

OVOVIVIPARITY IN TENEBRIONID BEETLES OF THE MELANOCRATOID PLATYNOTINA (COLEOPTERA: TENEBRIONIDAE: PLATYNOTINI) FROM MADAGASCAR, WITH NOTES ON THE VIVIPAROUS BEETLES

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Abstract.— First stage larve of ovoviviparous tenebrionid beetles (melanocratoid Platynotina, Platynotini) from Madagascar are described and illustrated: *Sebastianus simplex* Iwan, *S. projectus* Iwan, *Styphacus bartolozzi* Iwan, *S. kochi* Iwan, *Melanocratus ferreri* Iwan. Viviparity in beetles (Carabidae, Chrysomelidae, Micromalthidae, Staphylinidae and Tenebrionidae) is discussed.



Key words.— Coleoptera, Platynotini, Tenebrionidae, Carabidae, Chrysomelidae, Micromalthidae, Staphylinidae, Madagascar, South Africa, viviparity.

VIVIPARITY – DEFINITION AND CLASSIFICATION

In 1948 Hagan defined viviparity as “the birth of offspring without an enveloping egg shell”. He made a reservation, however, that “... eggs are also laid that may contain embryos of any developmental age, even eggs with fully grown embryos ready to fend for themselves immediately upon extrusion and, finally, insects give birth to living offspring which have hatched from the egg within the mother’s body, or the eggs may never have been initially provided with a shell ...”. For such cases Hagan established a separate category which he termed ovoviviparity. Ovoviviparous insects differ from oviparous ones in that they lay eggs which contain sufficient yolk to nourish the embryo till hatching occurs and the offspring is deposited. The remaining three types of viviparity are: adenotrophic, metagonadic and pseudoplacental viviparity. In 1951, in his fundamental work “Embryology of the viviparous insects” Hagan presented the current knowledge of viviparity in particular insect taxa (mainly in two chapters: Female Reproductive System and Development of Embryo). In one of the initial chapters the author discussed the previous divisions and definitions of insect viviparity and presented his own, modified (Hagan 1948) classification of viviparity in insects (Table 1).

Seller (1955) adopted the above division and developed a concept of ovoviviparity, recognising three kinds (depending on the site of incubation): in the ovariole (Homoptera: Coccidae; Coleoptera: Chrysomelidae), in the uterus (Diptera), and in special organs (Blattodea).

Hagan’s (1951) classification has become commonly adopted and is used in various modern entomology hand-

books, but various authors supplement it, adding or extending interpretation of its components. In “The Insects of Australia” Hinton and Mackerras (1970) point out that the term ovoviviparity is also used when hatching occurs immediately after deposition, but usually the young larvae hatch in the vagina and are later deposited. They add that “...the vaginal wall may be richly tracheated irrespective of the kind of deposition and there is no physiological differ-

Table 1. Classification of viviparity (Hagan 1951)

1. **Ovoviviparity.** The egg contains sufficient yolk to nourish the embryo until hatching and maternal deposition of offspring. No special nutritional structures are developed.
2. **Adenotrophic (Intussuctio-) viviparity.** The egg contains sufficient yolk to nourish the embryo until hatching. Specialized maternal organs nourish the larva in the uterus.
3. **Haemocoelus (Exgenito-) viviparity.** Embryonic development is in the haemocoel, not in genital ducts, and nutriment is acquired from maternal tissues by means of a trophamnion, trophserosa, or trophchorion.
4. **Pseudoplacental viviparity.** The embryo in the maternal genital tract obtains at least part of its nutriment by means of a placenta.
 - a. **Attached embryo type.** A pseudoplacenta, derived from maternal or embryonic tissue or from both sources, firmly unites parent and egg or embryo for a nutritional period of varying duration.
 - b. **Free embryo type.** Pseudoplacenta wholly of embryonic origin. Contact of egg, pseudoplacenta, or embryo with maternal genital tract due only to pressure or proximity.

ence between these two conditions...". Gillot (1995), describing ovoviviparity in his handbook, states that the eggs usually are laid before they hatch. He draws attention to the significance of viviparity as a form of parental care, and the associated reduction of the number of eggs laid (in extreme cases in some Diptera to one only).

VIVIPARITY IN BEETLES

First mentions of beetle viviparity pertained to termitophilous staphylinid species of *Corotoca* (Schiödte 1853) and chrysomelid species of *Oreina* (Perroud 1855). Till 1951, cases of viviparity were described for three families: Micromalthidae, Staphylinidae and Chrysomelidae. Hagan (1951: 61, table 6) classified all the cases of beetle viviparity as ovoviviparity. In 1978 Tschinkel recorded ovoviviparity in some tenebrionid beetles (tribe Platynotini), and in 1985 Liebherr and Kavanaugh in carabid beetles of the genus *Pseudomorpha*.

Micromalthidae

Only one species – *Micromalthus debilis* Leconte, with a very complex metamorphosis, additionally complicated by paedogenesis, parthenogenesis and cyclic shifts from oviparity to ovoviviparity – is ovoviviparous. Its reproductive mode and details of embryonic development were studied by Barber (1913a, 1913b), de Peyerimhoff (1913, 1933), Scott (1936, 1938) and Pringle (1938).

Staphylinidae

Schiödte (1853, 1856) was the first to observe viviparity in this family, in the following termitophilous species: *Corotoca melantho* Schidte, *C. phylo* Schiödte and *Spirachtha eurymedusa* Schidte. He found larvae of various development stages in dissected females. Hagan (1951) classified these species as ovoviviparous, but only because of the lack of detailed information on their reproduction. Wassmann's (1915a, 1915b) reports on viviparity in myrmecophilous species of the genera *Lomechusa* and *Atemeles* were later questioned by Donisthorpe (1909, 1916, 1926) and Jordan (1913). It remains uncertain if the species are actually viviparous, and if so, what type of viviparity is concerned.

