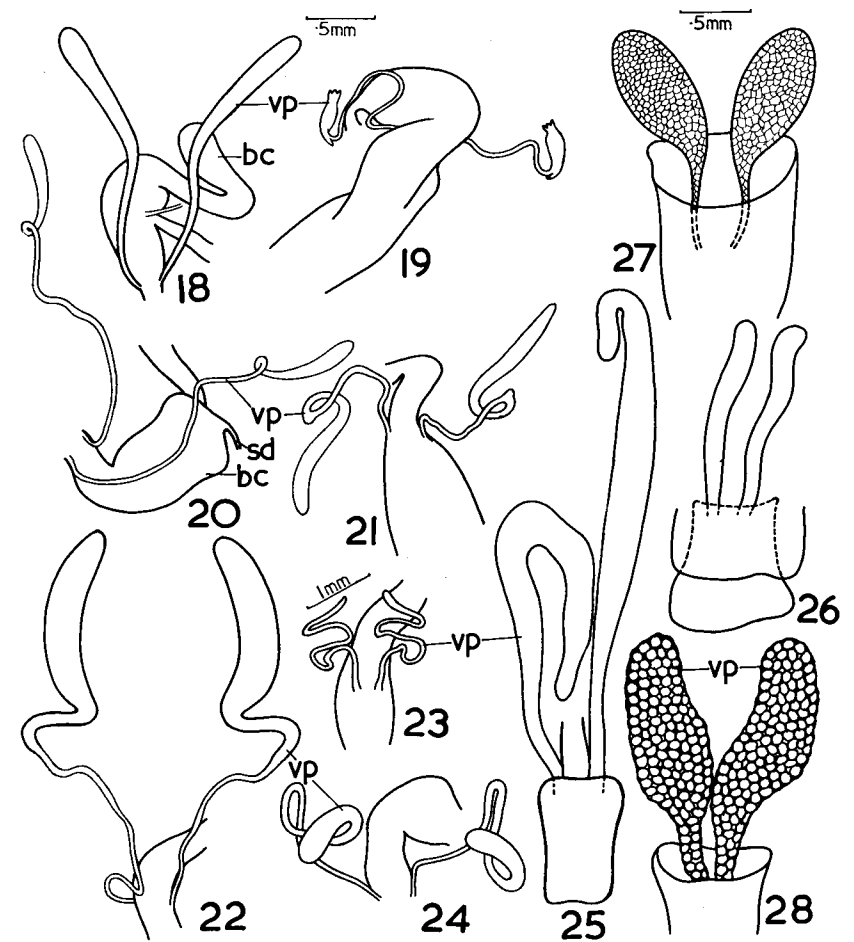
- bc — bursa copulatrix
- cov — common oviduct
- gs — gastric caeca
- lov — lateral oviduct
- mt — Malpighian tubules
- pgs — posterior gastric caeca
- sd — spermathecal duct
- vp — vaginal pouch



Figs. 6-17, Vaginal pouches of:

- 6, *Sagra stevensi* Baly
- 7, *Sagra congoana* Clav.
- 8, *Sagra senegalensis* Klug
- 9, *Cassida syratica* Bhm.
- 10, *Cassida enervis* Bhm.
- 11, *Oocassida cruenta* F.
- 12, *Oocassida pudibunda* Bhm.
- 13, *Lacoptera nepalensis* Bhm.
- 14, *Glyphocassis trilineata* Hope
- 15, *Glyphocassis trilineata* var. *melanosticta* Spaeth
- 16, *Platypria erinaceus* F.
- 17, *Platypria erinaceus* (branches reopened)

generation, in a secretion smeared onto the egg-shells which are eventually eaten by the larvae after hatching. Kasap (1975) recorded similar structures in some Australian eumolpines. Our studies of this subfamily reveal that in the tribe Spilopyrini, the pouches are club-like, with a long neck in *Spilopyra*



Figs. 18-28. Vaginal pouches of:

- 18, *Basilepta variabile* Duv.
- 19, *Colasposoma ornatum* Jac.
- 20, *Colasposoma auripenne* Motschy.
- 21, *Colasposoma* ? *asperatum* Lefev.
- 22, *Nodina crassipes* Jac.
- 23, *Platycorynus pyrophorus* Parry
- 24, *Macrocoma* sp.
- 25, *Trichotheca aeneopicea* Bry.
- 26, *Endocephalus lineatus* F.
- 27, *Metaxyonycha granulata* Germ.
- 28, *Colaspis brunnea* F.

sumptuosa, whereas in Nodinini they are long, tubular, and dilated distally, opening to the vagina in the species of genera *Basilepta*, *Cleorina*, *Nodina*, and *Typophorus*, and to the junction of the lateral oviducts in *Nodina aeneicollis* (Kasap 1975).

