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Biology of *Blepharida*-group flea beetles with first notes on natural history of *Podontia congregata* Baly, 1865 an endemic flea beetle from southern India (Coleoptera, Chrysomelidae, Galerucinae, Alticini)*

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Abstract

The biology, host plants, and pest status of *Podontia* Dalman, 1824 species are reviewed. Natural history of *Podontia congregata* Baly, 1865 a flea beetle endemic to southern India, is reported for the first time. It is distributed from the Western Ghats Mountains westward to the plains. Clusiaceae is reported as a new host plant family for *Blepharida*-group species, with *Garcinia gummi-gutta* (L.) N. Robson (Clusiaceae) as the host plant for *P. congregata*. Pentatomid bugs attack the larvae but not eggs, pupae, or adults. A new egg parasitoid species, *Ooencyrtus keralensis* Hayat and Prathapan, 2010 (Hymenoptera: Encyrtidae), was discovered. Aspects of *P. congregata* host selection, life cycle, and larval fecal defenses are consistent with its inclusion in the *Blepharida*-genus group.

Keywords

Leaf beetles, *Podontia congregata*, Pest, *Garcinia*, Clusiaceae, India

Introduction

The *Blepharida*-group of genera consists of robust and brightly colored flea beetles (Figs 1–10). Furth (1998) lists 16 genera in the *Blepharida*-group, which are united

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by characters of the eye shape, metatibial, aedeagal, and spermathecal morphology. Medvedev (1999) added three new genera, *Asiophrida* Medvedev, *Blepharella* Medvedev, and *Furthia* Medvedev from the Oriental region, making 19 genera in total. The *Blepharida*-group has a primarily Old World tropical distribution, with the exception of *Euplectroscelis* Crotch being endemic to Mexico (Furth 1992; Furth and Lee 2000). We follow Furth and Lee (2000: 27, Table 1) on the composition of the *Blepharida*-group genera as this is the most recent discussion of these genera, building from his morphological and classificatory discussions (Furth 1992, 1998) and pointing out the limitations of catalogue phylogenies. A modern phylogenetic analysis of relationships among these taxa and with other flea beetles is badly needed.

Species in the *Blepharida*-group are documented most commonly on host plants in the Anacardiaceae, Bignoniaceae, Burseraceae, and Sapindaceae (Table 1). However, there are several single species records from Apocynaceae, Caesalpiniaceae, Elaeocarpaceae, Fabaceae, Lythraceae, Meliaceae, Moraceae, and Verbenaceae, which raise interesting questions about diet evolution as well as the distinct possibility of questionable host reports. Additionally, Furth (1998) indicated how the lack of reference sources in Jolivet and Hawkeswood (1995) could mislead about true chrysomelid-plant associations. Host chemistry may likely have played an important role in the co-evolution of *Blepharida* Chevrolat (73 species; Figs 2–3) with their hosts in *Bursera* Jacq. ex L. (Burseraceae) (Becerra 1997, 2003, 2004a, b, 2007; Becerra and Venable 1999; Becerra et al. 2001). Host acquired secondary metabolites also appear to contribute to the effectiveness of an unusual larval fecal defense in *Blepharida* (Morton 1997; Morton and Vencl 1998; Vencl and Morton 1998, 1999).

Furth and Lee (2000) provided a morphological synthesis of the *Blepharida*-group, and reported that morphological data for immature stages were available for only nine species in *Blepharida* Chevrolat, *Diamphidia* Gerstaecker, *Euplectroscelis* Crotch, *Ophrida* Chapuis, and *Podontia* Dalman. Within this broader group, Takizawa (2005) recognized a *Podontia*-genus group comprised of *Blepharida* (Figs 2–3), *Ophrida* (Fig. 6), and *Podontia* (Figs 7–9), based on larval setal patterns and deposition of eggs in rows. Chaboo et al. (2007) added data for three more species in the southern African genera *Diamphidia* and *Polyclada* Chevrolat and Lee and Cheng (2007) added data for two Taiwanese species—*Ophrida spectabilis* (Baly) and *Podontia lutea* (Olivier) (Figs 6 and 8 respectively).