Chrysomelidae

First mentions of results of dissection of females and the presence of hatched larvae in their reproductive tract date from 1855; the studies were done by Perroud and involved two species of the genus *Oreina* (*speciosa* and *superba*). Based on literature data (Perroud 1855, Cornelius 1857, Weise 1885, Rupertsberg 1870, Bleuze 1874, Mayet 1874, Hacker 1888, Calloni 1889, Shenkling 1900, Chapman 1900, 1903, Champion and Chapman 1901, Williams 1914, Notman 1921, Rethfeldt 1924, Barnes 1925, Hennenberg 1927, Vetter 1937, Maneval 1938), Hagan (1951) mentioned 11 species of ovoviviparous chrysomelid beetles and divided them in two groups (offspring at birth enclosed in chorion and without

chorion); some species belonged to both groups at once. The author described in detail the female reproductive system and development of the embryo, summarizing the previous results (Kowalevsky 1871, Graber 1888, 1890, Lécaillon 1898a, 1898b, Korschelt and Heider 1899, Champion and Chapman 1901, Holmgren 1904, Strindberg 1913, Hirschler 1924, Rethfeldt 1924, Imms 1925, Eastham 1930, Paterson 1931a, 1931b, 1932, Snodgrass 1935).

The most penetrative and elegant paper on the viviparity in Chrysomelidae is that by Christian Bontems (1984). The author presented adaptations to viviparity: the ovariole (reduced germarium and vitellarium because of the reduced number of produced eggs; well-developed, elongate pedicel forming an incubation chamber in which larvae develop); the chorion (simplified, thin, permitting access of maternal nutritive substances to the embryo); small eggs (in the most advanced viviparous species the volume ratio of larva in oviduct to egg amounts to 80, while in oviparous species it equals 1). The above characters in chrysomelid beetles are graded, from the original condition to advanced adaptations (the most advanced species with respect to viviparity are members of the genus *Oreina*, especially *O. speciosa*, *O. ganglbaueri* and *O. alpestris*). Bontems (1985) stated that viviparity appeared as a character of chrysomelid beetles independently in several taxa and thus provided a poor basis for phylogenetic inferences. The author pointed out that in this beetle group, because of numerous intermediate cases, Hagan's (1951) classification was useless. In his paper he used neither the term ovoviviparity, nor the remaining terms for viviparity types, and made no attempt at assigning species to these types. To solve the problem of classification and terminology, Bontems adopted Carayon's (1961) definition of viviparity, according to which viviparous are species in which at least a part of embryonic development takes place within maternal organism. Based on this definition, he singled out 49 species which were viviparous or showing viviparous tendencies (e.g. facultative viviparity in *Oreina bidentata*, which at the beginning of the reproductive period lays eggs with no developed embryos, but with advancement of reproduction the eggs laid contain increasingly developed embryos). These species represent six genera (*Chrysolina* – 15, *Oreina* – 18, *Doryphora* – 7, *Phytodecta* – 6, *Paropsides* – 1, *Pyrgo* – 2) from the Palaearctic, Neotropics and Orient. Additionally, he found no dependence between viviparity and occurrence of species at high altitudes (mountain species) or the absence of spermatheca (most viviparous chrysomelids have no spermatheca, but some oviparous species are also devoid of it).

Chinese entomologists studied viviparity in chrysomelid beetles (Zhang 1984, Yang 1898), but their papers are written in Chinese and thus unavailable to me. The observations pertained to members of the genus *Gonioctena* Chevrolat (*fulva*, *rubripennis* and *rufipes*).

In 1994 Schroder et al. noted viviparity in *Platyphora quadrisignata* from Brazil, a member of a genus which is very closely related to *Doryphora* Illiger and *Leptinotarsa* Stål. The paper contains detailed information on cul-

ture of larvae and excellent illustrations of dissected female internal genitalia and embryo.

Tenebrionidae

In 1978 Tschinkel discovered ovoviviparity in tenebrionid beetles. Females of two species from South Africa, *Eurynotus capensis* (F.) (Oncotini) and *Melanopterus marginicollis* Muls. et Rey (trigonopoid Platynotina, Platynotini), carried fully developed larvae within their vaginae. The author states that "...other possible ovoviviparous species are *Schelodontes* sp. [trigonopoid Platynotina, Platynotini] and *Anomalipus variolosus* (Sol.) [Anomalipina, Platynotini], both of which carried a single, large egg in the vagina...".

Further ovoviviparous tenebrionid beetles were listed by Iwan (1996) in his revision of Madagascan melanocratoid Platynotina (Platynotini): *Melanocratus ferreri* Iwan, *Sebastianus projectus* Iwan, *Styphacus decorsei* Fairm. and *S. kochi* Iwan. Dissected females of these species were found to contain larvae in their bursa copulatrix and, in two further species – *M. validipes* Fairm. and *Styphacus neuter* (Fairm.) – single, large eggs were found.

Carabidae

Liebherr and Kavanaugh (1985) were the first to describe ovoviviparity in carabid beetles. They examined two myrmecophilous species of the genus *Pseudomorpha* from Arizona (*P. hubbardi* Notman and *P. angustata* Horn), in whose dissected females they found eggs with undeveloped and fully developed embryos, and larvae (completely free of egg chorion). Hatched larvae could be found within lateral oviducts, bursa copulatrix and vagina. The observations on enclosed larvae provide evidence that they are not active while held inside the female prior to larviposition, which is timed to coincide with summer rains. The authors suggest that the larviposition is aimed at eliminating egg mortality due to predation by ant hosts.