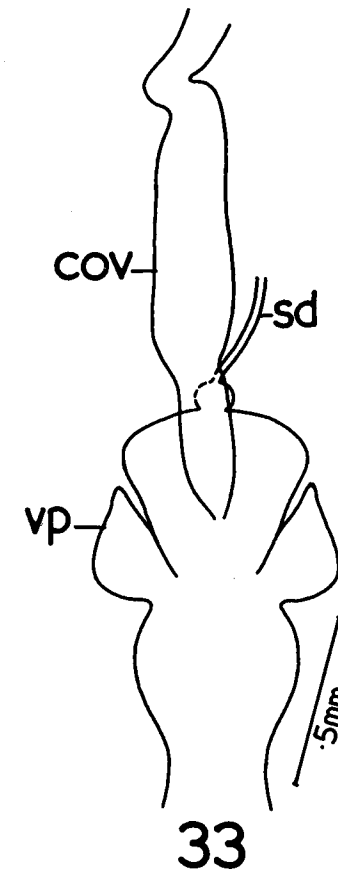
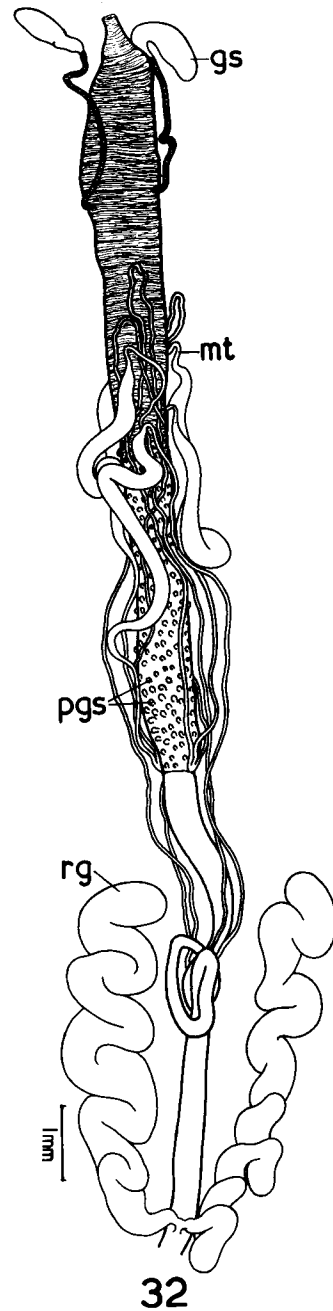
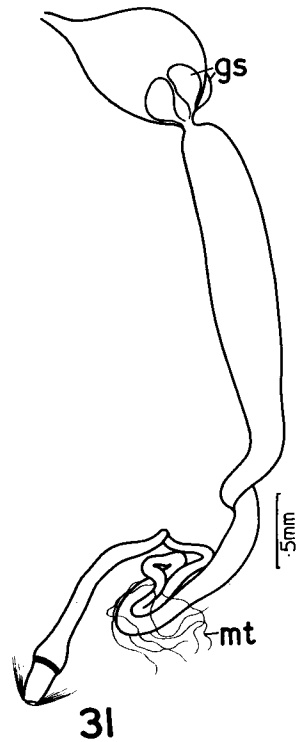
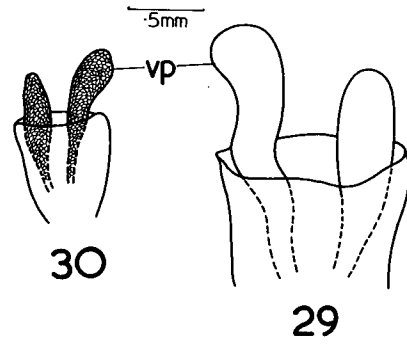


Fig. 33, *Aulacoscelis melanocera* Stål, ovipositor

In the tribe Eumolpini, the pouches vary in shape and size, being long, tubular, and somewhat dilated at their distal ends in *Eumolpus* sp., *Geloptera jugularis*, and species of genus *Colasposoma* studied; and elongated with an elliptical terminal structure in *C. ornatum* (Fig. 19). The pouches are dorso-ventrally compressed and much flattened, draining to the vagina through a thin tubular duct in *Metaxyonycha granulata*, *M. bogotensis*, *Colaspis brunnea*, and *C. flavipes*.