In *Blepharida*, *Diamphidia*, *Podontia*, and *Polyclada*, larvae retain their feces directly on the dorsum. This coating acts as a deterrent to attacking enemies such as ants (Vencl and Morton 1998, 1999). The fecal coat may also serve to moderate body temperature or to reduce water loss but the functions have not been tested. Fecal retention and the dorsally-positioned anus represent complex characters supporting the monophyly of the *Blepharida*-group (Paterson 1943).

The genus *Podontia* Dalman 1824 (Figs 7–9) comprises 14 Asian species ranging from Indonesia to Indo-China, with one species occurring in northern Australia (Baly 1865; Heikertinger and Csiki 1940). *Podontia* adults are distinguished from other *Blepharida*-group species by bifurcate prosternum, saddle-shaped mesosternum and strongly inwardly curved bifid tarsal claws (Medvedev 1999; Becerra 2004a). *Podontia* larvae vary in the presence and shapes of meso and metathoracic tubercles (Kimoto and

Table 1. Host plants of species of the *Blepharida*-group. Known questionable records are indicated by "(?)". Plant names follow the International Plant Names Index (2011).

Species	Host plant	Reference
***Asiophrida* Medvedev**		
Asiophrida marmorea (Wiedemann)	Anacardiaceae: *Spondias* L. sp.	Furth and Lee 2000
	Apocynaceae: *Holarrhena pubescens* Wall. (=*antidysenterica* (L.) Wall)	Stebbing 1914; Maulik 1926; Takizawa 1978; Medvedev 1999
	Burseraceae: *Garuga pinnata* Roxb.	Mathew and Mohandas 1989
	Garuga Roxb. sp.	Medvedev 1999
Asiophrida (Trichophrida) hirsuta (Wiedemann)	Burseraceae: *Boswellia serrata* Roxb. ex Colebr.	Stebbing 1914; Maulik 1926; Scherer 1969; Medvedev 1999
Asiophrida scaphoides (Baly)	Anacardiaceae: *Rhus* L.	Medvedev 1999
	Burseraceae: *Canarium* L.	Medvedev 1999
***Blepharida* Chevrolat**	Anacardiaceae	Furth 1999; Furth and Lee 2000
	Anacardiaceae: *Cotinus* Mill.	Jolivet and Hawkeswood 1995
	Rhus L. sp.	Jolivet and Hawkeswood 1995; Scherer 1973; Furth 1998
	Schinus L. sp.	Jolivet and Hawkeswood 1995
	Burseraceae	Furth 1999; Furth and Lee 2000; Newbold et al. 2007
	Bursera Jacq. ex L.	Becerra and Venable 1999; Becerra et al. 2009; Noge and Becerra 2009; Becerra 1994, 1997, 2003, 2007; Jolivet and Hawkeswood 1995; Becerra and Venable 1999; Jolivet and Verma 2002; Becerra et al. 2009
	Bursera schlechtendalii Engl.	Becerra 1994; Becerra and Venable 1990; Becerra et al. 2001
	Burseraceae: *Commiphora* Jacq. sp.	Becerra 2003
	Sapindaceae: *Allophylus* L. sp.	Jolivet and Hawkeswood 1995
	Matayba Aubl.	Jolivet and Hawkeswood 1995
Blepharida alternata Jacoby	*Bursera arborea* L. Riley	Furth 1998; Becerra 2007
	Bursera attenuata L. Riley	Furth 1998; Evans et al. 2000; Becerra et al. 2001, Becerra 2004a, b; 2007
	Bursera bicolor Engl.	Becerra 2004a, b, 2007
	Bursera chemapodicta Rzed. & E. Ortiz	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2004a, b, 2007
	Bursera citronella McVaugh & Rzed.	Becerra 2007
	Bursera cuneata Engl.	Becerra 2004a, b, 2007
	Bursera excelsa Engl.	Becerra 2004a, b, 2007
	Bursera fragilis S. Watson	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2004a, b, 2007