MATERIALS AND METHODS

Females were dissected and whole abdomens were cleared in 10% cold potassium hydroxide overnight. The dissected larvae were stained in chlorazol black dissolved in glycerine.

Eggs

Melanocratus validipes Fairm. – Madagascar Sud, plateau Mahafaly, 11/12 km Ouest d'Ankalirano, 250 m, 1/6-11-1974, P. Viette et A. Peyrieras; Museum Paris (2 ex.) (MNHN); Madagascar Sud, S. E. de Tranomaro, Androatsabo, 400 m, Peyrieras, XII-1971; Museum Paris (1 ex.) (MNHN);

Melanocratus fairmairei Iwan – Itampolo, Ampanihy Distr.; Madagascar, I. 1956, C. Koch leg. (1 ex.) (TMNH); Museum Paris, Madagascar, prov. de Tular, G. Petit 1926 (1 ex.) (MNHN);

Sebastianus major (Fairm.) – Ankororoka, Tulear Distr.; Madagascar, I. 1956, C. Koch leg. (1 ex.) (TMNH);

Styphacus decorsei Fairm. – Museum Paris, III. 69, Anjahantelo – Amboasary, Madagascar Sud, Vadon & Peyrieras (1 ex.) (MNHN);

Styphacus neuter (Fairm.) – Madagascar Sud, S. E. de Tranomaro, Androatsabo, 400 m, Peyrieras, XII-1971; Museum Paris (1 ex.) (MNHN);

Hovademus pauliani Ardoin – Andohahelo, (1.800 m), 1.54, (R.P.); Institut Scientifique, Madagascar (1 ex.) (MNHN);

Melanopterus varus Koch – Grahamstown, A. Vogt (1 ex.) (TMNH);

Eurynotus granulatus F. – Resolution, Albany Distr., VI. 1928, A. Walton (1 ex.) (TMNH);

Bantodemus mariepsus Koch – Marieps Mnt., Dec. 1925, G. van Son. (1 ex.) (TMNH);

B. imitator – Natal, Howick, Purcell (1 ex.) (TMNH);

B. lucidus Koch – Punda Milia, Kruger Nat. Park, III. 1960, C. K. Brain (1 ex.) (TMNH);

B. typhon (Muls. et Rey) – Johannesburg, Transvaal, G. Kobrow, 2.35 (1 ex.) (TMNH);

B. tristis Koch – Z. A. 93, Leydenburg D., Orhigstad; Humus, III. 62; N. Leleup leg. (1 ex.) (TMNH);

B. vescus Koch – Ironerown-Wolkberg, nr. Haenertsburg, E. Tvl., 17-26. XI. 1970, L. Prozesky and A. Strydom (1 ex.) (TMNH).

First instar larvae

Sebastianus simplex Iwan – Itampolo, Ampanihy Distr.; Madagascar, I. 1956, C. Koch leg. (TMNH) (1 ex.);

Sebastianus projectus Iwan – Madagascar Sud, plateau Mahafaly, 11/12 km Ouest d'Ankalirano, 250 m, 11/17-I-1974, P. Viette et A. Peyrieras; Museum Paris (1 ex.) (MNHN); Androka, Ampanihy Distr., Madagascar, I.1956, C. Koch leg. (1 ex.) (TMNH);

Styphacus bartolozzi Iwan – Madagascar Sud, plateau Mahafaly, 11/12 km Ouest d'Ankalirano, 250 m, 11/17-I-1974, P. Viette et A. Peyrieras; Museum Paris (2 ex.) (MNHN);

Styphacus kochi Iwan – S. o. Ctr. Madagaskar, Ljungqvist (1 ex.) (TMNH);

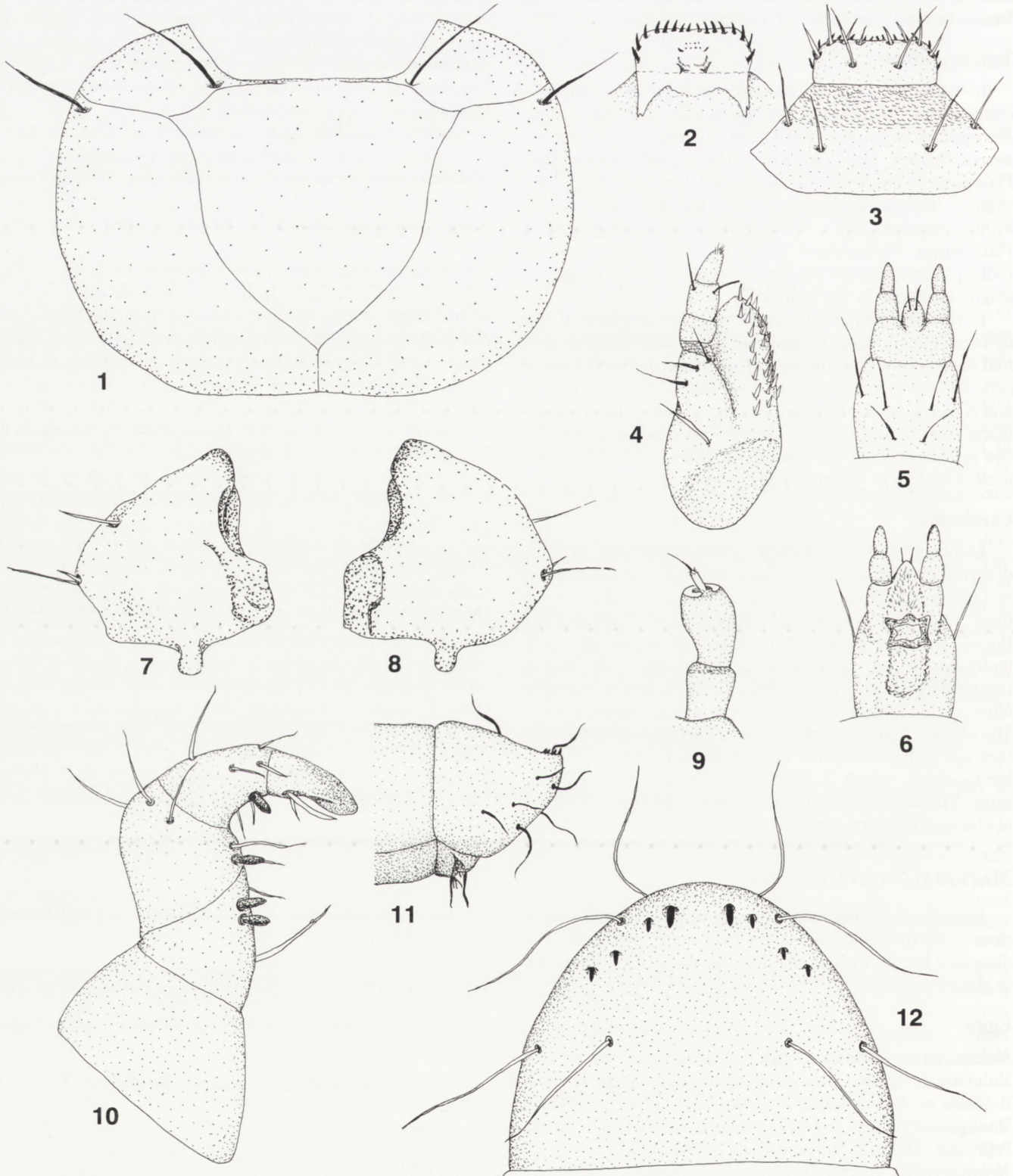
Melanocratus ferreri Iwan – Museum Paris, Madagascar S., District de Tsihombé, Beloha, Lieut. Decary 1919, avril (1 ex.) (MNHN).