The tribes Adoxini and Colaspoidini have a pair of long, tubular pouches opening to the vagina, e.g., in the species of genera *Eubraxis*, *Macrocoma*, *Trichotheca*, *Platycorynus*, *Endocephalus*, and *Bromius* (Stammer 1936).

MID-GUT CAECA IN CHRYSOMELIDAE

In all species of Eumolpinae in which we have been able to study the adult alimentary canal, the mid-gut has two types of caeca—an anterior group of a few large ones, and a posterior group of a larger number of small ones, as

Figs. 29–30. Vaginal pouches of:

29, *Eumolpus* sp.

30, *Typophorus viridicyaneus* Crotch

Fig. 31, Alimentary canal of larva of *Typophorus viridicyaneus*

Fig. 32, Alimentary canal of larva of *Megalopus jacobyi* Bruch

described by Stammer (1936) in *Bromius obscurus*; a similar condition was found by us in the only Eumolpinae larva we were able to dissect, of *Typophorus viridicyaneus* (Fig. 31), and was described by Stammer in larval *Bromius obscurus*, so that it is likely to be general in larvae of the subfamily.

In adult Cassidinae, anterior mid-gut caeca were found in all species possessing vaginal pouches of which we studied the alimentary canal; the only species we found to lack such caeca were *Cassida nebulosa* and *C. flaveola*, both of which also lacked vaginal pouches. A parallel situation seems to exist in the allied Hispinae; those species in which the adult alimentary canal has been studied and found to have anterior mid-gut caeca (*Promecotheca*, *Aproidea*, also *Platypria* and *Dactylispa* studied by us) all had vaginal pouches, whereas *Hispa* (Kasap 1975), and *Asamangulia* and *Rhadinosa*, studied by us, lacking vaginal pouches, also lacked mid-gut caeca. Mid-gut caeca were found by Stammer (1936) and by us in larvae of *Cassida rubiginosa*, whose adult also has them. We have seen no description of larval alimentary canal in Hispinae.

Mid-gut caeca have been found, in the larva only, in *Sagra* (Tayade *et al.* 1976) and *Donacia* spp. (Stammer 1935) and are probably general in larvae of these groups, though lacking in adults of all species of them studied by us or by others. They have recently been found to be absent in larval (Vats 1976) as well as adult Bruchinae, and have not been found in either stage of any Criocerinae studied by us or by others (Venturi 1949).

An unexpected finding by us is the presence of what appear to be specialised caeca on the mid-gut of larvae of *Megalopus jacobyi* (Fig. 32); no caeca were found in the only adult of this group whose gut we examined (*Sphondylia* sp.), nor were vaginal pouches found in any species of Megalopodinae. Mid-gut caeca were also absent in adults of all species dissected by us or described in the literature of Orsodacninae, Synetinae, Galerucinae, Halticinae, Chrysomelinae, Zeugophorinae, and Camptosomata.

Family Disteniidae: (Fig. 34)

There is a pair of thin and elongated finger-like processes, the vaginal pouches, in *Cheloderus childreni*. The pouches are ventrolateral and open at the junction of the common oviduct with the bursa copulatrix. The wall of the pouches is continuous with those of the bursa and the common oviduct. Each pouch is dilated at its distal end.

DISCUSSION AND CONCLUSIONS

From our observations, and published literature, it appears that all Chrysomelidae with vaginal pouches in the adults have mid-gut caeca at least in the larvae; this fact strongly supports the idea that these organs are concerned in the transmission and maintenance of symbiotic bacteria, in the manner described by Stammer (1936) for *Bromius* and *Cassida*.

