REPRODUCTIVE BIOLOGY AND NESTING BEHAVIOUR OF THE PROMINENT DUNG BEETLES (SCARABAEINAE: COLEOPTERA) IN THE AGRIBELTS OF MALABAR COAST

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BY

PRAMEELA K.

Under the Guidance of

Dr. SABU K. THOMAS

P. G. & RESEARCH DEPARTMENT OF ZOOLOGY,

ST. JOSEPH'S COLLEGE (AUTONOMOUS), DEVAGIRI,

KOZHIKODE - 673 008, KERALA.

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P.G. & RESEARCH DEPARTMENT OF ZOOLOGY
ST. JOSEPH'S COLLEGE DEVAGIRI (AUTONOMOUS)
KOZHIKODE - 673 008, KERALA
www.devagiricollege.org
email: sabukthomas@gmail.com

Dr. Sabu K. Thomas
Professor

Date:

Certificate

This is to certify that the thesis entitled "**REPRODUCTIVE BIOLOGY AND NESTING BEHAVIOUR OF THE PROMINENT DUNG BEETLES (SCARABAEINAE: COLEOPTERA) IN THE AGRIBELTS OF MALABAR COAST**" submitted to the University of Calicut for the award of degree of Doctor of Philosophy in Zoology, is the record of the original work done by **Mrs. PRAMEELA K.** in the PG & Research Department of Zoology, St. Joseph's College (Autonomous), Devagiri, Kozhikode, under my supervision and guidance, and that it has not formed the basis for the award of any degree/diploma or other similar titles to any candidate of any University.

Dr. Sabu K. Thomas
Supervising Teacher

P.G. & RESEARCH DEPARTMENT OF ZOOLOGY
ST. JOSEPH'S COLLEGE DEVAGIRI (AUTONOMOUS)
KOZHIKODE - 673 008, KERALA
www.devagiricollege.org
email: sabukthomas@gmail.com

Dr. Sabu K. Thomas
Professor

Certificate

Certified that the publication, "Prameela K. & Sabu K. Thomas, Life Cycle of the dung beetle *Onthophagus cervus* (Fabricius,1798) (Coleoptera: Scarabaeidae: Scarabaeinae) in moist belts of south India, *Entomon* 45 (4), pp 243-252" is published in a peer reviewed journal.

Place: Devagiri
Date :

Dr. Sabu K. Thomas
Supervisor & Guide

Declaration

I do hereby declare that the work entitled "**REPRODUCTIVE BIOLOGY AND NESTING BEHAVIOUR OF THE PROMINENT DUNG BEETLES (SCARABAEINAE: COLEOPTERA) IN THE AGRIBELTS OF MALABAR COAST**" is an authentic record of the work carried out by me under the supervision and guidance of Dr Sabu K. Thomas, Principal, St. Joseph's College (Autonomous), Devagiri, Kozhikode, and that no part of this has been published previously or submitted to the award of any other degree/diploma.

Place: Devagiri

Date: **PRAMEELA K.**

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Prameela K.

Dedicated to my Parents

and Teachers

CONTENTS

Chapter 1

INTRODUCTION

INTRODUCTION

Dung beetles belonging to the subfamily Scarabaeinae is a highly diverse and broadly distributed group, characterized by dung and organic debris at both the adult and larval stages (Hanski and Cambefort, 1991).The dung beetles include three subfamilies of Scarabaeidae (Insecta: Coleoptera), Aphodiinae, Geotrupinae and Scarabaeinae. Within the subfamilies, Scarabaeinae is the only group that is mainly coprophagous (faeces eating). The majority of Aphodiinae and Geotrupinae are saprophagous (eaters of decaying organic matter), not true dung beetles (Halffter and Matthews, 1966; Scheffler, 2002). Dung beetles are categorised into 12 tribes which included Coprini, Dichotomini, Phanaeini, Oniticellini, Onitini, Onthophagini, Eucraniini, Eurysternini, Canthonini, Gymnopleurini, Scarabaeini and Sisyphini (Lawrence and Newton, 1995).

Based on their nesting strategies dung beetles are divided into three functional groups, namely, rollers (telecoprid nesters), tunnelers (paracoprid nesters) and dwellers (endocoprid nesters) (Cambefort and Hanski, 1991). In Scarabaeinae, dwelling is associated with tribe Oniticellini and tunneling with tribes Coprini, Onitini and Onthophagini, dung rolling is associated with tribes Scarabaeini, Gymnopleurini, Sisyphini and Canthonini (Halffter and Edmonds, 1982). Regarding the morphological changes between the functional groups, the tunneling dung beetles have comparatively smaller hind legs and the front legs are well suited for digging. The presence of horns is common in tunneling dung beetles. The rollers commonly have long hind legs. The rollers roll the dung ball using their back legs (Hanski and Cambefort, 1991; Scholtz *et al*., 2009).

Most dung beetles use one of the three wide nesting strategies, tunnellers, rollers and dwellers. Tunneller (Paracoprid) species bury brood balls in vertical chambers in the locality of the original deposition site. Roller (telecoprid) species carry balls to some horizontal distance away, before burial below the soil surface. Dweller (endocoprid) species brood their young inside the dung mass itself (Halffter and Edmonds, 1982). This functional stratification permits dung beetles to decrease the intense struggle for limited food and space and protect the food from adverse environmental conditions such as heat and extreme dryness (Halffter and Edmonds, 1982; Cambefort and Hanski, 1991).

1.1. Distribution of dung beetles.

Provincial lists of dung beetles are obtainable from South Africa (Péringuey, 1900; Chown *et al*., 1995), African Tropical region (Gillet, 1908, 1911), Sumatra (Gillet, 1924), China (Gillet, 1935; Nakane and Shirahata, 1957; Bin -Hong Ho, 2018), Central America, the West Indies South America (Blackwelder, 1944) Afghanistan (Balthasar, 1955), Japan (Nakane and Tsukamoto, 1956), Florida (Woodruff, 1973), Panama and Costa Rica (Howden and Young, 1981; Howden and Gill, 1987; González-Maya and Mata-Lorenzen, 2008), Nebraska (Ratcliffe, 1991; Wagner *et al*., 2020), Europe (Baraud, 1992), Colombia (Lopera, 1996), Nearctic Realm (Smith, 2003) and Palaearctic region (Löbl and Smetana, 2006). World checklists of dung beetles were prepared by Krajcik (2006) and Schoolmeesters (2019). Checklists of dung beetles of Pakistan (Siddiqui *et al.,* 2014), Northern Brazil (Pacheco and Vaz-de-Mello, 2019), the Mediterranean region (Löbl and Löbl, 2016), Ecuador (Espinosza and Noreiga, 2018), Mexico (Sanchez - Hernandez *et al.*, 2020), Southwest Arabia (Paulian, 1938; Ziani, 2021), Neotropical region (Gonzalez and Vaz-de-Mello, 2021) and Cambodia (Han *et al.*, 2021) are available.

Arrow (1931) and Balthasar (1963a, b) provided comprehensive information about the dung beetles in the Indian subcontinent. Recent works on the taxonomy of dung beetles from different parts of India are Biswas and Chatterjee,1985; Veenakumari and Veeresh,1996; Mittal,1999; Chatterjee and Biswas, 2000; Chandra, 2005; Sewak, 2006; Schoolmeesters and Sabu, 2006; Chandra and Ahirwar, 2007; Vinod and Sabu, 2007; Vinod, 2009; Sarkar *et al*., 2010; Latha *et al*., 2011; Sabu *et al*., 2011; Venugopal *et al.*, 2012; Sarkar *et al*., 2015; Sathiandran *et al*., 2015; Karimbumkara and Priyadarsanan, 2013, 2016 ; Gajendra and Prasad, 2016; Subha and Sabu, 2017; Kalawate, 2018; Patole, 2019 and Kharel *et al*., 2020).

1.2. Ecological importance of dung beetles.

Dung beetles are an economically important group of beetles that play a central role in forest soil conditioning, as they are the chief agents in soil aeration, improving soil structure and water circulation and modify organic debris, making it usable for other organisms (Halffter and Mathews, 1966; Bornemissa and Williams, 1970; Nealis, 1977; Mittal, 1993). Faeces decompose four times faster in the presence of dung beetles (Gillard, 1967), thus the rate of nutrient cycling is increased (Miranda *et al.*, 1998). Dung beetles have very low efficiency of assimilation of energy (Holter, 1975) and much of what they ingest is quickly egested and is thus rapidly available to other organisms (Scheffler, 2002). Dung beetles also accelerate bacterial growth and, unlike earthworms, incorporate manure and carrion and plant material in the soil (Lutz, 1931). Dung beetles are among the most important invertebrates to dung decomposition in temperate and tropical agricultural grasslands (Gittings *et al.*, 1994; Davis, 1996; Horgan, 2001; Lee and Wall, 2006; Slade *et al.*, 2011; Kaartinen *et al*., 2013). Dung removal, seed dispersal, nutrient cycling and reduction of greenhouse gas emissions are the major ecosystem services provided by dung beetles (Slade *et al.*, 2011; Lugon *et al*., 2017; Menendez *et al.,* 2016; Nervo *et al*., 2017 and Piccini *et al*., 2017).

1.3 Prominent dung beetles in different regions.

Dominant dung beetle species varies among different regions. *Oniticellus pseudoplanatus* Balthasar, 1964 in moist forests of Ivory Coast (Cambefort and Walter, 1991); *Onthophagus vulpus* Harold, 1877 and *Sisyphus thoracicus* Sharp, 1875in the rainforest in Malaysia (Davis, 2000); *Dichotomius amplicollis* Harold, 1869, *Deltochilum gibbosum* (Fabricius, 1775) and *Onthophagus landolti* Harold, 1880 in Mexican dry forest (Andresen 2005, 2008); *O. wallacei* Harold, 1871, and *O.fuscostriatus* Boucomont,1914 in Indonesian forest (Shahabuddin,2010); *Dichotomius nisus* (Olivier, 1789), *Trichillum externepunctatum* (Preudhomme de Borre, 1880), *Canthon podagricus* (Harold,1868), *Onthophagus hirculus* (Mannerheim, 1829), *Pseudocanthon perplexus* (LeConte, 1847), *Ontherus sulcator* (Fabricius, 1775) and *Ataenius platensis* (Blanchard, 1846) in the Argentine cattle ranches (Damborsky *et al*., 2015), *Canthon histrio* Serville, 1828, *Onthophagus hirculus* (Mannerheim, 1829) and *Deltochilum verruciferum* Felshe, 1911 in Brazilian dry forest (Novais *et al*., 2016), *Canthonquinque maculatus* Castelnau,1840 *Canthon conformis* Harold, 1868, *Dichotomius serices* (Harold, 1867) in Southern Atlantic forest of Argentina **(**Andrés Gómez, 2017), *Ontherus pubens* Genier, 1996 in Ecuador (Espinosza and Noreiga, 2018), *Deltochilum mexicanum* (Burmeister, 1848) and *Dichotomius satanas* (Harold, 1867) in Mexico (Barretto *et al*., 2019), *Onthophagus hecate* (Panzer, 1794), *O. pennsyl vanicus* Harold, 1871 and *Diapterna pinguella* (Brown, 1929) in the Nebraska Sandhills Ecosystem (Wagner *et al*., 2020), *Eurysternus caribaeus* (Herbst,1789), *E. nigrovirens* Génier, 2009, *Dichotomius carbonarius* (Mannerheim, 1829), *Onthophagus hirculus* (Mannerheim, 1829), *O. buculus* Mannerheim, 1829, *Canthon simulans* (Martinez, 1950), *C. fortemarginatus*

Balthasar,1939, and *Canthidium barbacenicum* (Preudhomme de Borre,1886) in south Western Brazil Cerrado (Silva *et al*., 2021).

1.4. Prominent dung beetles in India.

Dominant dung beetles in India are *Digitonthophagus gazella* (Fabricius, 1787), *Onthophagus rectecornutus* Lansberge, 1883, *Copris repertus* Walker,1858, *C. fricator* (Fabricius, 1787) in Deccan region in south India (Veenakumari and Veeresh, 1996, 1997); *Caccobius ultor* Sharp, 1875 in the forests of Haryana in North-Western India (Mittal, 2005; Kakkar and Gupta, 2009, Kakkar, 2010); *Caccobius vulcanus* (Fabricius, 1801), *C. ultor* Sharp,1875, *Onthophagus centricornis* Fabricius, 1798, *O.cervus* (Fabricius, 1798), *O. fasciatus* Boucomont, 1924, *O. dama* (Fabricius, 1798), *Tiniocellus spinipes* (Roth, 1851), *Sisyphus longipes* (Olivier, 1789) and *Tibiodrepanus setosus* (Wiedemann, 1823) in the moist belts of south India (Vinod, 2009; Thomas *et al*., 2011; Venugopal *et al*., 2012; Nithya, 2012; Nithya *et al*.,2015; Shobhana, 2016; Sabu, 2012 and Subha, 2018). Patole (2019) reported *Catharsius pithecius* (Fabricius, 1775) and *Gymnopleurus cyaneus* (Fabricius, 1798) from the agriculture belts in Maharashtra. Two *Tiniocellus* species, *Tiniocellus imbellis* (Bates, 1891) and *T. spinipes* (Roth, 1851) were reported in the Tropical Forest of the Himalayan foothills, West Bengal, India. (Sarkar and Kharel, 2020).

1.5. Nesting behaviour and biology of dung beetles.

Like all insects, scarabs undergoes four stages in their life cycle: egg, larvae, pupae and adult. (Halffter and Mathews,1966; Hanski and Cambefort, 1991; Scheffler, 2002). All known Scarabaeinae exhibit some degree of nesting behaviour, Juvenile development takes between 30–50 days from egg to adult and in adverse conditions over a year. After emergence from the nest adults undergoes a prolonged feeding period for three to four months to develop gonads and eggs. The average life span of

60 days to three years (Scheffler, 2002). Nest preparation and brood mass construction are the pioneers of the next step in the breeding process (Halffter and Edmonds, 1982). Reproductive biology and nesting behaviour of dung beetles have been broadly studied and critically analysed in different parts of the world. Klemperer (1983) described the subsocial behaviour of *Oniticellus cinctus* (Fabricius,1775), from Birmingham. Biology and nesting behaviour of *Onitis viridulus* Boheman, 1857, *O. fulgidus* Castelnau, 1840, *O. obscures* Lansberge,1886 *O. alexis* Klug, 1835, *O. perpunctatus* Balthasar, 1963a, *O. caffer* Boheman,1857. *O. aygulus* (Fabricius, 1781), *O. tortuosus* Houston, 1983 *O. receptor, O. uncinatus* Klug, 1855, *O. picticollis* Boheman, 1857 and *O. pecuarius* Lansberge,1875 from South Africa were studied by Edwards and Aschenborn(1987). Life history of *Onthophagus medorensis* Brown, 1929 Hunter *et al*., (1991). Studies on reproductive biology and nesting of *Onthophagus stylocerus* Graells, 1851 by Romero and Piera (1995). Studies on the brood care behaviour and nest structure of the dung beetle *Onthophagus vacca* (Linnaeus, 1767) by Sowig (1996). Studies on the life history of *O. depressus* Harold, 1871 by Hunter *et al.,* (1996). The reproductive biology of the *O.incensus* (Say, 1835) was studied in Mexico by Martínez *et al*., (1998). Biology of the dung beetle *O. hirculus* Mannerheim, 1829 done by Gonzalez-Vainer and Morelli (1999). Reproductive biology of *Onitis belial* (Fabricius, 1789) from Morocco, *O. anthracinus* Felsche, 1907 and *O.vanderkelleni* Van Lansberge,1886 from Kenya, by Palestrini *et al*., (2002). The cost of reproduction of dung beetle *Onthophagus binodis* (Thunberg, 1818) was studied in Australia by Kotiaho and Simmons (2003). Comparative analysis of reproductive and nesting behaviour in several species of *Eurysternus* Dalman, 1824 by Huerta *et al*.,(2003). Studies on fecundity and offspring survival of *Copris tripartitus* Waterhouse, 1875 from Mexico was done by Huerta and Bang (2004). Studies on the life cycle,

preimaginal development and phenology of *Onthophagus landolti* Harold, 1880 in Mexico was done by Pérez-Cogollo *et al.*, (2015) and the cost of reproduction of *Callosobruchus maculatus* (Fabricius,1775) was done by Paukku and Kotiaho(2005). The rolling and tunneling behaviour of large-sized subsocial African dung rolling beetle *Scarabaeus catenatus* (Gerstaecker,1871) were studied by Sato (2007). Reproductive development and seasonal activity of two Korean native *Coprini* species *Copris ochus* (Motschulsky, 1860) and *C. tripartitus* Waterhouse, 1875 studied by Bang *et al*., (2008). Reproductive activity of *Onthophagus granulatus* Boheman, 1858 was studied in New Zealand by Forgie (2009). Studies on pre-imaginal stages of *O. incensus* (Say, 1835) by Huerta *et al*., (2010). Nesting behaviour of *O. incensus* (Say, 1835) was studied in Mexico by Huerta and Hernández (2013). Pérez - Cogollo *et al*.,(2015) studied the life history of *O. landolti* Harold, 1880, in Mexico. The feeding, reproductive and nesting behaviour of *Canthon bispinus* (Germar, 1824) from Uruguay (González-Vainer, 2015). Comparative studies on the nesting and food relocation behaviour of *Eucranium* Brulle, 1834 with that of the morphologically similar South African subgenus *Scarabaeus* (*Pachysoma*) Macleay,1821 was done by Ocampo and Philip (2017). The life history of the dung beetle *Onthophagus lecontei* Harold, 1871 was studied in Mexico by Arellano *et al*., (2017). The reproductive biology of *Euoniticellus intermedius* (Reiche, 1848) was studied in Mexico by Martinez *et al*., (2019). Medina *et al*., (2020) conducted a study on the feeding and reproductive behaviour of the dung beetle *Canthon rutilanscyanescen*s Harold, 1868 in Brazil.