DESCRIPTIONS OF THE FIRST-STAGE LARVAE OF THE MELANOCRATOID PLATYNOTINA

Sebastianus simplex Iwan, 1996

The description is based on a well developed first instar larva 12.0 mm long, 1.4 mm wide, head-capsule 1.2 mm broad (Fig. 18). Body subcylindrical; cuticula white-ivory; apices of mandibles and tips of the tarsungulus weakly sclerotized, darker. Egg-bursters absent.

Head. Prognathous type. Cranium transverse, slightly convex, narrower than pronotum, sides rounded. Epicranial suture Y-shape; epicranial stem short, about 7



Figures 1–12. *Sebastianus simplex*: (1) head, dorsal view; (2) ventral view of labrum; (3) labrum and clypeus; (4) maxilla; (5) dorsal and (6) ventral view of labium; (7) ventral and (8) dorsal view of left mandible; (9) antennae; (10) dorsal view of left fore leg; (11) lateral and (12) dorsal view of ninth abdominal segment.

times shorter than length of the head capsule (measured from the occipital foramen to the frontoclypeal suture); frontal arms extend to the antennal insertion, there is an additional oblique ecdysial line derived from each arm near its anterior end, these lines directed inwards and extend to the frontoclypeal suture (Fig. 1). Antennae 3-segmented (Fig. 9), with second segment about 1.7 times longer than first; segment 3 minute, about one-third of second one, with three short setae; apical area of segment 2 occupied by a sensillum (an incomplete ring around the base of segment 3); antennal insertion lateral, separated from the mandibular articulation by a narrow strip of membrane. Stemmata absent. Frontoclypeal suture distinct. Clypeus trapezoidal, about 2 times wider than long (Fig. 3); the postclypeus with two setae latero-medially on each side. Labrum transverse, with four setae along antero-lateral margin on each side and two long setae in the centre (Fig. 3). Epipharynx transverse-ovate; with eight short spines along anterior margin and pair short spines in the centre, two lateral setose patches below its, and strongly sclerotized, triangular pair of the posterior plates (Fig. 2). Mandibles asymmetrical, protruding laterally (Figs 7–8); the bifid obtuse apices sclerotized and dark coloured; right molar part prominently produced; on both mandibles ventrally one seta near the medianly broken curve of its exterior contour, and another two setae at base. Maxilla with well-developed transverse cardo (Fig. 4); elongate stipes bears 4 long setae; 3-segmented maxillary palpus: first segment subquadrate, second one 1.5 times longer than first (and bears three setae anteriorly), segment 3 conical, and slightly longer than first; mala with an inner surface densely covered by strong spines, and slightly notched at the inner apical angle. Labium with distinct prementum, mentum and submentum, gula not well-developed (Fig. 5); ligula with two setae on the tip, labial palps 2-segmented, second seg-

ment conical with setose area on apex; mentum elongated, with pair of setae at base and 4 ones medianly. Hypopharynx densely setose medianly, with tricuspidate hypopharyngeal sclerome (weakly sclerotized) (Fig. 6).