The published data on symbionts in Chrysomelidae almost exclusively record species in which they have been found, without specific mention of species in which symbionts have been sought without success. Stammer (1936) referred to "eine grosse Zahl von Chrysomeliden" studied by him with negative results; the only species he specifically noted as lacking symbionts were *Lamprosoma* (= *Oomorphus*) *kolbei*, *Cassida nebulosa*, and *C. flaveola*. It is likely that he would have studied some of the commoner Central European species of Chrysomelinae, Criocerinae, Galerucinae, Halticinae, Cryptocephalinae, and Clytrinae. He also neglected to describe his general methods of looking for symbionts.

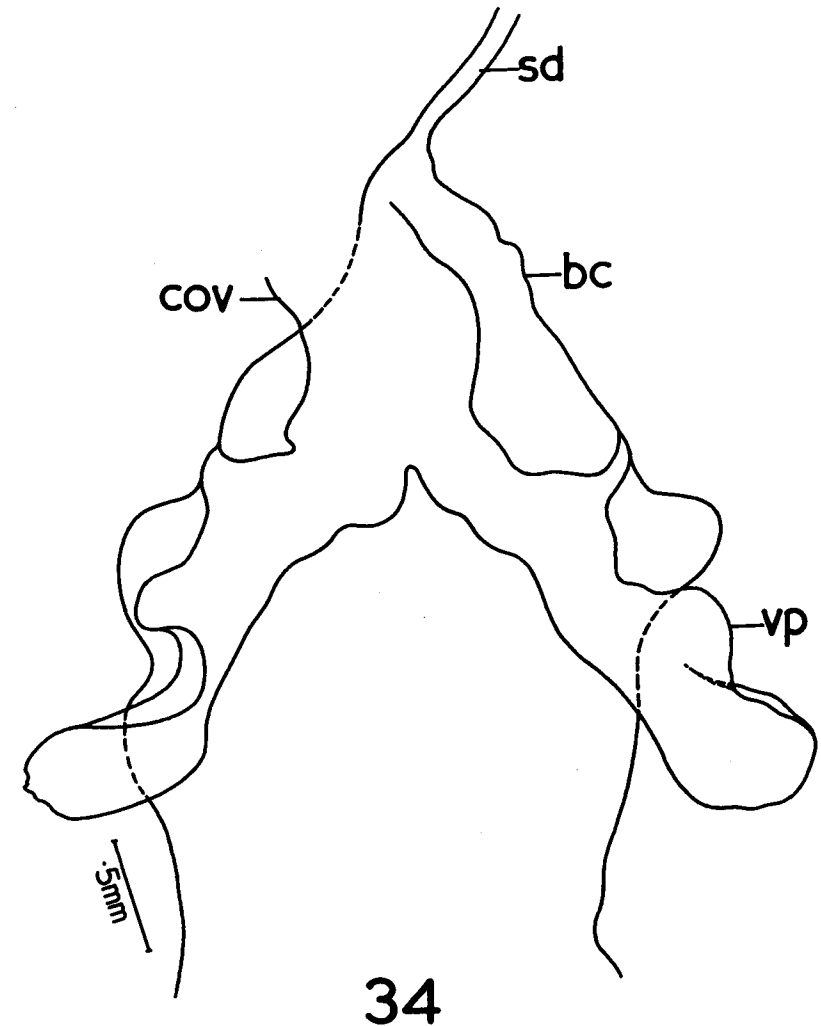


Fig. 34, *Cheloderus childreni*, ovipositor

Our findings of dilated Malpighian tubules in *Oomorphus* and *Megalopus* late larvae might suggest an adaptation for symbiont transmission, on the model of *Donacia*. The indications are that symbionts, where present, are mainly functional in the larval stage; Stammer did not state whether he had studied larvae of groups other than the Eumolpinae, Cassidinae, and Donaciinae, nor whether he had investigated the developing eggs in the ovarioles, on the analogy of those curculionid groups in which symbionts have been found to be transmitted direct to the eggs. Our findings of posterior mid-gut caeca in larval *Cryptocephalus*, and of anterior ones in larval *Megalopus* (representing a group unlikely to have been studied by Stammer), suggest possible presence of sym-