1.6. Nesting behaviour and biology of dung beetles in India.

Only scant information is available on the life-cycle of Indian dung beetle species and the details are as follows; Joseph (1994) carried out a study on sexual dimorphism and intra sex variations of the giant dung beetle *Heliocopris dominus* Bates (1868). Veenakumari and Veeresh (1996b) studied the feeding and breeding behaviour of *Gymnopleurus gemmatus* (Harold, 1871) and *G.miliaris* (Fabricius 1775). Studies on the reproductive biology of the two commonly occurring south Indian species *Onthophagus gazella* (Fabricius, 1787) and *O.rectecornutus* Lansberge, 1883 was done by Veenakumari and Veeresh (1996c). Subsociality in *Copris repertus* Walker, 1858 and *C. indicus* Gillet, 1910 was studied by Veenakumari and Veeresh (1997). Joseph (1998) conducted studies on the life biology and breeding behaviour of *Heliocopris dominus* Bates (1868). Studies on the life cycle, ecological role and biology of immature stages of *H. dominus* Bates, 1868 was done by Joseph (2003). Nidification behaviour of three dung beetle species, *Onthophagus catta* (Fabricius 1787), *Onitis philemon* (Fabricius, 1801) and *Liatongus rhadamistus* (Fabricius, 1775) were studied in Maharashtra by Gaikwad and Bhawane (2015). Study of nesting and biology of the dung beetle *Scaptodera rhadamistus* (Fabricius, 1775) from Maharashtra was done by Khadakkar *et al*., (2018). Analysis of the nesting architecture, life cycle, and brood ball morphometry of the dung beetle *Oniticellus cinctus* (Fabricius, 1775) was studied in Dehradun by Singh *et al*., (2019).

It is impossible to interpret the exact mechanism behind the seasonality and abundance of individual species and genera due to lack of knowledge on the biology and ecology of prominent dung beetles species (Sabu, 2012; Vinod, 2009; Nithya, 2012; Latha, 2011; Sobhana, 2016; and Subha, 2018). The present study has been undertaken to understand the life-history traits of the five prominent dung beetle species, *Onthophagus cervus* (Fabricius, 1798), *Onthophagus fasciatus* Boucomont, 1924, *Tiniocellus spinipes* (Roth, 1851), *Sisyphus longipes* (Olivier, 1789), and *Tibiodrepanus setosus* (Wiedemann, 1823) in the agribelts of Malabar Coast region in south India.

The genus *Onthophagus* Latreille, 1802 is a hyperdiverse and largest genus, within the tribe Onthophagini of the subfamily Scarabaeinae. The peculiarity of the *Onthophagus* genus is characterized by their excavation habit of construction galleries beneath the dung, and females are produced a large number of eggs (Fecundity is high) (Halffter and Edmonds, 1982; Delgado,1997; Pulido and Zunino,2007). *Onthophagus* is a well-adapted species capable of surviving in a variety of habitats including disturbed habitats like crop fields and may produce several broods per year as common in small tunnelers (Cambefort and Hanski, 1991). The tribe Onthophagini belong to two species, *Onthophagus cervus* (Fabricius, 1798) and *Onthophagus fasciatus* Boucomont, 1924 are the prominent tunneller species in the moist belts of south India (Vinod, 2009; Thomas *et al.,* 2011*;* Venugopal *et al.,* 2012; Nithya, 2012; Nithya *et al*; 2015; Shobhana, 2016; Sabu, 2012 and Subha, 2018).

The tribe Oniticellini Kolbe, 1905 include 4 subtribes namely *Drepanocerina* van Lansberge, 1875, *Oniticellina* Kolbe, 1905, *Helictopleurina* Janssens, 1946 and *Eurysternina* Volcano, Martinez and Pereira, 1960 (Branco, 2010 and Philips, 2016). *Tiniocellus spinipes* (Roth, 1851) comes under the soil tunneling genus *Tiniocellus* of the subtribe Oniticellina (Cambefort and Lumaret, 1983). Oniticellina sub-tribe differ from other sub-tribes due to these characters are as follows, the pygidium lacks the basal transverse carina, the dorsal face is either glabrous or with simple pilosity, and the scutellum is small but always distinct (Janssens, 1949). So far only the data available on the biology of subtribe Oniticellina species namely, *Liatongus rhadamistus* (Fabricius, 1775) in West India (Gaikwad and Bhawane, 2015) and *Euoniticellus intermedius* (Reiche, 1848) in Mexico (Martinez *et al*., 2019) have been reported. *Tiniocellus spinipes* is a small-sized beetle having, Length of 6 mm, a breadth of 2.5mm; and inhabited in Mammalian dung. *Tiniocellus* Péringuey, 1901 is a species-poor genus and has only seven species throughout the world. *Tiniocellus. spinipes* (Roth,1851), The Asiatic *T. imbellis* (Bates, 1891); *T. asmarensis* Balthasar, 1968 the African *T. setifer* (Kraatz,1895), *T. praetermissus* (Branco, 2010), *T. dolosus* (Branco,2010) and *T. eurypygus* (Branco, 2010).Two species, *T. imbellis* (Bates, 1891) and *T. spinipes* (Roth, 1851) are known from India, Schoolmeesters (2019).

Sisyphini is regarded as the true dung ball rollers (Daniel *et al*., 2020) and *Sisyphus longipes* (Olivier, 1789) belongs to the tribe Sisyphini. As a member of the roller guild, it has the following features that assist the species in dung rolling. It contains eight antennal articles, comparatively short bodies that are laterally compressed and flattened, especially at the sides of the pronotum, elytra that are broad proximally but attenuate posteriorly and the exceptionally long middle and hind legs. The tribe contains species of minor to moderate body size averaging 7.0–10.0 mm. The *Sisyphus* species in India are *Sisyphus longipes* (Olivier, 1789) *S. neglectus* Gory, 1833, *S. araneolus* Arrow 1927, *S. hirtus* Wiedemann, 1823 (Arrow 1927), and *S. indicus* Hope, 1831. *Sisyphus longipes* as the dominant roller species in the moist belts of South India (Vinod, 2009; Sabu, 2011; Mathew, 2011; Simi, 2012; Nithya, 2012; Nithya *et al*., 2015 Subha, 2018) and showed significant seasonal variation with high abundance in the Monsoon season (Sabu, 2011).

The genus *Tibiodrepanus* was introduced by Krikken (2009) *Tibiodrepanus setosus* (Wiedemann, 1823) comes under the dwelling subtribe Drepanocerina. The subtribe *Drepanocerina* is composed of 11 genera and 46 species (Schoolmeesters, 2019). The prominent dweller species in the moist belts of South India is *Tibiodrepanus setosus* (Vinod, 2009; Sabu, 2011; Mathew, 2011; Simi, 2012; Nithya, 2012; Nithya *et al*., 2015 Subha, 2018).

OBJECTIVES

Study of following aspects of prominent dung beetle species in the agricultural fields in the Malabar Coast region.

1. Life biology and
2. Fecundity, egg mortality, larval and pupal duration, adult life span, nesting strategies and voltinism of prominent dung beetles species.

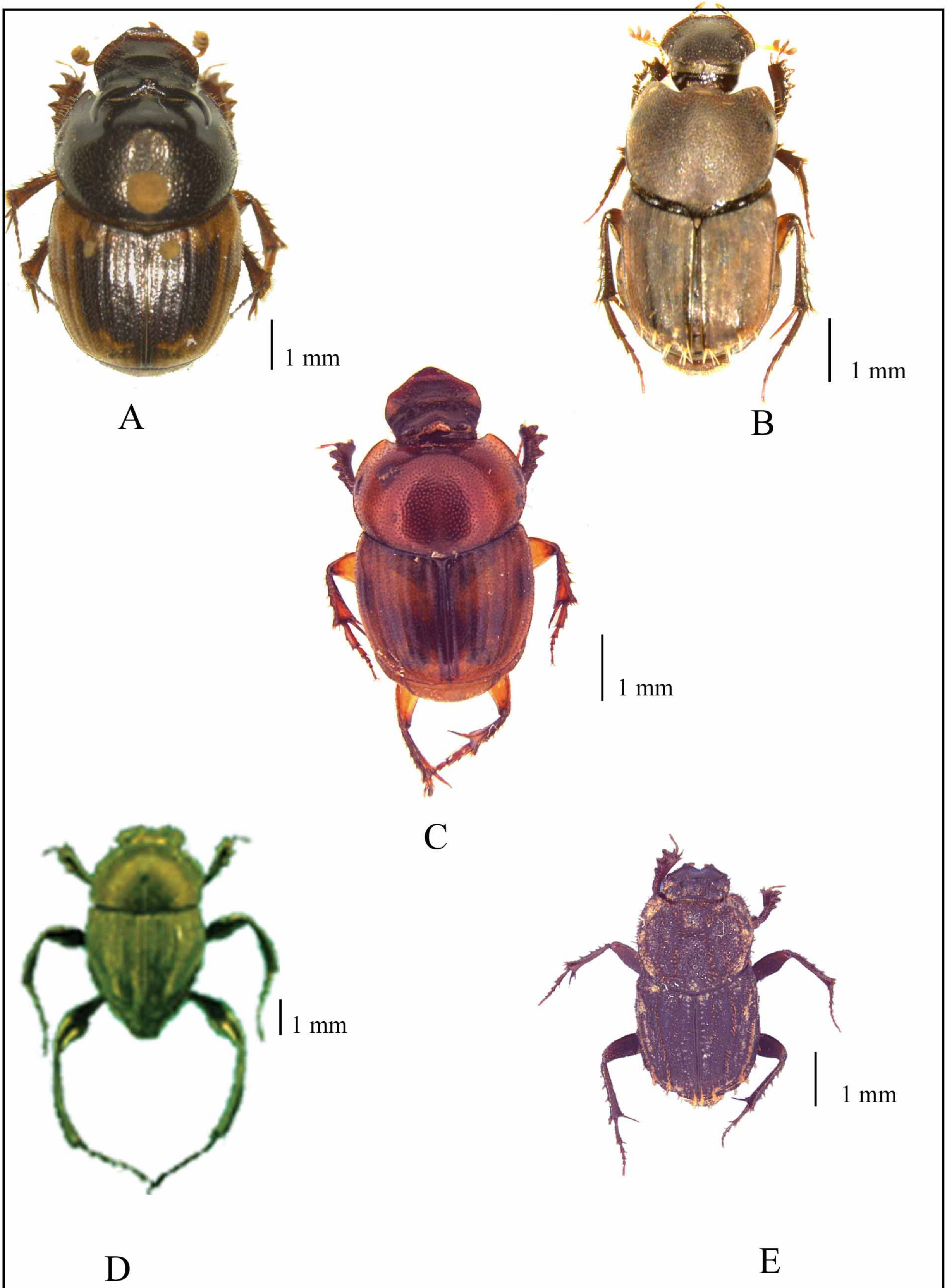

Figure 1. A) *Onthophagus cervus* (Fabricius, 1798); B) *Tiniocellus spinipes* (Roth, 1851); C) *Sisyphus longipes* (Oliver, 1798); D) *Onthophagus fasciatus* Boucomont, 1914; E) *Tibiodrepanus setosus* (Wiedemann, 1823)

Chapter 2

REVIEW OF LITERATURE

REVIEW OF LITERATURE

2.1. Taxonomy of dung beetles of the world

The dung beetles were categorized under subfamily Scarabaeinae and members of the suborder Lamellicornia were included by Linnaéus (1758) under a single genus, the *Scarabaeus.* The dung beetles derived from the Linnean *Scarabaeus* and constituted a new genus *Copris* by Fourcroy (1785). Latreille (1796) placed the species with 11-jointed antennae under the name *Geotrupes*. Two new genera *Oryctes* and *Aphodius* were introduced by Illiger (1798). Fabricius (1798) separated genus *Onitis* from genus *Copris.* Creutzer (1799) suggested the name *Actinophorus* for the ball rolling beetles now comprised in the genera *Scarabaeus* and *Gymnopleurus*. Weber (1801) introduced the name *Ateuchus sacer* for *Scarabaeus sacer*. The largest dung beetle genus, *Onthophagus* was introduced by Latreille (1802). The genus *Gymnopleurus* was introduced by Illiger (1803). Latreille (1807) introduced the genus *Sisyphus. Oniticellus* genus was introduced by Serville (1825). Genus *Drepanocerus* was introduced by Kirby (1828). The two new genera, *Catharsius* and *Heliocopris* comprising large dung beetles introduced by Hope (1837). The genus *Caccobius* was introduced by Thomson (1863). The genus *Liatongus* was introduced by Reitter (1892) and the genus *Tiniocellus* by Péringuey (1900). Boucomont (1914) introduced the genus *Phacosoma.* Due to homonymy, Vaz-de-Mello (2003) renamed the genus *Phacosoma* as *Ochicanthon.* The genus *Tibiodrepanus* was introduced by Krikken (2009) which is formerly supposed to be the genus *Drepanocerus* Kirby, 1828.

Arrow (1931) discarded the classification system suggested by Lacordaire (1856) and classified dung beetles in four divisions (= tribes) *viz*. Scarabaeini, Sisyphini, Coprini, and Phanelini under subfamily Coprinae with which he considered the Scarabaeinae synonymous. Scarabaeinae subdivided into six tribes: Coprini, Eurysternini, Oniticellini, Onitini, Onthophagini and Scarabaeini by Janssens (1949).

Later, Balthasar (1963a,b) positioned the group as a family including two behaviourally diverse subfamilies: Coprinae and Scarabaeinae. The previous subfamily involved the tribes Coprini, Dichotomini, Phanaeini, Oniticellini, Onitini and Onthophagini while the latter subfamily included the tribes Eucraniini, Eurysternini, Canthonini, Gymnopleurini, Scarabaeini, and Sisyphini. A study by Zunino (1984), which focused on the systematics of the subfamily Scarabaeinae based on the comparative analysis of the male and female genitalia disputed the monophyly of the tribes Onitini, Coprini, and Dichotomini.

Lawrence and Newton (1995) placed all 12 tribes in the subfamily Scarabaeinae which they consider the Coprinae synonymous. Krikken (2009) revised and discussed the taxonomic and biogeographic status of the genus *Drepanocerus* Kirby, 1828 and split the genus into five new subgenera namely, *Afrodrepanus*, *Clypeodrepanus*, *Latodrepanus* , *Sulcodrepanus* and *Tibiodrepanus.*

Dung beetles were recorded from South Africa (Péringuey ,1900; Chown *et al.*, 1995; Davis ,2002), African Tropical region (Gillet ,1908, 1911), Sumatra (Gillet 1924), China (Gillet 1935; Nakane and Shirahata 1957 and Bin -Hong Ho 2018), Southwest Arabia (Paulian , 1938; Ziani, 2021), Central America, the West Indies and South America (Blackwelder 1944; Afghanistan (Balthasar, 1955), Japan (Nakane and Tsukamoto 1956), Florida (Woodruff ,1973), Panama and Costa Rica (Howden and Young 1981; Howden and Gill 1987; González-Maya and Mata-Lorenzen 2008), Nebraska (Ratcliffe 1991; Wagner *et al.*, 2021), Europe (Baraud, 1992), Colombia

(Lopera ,1996), Nearctic Realm (Smith, 2003) and Palaearctic region (Löbl and Smetana, 2006). Krajcik (2006) and Schoolmeesters (2011) prepared world checklists of dung beetles. Siddiqui *et al.,* (2014) gave an annotated list of scarabs collected from vicinities of Pakistan with the faunal composition. The distribution and species diversity of dung beetles from the Mediterranean region were reported by Löbl and Löbl (2016). Philips (2016) described the tribe, *Oniticellini* Kolbe, 1905 and it has four subtribes, viz. *Drepanocerina* van Lansberge, 1875, *Oniticellina* Kolbe, 1905, *Helictopleurina* Janssens, 1946 and *Eurysternina* Volcano, Martinez and Pereira, 1960 and provided the worldwide data on the tribe Oniticellini Kolbe, 1905 and it belongs to 26 genera and 252 species Branco (2010). Silva (2017) presented an annotated list of the dung beetle species from, Southern Brazil. Espinosza and Noreiga (2018) provided distributional data and recorded 14 genera and 54 species from Ecuador. Salomao *et al.,* (2019) analyzed a total of 945 species from the mosaic habitat at the ecotone of Savanna ecosystems in North-Eastern Brazil. Schoolmeesters (2019) provided worldwide records of dung beetles. Sanchez-Hernandez *et al*., (2020) reported 112 species and 7 subspecies belonging to 23 genera, 7 tribes, and 4 sub-tribes of the subfamily Scarabaeinae from Natural Protected Areas in Mexico. González-Alvarado and Vaz-de-Mello (2021) provide a complete taxonomic revision of the Neotropical dung beetle of sub genus *Deltochilum* (*Deltohyboma*) Lane 1946.