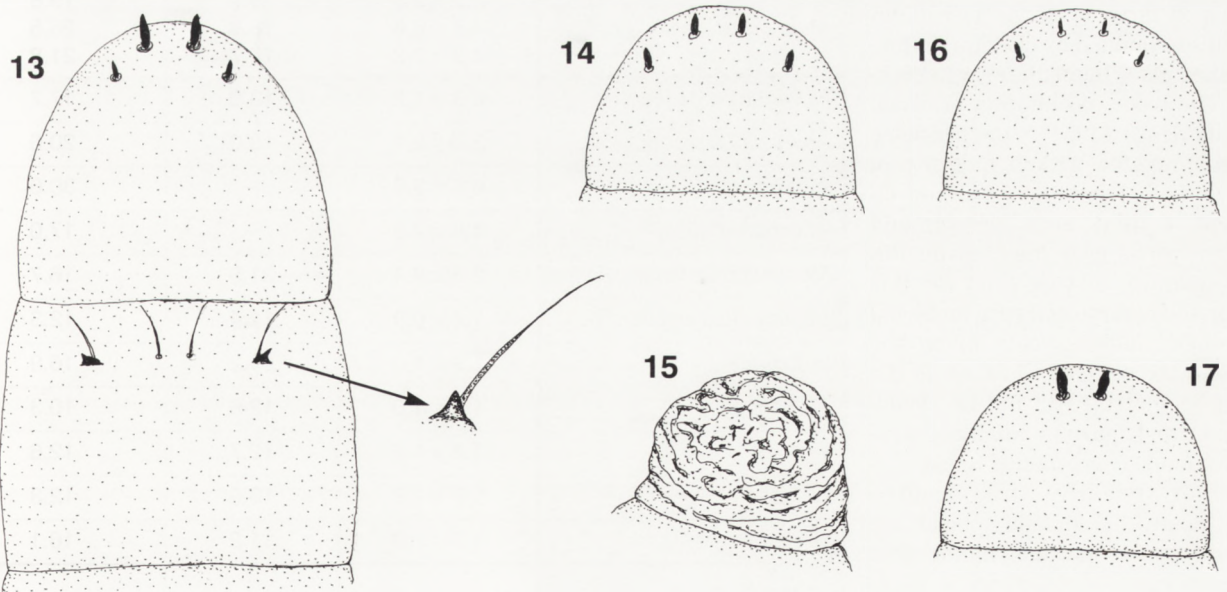
Thorax. Prothorax subquadrate about as long as wide, and 2 times longer than meso- or metathorax. Fore legs longer and stouter than mid and hind legs, setal arrangement as in Fig. 10; fore coxae nearly subquadrate, with strongly convex ventral margin; trochanter elongated, anteriorly with two heavily sclerotized tubercle; inner margin of femur subrectangularly bent, with one strongly sclerotized tubercle; tibia elongated, somewhat longer than tarsungulus, with one tubercle; tarsungulus wide, spade-like, strongly sclerotized, with 2 setae (not divided).

Abdomen. Ninth sternum reduced; pygopodia well visible (Fig. 11); ninth abdominal notum broadly heart-shaped, with 8 short spines along apex (2 median ones stouter than the other) (Fig. 12).

Comments. A general description of the first-stage larvae of the remaining species corresponds to the earlier-presented description of *Sebastianus simplex*. The differences involve mainly the number and shape of spines on the ninth abdominal notum (Figs 12–14, 16–17) and the presence of egg-bursters (Table 2). When the latter structure is present, it is located on the notum of thorax and abdomen as a pair of sharp dentates (Fig. 13). The last abdominal segment in not fully mature larvae is multiply concentrically wrinkled and flattened (Fig. 15), only later it assumes a cylindrical shape.

DISCUSSION

A common character of all beetles is that the 1st instar larva is born. After hatching it does not feed on maternal secretions and does not pass its whole larval development



Figures 13–17. Last abdominal segments: (13) *Sebastianus projectus* (inset. egg-burster); (14–15) *Styphacus bartolozzi*; (16) *Styphacus kochi*; (17) *Melanocratus ferreri*.

Table 2. Some differences between ovoviparous Platynotini.

species	larval length [mm]	head width [mm]	female length [mm]	egg-bursters	number of spines on abdominal sternite IX
<i>Melanocratus ferreri</i>	11.5	1.3	16.5	present	2
<i>Sebastianus simplex</i>	12.0	1.2	17.5	absent	8
<i>Sebastianus projectus</i>	8.0 7.0	1.0 1.0	17.5 18.5	present	4
<i>Styphacus bartolozzi</i>	10.0 10.5	1.2 1.2	14.5 15.5	absent	4
<i>Styphacus kochi</i>	4.5	0.7	18.5	present	4

in a specially modified section of the bursa called uterus (as is the case with adenotrophic viviparity in e.g. Diptera, Glossinidae). According to Hagan's (1951) classification this mode of reproduction can be classified within ovoviviparity in broad sense. Adopting the broadest definition of the term, i.e. its interpretation by Hinton and Mackerras (1970), Carayon (1961) and Bontemps (1985), ovoviviparity will include both laying eggs with partly formed embryos and larviposition (fully developed larva of instar 1) without or still surrounded by chorion (hatching takes place immediately after laying). The basic assumption of ovoviviparity (Hagan 1951) is the presence of egg provided with a quantity of yolk sufficient for embryonic development. I think that chrysomelid species whose eggs have an insufficient quantity of yolk (and for this reason the embryo, fed with maternal secretions, moves freely along the ovary to the oviduct and then to the bursa copulatrix) can not be classified as ovoviviparous. Such a reproductive mode corresponds to pseudo-placental viviparity (free embryo type). Some chrysomelid species are probably ovoviviparous. In the first group of chrysomelids and in carabids, larvae are born without chorion, which is thin and elastic suggest-

ing – in carabid beetles – viviparity (the more so that their eggs and hatched larvae are surrounded and separated from each other by a gelatinous matrix).

According to Bontemps (1985) viviparity in Chrysomelidae appeared independently and, contrary to what other authors postulated, is not associated with the occurrence of these beetles in mountain areas (it does not depend on climatic conditions at all). Contrary to Bontemps' opinion on Chrysomelidae, I assume that the development strategy of viviparity in Tenebrionidae (some genera of Platynotini

Table 3. Major axis of egg as a percentage of length of body female from vertex of head to tip of abdomen by Hinton (1981).