Species	Host plant	Reference
	Bursera heteresthes Bullock	Becerra 2007
	Bursera instabilis McVaugh & Rzed.	Becerra 1997, 2004a, b, 2007; Furth 1998; Evans et al. 2000; Becerra et al. 2001
	Bursera palmeri S. Watson	Furth 1998; Becerra 2004a, b, 2007
	Bursera submoniliformis Engl.	Furth 1998; Becerra 2004a, b, 2007
Blepharida atripennis Horn	*Bursera epinnata* (Rose) Engl.	Furth 1998; Lee 1999; Furth and Lee 2000
	Bursera odorata T.S. Brandeg	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2004a, b, 2007
	Bursera ruticola Pérez-Navarro	Becerra 2004a, b, 2007
Blepharida balyi Bryant	*Bursera copallifera* (Sessé & Moc. ex DC.) Bullock	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2004a, b, 2007
	Bursera bipinnata (DC.) Engl.	Furth 1998; Becerra and Venable 1999; Becerra 2004a, b, 2007
	Bursera discolor Rzed.	Furth 1998; Becerra 2004a, b, 2007; Becerra and Venable 1999
	Bursera diversifolia Rose	Furth 1998; Becerra 2004a, b, 2007
	Bursera Jacq. ex L. sp.	Furth 1998
Blepharida bryanti Furth	*Bursera excelsa* (Kunth) Engl.	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2004a, 2007
Blepharida condrasi (Weise)	*Rhus tripartita* (Ucria) Grande	Furth and Young 1988
Blepharida conspersa (Horn)	*Bursera epinnata* (Rose) Engl.	Furth 1998; Becerra 2004a, b, 2007
	Bursera filicifolia T. S. Brandeg.	Furth 1998; Becerra 2004a, b, 2007
	Bursera hindsiana Engl. in DC.	Becerra 2004a b, 2007
Blepharida flavocostata Jacoby	*Bursera aspleniifolia* T. S. Brandeg.	Furth 1998; Evans et al. 2000; Becerra and Venable 1999; Becerra et al. 2001; Becerra 2003, 2004a, b, 2007
	Bursera bicolor Engl.	Becerra 2003
	Bursera biflora (Rose) Standl.	Furth 1998; Becerra and Venable 1999; Evans et al. 2000; Becerra et al. 2001; Becerra 2003, 2004a, b, 2007
	Bursera bipinnata (DC.) Engl.	Becerra 2004a, b, 2007
	Bursera bonetii Rzed.	Furth 1998; Becerra and Venable 1999; Becerra 2003, 2004a, b, 2007
	Bursera copallifera (DC.) Bullock	Furth 1998; Evans et al. 2000; Becerra et al. 2001
	Bursera hintonii Bullock	Furth 1998; Becerra and Venable 1999; Evans et al. 2000; Becerra et al. 2001; Becerra 2003, 2004a, b, 2007
	Bursera sarukhanii Guevera & Rzed.	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2003, 2004a, b, 2007
	Bursera schlechtendalii Engl.	Furth 1998
	Bursera submoniliformis Engl.	Furth 1998; Becerra and Venable 1999; Becerra 2003, 2004a, b, 2007
	Bursera velutina Bullock	Furth 1998; Becerra and Venable 1999; Evans et al. 2000; Becerra et al. 2001; Becerra 2003, 2004a, b, 2007
	Bursera xochipalensis Rzed.	Becerra 2004a, b