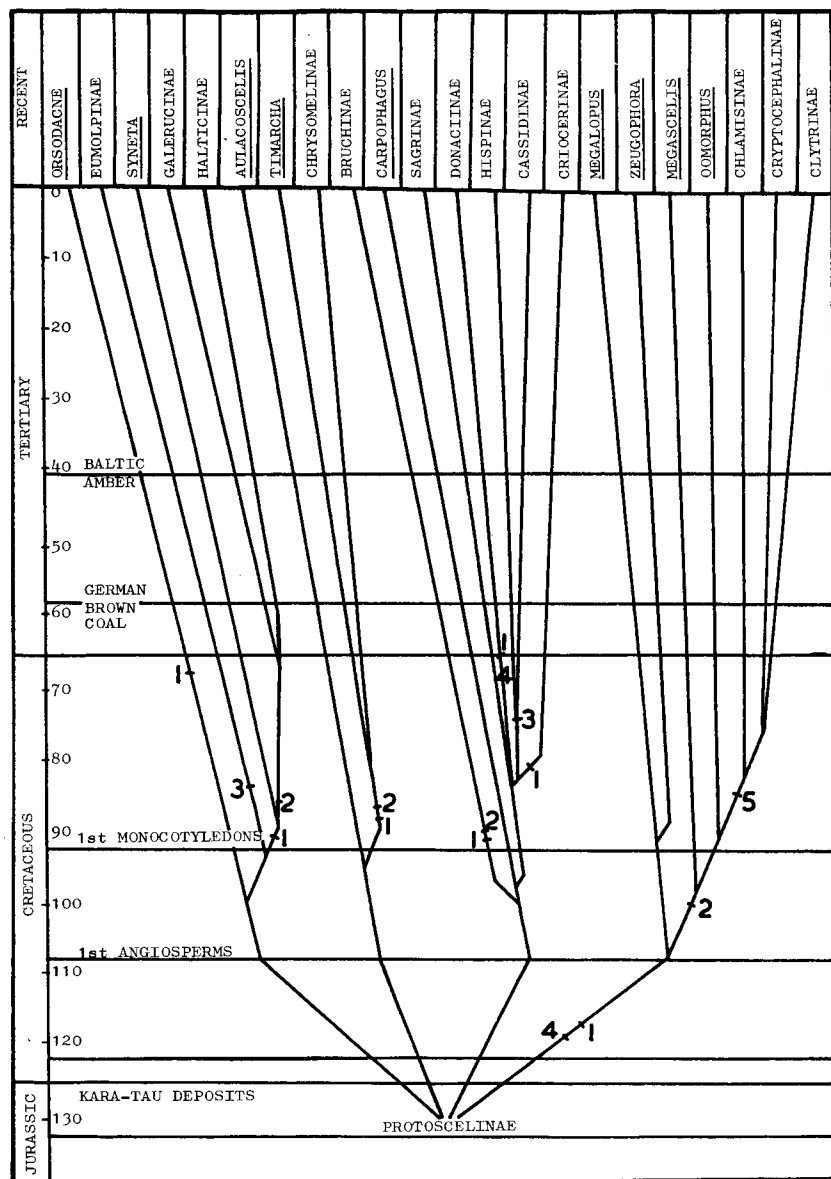


Fig. 35. Phylogenetic dendrogram

Description of the Numbers Used in the Phylogenetic Dendrogram

- 1, Loss of vaginal pouches.
- 2, Loss of larval mid-gut caeca.
- 3, Development of adult mid-gut caeca.
- 4, Secondary development of inflated malpighian tubules in adults.
- 5, Loss of inflated malpighian tubules in adults.

bionts, but call for proper histological study to confirm their presence; the absence of modified Malpighian tubules, or of vaginal pouches, in adult *Cryptoccephalus* implies that if symbionts are present in the genus, they are probably transmitted in the curculionoid manner, by way of the ovarioles.

The presence of what appear to be vaginal pouches in *Aulacoscelis* as well as in *Sagrinae* favours the theory that such structures, and presumably symbionts of some kind, were present in ancestral Chrysomelidae, these modern groups showing the closest resemblance to the oldest fossil Chrysomelidae, *Protoscelis* and *Pseudomegamerus*, described by Medvedev (1968) from late Jurassic deposits. It may not be accidental that scanty published records (Monros 1954) seem to indicate associations of both *Aulacoscelis* and the Australian *Sagrinae* *Carpophagus* with *Cycadaceae*, a very old group of *Gymnospermae*, represented by fossils in the same deposits as Medvedev's *Protoscelinae*.