Tenebrionidae	– 11.56
Staphylinidae	– 13.90
Dermestidae	– 16.84
Lathridiidae	– 26.98
Anisotomidae	– 34.60

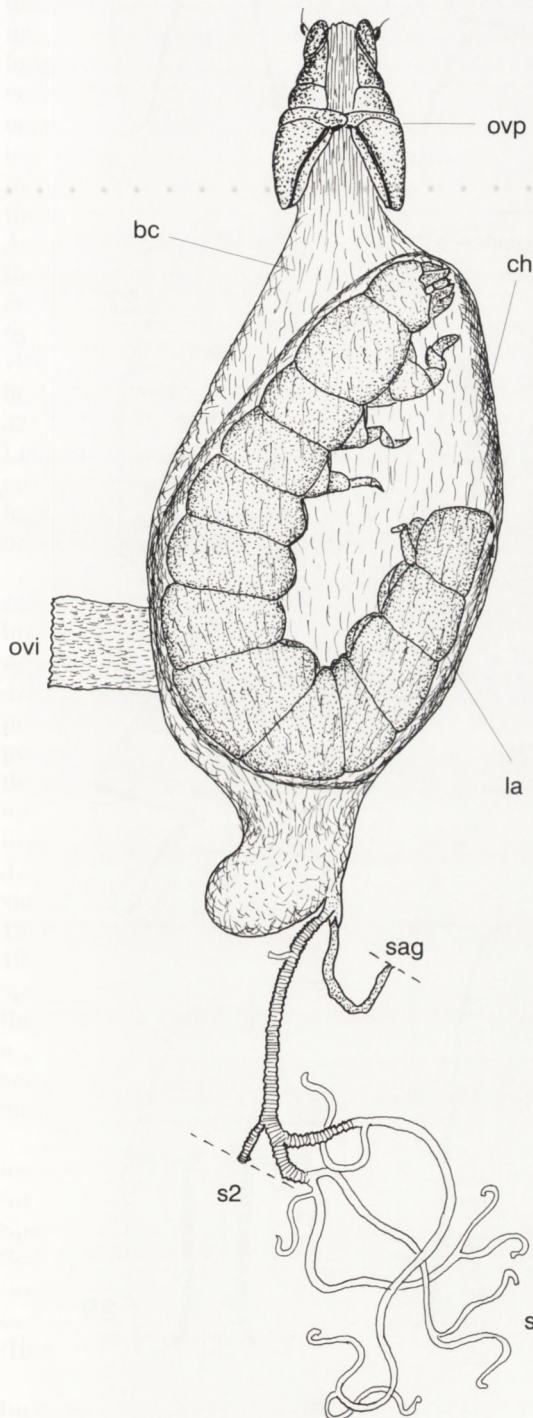
Table 4. Egg dimensions and the ratio female/egg length in some species of the Tenebrionidae, [* – ovoviviparous species; (1) – data after Endrödy-Younga (1988)].

speciess	egg dimensions [mm]	female length [mm]	major axis of egg as a % of length body female
Platynotini			
<i>Styphacus neuter</i> *	3.7 × 1.8	17.8	20.8
<i>Styphacus decorsei</i> *	3.6 × 1.7	20.0	18.0
<i>Sebastianus major</i> *	4.5 × 2.4	19.5	23.1
<i>Melanocratus fairmairei</i> *	5.0 × 2.6 3.1 × 1.5	13.9 15.5	36.0
<i>Melanocratus validipes</i> *	3.9 × 2.3 4.8 × 2.6 4.3 × 2.2	19.7 18.8 19.7	19.8 25.5 21.8
<i>Hovademus pauliani</i>	2.3 × 1.2	13.0	17.7
<i>Anomalipus plebejus</i>	3.6 × 2.1	18.0	20.0
<i>A. braini</i> (1)	6.8 × 3.0	–	30.0
<i>A. expansicollis</i> (1)	4.6 × 2.8	–	17.0
<i>Melanopterus varus</i>	3.6 × 2.4	21.5	16.7
<i>Bantodemus imitator</i>	1.4 × 0.9	11.4	12.3
<i>B. lucidus</i>	1.9 × 1.0	11.2	16.9
<i>B. mariepsus</i>	1.3 × 1.0	12.6	10.3
<i>B. tristis</i>	1.6 × 1.2	12.7	12.6
<i>B. typhon</i>	1.6 × 1.2	13.0	12.3
<i>B. vescus</i>	1.8 × 1.0	11.2	16.1
Oncotini			
<i>Eurynotus granulatus</i> *	2.6 × 1.5	18.7	13.9

and Oncotini) is associated with extremely adverse habitat conditions. In the distribution area of the discussed tribes in South Africa and south-western Madagascar the annual rainfall ranges from 400 to 1000 mm, and in some areas is even below 400 mm (Madagascar); both humidity and temperature show high diurnal

Table 5. Date on the biology of some tenebrionid beetles after Hinton (1981) (1), Gołębiewska and Nawrot (1976) (2), and Endrödy-Younga (1988) (3),