2.2. Distribution of dung beetles in India.

Data on the occurrence of dung beetles are mainly based on the publications of the Zoological Survey of India and the works carried out regionally from different parts of India. Arrow (1931) recorded 48 species of dung beetles from the western slopes of the south Western Ghats. Biswas and Chatterjee (1985) reported 7 new species namely, *Oniticellus namdaphensis*, *Oniticellus subhendui*, *Oniticellus gayeni*, *Onthophagus tirapensis*, *Onthophagus arunachalensis*, *Onthophagus songsokensis* and *Onthophagus royi* from Namdapha wildlife sanctuary. Biswas and Chatterjee (1986) reported 3 new species namely *Onthophagus keralicus, Onthophagus sahai,* and *Onthophagus taruni,* and recorded 16 species from the Silent Valley National Park. Veenakumari and Veeresh (1996a) described 61 species of Scarabaeinae belonging to three tribes from Bangalore in the Deccan region. Chatterjee and Biswas (2000) reported 27 species from Tripura State. Chandra (2000) published an inventory of 96 species of scarab beetles and their dispersal from the protected areas of Madhya Pradesh. Biswas and Mulay (2001) noted 71 species from Nilgiri Biosphere Reserve. As part of the biodiversity documentation program by the Kerala Forest Research Institute, 37 species of dung beetles from Kerala was reported by Mathew (2004). An account of the scarabaeid beetles of Himachal Pradesh was published by Chandra (2005). A new species, *Onthophagus devagiriensis* from a moist deciduous forest in the Wayanad region of Kerala State was reported by Schoolmeesters and Sabu (2006). Chandra and Ahirwar (2007) provided a comprehensive account of the scarab beetles of Chhattisgarh and Madhya Pradesh. Vinod (2009) prepared a checklist of 58 species, including 13 genera and 7 tribes of the Wayanad region. Latha *et al.,* (2011) gave a revision of the taxonomic status of the Scarabaeinae genus *Ochicanthon* Vaz-de-Mello 2003 and 15 species were reported with 8 new species from the Western Ghats. Sabu *et al.,* (2011) prepared a checklist of 142 species from the moist South Western Ghats including five new species. Karimbumkara and Priyadarsanan, (2013) published a comprehensive list of 145 species of dung beetles belonging to 9 tribes and 23 genera reported from Karnataka. Sarkar *et al.,* (2015) described the systematics of 19 Scarabaeinae species under 6 genera reported from Buxa Tiger Reserve, West Bengal.

Sathiandran *et al.*, (2015) published an illustrated checklist of 36 species of dung beetles from the Periyar Tiger Reserve in the southern Western Ghats. Mittal and Jain (2015) studied the taxonomy of the Indian dung beetle and recorded 420 species in 38 genera. Karimbumkara and Priyadharsanan (2016) reported three new species *Onthophagus jwalae* (Kerala), *O. pithankithae* (Karnataka), and *O. tharalithae* (Assam) from India. Subha and Sabu (2017) reported bioindicator dung beetles from a shaded coffee plantation in the Nilgiri Biosphere Reserve of the south Western Ghats. Kalawate (2018) gave a preliminary study on the dung beetles of the Northern Western Ghats, Maharashtra, Khadakkar et al., (2019**)** collected and identified a total of 97 scarab beetles species of 39 genera belonging to 7 subfamilies, where 10 species were newly recorded from different habitats of the Vidarbha region of Central India. Patole (2019) analyzed the diversity and relative abundance of dung beetles from Sakri tahsil, Dist Dhulia Maharashtra. Latha and Sabu (2018) collected 34 species, belonging to 11 genera and 7 tribes from Nelliampathy. Sarkar and Kharel (2020) provided the first faunistic account on the *Onthophagus* Latreille, 1802 of the Nadia district, West Bengal. Chauhan and Uniyal (2020)_prepared a checklist of dung beetles of Uttarakhand. Sarkar and Kharel (2020) published the first faunistic study on the tribe *Oniticellini* Kolbe, 1905 (Coleoptera: Scarabaeidae) of Baikunthapur Tropical Forest in the Himalayan foothills, West Bengal.

2.3. Prominent dung beetle species in the world

Dominant dung beetle species vary among different global regions. Cambefort and Walter (1991) reported *Oniticellus pseudoplanatus* Balthasar, 1964 as the prominent species in moist forests of the Ivory Coast. *Othophagus vulpus* Harold, 1877 and *Sisyphus thoracicus* Sharp, 1875 were reported as the dominant dung beetle species in the tropical rainforests of Malaysia Davis (2000). *Dichotomius amplicollis* (Harold,1869), *Deltochilum gibbosum* (Fabricius,1775) and *Onthophagus landolti* Harold,1880 were recorded as the prominent beetles from Mexican dry forest (Andresen 2005, 2008). Shahabuddin (2010) recorded *O. wallacei* Harold, 1871 and *O. fuscostriatus* Boucomont, 1914 as the dominant species from an Indonesian forest. *Onitis crassus* Sharp, 1875 was reported as the major species from Pakistan by Ali *et al*., (2015). *Canthon histrio* Serville, 1828, *Onthophagus hirculus* Mannerheim, 1829, and *Deltochilum verruciferum* Felshe, 1911 were reported as the prominent species in Brazilian dry forest by Novais *et al*., (2016). *Canthon quinque maculatus Castelnau, 1840, Canthon conformis Harold,1868 and Dichotomius sericeus Harold,1867 were reported as the dominant species in the southern* Atlantic forest of Argentina **(**Gomez Cifuentes *et al*., 2017). Espinosza and Noreiga (2018) reported *Ontherus pubens* Genier, 1996 as the abundant species from Ecuador. Wagner *et al*., (2021) reported *Onthophagus hecate* Panzer, 1794, *O. pennsylvanicus* Harold, 1871 and *Diapterna pinguella* Brown, 1929 as the abundant species from the Nebraska Sandhills Ecosystem in the USA.

2.4. Prominent dung beetles species in India

Onthophagus gazelle Fabricius, 1787, *O. rectecornutus* Lansberge, 1883, *Copris repertus* Walker, 1858, and *C. fricator* Fabricius, 1787 were reported as the prominent species from the Deccan region in south India (Veenakumari and Veeresh 1996a,1997). Three prominent species, *Tiniocellus spinipes* (Roth, 1851), *Tibiodrepanus sinicus* Harold, 1868 and *Caccobius ultor* Sharp, 1875 were reported from the forests of Haryana (Mittal 2005; Kakkar and Gupta, 2010). Vinod, (2009); Sabu, (2011); Simi *et al.*, (2012); Nithya, (2012); Latha,(2013); Shobhana, (2016); and

Subha, (2018) reported *Caccobius vulcanus* Fabricius, 1801, *C. ultor* Sharp, 1875, *Onthophagus centricornis* Fabricius, 1798, *O. cervus* (Fabricius,1798), *O. dama* (Fabricius, 1798), *Tiniocellus spinipes* (Roth, 1851), *Tibiodrepanus setosus* Weidemann, 1823 and *Sisyphus longipes* (Olivier, 1789) as the prominent species from the 'moist belts of South India. *Catharsius pithecius* (Fabricius, 1775) and *Gymnopleurus cyaneus* (Fabricius, 1798) were reported as dominant dung beetle in the agriculture belts of Maharashtra Patole (2019). Sarkar and Kharel (2020) reported *Tiniocellus imbellis* (Bates,1891) and *T.spinipes* (Roth,1851) as the dominant species in the Tropical Forest of the Himalayan foothills, West Bengal.

2.5. Reproductive biology of dung beetles in the world

Several features of the biology of dung beetles had been broadly studied and critically analyzed in different regions of the world (France, South American countries, South Africa, Germany, etc.). Halffter and Edmonds (1982) compiled information on the nesting behaviour of subfamily Scarabaeinae and analyzed the relationship between ecological conditions, morphology and behaviour of dung beetles. Subsocial behaviour of *Oniticellus cinctus* (Fabricius, 1775) was described by Klemperer (1983) from Birmingham and found that the nest chambers of *Oniticellus cinctus* contained twenty brood balls, and the whole period of development took one month. Edwards and Aschenborn (1987) observed the nesting biology of *Onitis viridulus* Boheman,1857, *O. fulgidus* Klug,1855, *O. obscurus* Lanseberge, 1886, *O. alexis* Klug, 1835, *O. perpunctatus* Balthasar, 1963, *O. Caffer* Boheman, 1857, *O. aygulus* (Fabricius, 1781), *O. tortuosus* Houston, 1983, *O. deceptor* Peringuey, 1901, *O. uncinatus* Klug, 1855, *O. picticollis* Boheman 1857 and *O. pecuarius* Lanseberg, 1875 from South Africa. Hunter *et al*., (1991) worked on the life history studies of

Onthophagus medorensis Brown, 1929 and described each stage of its life cycle and the whole developmental period took 46 days. A study on the reproductive biology, nesting and ontogenetic development of *O. stylocerus* Graells, 1851 revealed that the species was univoltine (Romero and Piera, 1995). Studies on the brood care behaviour and nest structure of the dung beetle *O. vacca* (Linnaeus, 1767) was done by Sowig (1996). Hunter *et al.*, (1996) studied the life history of *O. depressus* Harold, 1871. Sato (1997) detailed the nesting, rolling and tunnelling behaviour of large-sized subsocial African dung rolling beetle *Scarabaeus catenatus* (Gerstaecker, 1871). The reproductive biology of the *Onthophagus incensus* (Say, 1835) in Mexico has been studied by Martínez *et al.*, (1998). Gonzalez-Vainer and Morelli (1999) studied the biology of the dung beetle *Onthophagus hirculus* Mannerheim, 1829 from Uruguay. Palestrini *et al*., (2002) worked on the reproductive biology of *Onitis belial* Fabricius, 1789 from Morocco, *O. anthracinus* Felsche, 1907 and *O. vanderkelleni* Van Lansberge, 1886 from Kenya and it was revealed that *O. vanderkelleni* Lansberge, 1886 constructed a poorly enlarged nest and laid a greater mean number of eggs, and *O. belial* Fabricius 1798, *O. anthracinus* Felsche, 1907 spent a more amount of energy for the construction of the nest. The longevity cost of reproduction for males and females in the dung beetle *Onthophagus binodis* Thunberg, 1818 was studied in Australia by Kotiaho and Simmons (2003). Huerta *et al.*, (2003) analyzed the reproductive biology and nesting behaviour of several species of *Eurysternus* Dalman, 1824 and observed that *Eurysternus*, a morphologically quite homogeneous genus, showed two distinct types of nesting behaviour. Analysis of the fecundity and offspring survival of *Copris tripartitus* Waterhouse 1875 from Mexico was done by Huerta and Bang (2004). The cost of reproduction in *Callosobruchus maculatus* (Fabricius 1775) was studied by Paukku and Kotiaho (2005).The study of reproductive development and seasonal activity of *Copris ochus* Motschulsky, 1860 and *C. tripartitus* Waterhouse, 1875 from Korea was done by Bang *et al*., (2008) and their study revealed that *C. ochus* and *C. tripartitus* appeared as univoltine species. A study of reproductive activity of *Onthophagus granulatus* Boheman, 1858 from New Zealand by Forgie (2009), showed that *O. granulatus* was univoltine species. Huerta *et al*., (2010) worked on pre-imaginal stages of the *O. incensus* (Say ,1835) from Mexico. Simmons and Ridsdill-Smith (2011) studied the sexual dimorphism, reproductive success and the parental investment of two *Onthophagus* species *O. taurus* (Schreber, 1759), and *O. vacca* (Linnaeus, 1767). Nesting behaviour of *O. incensus* (Say ,1835) from Mexico was studied by Huerta and García-Hernández (2013). Pérez - Cogollo *et al*., (2015) studied the life history of *O. landolti* Harold (1880) from Mexico and described its pre-imaginal stages of development. The feeding, reproductive, and nesting behaviour of *Canthon bispinus* (Germar, 1824) was studied in Uruguay by González-Vainer (2015). Ocampo and Philip (2017) Studied the biology and food relocation behaviour of *Eucranium* species and compared it with South African subgenus *Scarabaeus* (*Pachysoma*) Macleay,1821 .Study on nesting biology and life history of the dung beetle *Onthophagus lecontei* Harold, 1871 from Mexico by Arellano *et al.*, (2017), revealed that a type 1 pattern of nesting behaviour was observed and pairs built one to seven brood masses. This study showed the pre-nesting period (Feeding) lasted for 16 days, the egg stage for 2 days, the larval period for 22 days and the pupal period for 11 days. Studies on the reproductive biology of *Euoniticellus intermedius* (Reiche, 1848) by Martinez *et al*., (2019) observed that development from egg to imago ranged from 25 to 28 days and the lifespan of this species was recorded as 30 to 60 days. Hernandez *et al*., (2020) provided details of the

Feeding and reproductive behaviour of the dung beetle *Canthon rutilans cyanescens* Harold, 1868 from Brazil.

2.6. Reproductive biology of dung beetles in India

Very few reports are available on the life history and behaviour of the dung beetle species in India. Joseph (1994). Studied the Sexual dimorphism and intra sex variations of the giant dung beetle *Heliocopris dominus* Bates, 1868. Feeding and breeding behaviour of *Gymnopleurus gemmatus* (Harold, 1871) and *Gymnopleurus miliaris* (Fabricius, 1775) done by Veenakumari and Veeresh (1996b) detailed that feeding, ball making and rolling, mating, competition, and predation of two species. Life history of two commonly occurring south Indian species, *Onthophagus gazella* (Fabricius, 1787) and *O. rectecornutus* Lansberge, 1883 were done by Veenakumari and Veeresh (1996c). Subsocial behaviour in *Copris repertus* Walker, 1858 and *Copris indicus* Gillet,1910 was studied by Veenakumari and Veeresh (1997). Studies on the life cycle, ecological role and biology of immature stages of *Heliocopris dominus* Bates, 1868 have been done by (Joseph, 1998, 2003). Gaikwad and Bhawane (2015) studied the nidification behaviour of three dung beetle species, *Onthophagus catta* (Fabricius, 1787), *Onitis philemon* (Fabricius, 1801) and, *Liatongus rhadamistus* (Fabricius, 1775) from Maharashtra and analyzed that *Onthophagus catta* constructed a simple nest composed of a single unbranched vertical gallery, *Onitis philemon* made a simple unbranched numerous and extensive vertical galleries and *Liatongus rhadamistus* have constructed a tunnel just beneath the dung pads up to 9 cm deep. Studies on the life cycle and nesting behaviour of dung beetle *Onthophagus catta* (Fabricius, 1787) from Maharashtra by Gaikwad and Bhawane (2016) showed that the adult longevity ranged between 42-85 days. Nesting and biology of dung beetle

Scaptodera rhadamistus (Fabricius, 1775) was studied in Maharashtra by Khadakkar (2018). Singh *et al*., (2019) studied the nesting architecture, life cycle, and brood ball morphometry of the dung beetle *Oniticellus cinctus* (Fabricius, 1775) in Dehradun the study revealed that the total period for the development of the beetles took one month.

Analysis of the literature revealed that no data is available on the prominent dung beetle species, reproductive biology and nesting behaviour in the Agribelts of the Malabar Coast region.