Species	Host plant	Reference
Blepharida florhi Jacoby	*Bursera bipinnata* (DC.) Engl.	Furth 1998; Becerra and Venable 1999; Becerra 2004a, b, 2007
Blepharida gabrielae Furth	*Bursera aptera* Ramirez	Evans et al. 2000; Becerra et al. 2001
	Bursera discolor Rzed.	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2004a, b, 2007
	Bursera fagaroides Engl.	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2004a, b, 2007
	Bursera paradoxa Guevera & Rzed.	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2004a, b, 2007
	Bursera trifoliolata Bullock	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2004a, b, 2007
	Bursera Jacq. ex L. sp.	Furth 1998
Blepharida hinchahuevosi Furth	Anacardiaceae: *Pseudosmodingium perniciosum* (Kunth) Engl.	Furth 1998; Becerra 2004a, b
Blepharida humeralis Furth	*Bursera submoniliformis* Engl.	Furth 1998; Becerra and Venable 1999; Becerra 2004a, b, 2007
Blepharida irrorata Chevrolat	Sapindaceae: *Allophylus cominia* Sw.	Brunner et al. 1975; Furth 1998; Takizawa 2003; Becerra 2004a
	Allophylus occidentalis Radlk.	Brunner et al.1975; Furth 1998; Takizawa 2003; Becerra 2004a
	Matayba Aubl.	Wolcott 1936; Furth 1998; Takizawa 2003; Becerra 2004a
	Bursera simaruba (L.) Sarg.	Furth 1998; Takizawa 2003; Becerra 2004a
Blepharida johngi Furth	*Bursera glabrifolia* (Kunth) Engl.	Furth 1998; Becerra 2004a, 2007
	Bursera Jacq. ex L. sp.	Furth 1998
Blepharida judithae Furth	*Bursera ariensis* (Kunth) McVaugh & Rzed.	Furth 1998; Becerra and Venable 1999; Becerra 2004a, b, 2007
Blepharida lineata Furth	*Bursera crenata* P. G. Wilson	Furth 1998; Evans et al. 2000; Becerra and Venable 1999; Becerra et al. 2001; Becerra 2003, 2004a b, 2007
	Bursera denticulata McVaugh & Rzed.	Becerra and Venable 1999; Evans et al. 2000; Becerra et al. 2001; Becerra 2003, 2004a b, 2007
	Bursera kerberi Engl.	Evans et al. 2000; Becerra et al. 2001; Becerra 2004a, b, 2007
	Bursera trimera Bullock	Furth 1998; Evans et al. 2000; Becerra and Venable 1999; Becerra et al. 2001; Becerra 2003, 2004a, b, 2007
Blepharida maculicollis Furth	*Bursera submoniliformis* Engl.	Furth 1998
	Bursera xochipalensis Rzed.	Becerra 2004a
Blepharida marginalis Weise	*Rhus natalensis* Bernh. ex Krauss, *Rhus tripartita* DC., *Rhus vulgaris* Meikle	Furth and Young 1988
Blepharida melanoptera (Fall)	*Bursera infernidialis* Guevera & Rzed.	Furth 1998; Becerra and Venable 1999; Becerra 2004a, b, 2007
	Bursera laxiflora S. Watson	Furth 1998; Becerra 2004a, b, 2007