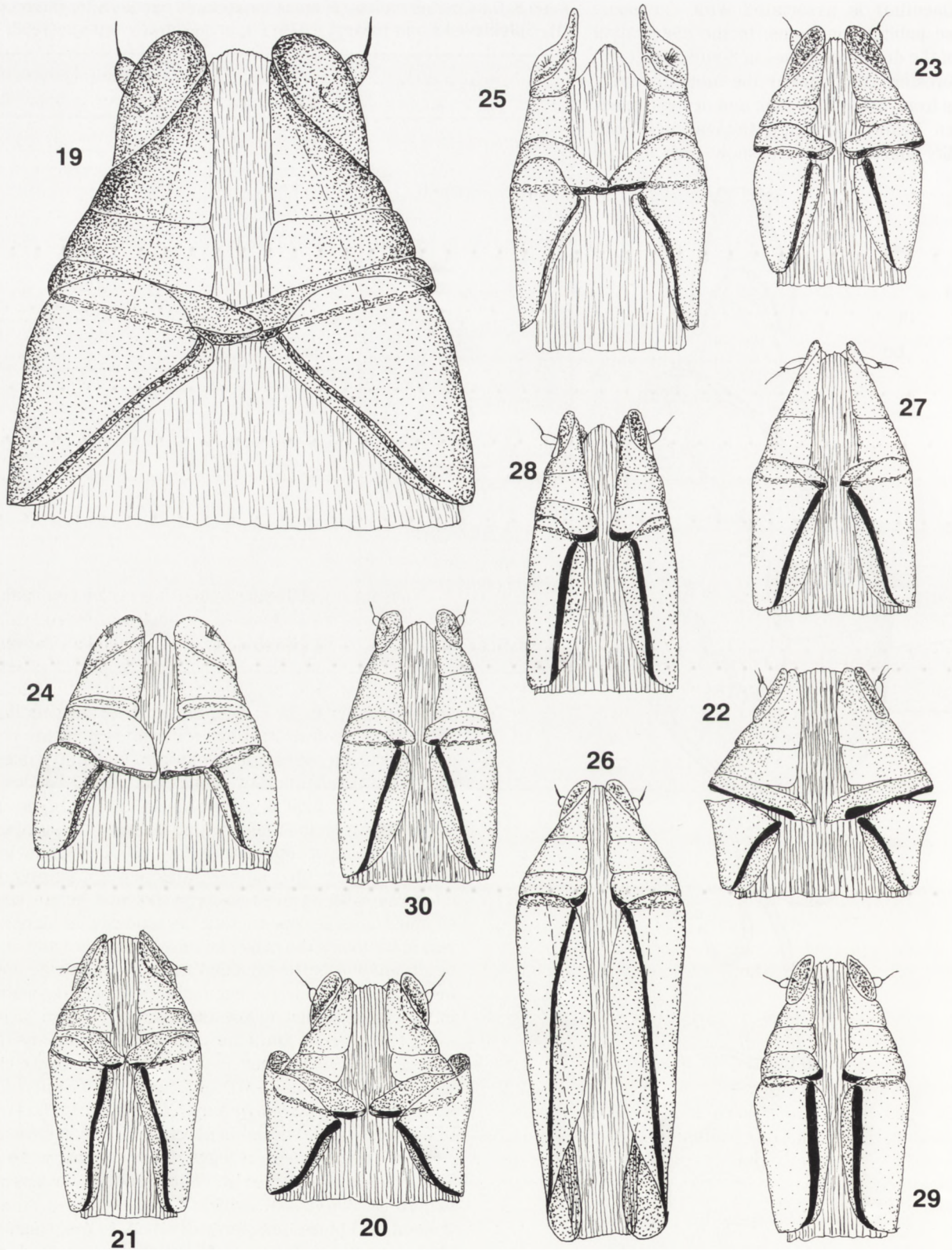
Species	Eggs (numbers)	Oviposition (days)	Female longevity (days)
<i>Tenebrio molitor</i> L. (1)	77–576 (276)	21–67	37–96 (65)
<i>Tenebrio molitor</i> L. (2)	500	130	147
<i>Tenebrio obscurus</i> F. (1)	73–970 (463)	22–137	42–152 (84)
<i>Tenebrio obscurus</i> F. (2)	460	–	90
<i>Tribolium castaneum</i> (Herbst) (1)	(360)	–	–
<i>Tribolium castaneum</i> (Herbst) (2)	485	–	720
<i>Tribolium confusum</i> Duv. (2)	max. 976 (400)	–	1280
<i>Mesomorpha villiger</i> (Blanch.) (1)	100+	–	190+
<i>Palorus subdepressus</i> Woll. (2)	116–695	–	8–240
<i>Gnathocerus cornutus</i> Fabr. (2)	100–400	–	300
<i>Anomalipus</i> spp. (3)	2–18 (per season)	–	~2200



Figures 18. *Sebastianus projectus*, female internal genitalia (bc – bursa copulatrix, ch – chorion, la – larva, ovi – oviduct, ovp – ovipositor, s1 and s2 – symmetrical parts of spermatheca, sag – spermathecal accessory gland).

amplitudes (Werger 1978, Davis 1964, Battistini and Richard-Vindard 1972). However, the areas mentioned are not deserts; the climate is semiarid to moderately mesic. In their 1993 paper Endrödy-Younga and Tschinkel described in detail their field observations of beetles of the genus *Anomalipus* hiding underground during unfavourable periods (in the night and during the cold, dry winter months when adults are hibernating), while surface activity occurs after rain and during relatively cool and humid hours of summer days. It appears that the tendency to increase egg size in beetles of the tribe Platynotini (Tables 3 and 4), could be an adaptation to dry conditions. A favourable, low volume/surface ratio of the egg facilitates retaining water and increases resistance to low temperatures.