Chapter 3

MATERIALS & METHODS

METHODOLOGY

3.1. Rearing of Dung Beetles

Adult beetles were collected using dung baited pitfall traps and handpicking from the agricultural fields in different regions of the Malabar Coast, namely, an open agricultural field consisting of mainly coconut plantation with intervening grasslands close to Devagiri College campus (11015’N, 75048’E), Kozhikode district, an open agricultural field at Naduvattam **(**$10^0$52'55.92''N, $76^0$0'29.59''E) and paddy field at Thavanoor **(**10.8412°N,75.9938°E**)** Malappuram district, Kerala (India) and paddy field at Kumbidi (10.8337°N,76.0489°E**)** Palakkad district, Kerala (India)**,** were collected during June 2016 to December 2017 period. To collect live dung beetles, pitfall traps made of plastic basins, 10 cm in diameter and 15 cm deep with the minimum quantity of water to prevent the drowning of the fallen beetles, were placed in the field from 8:00 am to 12:00 pm. Preliminary verification, separation, and sexing of the collected beetles were done by comparing with verified specimens present in the insect collections of St. Joseph’s College, Devagiri, Kozhikode and taxonomic keys in Arrow (1931). Based on morphological characters such as small body size and colour, beetles of uniform age were selected and grouped. Adult *Onthophagus cervus* were sexed with the male having a pair of horns behind the eyes, slanting backward, wide at the base but not united, each bent at a right angle inside just beyond the base, curved outward and rapidly narrowed. The clypeus is slightly produced, but truncate and not pointed, very shining, lightly punctured with intermixed large and small punctures and separated from the forehead by not very strong carina. The clypeus is powerfully and closely punctured and not shining, separated from the forehead by a strong carina, and there is a similar carina between the eyes are present in females *Onthophagus fasciatus* .In male, the clypeus is feebly punctured in the middle and more intensely and closely at the sides produced to a point, gently reflexed and divided by a slightly curved carina from the sparsely punctured forehead. The posterior margin of the head is produced backward and gently curved upward, the median part developing a curved tongue-like process at the sides ,a pair of closely parallel horns, which is wide at the base and tapering to the tips. The pronotum is almost vertical and finely and sparsely punctured in front. Females, having features such as the clypeus is transversely rugose, the sides are convergent, and the front margin is strongly reflexed and nearly straight in the middle, the forehead is relatively strongly punctured and separated from the clypeus by a strong nearly straight carina and there is a second strong carina upon the vertex. The pronotum bears a well-marked transverse carina in the middle just behind the front margin), and *Tiniocellus spinipes* were sexed based on the pronotum shape (the clypeus is short with its margin rounded and extremely feebly excised in the middle. The front tibia is broad with four short sharp external teeth almost at right angles in males and the female. The clypeus is slightly produced and distinctly excised at the front margin. The front tibia is broad with very strong external teeth, the terminal one .very oblique). *Sisyphus longipes* males showed remarkable peculiarities in the legs. In *Tibiodrepanus setosus* the head is rather narrow,unevenly and unequally punctured with the sides nearly straight and parallel behind. The pronotum has a small anterior lateral depression on each side and a big posterior depression, from the middle of the latter springs, a slender dorsal horn directed obliquely forward, its extremity with a little bifurcate, but the tips scarcely diverging. The males having a horn present. Female having the pronotum with a rather large median posterior depression a smaller one in front of it, and an anterior lateral depression on each side (Arrow, 1931).

Ten mating pairs were selected. Each pair was placed in an individual wide-mouthed earthen pot with diameter of 51.5 cm, thickness 0.9 cm and length 14 cm and filled with finely sieved clay soil collected from the collection site and moistened with water by a depth of 13.5 cm and fresh cow dung on top for food and the construction of brood balls and each pair were provided with fresh cow dung twice a week. The top of the earthen pots was covered with a mesh net (mesh size 0.053 µm) to prevent the escape of the beetles and the pots were kept at controlled room conditions (Temperature 23^0C-25^0C; humidity 75%) and in plastic troughs containing moist sand. Water was sprayed with a mist sprayer on alternate days to prevent desiccation (Fig.2 A-F). Daily observations for all life events, such as brood ball formation, egg-laying, egg hatching, duration of the larval and pupal phase and adult emergence were noted, and parallel laboratory culture was maintained for observing each life cycle stage of the development and also for studying the nest architecture. To monitor the life cycle and development of the egg, different stages of larval development, pupa and until adult emergence were recorded by making a small opening on each brood ball, which was closed by pasting with a layer of dung and soil after each observation and the brood masses/balls were retained in individual earthen pots arranged with moist soil. Observations were made twice a week until the emergence of new adults. The number, length and width of the brood masses, number of larvae, pupae and adults, and the size of the adults were recorded. Newly emerged beetles were collected, paired and counted, and transferred to new individual earthen pots topped with fresh cow dung and were kept until their natural death. Adult longevity (after emergence from their brood ball) is known only in laboratory-reared specimens and the survival period was noted for each beetle. The experiment setup was kept moist by sprinkling water to prevent desiccation. After two weeks, the earthen pot was opened with care and notes were being made on the nest architecture, ball making, and the length of the tunnel was taken. Photographs were taken using Nikon digital camera D90 and LEICAS8APO (Trinocular stereo zoom microscope).

3.2. Study of Nesting Pattern

Adult beetles got from the collection site were placed in a wide-mouthed earthen pot. The earthen pot was filled with moist soil and topped with fresh cow dung droppings. The top of the earthen pot was covered with a mesh net, after introducing the beetles to prevent their escape. These wide-mouthed circular earthen pots (16×40cm) were found to be the most suitable for the rearing of roller and dweller species.

Preliminary analysis was done in the field beneath the dung pats to get an idea about the tunneling behaviour of tunneling species, brood ball construction, nesting preparation and also done by open the tunnels by digging in the agricultural field from where the beetle collections were made. For the study of the nest architecture of tunneling species, adult beetles got from the collection site, were placed in plastic pots (15×1×16 cm) which were cut into half lengthwise and rejoined with masking tape to retain their original shape. The rejoined plastic pot was filled with moist soil up to a depth of 12 cm and topped with fresh cow dung droppings. Beetles were shifted to the pre-arranged plastic pot containing soil and cow dung topping. The top of the plastic pot was covered with a mesh net, after introducing the beetles to prevent their escape. The experimental setup was kept moistened by sprinkling water to prevent desiccation. After two weeks, the rejoined plastic pot was opened with care and the notes were being made on the nest architecture, ball making and the length of the tunnel was taken (Fig.3 A-E). For data analysis, (Mean±SD) values are calculated from raw data values with the use of Microsoft excel 2010.

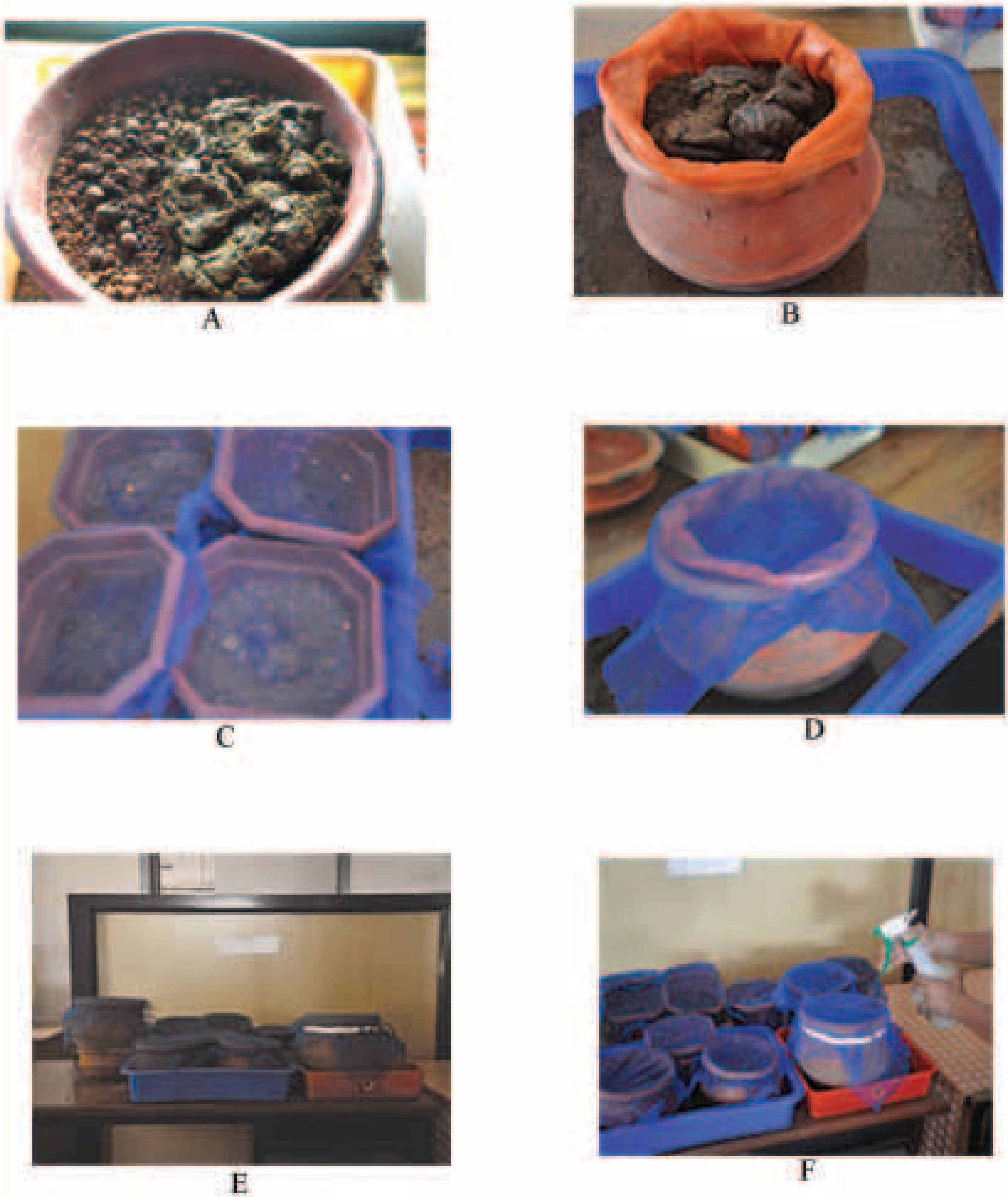

Figure 2. Laboratory cultural setup of Dung beetles; A) Rearing of roller species; B)Tunneler species; C) Dweller species; D) Earthern pot topped with fresh cow dung and covered with mesh net; E) Maintenance of cultural set up in a controlled room condition; F) Experimental setup sprayed with mist sprayer

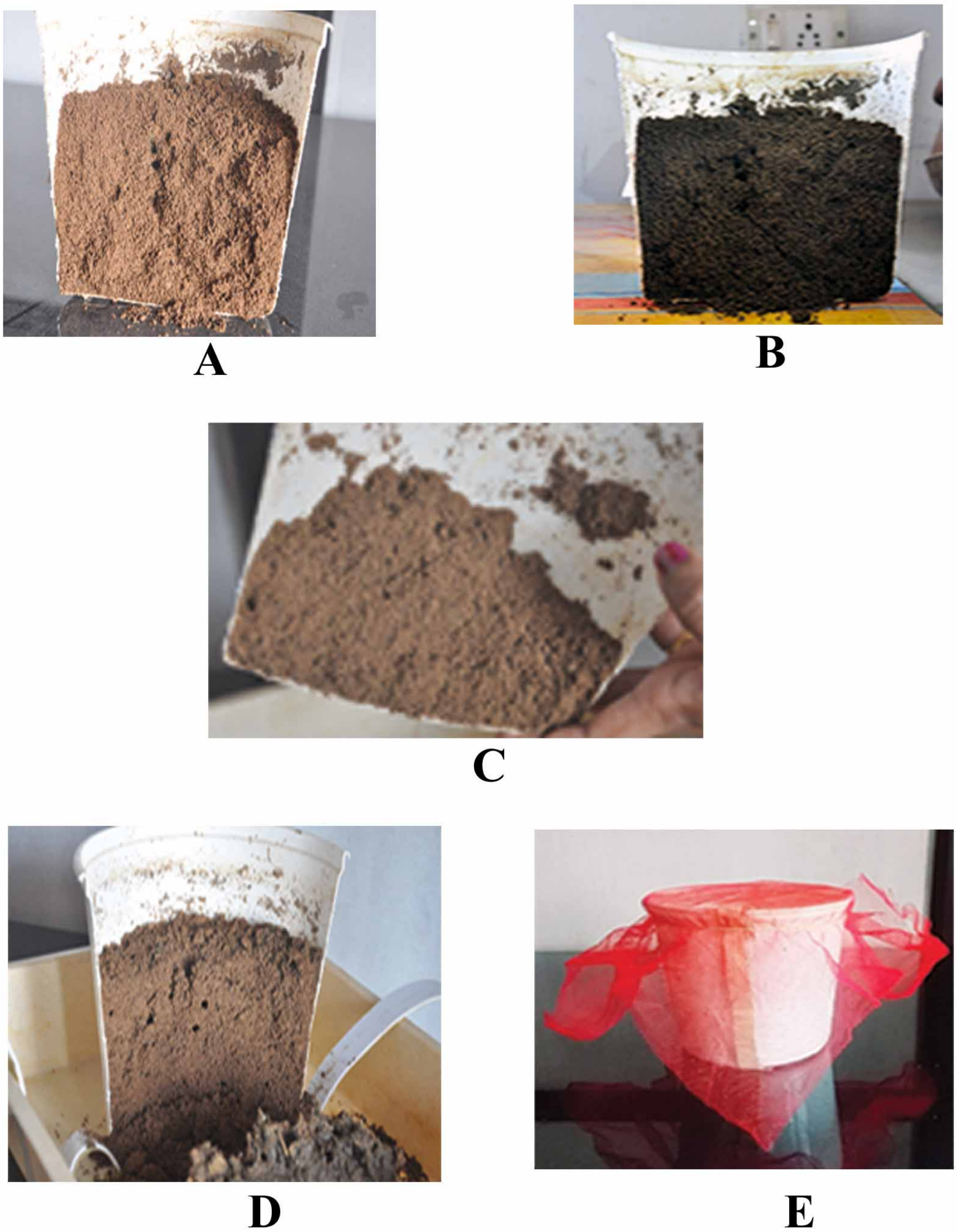

Figure 3. Nest architecture study of dung beetles;
A, B & C) Plastic pot cut in half lengthwise;
D) Rejoined with masking tape; E) Rejoined plastic pot tied with mesh net

Chapter 4

RESULTS

RESULTS

4.1. Life biology of *Onthophagus cervus* (Fabricius, 1798)

Life biology involved four stages namely egg, larva, pupa and adult. The egg stage lasted for 3.60±0.51 days, the larval stage for 16.70 ±1.87 days, the pupal stage for 10.20±1.03 days and the adult stage for 60.17± 2.08 days.

Brood mass and eggs (Fig 4. A-N): Adult beetles constructed brood balls after 12.4±0.69 days. A single mating pair produced 14.10±5.69 brood balls during its period of the life cycle. Oval- shaped brood balls have a length of 20.4±0.97 mm, width 32.8±1.62 mm and were coated by a layer of soil and dung (Fig 4. A). The brood masses were formed of dung mass with an egg chamber with the egg glued to the wall of the egg chamber (Fig 4. B). Brood masses were attached to the wall and end of the tunnels. Eggs were elongated oval in appearance and creamy white, during the first two days. Before hatching (3^{rd} day), the egg became yellowish and the eggshell became transparent (3^{rd} and 4^{th} day) and the larva was visible through the chorion. The egg stage lasted for 3.6±0.51 days. A single mating pair produced 21.7±6.69 surviving eggs during its lifetime. Low egg mortality (14.57%) was recorded (Table.1).

Larva: Three larval instars (Fig 4. C, D, E) were recorded. Newly emerged larvae were transparent with the tips of the mandible being dark brown. Larvae were found in a cavity inside a brood ball and they consumed the dung ball from inside. Newly hatched larvae were creamy white fleshy “grubs”. All larvae have the characteristic “coprine hump” and the flattened, fleshy-lobed anal segment. The larval period lasted 16.7±1.87

days. Low larval mortality (16.12%) was recorded. A single mating pair produced 18.2±6.58 surviving larvae.

Pupa: Pupae were present inside the thin-walled pupal cell or cocoon constructed by larva inside the brood ball. The inner surface of the pupal cell was smooth and was coated with soft dried dung and soil (Fig 4. F). Newly formed pupae were creamy white, shiny with four pairs of finger-like processes on the dorsolateral region of the abdomen and a large blunt pronotal projection extending over a posterior portion of the head. Later on the pupae turned golden brown (Fig 4. G, H). The pupal period lasted for 10.2 ± 1.03 days. Pupal mortality (27.48%) was recorded. A single mating pair produced 13.2±4.88 pupae.