On this theory, there must have been very polyphyletic loss of vaginal pouches, and presumably of symbionts, within Chrysomelidae. In *Donaciinae*, and possibly in *Megalopodinae*, there should have been switches to symbiont transference via the Malpighian tubules, with loss of vaginal pouches. Loss of vaginal pouches and presumably of symbionts should have occurred independently on the lines leading to *Bruchinae*, *Criocerinae*, *Orsodacninae*, *Synetinae*-*Galerucinae*-*Halticinae*, *Chrysomelinae*, and at least the higher *Campitosomata*, as well as in certain *Cassidinae* and *Hispinae*. That is, on the assumption that our previous dendrogram is at least topologically correct (Mann and Crowson 1981). If symbionts are mainly functional in the larval stage, one might expect their loss to be related to changes either in the larval food or in the larva's own mode of digestion. Assuming that the original larval habit was internal stem-feeding (as in *Sagrinae* and *Megalopodinae* today), loss of symbionts seems to have occurred only in groups which have moved away from this habit, but in by no means all of them. It is very hard to explain why symbionts should be lost in root-eating larvae of *Syneta* (and many *Galerucinae*-*Halticinae*) but retained in *Eumolpinae* larvae of similar habits, or why leaf-eating larvae of *Cassidinae* should retain them while they are lost in *Criocerinae* and *Chrysomelinae*.

The tendency to loss of vaginal pouches, and of larval mid-gut caeca, is manifest also in *Cerambycidae*. Both types of organ have been found in all *Aseminae* studied, and in many but not all *Lepturinae* (Schomann 1937), both groups appearing to be primitive types in the family; they have been found in a few apparently primitive types of *Cerambycinae* and *Prioninae*, but in no *Lamiinae*. In *Cerambycidae*, species whose larvae develop in still living, fresh, or unseasoned trunks or branches seem rarely if ever to have vaginal pouches whereas, at least in *Lepturinae*, these seem to be present when the larvae develop in seasoned or decayed wood.

In the allied but basically more primitive *Disteniidae* (Crowson 1981), which may be more closely allied to *Chrysomelidae* than are *Cerambycidae* proper, we found well developed vaginal pouches in the *Oxypeltinae* *Cheloderus*, while Schomann (1937) reported reduced and possibly nonfunctional ones in *Distenia* and *Vesperus*, representing the subfamilies *Disteniinae* and *Vesperinae*; nothing is known to us of such structures in the 4th subfamily, *Philinae*. According to Scott Cameron and Real (1974), the larvae of *Cheloderus* develop in living branches and trunks of *Nothofagus*, while larvae of *Vesperus* are well known to live free in the soil feeding on roots after the manner of *Eumolpinae* larvae which they somewhat resemble. Larvae of *Distenia* in the U.S.A. and Russia

(Craighead 1923; Cherepanov 1979) are reported to develop under the bark of roots and underground parts of trunks of dead or moribund trees. Thus the known habits of disteniid larvae resemble those of Cerambycid groups like Lamiinae which do not have symbionts. It thus seems possible that disteniid symbionts will prove to be analogous to those of Chrysomelidae rather than Cerambycidae, bacterial rather than yeast-like.

It begins to appear likely that symbionts of some kind, transmitted to the eggs by vaginal pouches, were present in the ancestral Chrysomeloidea, well back in the Jurassic period. There is now little doubt that the nearest living allies of Chrysomeloidea are to be found in Curculionoidea, a group in which symbionts, often housed in mid-gut caeca of the larva, are widespread, and nearly always bacterial. However, vaginal pouches are rare in Curculionoidea, being known only in one subfamily, Cleoninae. In others of the group, symbionts are transmitted either via the Malpighian tubules (as in many Apionidae) or directly through the ovaries. Unfortunately, we have found little or no information on the possible occurrence of symbionts in the more primitive groups like Nemonychidae, Anthribidae, Belidae, or even Attelabidae. If symbiotic adaptations are eventually found in these groups, it will greatly strengthen the hypothesis that symbionts were already present in a common ancestor of Chrysomeloidea and Curculionoidea, probably in the middle or lower Jurassic.