It follows from the data contained in Bontems' (1985) (Table 3, p. 977) paper that eggs of viviparous chrysomelids are very small – 0.6 × 0.2 mm in *O. ganglbaueri* (in an oviparous *O. elongata* only 1.4 × 0.5 mm). The increase in egg size in Platynotini is accompanied by a clear reduction of the number of eggs laid, compared to other Tenebrionidae (Table 5). The process involves also oviparous Platynotini, which suggests that it should be treated as a phase preceding ovoviviparity. A possibility to choose the time and place of oviposition (because of very adverse environmental conditions) was possible only when the eggs could be retained for some time in the female's organism. In all dissected females of Platynotini I always found only a single egg in the bursa copulatrix; I never



Figures 19–30. Ovipositor: (19) *Sebastianus projectus*, Madagascar; (20) *Styphacrus nimius*, Madagascar; (21) *Melanocratus ferreri*, Madagascar; (22) *Sebastianus simplex*, Madagascar; (23) *Amblychirus tenebrosus*, South Africa; (24) *Anomalipus mastodon*, South Africa; (25) *Gonopus agrestis*, South Africa; (26) *Eurynotus capensis*, South Africa; (27) *Opatrinus moestus*, South America; (28) *Phallocentron praelaciniatum*, tropical part of Africa; (29) *Anchophthalmus variabilis*, tropical part of Africa; (30) *Pseudoblaps strigipennis*, Orient.

found other eggs in other sections of the female genital tracts or inside the abdomen (after dissection in KOH). My observations are confirmed by Tschinkel's (1978) note and Endrödy-Younga's (1988) mention of an oviparous *Anomalipus* in which "...the last eggs had not yet formed at the time when the first one was laid...". It is thus not accidental that the embryonic development in viviparous tenebrionids takes place only in the bursa copulatrix, and not in the earlier sections of the female genital tract. A longer retention of eggs inside the female enables the embryo to pass the incubation period inside the maternal organism and offers two benefits: embryo protection during its incubation and already active stage (1st larval instar), capable of vertical and horizontal migration and thus search for shelter, facing the adverse habitat. Assuming that this type of ovoviviparity may evolve further, the way will lead to adenotrophic, and not pseudoplacental, viviparity (only one offspring at a time is cared for by the mother). In the case of chrysomelid and carabid viviparous beetles the number of eggs produced per female is fairly high. Browdij (1970) observed larviposition of 32–54 larvae during 20 days by one isolated female. Liebherr and Kavanaugh (1985), studying carabids, reported that the total number of eggs plus free larvae found per female (dissected) averaged 32 (max. about 60) for *P. angustata*, and 34 (max. about 70) for *P. hubbardi*.

In tenebrionid beetles the fertility (associated with reduction of the number of eggs) is increased by prolonging the oviposition period due to individual longevity. According to Endrödy-Younga (1988) in oviparous *Anomalipus* the female lays eggs during about 5 months per year, the total number being 2 to 18 eggs, mean 9.2 eggs per female per season. The author reports also that a beetle of the genus *Gonopus* (closely related to trigonopoid and melanoceroid Platynotina) kept in the laboratory, lived for about 8 years, and a member of the genus *Anomalipus* – 5 years and 8 months; in the wild 20% individuals of *A. mastodon* marked in a population study in 1979 and 1980 still appeared in daily counts during the 1982/83 season. The female's ability to store sperm in the spermatheca for a long time seems to be a consequence of the above processes. According to Endrödy-Younga (1988) a single female lays fertile eggs during two consecutive seasons, which means that it stores sperm in the spermatheca during ca. 19 months after the last copulation.

The phenomenon (retention of incubated eggs inside female) may be regarded as a form of parental care. Care for laid eggs is known in such families as Carabidae, Spercheidae, Hydrophilidae, Silphidae, Staphylinidae, Scarabaeidae, Passalidae, Heteroceridae, Chrysomelidae, Scolytidae, Platypodidae; a single case – *Phrenapates bennetti* Kirby – was noted in the family Tenebrionidae (Hinton, 1981).

My studies on the evolutionary tendencies in the structure of the female reproductive system (in preparation) indicate clear changes in the development of particular components of ovipositor in ovoviviparous and related oviparous species (producing large eggs). The changes

include a considerable shortening of paraproct (reduction of its anterior margin), and the first coxite (very narrow, transverse), often resulting in an ovipositor in the shape of triangle with a rather broad base, are adaptations to laying large eggs or to larviposition (cf. Figs 19–25 and 27–30). Members of the genus *Eurynotus* (Oncotini) depart from this scheme – their characteristic feature is a strongly elongate paraproct (probably depending on substratum for ovi- or larviposition) (Fig. 26). It appears that in spite of close relationship, ovoviviparity in particular groups of tenebrionid beetles could evolve independently. A more important fact is the occurrence of preadaptations to this mode of reproduction in South African Platynotini: production of large, single eggs and modifications in the ovipositor structure. The tribe Oncotini is probably a polyphyletic group and its relationships to Platynotini are unclear, since adopting Koch's (1956) interpretation results in one of these taxa being paraphyletic. Tendencies to viviparity in only some taxa of both these tribes provide another argument against Koch's (1956) classification and indicate a necessity of a modern analysis and verification of the system of opatrine lineage (sensu Doyen i Tschinkel 1982).

CONCLUSIONS

Ovoviviparity in Tenebrionidae has evolved independently and differs from comparable modes of reproduction in other beetles (Micromalthidae, Chrysomelidae, Carabidae). Tenebrionid beetles produce in a given period of embryo incubation only one large egg, retained by the female in the bursa copulatrix. Their larvae are born surrounded by chorion and hatch outside the maternal organism.

Ovoviviparity evolution in Tenebrionidae is associated with earlier formation of large eggs and the associated modification of ovipositor. Eggs containing embryos at various development stages, up to full grown first instar larvae may be expected inside females of various species.

Longevity of adult beetles favours the discussed mode of reproduction. Its efficiency is evident in an area of adverse humidity and temperature conditions (large diurnal and annual amplitudes).

Ovoviviparity and preadaptations (large, single eggs) of tenebrionid beetles involve a group of genera of related tribes Platynotini and Oncotini, inhabiting South Africa and Madagascar (opatrine lineage sensu Doyen and Tschinkel 1982).

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