Adult: Teneral period lasted 2.40 ±0.51 days. The teneral adult was light orange-red (Fig. 4. I). Adult emerged by cutting a hole in the brood ball (Fig 4. J). 67.42% of adults emerged (30 females and 10 males) and the sex ratio of 3:1 was observed. Newly formed adults took 1.40±0.52 days for the complete melanization. On exit from the brood ball, newly emerged beetles constructed the tunnels. Sexual maturity was attained by 11±1.05 days of emergence. Adult male (Fig 4. K) duration of 35.2±8.65 days and female (Fig 4.L) duration of 60.17± 2.08 days were observed. Egg to teneral adults took 28.2 ±1.03 days. A single mating pair produced 4±2.21 surviving adults during its lifetime.

Nesting behaviour: Adult beetles (males and females), upon releasing, made vertical (Fig 4. M) and horizontal tunnels (Fig.4.N). Both males and females were involved in tunnel construction and handling of dung. Both vertical and horizontal tunnels were made and were interconnected. Vertical tunnels with a depth of 6.96±1.30 cm and horizontal tunnels with a length of 2.25±0.59 cm, were observed.

Brood masses were present at the bottom of the tunnels. Brood balls were seen in single or in mass.

4.2. Life biology of *Onthophagus fasciatus* Boucomont, 1914

The lifecycle comprises four phases namely egg, larva, pupa, and adult. The egg stage took 3.1±0.57 days, the larval stage for 18.1±0.31 days, the pupal stage for 11.1±0.57 days and the (egg to teneral adult) for 38.5 ±0.52 days. Adult period for 64.1± 2.42 days.

Egg and Brood ball (Fig 5. A-I) :

Egg: Eggs were elongated ovoid in appearance and creamy white, during the first 2 days (Fig 5. A). Earlier to hatching (3rd day), the egg developed yellowish and the eggshell became transparent (3rd and 4th day) and the larva was visible through the chorion. The egg period took 3.1±0.57. A single mating pair formed 12.5 ±10.60 eggs during its lifetime. Low egg mortality (13.29 %) was recorded (Table 2).

Brood ball: Adult beetles constructed brood balls subsequently 12.2±0.42 days. A single mating pair made 13.2±3.68 brood balls throughout its period of the lifecycle. Oval-shaped brood balls have a length of 14.4±1.42 mm, width 22.9±2.23 mm, and were layered by a film of soil and dung (Fig 5. B) **.** Brood masses are attached to the wall and end of the tunnels. The brood masses are formed of dung mass with an egg chamber with the egg attached to the wall of the egg chamber

Larva: Three larval instars were observed (Fig 5. C, D, E). Newly developed larvae were clear with the tips of the mandible being dark brown. Larvae were seen in a cavity inside a brood ball and they used up the dung ball from inside. Newly produced larvae were creamy white fleshy “grubs”. “Coprine hump” and flattened, fleshy-lobed anal segment are the characteristics feature of all larvae. The larval period lasted for 18.1

±0.31 days. Low larval mortality (28.03 %) was recorded.The third segment of the abdomen with a setose present.

Pupa: The newly formed pupae were creamy white, shiny, with large, blunted pronotal projection lengthening over the posterior portion of the head and small mesonotal and metanotal projections present. Large finger-like lateral tergal projections on segments 3-6 and caudal projections callous-like. (Fig 5. F). Pupae were present inside the thin-walled pupal cell or cocoon made by larva inside the brood ball. The inner surface of the pupal cell was smooth and was covered with soft dried dung and soil (Fig 5. G). The pupal period lasted for 11.1±0.57 days. Pupal mortality was recorded at 61.68 %.

Adult: Teneral adults continued in the pupal cell for 3 days. The teneral adult is light orange-red. Adult emerged by cutting a hole in the brood ball 36.84 % of adults emerged (25 females and 10 males) and the sex ratio of 5:2 was observed. Newly formed adults took 1.4±0.52 days for the complete melanization. On leaving the brood ball, newly emerged beetles constructed the tunnels. Sexual maturity was attained by 11±1.05 days of emergence. Adult male (Fig 5. H) duration of 51.4±5.19 days and female (Fig 5. I) duration of 64.1± 2.42 days were observed. Egg to teneral adults took 38.5 ±0.52 days.

Nesting behaviour: Paired males and females upon releasing, made vertical and horizontal tunnels. Construction of tunnels and handling of dung is done by both males and females, vertical and horizontal tunnels were made. Vertical tunnels with a depth of 7.3±0.63 cm and horizontal tunnels with a length of 4.3±0.49 cm, were observed. Brood masses were present at the bottom of the tunnels. Brood balls are seen in single or in mass.

4.3 . Life biology of *Tiniocellus spinipes* (Roth, 1851)

Life biology contains four stages namely egg, larva, pupa, and adult. The egg stage lasted for 4.2±0.42 days, the larval stage for 20.6 ±1.26 days and the pupal stage for 12.3±0.82 days and the developmental period (egg to teneral adult) for 39.2 ± 0.63 days.

Egg and brood mass (Fig 6. A-H):

A single mating pair produced 14.3±5.57 brood balls during its period of one life cycle. Oval-shaped brood balls have a length of 29.5±0.70 mm, width 50.5±2.83 mm and are covered by a layer of soil and dung. The brood masses are made of dung mass with an egg chamber with the egg attached to the wall of the egg chamber. Brood masses are produced after 6.6±0.69 days and are attached to the end of the tunnels.

Egg: The egg is usually found adhering to the wall of the brood ball (Fig 6. A). As development continues, there is an increase in width, so that the eggs just before hatching the chorion is transparent (3^{rd} and 4^{th} day), the dark mandibles and the segmentation of the body can be distinguished through it. Eggs were lengthened oval in appearance and creamy white, during the first 2 days. The egg stage lasted 4.2 ± 0.42 days. 24.4 ± 6.91 eggs are produced during their lifetime. Egg mortality 28.27 % and egg hatchability 71.72% were recorded. (Table 3).

Larva: Three larval instars (Fig 6. B, C, D) were recorded. Newly developed larvae were transparent with the tips of the mandible being dark brown. Larvae were found in a cavity inside a brood ball and they consumed the dung ball from inside. Newly hatched larvae were creamy white fleshy "grubs", "Coprine hump" and the flattened, fleshy-lobed anal segment. The larval period lasted for 20.6 ±1.26 days. Larval mortality (18.85 %) was recorded. A single mating pair produced 14.2±6.52 surviving larvae. Larval survivability 81.14% was recorded.

Pupa: Pupae were present inside the thin-walled pupal cell (Fig 6. E) or cocoon constructed by larva inside the brood ball. The internal surface of the pupal cell was smooth and was coated with soft dried dung and soil. The newly formed pupae were creamy white, shiny, with four pairs of finger-like processes on the dorsolateral area of the abdomen and a large, blunt pronotal projection prolonging over a posterior portion of the head. The pupal period lasted 12.3±0.82 days. Pupal mortality was recorded at 48.59 %. A single mating pair produced 7.3 ±3.27 pupae. Pupal survivability of 51.40% were observed.

Adult: Teneral adults remained in the pupal cell for 2.4 ±0.51 days and 41.09% of adults are emerged by making a hole in the brood ball (Fig .6, F). The teneral adult is light orange-red in colour. Complete melanization of teneral adults required 1.4±0.52 days. Sexual maturity was attained by 12.5±0.98 days after emergence. Adult female (Fig 6. G) duration of 70.7± 6.42 and male (Fig 6. H) duration of 72±3.65 days and days were recorded. Egg to teneral adults, took 39.2 ± 0.63 days. A single mating pair produced 3.±2.05 surviving adults during its lifetime, 41.09% of adult survivability were observed (30 females and 20 males) and the sex ratio of 3:2 was observed. Adult mortality (58.90 %) was recorded.

Nesting behaviour: Adult beetles made shallow vertical tunnels. Both males and females were involved in tunnel construction and handling of dung. Vertical tunnels with a depth of 9.65±0.74 cm (tunnel length of 2.7±0.49 cm inside the dung pat; 6.95±0.25 in the soil).

4.4. The life biology of *Sisyphus longipes* (Olivier, 1789)

Life biology contains four stages namely egg, larva, pupa, and adult. The egg stage lasted for 6.8±1.22 days, the larval stage for 25.3± 0.68 days and the pupal stage for 15.5± 0.70 days and the developmental period (egg to teneral adult) for 47.3 ±1.63 days.

Brood ball construction: (Fig 7. A-J): Paired beetles built brood balls after 13.56±2.05 days, A single mating pair created 20.1±5.13 brood balls and food balls 9.6 ±4.40 during its period of the life cycle. The adult beetles (males and females) upon releasing, make a brood ball from the dung pad and it is rolled away from the dung. The dung ball is buried with a depth of 3.6±0.69 cm or the sides of the earthern pot and some are not buried in the soil. When the brood ball is completely formed from the dung and it is rolled away by the pair or by the single adult alone, using the long hind limbs with pushing using the back legs and pulling using the front legs and fashioned into spherical balls. Food balls are smaller than brood balls or they may be of similar size. Spherical-shaped brood balls have a diameter of 12.1±1.51 mm and the feeding ball has a width of 6.37 mm. The adult-making brood balls in which eggs are laid may be coated with soil.

Egg: The adult beetle constructed a spherical brood ball (Fig 7. A) and is buried at the end of a shallow tunnel underneath the moist soil in the earthern pot and lays an egg in the brood ball and eggs are present inside the brood ball. Eggs were lengthened oval in appearance and creamy white, soft and yolky. The egg stage lasted for 6.8±1.22 days (Fig 7. B).

Larva: The larvae present inside the brood ball, (Fig 7. C, D, E) they eat the dung from inside the brood ball. The newly formed larvae were translucent, fleshy “grubs”, C-shaped body, the adjacent area of the mandible with two setae, pronotum with separate shields bearing anterior angels; legs with prominent lengthen terminal papillae, third abdominal segment absent dorso middle prominence; maxillary stridulatory teeth absent. Legs two- or three-segmented. The hindgut enlarged portion of larvae stores larval excrement that has grey-brownish paste. The larval period lasted for 25.3±0.68 days.

Pupa: The newly formed pupae are shiny, creamy white, with numerous projections present on its dorsal surface, finger-like processes are detected on the dorsolateral region of the abdomen and pronotal projections absent, mesonotal and metanotal projections present, adjacent tergal projections finger-like, present on the abdomen (Fig 7. F). The pupal period lasted for 15.5± 0.70 days in the laboratory. Pupae are present inside the pupal cell (Fig 7. G) formed by the larva. Pupal survivability 44% were recorded (Table.4).

Adult: Adults are formed in the larval chamber prepared by larvae, they construct a hole in the chamber and the adults emerged (Fig 7. H) from the chamber after 15.5± 0.70 days of pupation , 44 % of adults arisen from the brood ball in which survivability of adults is 40.90% were observed (9 females and 9 males) and the sex ratio 1:1 were observed. The newly formed immature adults stay in the dung and the sexual maturity was attained after 14.5±0.52 days. Adult male (Fig 7. I) duration of 33±7.52 days and female (Fig 7. J) duration of 42.5± 2.63 days were observed in the laboratory.The developmental period from egg to teneral adults took 47.3 ±1.63 days were observed.

Nesting behaviour: Nest provision and brood mass creation are the symbols of the following stage in the breeding process. The adult beetles (males and females), built a brood ball from the dung pad rolled away from the dung mass and the eggs were positioned in the brood ball buried in the pit with the depth of 3.6±0.69 cm

4.5. Life biology of *Tibiodrepanus setosus* (Wiedemann, 1823)

Biology of *Tibiodrepanus setosus*: (Fig 8. A-I): Life biology involves four stages namely egg, larva, pupa, and adult. The egg stage lasted for 3.9 ±0.31 days, the larval stage for 15.4±1.07 days and, the pupal stage for 8.6 ±0.51 days and egg to teneral adult 30 ±0.44 adult stage for 50.9±6.79 days

Brood mass and Egg (Fig 8. A**):** Adult beetles laid eggs using much drier dung after 7.5±0.52 days. A single mating pair produced 10.2 ±1.54 eggs during its period of the life cycle. The eggs are laid directly in the food source with the eggs are present in the dung.

Egg: Eggs were elongated oval in appearance and creamy white, during the first 2 days (Fig 8. A). Before hatching (3rd day), the egg became yellowish and the eggshell became transparent (3rd and 4th day) and the larva was visible through the chorion. The egg stage lasted 3.9 ±0.31. A single mating pair produced 10.2 ±1.54 eggs during its lifetime. Low egg mortality of 13.72% was recorded (Table.5).

Larva: Three larval instars, (Fig 8 .B,C,D) were recorded. Larvae were found in a cavity inside a brood ball. Newly hatched larvae were creamy white fleshy “grubs”. All larvae have the characteristic “Coprine hump”. Most are c-shaped, white fleshy “grubs” with a well sclerotised head capsule and well-developed legs. The larval period lasted for 15.4 ±1.07 days. Low larval mortality of 22.72 % was recorded.

Pupa: Pupae were present inside the thin-walled pupal cell constructed by larva inside the brood ball. (Fig 8 .E). The inner surface of the pupal cell was smooth and was coated with soft dried dung and soil. The newly formed pupae were creamy white, shiny, with four pairs of finger-like processes on the dorsolateral region of the abdomen and a large, blunt pronotal projection lengthening over a posterior portion of the head (Fig 8. F). Later on, the pupae turned golden brown. The pupal period lasted for 8.6 ±0.51 days. Pupal mortality was recorded at 47.05 %.

Adult: Teneral adults (Fig 8. G) remained in the pupal cell for 3.1±0.31 days. Adult emerged by cutting a hole in the pupal cell. Adults emerged 55.55 % (12 females and 8 males) and the sex ratio of 3:2 was observed. Newly formed adults took 1.3 ±0.49 days for the complete melanization. Sexual maturity was attained by 12.4±0.51days of emergence. Adult male (Fig 8. H) duration of 50.9±6.79 days and female (Fig 8. I) duration of 50 ± 8.01 days were observed. Egg to teneral adults took 30 ±0.44 days

Nesting behaviour

Beetles use plenty of drier dung for building brood masses and each brood mass has one egg. Type 4 nests were observed, the beetles do not form nesting chambers or burrows, and the whole development within the dung pat itself.

Table 1. Fecundity, egg mortality, egg hatchability, larval survivability, pupal survivability, and adult mortality of *Onthophagus cervus* in the agribelts of the Malabar Coast region.

Parameters	Mean ±SD	Hatchability/ Mortality/ Survivability (%)
Fecundity	25.4±6.67	-
Egg hatchability	21.7±6.69	85.43
Egg mortality	3.7±2.31	14.57
Larval survivability	18.2±6.58	83.88
Larval mortality	3.5±1.50	16.12
Pupal survivability	13.2±4.88	72.52
Pupal mortality	5±2.62	27.48
Adult survivability	4±2.21	30.30
Adult mortality	9.2±2.57	69.69

Table 2. Fecundity, egg mortality, egg hatchability, larval survivability, pupal survivability, and adult mortality of *Onthophagus fasciatus* in the agribelts of the Malabar Coast region.

Parameters	Mean ±SD	Hatchability/ Mortality/ Survivability (%)
Fecundity	12.5± 10.60	-
Egg hatchability	13.7±4.28	86.7
Egg mortality	2.1±1.29	13.29
Larval survivability	10.7±3.49.	71.97
Larval mortality	3.0±0.94	28.03
Pupal survivability	4.1±0.88	38.31
Pupal mortality	6.6±3.40	61.68
Adult survivability	2.4±0.84	58.53
Adult mortality	1.5±0.70	41.47

Table 3. Fecundity, egg mortality, egg hatchability, larval survivability, pupal survivability, and adult mortality of *Tiniocellus spinipes* in the agribelts of the Malabar Coast region.

Parameters	Mean±SD	Hatchability/ Mortality/ Survivability(%)
Fecundity	24.4 ± 6.91	-
Egg hatchability	17.5±6.68	71.72
Egg mortality	6.9±3.38	28.27
Larval survivability	14.2±6.52	81.14
Larval mortality	3.3±0.82	18.85
Pupal survivability	7.3±3.27	51.40
Pupal mortality	6.9±3.51	48.59
Adult survivability	3±2.05	41.09
Adult mortality	4.3±1.77	58.90

Table 4. Fecundity, egg mortality, egg hatchability, larval survivability, pupal survivability, and adult mortality of *Sisyphus longipes* in the agribelts of the Malabar Coast region.