Assuming that ancestral Chrysomeloidea had symbionts, the question remains, were they bacterial as in Chrysomelidae, or yeast-like as in Cerambycidae? The published data on the functions of symbionts in beetles (Koch 1967) suggests that they may be rather different in bacteria and yeasts. Bacterial symbionts seem often to be important as sources of vitamin-like substances (e.g., steroids) deficient in the normal diet, whereas yeasts may be more important in synthesising essential amino acids, and perhaps at times in producing enzymes to break down substances which the larva could not digest.

The most obvious parallel to Chrysomeloidea may be in the systematically remote Bostrychoidea, in which Anobiidae usually have yeast-like symbionts in anterior mid-gut caeca of the larvae, and vaginal pouches in the adults (Koch 1967), whereas Bostrychidae usually have bacteria in mycetomes attached to the posterior mid-gut of the larvae, and lack vaginal pouches, transmission to the eggs being direct through the ovarioles as in many Curculionidae. As a rule, bostrychid larvae can develop successfully only in unseasoned wood, with considerable remains of cell-contents, whereas anobiid larvae commonly occur in thoroughly seasoned wood. Physiologically, and in some structural characters, it would be easier to imagine Anobiidae developing from some primitive bostrychid ancestor rather than *vice versa*. If *Cheloderus* proves to have bacterial rather than yeast-like symbionts, this will strengthen the hypothesis that in Chrysomeloidea, too, yeast-like symbionts have replaced prior bacterial ones.

Hinton (1981) described the structures in Cassidinae, which we have called vaginal pouches, under the name colleterial glands, indicating that they produced a secretion which serves either to cement the eggs to the substratum or to form a protective covering for the eggs. He also asserted that secretions serving this function were probably produced in all Chrysomelidae, though in Chrysomelinae and Criocerinae the cells concerned were situated in the calyx or the ends of the ovarioles of the ovaries, and in Camptosomata were in dorsal glands opening into the rectum. He made no reference to colleterial glands in Donaciinae or Eumolpinae. Possibly the transmission of symbionts is an ad-

Table 1. Showing the occurrence of gut caeca and vaginal pouches in the adults and larvae of families Chrysomelidae, Cerambycidae, and Disteniidae.

Family/Subfamily	Vaginal pouches (+/-)	Type of pouches	Gut caeca				Type of symbionts Bacteria/ Yeast-like
			Adult		Larva		
			Anterior (+/-)	Posterior (+/-)	Anterior (+/-)	Posterior (+/-)	
I Disteniidae	+	Unbranched	?	?	?	?	?
II Cerambycidae	+/-	Unbranched	+/-	-	+/-	-	Yeast-like
III Chrysomelidae	-	-	-	-	?	?	?
i) Orsodacninae	-	-	-	-	?	?	?
ii) Synetinae	+	Unbranched	+	+	+	+	Bacteria
iii) Eumolpinae	-	-	-	-	-	-	-
iv) Galerucinae	-	-	-	-	-	-	-
v) Halticinae	-	-	-	-	-	-	-
vi) Aulacoscelinae	+	Unbranched	?	?	?	?	?
vii) Chrysomelinae	-	-	-	-	-	-	-
viii) Bruchinae	-	-	-	-	-	-	-
ix) Sagrinae	+	Branched	-	-	+	+	?
x) Donaciinae	-	-	-	-	+	+	Bacteria
xi) Hispiniae	+	Branched	+/-	+/-	?	?	Bacteria
xii) Cassidinae	+	Branched	+/-	+/-	+/-	+/-	Bacteria
xiii) Criocerinae	-	-	-	-	-	-	-
xiv) Megalopodinae	-	-	-	-	-	-	-
xv) Megascelinae	?	?	?	?	?	?	?
xvi) Lamprosomatinae	-	-	-	-	-	-	-
xvii) Chlamisinae	?	?	?	?	?	?	?
xviii) Clytrinae	-	-	-	-	-	-	-
xix) Cryptocephalinae	-	-	-	-	-	-	-

ditional function which may be taken on by the colleterial glands—or alternatively, a colleterial function may be secondarily acquired by what were initially organs of symbiont transmission.

ACKNOWLEDGMENTS

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