Parameters	**Mean ±SD**	**Hatchability/ Mortality/ Survivability (%)**
Fecundity	15±5.66	-
Egg hatchability	12.8±4.75	85.33
Egg mortality	2.2±1.61	14.67
Larval survivability	10±4.88	78.12
Larval mortality	5.6±2.50	21.88
Pupal survivability	4.4±2.83	44
Pupal mortality	5.6±2.50	56
Adult survivability	1.8±0.79	40.90
Adult mortality	2.6±2.17	59.09

Table 5. Fecundity, egg mortality, egg hatchability, larval survivability, pupal survivability, and adult mortality of *Tibiodrepanus setosus* in the agribelts of the Malabar Coast region.

Parameters	Mean ±SD	Hatchability/ Mortality/Survivabilit y (%)
Fecundity	10.2 ±1.54	-
Egg hatchability	8.8±1.48	86.27
Egg mortality	1.4±0.51	13.72
Larval survivability	6.8±1.39	77.28
Larval mortality	2±1.69	22.72
Pupal survivability	3.6±0.97	52.94
Pupal mortality	3.2±1.69	47.05
Adult survivability	2±0.81	55.55
Adult mortality	1.6±0.51	44.44

Table 6. Number and size of brood balls and duration (days) of different life cycle stages of various *Onthophagus* species (Author details are provided in parenthesis; ND: no data available)

Species	Number of brood balls	Brood ball		Egg (Incubation period)	Larval duration	Pupal duration	Teneral adult days	Total duration (Egg to teneral adult) days	Adult longevity
		Length in mm	Width in mm						
O. cervus (present study)	14.1±5.69	20.4±0.97	32.8±1.62	3.6±0.51	16.7 ±1.87	10.2±1.03	2.4±0.51	28.2 ±1.03	60.17± 2.08
O. catta (Gaikwad and Bhawane, 2016)	22.5±17.67	27.7±3.79	5.4±1.49	2.38±0.8	31.5 ±6.37	13.46±0.8	3.5±0.70	48.33±4.49	66.7±11.98
O. gazella (Veenakumari and Veeresh, 1996c)	6	40.6±0.03	16.0±0.08	5.4±0.54	26.2±1.22	11.16±0.98	3.5±0.70	41.4±2.60	ND
O. rectecornutus Veenakumari and Veeresh,1996c)	12±2.5	34.7±0.33	11.3±0.11	4.0±0.47	19.0±2.00	10.88±1.05	4	31.8±1.93	ND
O. lecontei (Arellano *et al.*, 2017)	3.50±1.74	23.47±1.52	23.14±0.91	2	22±1.14	11±0.87	4±0.95	39	60±2.3
O. incensus (Huerta *et al.*, 2010)	5± 5.65	25±7.07	12.5±3.53	4	22	10±2.82	ND	36 ±2.82	93
O. landolti (Perez cogollo *et al.*, 2015)	14.5±13.43	ND	ND	2.2 ±0.70	21±1.41	7±1.41	ND	30	60
O. medorensis (Hunter *et al.*, 1991)	ND	10.27±4.63	ND	4	28	11.5±0.70	4±1.41	49.5 ±4.94	53±26.88
O. depressus (Hunter *et al.*, 1996)	ND	22±4.24	16±1.41	3.4±1.28	27	12	3	46.5±14.84	50
O. stylocerus (Romero and Piera,1995)	19.75±2.16	31.5±9.19	15.5±3.53	7.5±3.53	22.33±3.05	14±4.24	15	60.5±13.43	ND

Table 7: Number and size of brood balls and duration (days) of different life cycle stages of various *Onthophagus* species.
(Author details are provided in parenthesis; ND: no data available)

Species	Number of brood balls	Brood ball		Egg (Incubation period)	Larval duration	Pupal duration	Teneral adult days	Total duration (Egg to teneral adult) days	Adult longevity
		Length in mm	Width in mm						
O. fasciatus (present study)	13.2±3.68	14.4±1.42	22.9±2.23	3.1±0.57	18.1 ±0.31	11.1±0.57	3	38.5 ±0.52	64.1± 2.42
O. catta (Gaikwad and Bhawane, 2016)	22.5±17.67	27.7±3.79	5.4±1.49	2.38±0.8	31.5 ±6.37	13.46±0.8	3.5±0.70	48.33±4.49	66.7±11.98
O. gazella (Veenakumari and Veeresh, 1996c)	6	40.6±0.03	16.0±0.08	5.4±0.54	26.2±1.22	11.16±0.98	3.5±0.70	41.4±2.60	ND
O. rectecornutus (Veenakumari and Veeresh,1996c)	12±2.5	34.7±0.33	11.3±0.11	4.0±0.47	19.0±2.00	10.88±1.05	4	31.8±1.93	ND
O. lecontei (Arellano *et al.*, 2017)	3.50±1.74	23.47±1.52	23.14±0.91	2	22±1.14	11±0.87	4±0.95	39	60±2.3
O. incensus (Huerta *et al.*, 2010)	5± 5.65	25±7.07	12.5±3.53	4	22	10±2.82	ND	36 ±2.82	93
O. landolti (Perez cogollo *et al.*, 2015)	14.5±13.43	ND	ND	2.2 ±0.70	21±1.41	7±1.41	ND	30	60
O. medorensis (Hunter *et al.*, 1991)	ND	10.27±4.63	ND	4	28	11.5±0.70	4±1.41	49.5 ±4.94	53±26.88
O. depressus (Hunter *et al.*, 1996)	ND	22±4.24	16±1.41	3.4±1.28	27	12	3	46.5±14.84	50
O. stylocerus (Romero and Piera,1995)	19.75±2.16	31.5±9.19	15.5±3.53	7.5±3.53	22.33±3.05	14±4.24	15	60.5±13.43	ND

Table 8. Number and size of brood balls and duration (days) of different life cycle stages of various sub-tribe Oniticellina species

Species	Number of brood balls	Brood ball		Egg incubation period	Larval duration	Pupal duration	Teneral adult days	Total duration (egg to teneral adult) days	Adult longevity
		Length in mm	Width in mm						
T. spinipes (Roth,1851) (Present study)	96.33±1.3	29.5±0.70	50.5±2.83	4.2±0-42	20.6 ±1.26	12.3±0.82	2.4 ±0.51	39.2 ± 0.63	72±3.65
E. intermedius (Reiche,1848)	111±15	-	-	1.5±0.70	31	28	-	56	45± 21.21
L. rhadamistus (Fabricius,1775)	-	-	20.5±1.28	3.94±0.7	30±32.52	17±1.41	5.5±0.70	69.14±6.17	80.45±14.95

Table 9. Number, shape and size of brood balls and duration (days) of different life stages of *Sisyphus* species.

Species	Brood ball			Duration of different life stages						Adult number		Adult longevity	
	No	Shape	Diameter	Egg			Larva	Pupa	Egg adult	Male	Female	Summer	Winter
				Number		Duration							
				Summer	Winter								
***S. longipes* (Present study)**	20.1±5.13	Sphere	12.1±1.51	15±5.66	NA	6.8±1.22	25.3±0.68	15.5± 0.70	47.3±1.63	9	9	42.5±2.63	
S. sordidus	-	Dome on sphere	-	15±7.07	-	8	-	-	66.2	-	-	-	300-700
S. seminulum	-	Dome on sphere	-	26.0	17.5	6.5±2.12	-	-	47.1	-	-	125.2	186
S. mirabilis	-	Sphere with very short tip	16.2	46.8	46.2	9±1.41	-	-	77.3	175	175	144.1	214.6
S. fortutus	-	Sphere with tip	17.1	54.5	57.5	12±2.82	-	-	73.2	54	68	153.5	201.0
S. spinipes	-	Sphere with long tip	17.6	43.7	34.5	8.5±0.70	-	-	51.8	108	129	104.2	153.2
S. infusticatus	-	Sphere with tip	13.6	56.4	36.2	9±1.41	-	-	53.7	112	120	114.1	127.3
S. rubrus	40	Sphere with flat dome	14.7	36.4	24.8	-	-	-	64	131	136	116.8	148.6
S. calcaratus	48	Orange	10.6	41.2	25.5	7.5±0.70	-	-	59.7	160	178	133.6	221.0
S. muricatus	-	Orange	-	14		-	-	-	58	4	4	395	-
S. fasciculatus	-	Orange	-	18	-	-	-	-	60	18	21	395	-
S. barbarossa	-	Orange	-	-	-	-	-	-	-		9	9	-
S. tibialis	-	Sphere	-	-	-	-	-	-	-	-	-	-	-

Figure 4. A) Brood ball of *Onthophagus cervus;* B)Egg glued to the wall of brood mass; C) First instar larva; D) Second instar larva; E) Third instar larva; F) Pupal cell; G) Pupa- Early phase; H) Pupa- late phase I) Teneral adult; J) Emergence of adult from pupal cell; K) Adult male; L) Adult female; M & N) Nesting behaviour- vertical & horizontal tunnels.

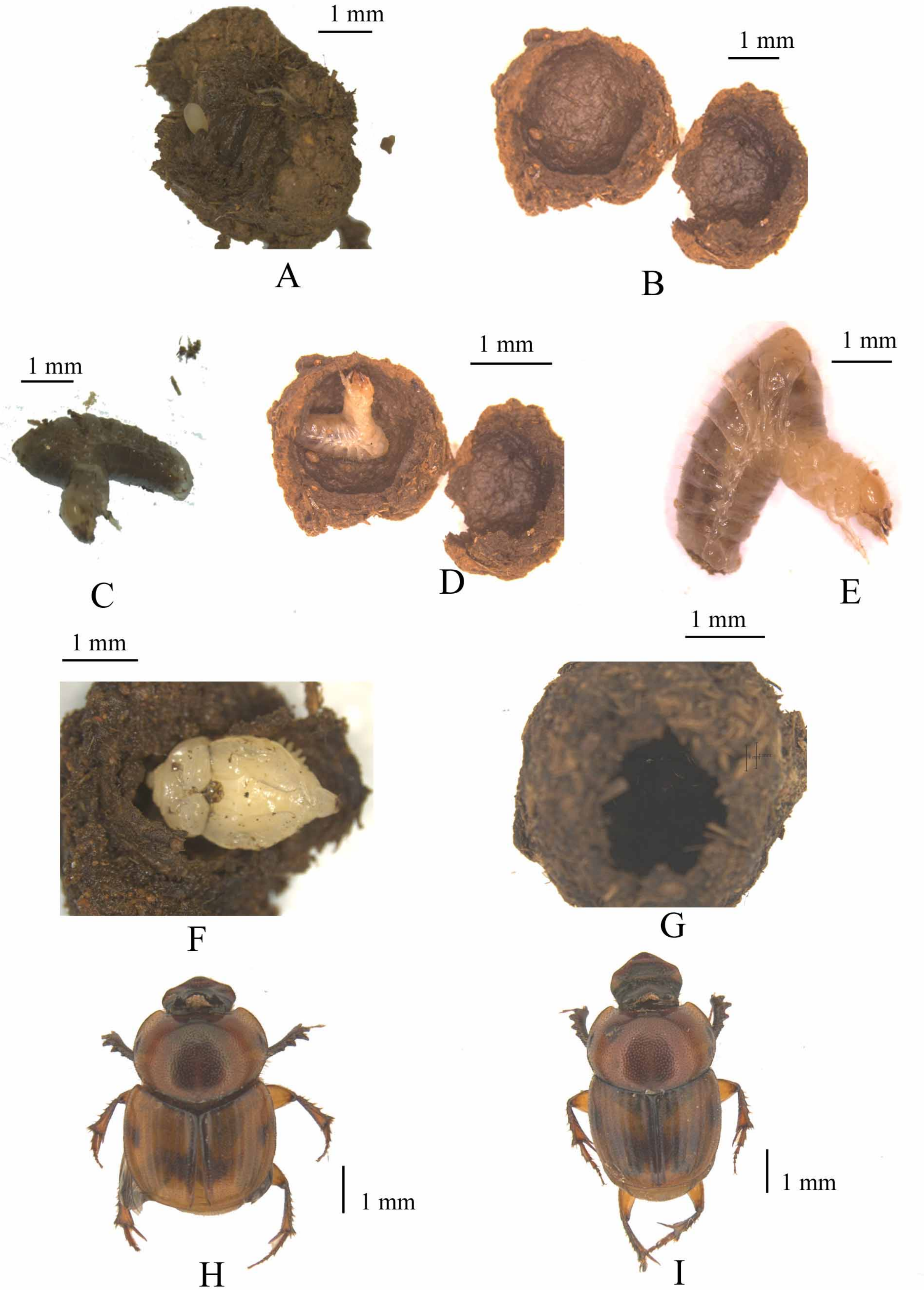

Figure 5. A) Egg of *Onthophagus fasciatus*; B) Brood ball; C) First Instar larva; D) Second Instar larva; E) Third Instar larva; F) Pupa; G) Pupal cell; H) Male; I) Female

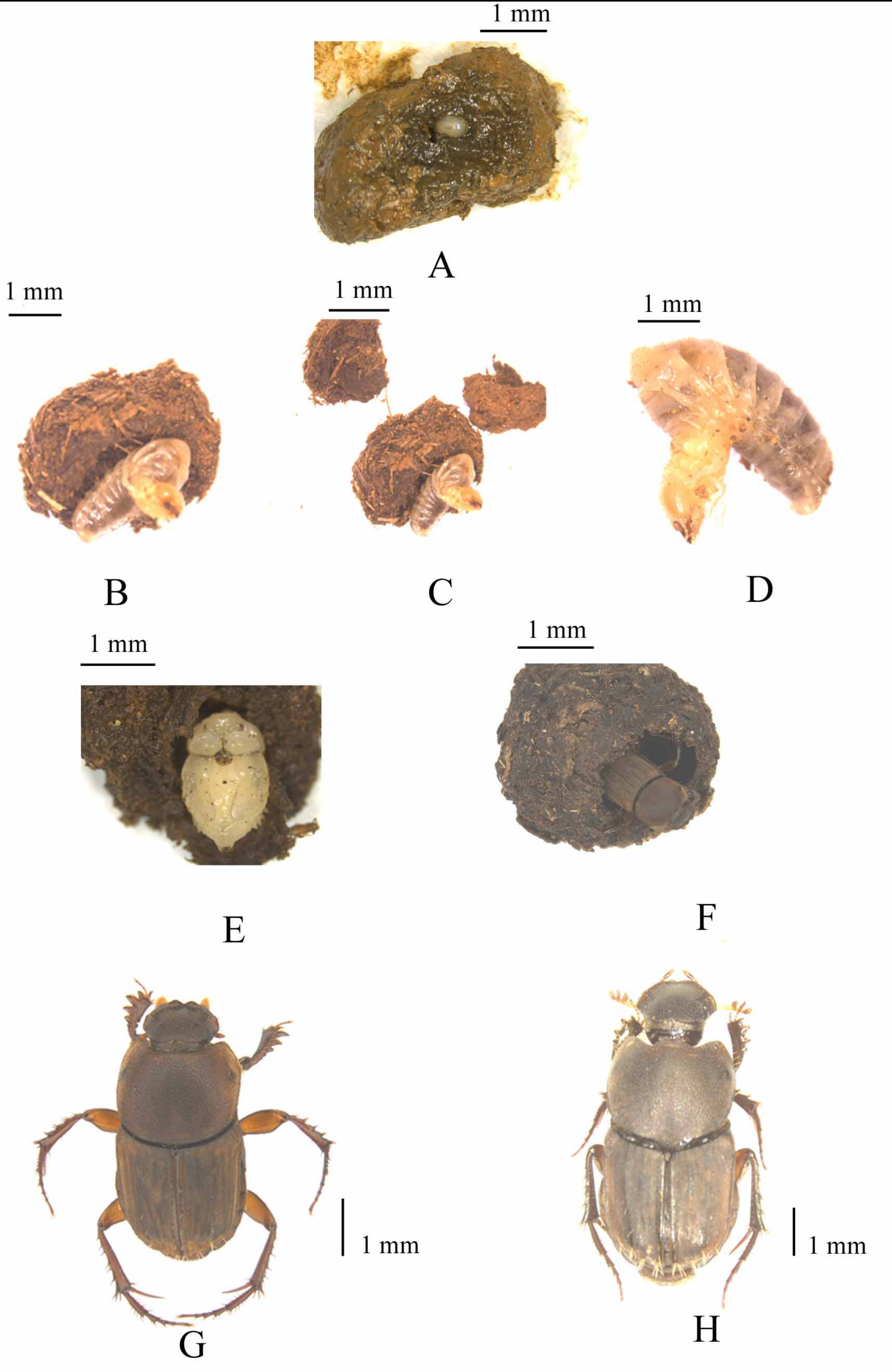

Figure 6. A) Egg of *Tiniocellus spinipes;* B) First Instar larva; C) Second Instar larva; D) Third Instar larva; E) Pupa; F) Adult emerged cutting a hole in the pupal cell; G) Female; H) Male

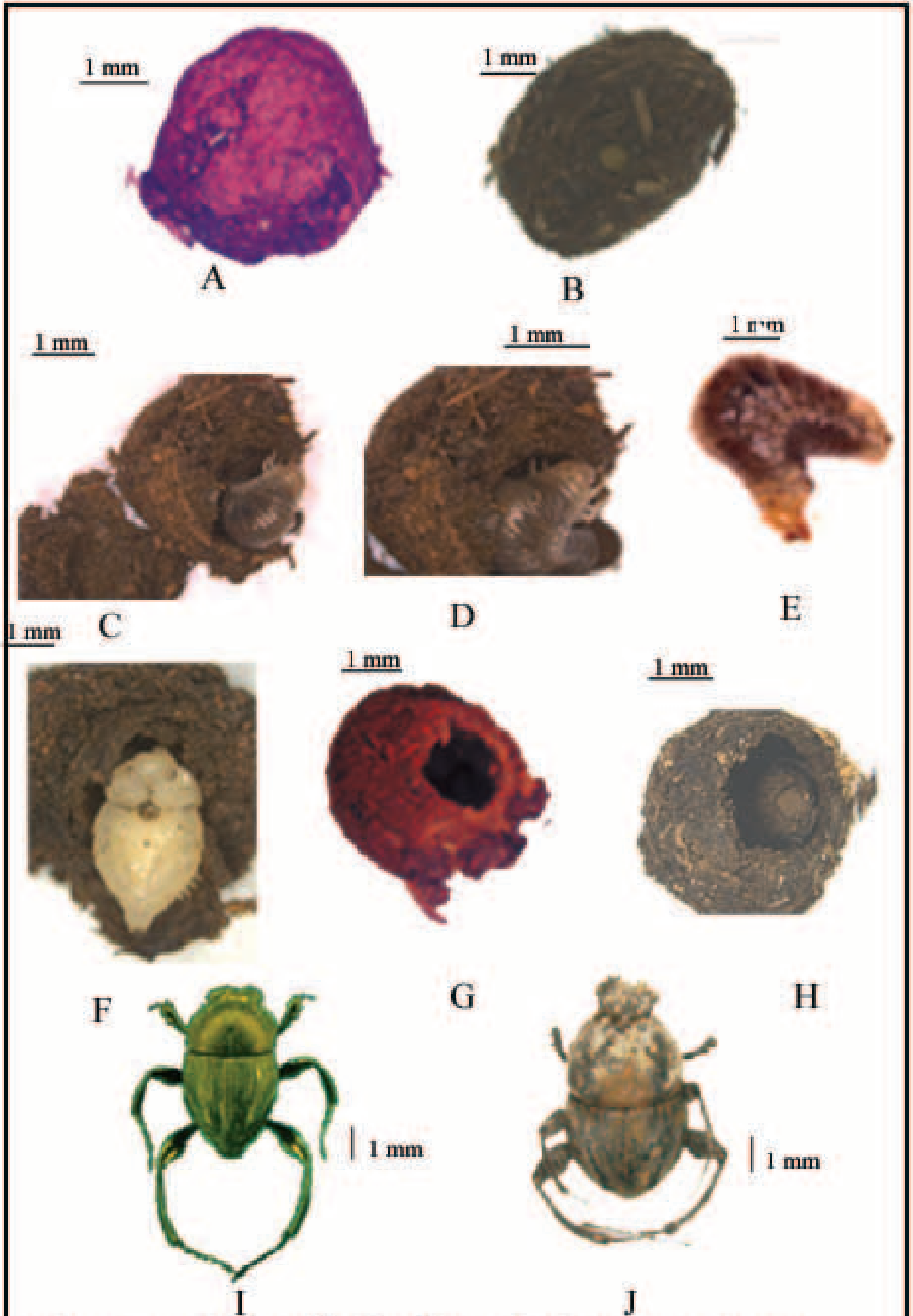

Figure 7. A) Brood ball of *Sisyphus longipes*; B) Egg; C) First Instar larva; D) Second Instar larva; E) Third Instar larva; F) Pupa; G) Pupal cell; H) Emerging adult; I) Male; J) Female

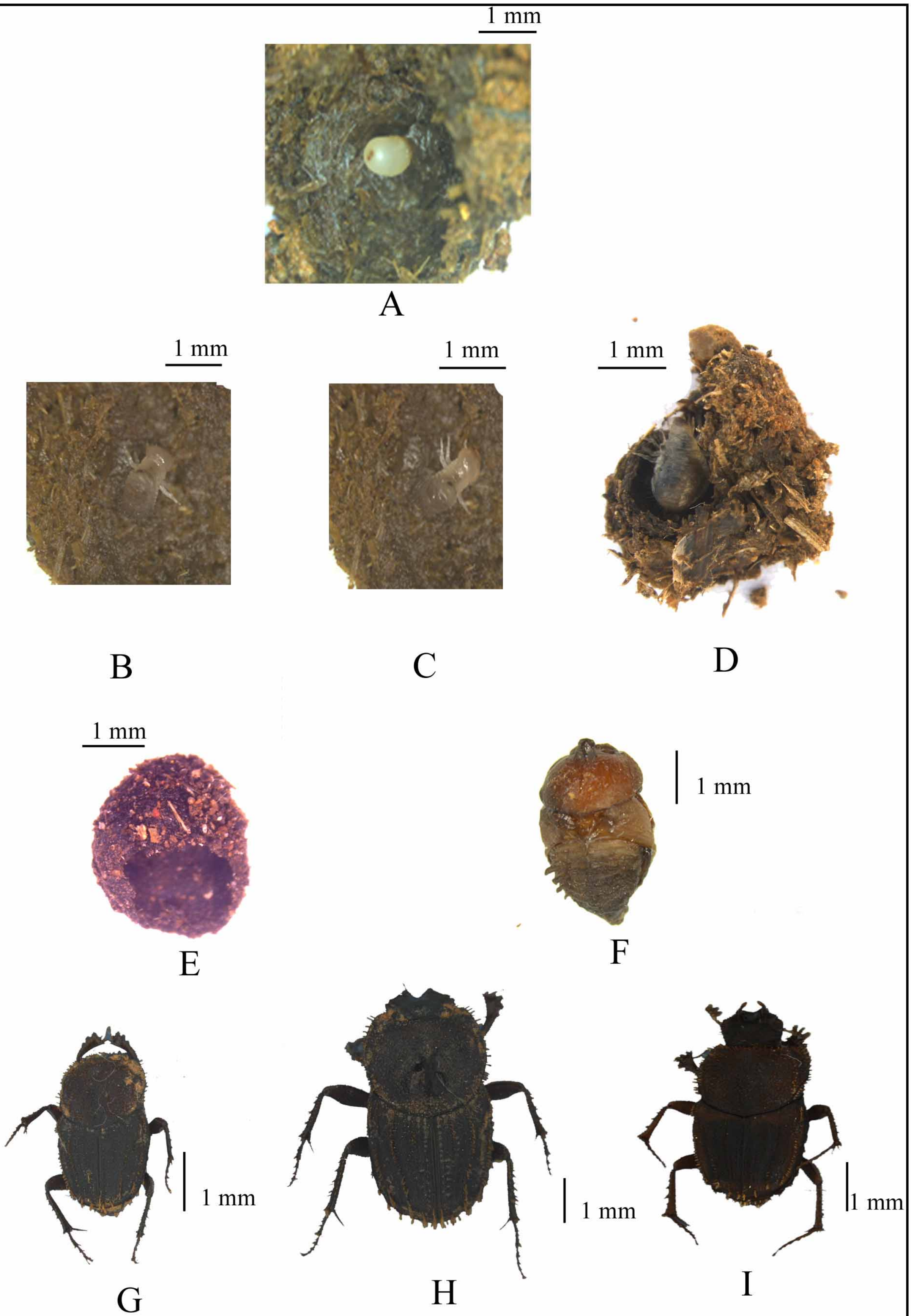

Figure 8. A) Egg of *Tibiodrepanus setosus*; B) First Instar larva; C) Second Instar larva; D) Third Instar larva; E) Pupal cell; F) Pupa; G)Teneral adult; H) Male; I) Female

Chapter 5

DISCUSSION

DISCUSSION

The present study provides data on the reproductive biology and nesting behaviuor of the five prominent dung beetle species *Onthophagus cervus, O. fasciatus* , *Tiniocellus spinipes*, *Sisyphus longipes*, and *Tibiodrepanus setosus* in the agribelts of the Malabar Coast region and the basic reasons for their abundance and dominance in the region**.**

5.1. *Onthophagus cervus* (Fabricius, 1798).

Comparison of data of brood mass production, fecundity, duration of egg, larval, pupal, adult stages, adult mortality, and life span of *Onthophagus cervus* with other *Onthophagus* species (listed out in **Table.6**) revealed that a broad categorization of *Onthophagus* species based on the life cycle characteristics is possible. Data on the brood mass production of different *Onthophagus* species showed that *Onthophagus* species can be categorized as high and low brood mass producers. *Onthophagus stylocerus* Graells,1851 (Romero and Piera, 1995); *O. rectecornutus* Lansberge,1883 (Veenakumari and Veeresh, 1996c); *O. landolti* Harold,1880 (Pérez-Cogollo*et al.*, 2015); *O.catta* (Fabricius,1787) (Gaikwad and Bhawane, 2016), and *O. cervus* (Fabricius,1798) comes under the category of high brood mass producers with a brood mass range of 1– 40 and; *O. hirculus* Mannerheim,1829 (Gonzalez- Vainer and Morelli, 1999); *O. incensus* Say,1835 (Huerta and Hernandez, 2013); *O. lecontei* (Harold,1871) (Arellano *et al.*, 2017) falls under the category of low brood mass producers with a brood mass range of 1–10. Similarly based on the size of brood ball, two categories of *Onthophagus* species are recognizable with a large-sized brood ball category consisting of, *O. stylocerus* (Romero and Piera, 1995); *O. rectecornutus* (Veenkumari and Veeresh, 1996c); *O. catta* (Gaikwad and Bhawane, 2016) and small brood ball category of *O. medorensis* Brown,1929 (Hunter *et al.,* 1991); *O. depressus* Harold,1871 (Hunter *et al.*, 1996); *O. hirculus* Mannerheim,1829 (Gonzalez –Vainer and Morelli, 1999); *O. lecontei* (Arellano *et al.,* 2017) and *O. cervus.*

Duration of egg incubation revealed a pattern of longer egg incubation period in *O. medorensis* (Hunter III *et al*., 1991); *O. stylocerus* (Romero and Piera, 1995); *O. depressus* (Hunter *et al.,* 1996); *O. rectecornutus* (Veenakumari and Veeresh, 1996c); *O. hirculus* (González-Vainer and Morelli, 1999); *O. incensus* (Huerta *et al.,* 2010), *O. cervus* and short egg incubation period in *O. landolti* (Pérez-Cogollo*et al*., 2015); *O. catta* (Gaikwad and Bhawane, 2016) and in *O. lecontei* (Arellano *et al.,* 2017).

Comparison of larval duration showed that *O. cervus* and *O. rectecornutus* (Veenakumari and Veeresh, 1996) belong to the shorter larval duration category compared to *O. medorensis* (Hunter *et al.,*1991); *O. stylocerus* (Romero and Piera, 1995); *O. depressus* (Hunter *et al.,* 1996); *O. incensus* (Huerta and Hernandez, 2013); *O. landolti* (Pérez-Cogollo*et al*., 2015); *O. catta* (Gaikwad and Bhawane, 2016)*;* and *O. lecontei* (Arellano *et al.,* 2017) with long larval duration period.

Comparison of pupal duration among the various *Onthophagus* species show that *O. landolti* (Pérez-Cogollo*et al*., 2015) has a short pupal period compared to longer pupal duration in *O. medorensis* (Hunter *et al.,* 1991); *O. stylocerus* (Romero and Piera,1995); *O. depressus* (Hunter *et al.,* 1996); *O. rectecornutus* (Veenakumari and Veeresh, 1996c); *O. catta* (Gaikwad and Bhawane, 2016); *O. cervus* and *O. lecontei* (Arellano *et al.,* 2017). Higher variability in egg hatchability, larval and pupal survivability under uniform conditions in many samples indicate that wider variation exists in the population and the exact reasons are not understood and could be genetic.

The developmental period of *O. cervus* **(**egg to a teneral adult**)** and Mexican species *O. landolti* (Pérez-Cogollo*et al.,* 2015) was the shortest among the various

Onthophagus species. The teneral adult period was shorter in *O. cervus* compared to other *Onthophagus* species. Comparison of adult duration showed that *O. cervus* and *O. medorensis* (Hunter *et al.,* 1991); *O. depressus* (Hunter *et al.*, 1996); *O. landolti* (Pérez-Cogollo *et al*., 2015); *O. lecontei* (Arellano *et al.,* 2017); were species with short adult longevity whereas,*O. stylocerus* (Romero and Piera,1995); *O. rectecornutus* (Veenakumari and Veeresh, 1996c); *O. incensus* ((Huerta and Hernandez 2013); and *O. catta* (Gaikwad and Bhawane, 2016); were with longer adult duration. Low pupal survivability compared to the high egg hatchability, larval survivability, and adult survivability of *O. cervus* indicated that the pupal phase is the crucial phase in the life cycle of *O. cervus*.

Type 1 pattern of nesting was present in *Onthophagus cervus* with a simple, shallow tunnel with a bottom containing brood masses and vertical and horizontal tunnels (Halffter and Edmonds, 1982). Similar type 1 pattern was reported in *O. taurus* (Fabre, 1918); *O. fucatus* (Main, 1922); *O. coenobita* (Burmeister, 1930); *O. catta* (Fabricius,1787) (Gaikwad and Bhawane, 2016); and *O. lecontei* Harold,1871 (Arellano *et al.*,2017). Some *Onthophagus* species constructed compound nest (Type 2) with galleries that may have one or more branches, which ended into brood cells in *O.nuchicornis* Linnaeus,1758, *O. fracticornis* (Burmeister, 1930), *O. medorensis* (Hunter *et al.,* 1991), *O. stylocerus* (Romero and Piera, 1995), *O. rectecornutus* (Veenakumari and Veeresh, 1996c) and *O. incensus* (Huerta and Hernandez 2013).

Among the tunneling species, large species tend to bury their brood balls at a deeper depth and small species at a shallower depth, which is thought to help reduce overall competition for nesting space (Hanski, 1991a; Rougon and Rougon, 1991; Hernández *et al.,* 2011). Tunnels were dug roughly perpendicular to the interface between soil and dung, resulting in interference competition for nesting space underneath dung pads, especially in areas where tunnels branch out into nesting chambers (Halffter and Edmonds, 1982; Hanski, 1991b; Macagno *et al.*, 2016). Higher longevity of females and female-biased sex ratio were seen in *O. cervus.* Why females live longer than male is generally unknown, either metabolic differences or differences in patterns of resource allocation between males and females probably account for the gender difference in lifespan (Fox *et al*., 2003). Alternatively, males may allocate a more significant proportion of their biomass to reproduction, or allocate those resources sooner, such that they become resource-stressed at a younger age. Gender-difference in energy expenditure explains at least some of the gender-difference in lifespan. Some of the difference in lifespan and mortality rates between genders is due to faster energy-water loss in males than in females (Fox *et al*., 2003).

Observed sex ratio bias in *O. taurus* females, is caused by the higher mortality of males and suggested that this might be linked to higher demand for nutritional resources during offspring development (House *et al.,* 2011). Differential mortality is common in species like dung beetles with both the sexes having distinct nutritional requirements and energy expenditures due to differential mobility and investment in parental care (Veran and Beissinger, 2009). Evaluation of the cost of male production studies with other groups (Jokela *et al*., 1997; Wolinska and Lively, 2008; Macagno *et al.,* 2019), have suggested a cost of producing males. Also, as per LMC (local mate competition), a female-biased sex ratio is favored if the mating competition takes place between male offspring (Hamilton, 1967), whereas an equal sex ratio is expected under random mating (Fisher, 1930). Hence the female-biased sex ratio noticed in *O. cervus* indicates that mating competition takes place between male offspring and the high cost of producing males might have led to the reduction in the ratio of males to females in *O. cervus.*

With traits that are common in an *r*-selective species such as high fecundity, multivoltine, small body size, low egg mortality, shorter larval duration, early maturity onset, and shorter developmental period (short generation time enables attaining maturity earlier together with female-biased sex ratio), longer duration of females (favoring high egg production) and shallow tunnels (which enable easy and fast tunneling process and development in thin soil topsoil layer) all of these morphological and physiological traits contribute to the higher abundance of *O. cervus* and make it the prominent dung beetle species in the agribelts of Malabar Coast in south India.

5.2 *Onthophagus fasciatus* Boucomont, 1914 .

The current study showed that the nesting pattern presented by *Onthophagus fasciatus* was Type 1 with a simple, shallow tunnel with a bottom containing brood masses and with the tunnels not going deeper into the soil and creating vertical and horizontal tunnels (Halffter and Edmonds, 1982). Similar type 1 pattern was reported in *O. catta* (Gaikwad and Bhawane, 2016); *O. lecontei* (Arellano *et al.,* 2017); *O. coenobite* (Burmeister1930); *O. tauruss* (Fabre, 1918); and *O. fucatus* (Main, 1922). Some *Onthophagus* species constructs compound nest (Type 2) with galleries that may have one or more branches, which ends into brood cells as in *O. gazelle* and *O. rectecornutus* (Veenakumari and Veeresh, 1996c); *O. nuchicornis* and *O. fracticornis* (Burmeister, 1930); *O .medorensis* (Hunter *et al.,* 1991); *O. incensus* (Huerta *et al.,* 2010); and *O. stylocerus* (Romero and Piera 1995).

The current study provides the first-time data on the nesting behaviour and life history of *Onthophagus fasciatus* and also enabled comparison of data with other *Onthohpagus* species (details listed out in **Table.7**). Comparison of the life cycle and brood mass construction, brood ball size, fecundity, duration of egg, larval, pupal and adult mortality, duration of adult phase, and life span of *various Onthophagus* species revealed the presence of the following categories. Based on the brood mass production *Onthophagus* species can be categorized as high and low brood mass producers. *Onthophagus fasciatus, O. catta* (Gaikwad and Bhawane, 2016), *O. rectecornutus* (Veenakumari and Veeresh, 1996c), *O. stylocerus* (Romero and Piera,1995) and *O. lentolti* (Perez-cogollo *et al.*,2015) comes under the category of high brood mass producers with a brood mass range of 1- 40. *O. gazelle* (Veenakumari and Veeresh,1996c), *O. incensus* (Huerta *et al.*, 2013), *O. lecontei* (Arellano *et al.*, 2017), and *O. hirculus* (González-Vainer and Morelli, 1999) falls under the category of mass producers with a brood mass range of 1-10. Similarly based on the size of brood ball two categories of *Onthophagus* species are recognizable with a large-sized brood ball category consisting of *O. gazella, O. rectecornutus* (Veenkumari and Veeresh, 1996c), *O. stylocerus* (Romero and Peira, 1995), *O. catta* (Gaikwad and Bhawane, 2016) and small brood ball category consisting of *O. lecontei* (Arellano *et al.*, 2017), *O. depressus* (Hunter *et al.*,1996), *O. fasciatus, O. hirculus* (González-Vainer and Morelli, 1999) and *O. medorensis* (Hunter *et al.*, 1991).

Based on the duration of egg incubation, a pattern of longer egg incubation period as in *O. stylocerus* (Romero and Peira, 1995), *O. rectecornutus* (Veenakumari and Veeresh, 1996c), *O. gazella* (Veenakumari and Veeresh, 1996b), *O. incensus* (Huerta *et al.*, 2010), *O. medorensis* (HunterIII *et al*., 1991), *O. depressus* (Hunter *et al.*, 1996), *O. fasciatus*, and *O. hirculus* (González-Vainer and Morelli, 1999) and short egg incubation period in *O. lecontei* (Arellano et *al.*, 2017), *O. catta* (Gaikwad and Bhawane, 2016), and in *O. landolti* (Pérez-Cogollo *et al*., 2015) is distinct.

Comparison of larval duration shows that *O. fasciatus* and *O. rectecornutus* (Veenakumari and Veeresh, 1996c) belongs to the shorter larval duration category compared to *O. catta* (Gaikwad and Bhawane, 2016), *O. lecontei* (Arellano *et al.*, 2017), *O. incensus* (Huerta *et al.,* 2010), *O. landolti* (Pérez –Cogollo *et al*., 2015), *O. gazelle* (VeenaKumari and Veeresh, 1996), *O. insensus* (Huerta *et al.,* 2015), *O. medorensis* (Hunter *et al.,*1991, *O. stylocerus* (Romero and Peira,1995) and *O. depressus* (Hunter *et al.,*1996) with long larval duration.

Comparison of pupal duration of various *Onthophagus* species shows that a short pupal period is present in *O. landolti* (Pérez-Cogollo *et al.,* 2015) compared to the longer pupal duration of *O. stylocerus* (Romero and Peira, 1995), *O. catta* (Gaikwad and Bhawane, 2016), *O .gazella* (Veenakumari and Veeresh, 1996), *O. lecontei* (Arellano *et al.,* 2009), *O. medorensis* (Hunter *et al.,* (1991), *O. depressus* (Hunter *et al.,*1996), *O. fasciatus* and *O. rectecornutus* (Veenakumari and Veeresh,1996c). High pupal mortality shows that the pupal phase as the crucial phase in the life cycle of *O. fasciatus.*

The developmental period of *O. fasciatus* (egg to a teneral adult**)** is closer to the developmental period in *O. incensus* (Huerta *et al.,* 2010), *O. lecontei* (Arellano *et al.*,2017), *O. rectecornutus* (Veenakumari and Veeresh, 1996) and the mexican species *O. landolti* (Perez cogollo *et al.,* 2015) is having the shortest developmental period. Comparison of adult duration shows that *O. incensus* (Huerta *et al.,* 2010), *O. rectecornutus* (Veenakumari and Veeresh, 1996c), *O. catta* (Gaikwad and Bhawane, 2016), *O. stylocerus* (Romero and Piera,1995), and *O. gazelle* (Veenakumari and Veeresh, 1996c) are species with longer adult duration and *O. landolti* (Pérez – Cogollo *et al*., 2015), *O. lecontei* (Arellano *et al.,* 2017), *O. medorensis* (Hunter *et al.,*1991), *O. depressus* (Hunter *et al.,* 1996) are species with short adult longevity.

Higher longevity of females and sex ratio biased towards females seen in *O. fasciatus.* Why females live longer than male is generally unknown, either metabolic differences or differences in patterns of resource allocation between males and females probably account for the gender difference in lifespan (Fox *et al.*, 2003).

The female-biased sex ratio noticed in *O. fasciatus* indicates that mating competition takes place between male offsprings and the high cost of producing males might have led to the reduction in the ratio of males to females in *O. fasciatus*. Traits such as low egg mortality, shorter larval duration, and shorter developmental period, short generation time, female-biased sex ratio, longer duration of females favouring high egg production lead to the higher abundance of *O. fasciatus* in the agribelts of the Malabar coast region.

5.3 . *Tiniocellus spinipes* (Roth, 1851).

The reproductive biology and life span of a member species *Tiniocellus spinipes* of the genus *Tiniocellus* of soil tunnelling sub-tribe Oniticellina of tribe Onitcinellini and dominant in the regional landscape in South India is analyzed. Additionally, the present study enabled a comparison of the life biology of representative species of the related soil tunneling genera of the subtribe Oniticellina namely, *Tiniocellus*, *Euoniticellus*, and *Liatongus.* Compared the present data on the brood mass production, fecundity, egg, larval, pupal, adult duration, adult mortality and life span of *Tiniocellus spinipes* with available data on the soil tunneling genera of the subtribe Oniticellina species *Euoniticellus intermedius* (Reiche,1848) and *Liatongus rhadamistus* (Fabricius,1775). The present study revealed that *Tiniocellus spinipes* is having the shortest larval, pupal, teneral adult, mature adult duration (details listed out in **Table.8)**. Short egg to teneral adult duration and high brood mass production compared to *Liatongus rhadamistus* (Gaikwad and Bhawane, 2015) and *Euoniticellus intermedius* (Martinez *et al.*, 2019*)* are taken as part of the reproductive strategy of *Tiniocellus spinipes* and is favouring the population build-up of the species. Advantages of the longer egg incubation period in *Liatongus rhadamistus* (Gaikwad and Bhawane, 2015) and *Tiniocellus spinipes*, and the short egg incubation period in *Euoniticellus intermedius* (Martinez *et al.,* 2019) are not understood. Egg incubation period ranging from 2-5 days is observed as a general pattern in many highly abundant dung beetles such as *Onthophagus gazella, O. rectecornutus* (Veenakumari and Veeresh.,1996c), and *Oniticellus cinctus* (Singh *et al.,* 2019).

Among the various life cycle stages the high pupal mortality of *Tiniocellus spinipes* is the crucial phase adversely affecting the life cycle of *T. spinipes.* Present data shows that *T. spinipes* is a soil-tunneling species producing a simple, shallow tunnel with bottom containing brood masses (Cambefort and Lumaret, 1983) and have high fecundity and is a multivoltine species. Differential mortality is common in dung beetles with both the sexes having distinct nutritional requirements and energy expenditures as a result of differential mobility and investment in parental care (Veran and Beissinger, 2009). The longevity of females and males in *T. spinipes* indicates the absence of differential mobility and the possible presence of an investment in parental care by both sexes.

Sex ratio biased towards females is seen in *Tiniocellus spinipes.* Evaluation of the cost of male production studies in other groups (Jokela *et al*., 1997; Wolinska *et al*., 2008; Macagno *et al.,* 2019), have suggested a cost of producing males. Also, as per LMC (Local mate competition), a female-biased sex ratio is favoured, if the mating competition takes place between male offsprings, whereas an equal sex ratio is expected under random mating (Fisher *et al*., 1930). Hence, the female-biased sex ratio noticed in *T. spinipes* indicates that mating competition occurs between male offspring.

5.4. *Sisyphus longipes* (Olivier, 1789).

The present study showed that *Sisyphus longipes* make spherical brood balls as reported for South African species *S. tibialis* Raffray 1877 (Paschalidis, 1974). Spherical brood balls of *S.longipes* differs from the dome and sphere-shaped brood ball in *S. seminulum,* Gerstaecker 1871, *S. costatus* Hunberg, 1818, *S. sordidus* Boheman, 1857, *S. caffer* Boheman, 1857, the pear-shaped brood ball in *S. impressipennis* Lansberge, 1886 and the sphere-shaped with a flat dome in *S. rubrus* and *S. macrorubrus* (Paschalidis, 1974), sphere-shaped with a very short tip in *S. mirabilis* Arrow 1927 and sphere with the long tip in *S. spinipes* Thunberg 1818 (Paschalidis, 1974). The diameter of brood ball of *S. longipes* is similar to the brood ball in other *Sisyphus* species, *S. rubrus, S. infusticatus* and *S. calcaratus*.

Comparison of data (details listed in **Table. 9**) on brood mass production in *Sisyphus longipes* showed that a lower number of brood balls are produced compared to other species, *S. rubrus* and *S. calcaratus* (Paschalidis, 1974). Duration of egg incubation revealed a pattern of longer egg incubation period in *S. fortuitus* Peringuey 1901, *S. infuscatus* Klugg, 1855 and *S. mirabilis* (Paschalidis, 1974) and short egg incubation period in *S. sordidus* (Boheman, 1857), *S. seminulum* (Gerstaecker, 1871), *S. calcaratus* (Klug, 1855), (Paschalidis, 1974) and in *S. longipes.* In *S. seminulum* (Gerstaecker, 1871) and *S. sordidus* (Boheman, 1857), one nest contains a single egg (Paschalidis, 1974) and the same pattern was observed in the present study. Paschalisidis (1974) reported that in *Sisyphus* species three larval instars can take less than 30 days to complete in the summer season and the same pattern with similar larval duration was observed in *Sisyphus longipes*.

Compared to the pupal duration in other *Sisyphus* species (*Sisyphus sordidus*, *S. mirabilis*, *S. fortuitus* and *S. fasciculatus*), the pupa transformed into an adult within 2-3 weeks as reported in the previous studies of (Paschalidis, 1974). High pupal mortality was observed in the present study. Based on their developmental period, *Sisyphus* species are categorized into two categories, species with a long developmental period (*Sisyphus sordidus*, *S. mirabilis*, *S. fortuitus*, and *S. fasciculatus*) and species with a shorter developmental period (*S. seminulum*, *S. spinipes*, *S. infuscatus*, *S. calcaratus*, *S. muricatus*, and *S. longipes*).

The sex ratio of 1:1 observed in the present study was reported in other species of the genus (*S. mirabilis*, *S. muricatus*, and *S.barbarossa*) also (Paschalidis, 1974). It is best explained by Fisher's principle (Hamilton 1967) and it says that in most sexually reproducing species, the ratio tends to be 1:1, given the assumption of equal parental expenditure on offspring of both sexes. Male births are less common than females and the new born male then has better mating prospects than a newborn female and therefore can expect to have more offspring. Therefore parents genetically disposed to produce males tend to have more than average numbers of grandchildren born to them. The genes for male-producing tendencies spread, and male births become more common. As the 1:1 sex ratio is approached, the advantage associated with producing males dies away. The same reasoning holds if females are substituted for males throughout. Therefore 1:1 is the equilibrium ratio and is the evolutionarily stable strategy (ESS).

In the current study, the female longevity is long compared to males, the same trend has been observed in the previous studies of other *Sisyphus* species viz., *Sisyphus sordidus, S. mirabilis, S. fortuitus, S. fasciculatus, S. seminulum, S. spinipes, S. infuscatus,* and *S.calcaratus* (Paschalidis, 1974). Why females live longer than males is generally unknown, it would be the metabolic differences or difference in patterns of resource allocation between males and females probably account for the gender difference in life span (Fox *et al*., 2003).

The type-2 pattern of nesting is the more typical pattern amongst rollers and usually some participation by both sexes (Halffter 1989) are involved. Several patterns of nesting, brood ball shape and burial are reported in the *Sisyphus* species (Paschalidis, 1974). Our results show that in *Sisyphus longipes,* shorter developmental period and female longevity contribute to the abundance of the species and it also helps to accelerate the population growth of the species in the moist belts of south India.

5.5. *Tibiodrepanus setosus* (Wiedemann, 1823).

The nesting biology of *Tibiodrepanus setosus* showed a Type 4 nesting pattern. *T. setosus* exploits comparatively drier dung for constructing brood masses with each brood mass containing one egg. Among the various life cycle stages of *T. setosus* pupal phase was the crucial phase adversely affecting the life cycle of *T. setosus.* Sex ratio biased towards females is seen in *T. setosus***.** Also, as per LMC (Local mate competition), a female-biased sex ratio is favored, if mating competition takes place between male offsprings. Whereas an equal sex ratio is expected under random mating (Fisher *et al*., 1930). Hence the female-biased sex ratio noticed in *T.setosus* indicates that the females have relatively high fecundity, with the females laying more eggs which are usually spread out in dung pats through their lifespan and multivoltine species. Relatively small size and high fecundity of inferior competitors help such species to avoid exclusion from the local species pool, even at high levels of competition (Hanski and Cambefort, 1991a). The present analysis of the life cycle indicates that *T. setosus* with traits that are common in an *r*-selective species

(MacArthur and Wilson 1967) such as high fecundity, small body size, low egg mortality, shorter larval duration, early onset of maturity, shorter developmental period, short generation time (multivoltine) together with female-biased sex ratio, contributed to the higher abundance of *T. setosus* in the region.

Chapter 6

CONCLUSION

CONCLUSION

The current study provides information on the life biology and nesting behaviour of the five prominent dung beetle species, ***Onthophagus cervus, O. fasciatus, Tiniocellus spinipes, Sisyphus longipes*** and ***Tibiodrepanus setosus*** in the agribelts of the Malabar Coast region.

1. *Onthophagus cervus*

Shorter larval duration, early onset of maturity, shorter developmental period, female-biased sex ratio, and longer duration of females (favouring high egg production) contribute to the higher abundance of tunneler species, *Onthophagus cervus,* in the Malabar Coast region. Type 1 nesting behaviour with vertical and horizontal tunnels extending to the deep soil was recorded.

2. *Onthophagus fasciatus*

Shorter larval duration, longer duration of females and female-biased sex ratio contribute to their abundance. Type 1 nesting behaviour with the vertical and horizontal tunnels reaching deep soil layer was recorded.

3. *Tiniocellus spinipes.*

Shorter larval and pupal developmental period, longer duration of females, female-biased sex ratio and Type 1 nesting behaviour with shallow tunnels in the top soil layer that enabled easier and fast tunnelling process lead to their abundance in the region.

4. *Sisyphus longipes.*

Short larval and pupal developmental periods and more extended female longevity contribute to the higher abundance of the roller species. *Sisyphus longipes* rolled the dung ball away from the dung pat and Type 2 nesting pattern with dung ball burial in the top soil layer recorded.

5. *Tibiodrepanus setosus*.

The relatively small size, female-biased sex ratio, shorter larval-pupal duration, and early maturity onset lead to the high abundance of *Tibiodrepanus setosus.* Type 4 nesting behaviour is observed with the whole development from egg to adults occurring within the dung pat itself recorded. Beetles used moderately wet dung for building brood mass construction and laid one egg per brood mass.

Chapter 7

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