Species	Host plant	Reference
Blepharida multimaculata Jacoby	*Bursera aptera* Ramirez	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2007
	Bursera discolor Rzed.	Furth 1998; Evans et al. 2000; Becerra and Venable 1999; Becerra et al. 2001
	Bursera fagaroides (Kunth) Engl.	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2004a, b, 2007
	Bursera fagaroides var. *purpusii* (Brandegee) McVaugh & Rzed.	Becerra and Venable 1999
	Bursera paradoxa Guevera & Rzed.	Furth 1998; Becerra and Venable 1999
	Bursera trifoliolata Bullock	Furth 1998; Becerra and Venable 1999
	Bursera Jacq. ex L. sp.	Furth 1998
Blepharida natalensis Baly	*Rhus lancea* L.f.	Becerra 2004b
	Rhus zeyheri Sond.	Scherer 1973
Blepharida nigromaculata Jacoby	*Rhus* L. sp.	Becerra 2004b
Blepharida nigrotesselata Baly	*Rhus* L. sp.	Paterson 1943
Blepharida pallida Blake	*Bursera arborea* (Rose) Riley	Becerra 2007
	Bursera aloexylon (Scheide ex Schlecht.) Engl.	Furth 1998; Becerra 2007
	Bursera bipinnata (DC.) Engl.	Becerra 2007
	Bursera coyucensis Bullock	Furth 1998; Becerra 2004a, b, 2007
	Bursera cuneata (Schlecht.) Engl.	Furth 1998
	Bursera excelsa (Kunth) Engl.	Becerra 2007
	Bursera glabrifolia Engl.	Becerra 2007
	Bursera grandifolia (Schlecht.) Engl.	Furth 1998; Evans et al. 2000; Becerra and Venable 1999; Becerra et al.2001; Becerra 2004a, b, 2007
	Bursera heteresthes Bullock	Furth 1998; Becerra 1997, 2007
	Bursera instabilis McVaugh & Rzed.	Becerra 2007
	Bursera kerberi Engl.	Becerra 2007
	Bursera penicillata (DC.) Engl.	Becerra 2007
	Bursera sarcopoda P. G. Wilson	Becerra 2007
	Rhus L. spp.	Scherer 1973
Blepharida parallela Furth	*Bursera discolor* Rzedowski	Furth 1998; Becerra 2004a, b, 2007
	Bursera schlechtendalii Engl.	Furth 1998; Becerra and Venable 1999; Becerra 2003, 2004a, b, 2007
Blepharida rhois (Forster)	Anacardiaceae: *Cotinus obovatus* Raf. Sullivan	Furth 1998; Becerra 2004a, b
	Rhus L.	Peterson 1953; Takizawa 1978; Furth 1998, 1999; Becerra 2004b
	Rhus aromatica Aiton	Mignot 1971; Scherer 1973; Furth 1998
	Rhus copallina Linnaeus	Mignot 1971; Frost 1973; Furth 1998; Lee 1999; Furth and Lee 2000
	Rhus cotinus Nutt.	Riley 1874; Furth 1998

Species	Host plant	Reference
	Rhus microphylla Engl.	Furth 1998
	Rhus trilobata Nutt.	Furth 1998
	Rhus typhina Linnaeus	Mignot 1971; Scherer 1973; Frost 1973; Furth 1998
	Rhus vernix Linnaeus	Mignot 1971; Frost 1973
	Rhus L. spp.	Takizawa 1978; Becerra 2004a, b
	Schinus terebinthifolius Raddi	Frost 1972, 1973; Takizawa 1978; Furth 1998; Becerra 2004a, b
	Schinus L. sp.	Mignot 1971; Frost 1972, 1973
	Apocynaceae: *Catharanthus (=Vinca) roseus* (L.) G. Don	Frost 1972
	Pinaceae: *Pinus palustris* Mill.	Mignot 1971; Frost 1972
	Rosaceae: strawberry	Mignot 1971
Blepharida sacra (Weise)	*Rhus natalensis* Bernh. ex Krauss	Furth and Young 1988
	Rhus tenuinervis Engl. & Gilg. (non-host)	Furth and Young 1988
	Rhus tripartita DC.	Furth 1982, 1985, 2004; Furth and Young 1988; Lee 1999; Furth and Lee 2000
	Rhus vulgaris Meikle	Furth and Young 1988
Blepharida schlechtendalii Furth	*Bursera aptera* Ramirez	Furth 1998; Becerra 2004a, b, 2007
	Bursera heteresthes Bullock	Furth 1998
	Bursera schlechtendalii Engl.	Furth 1998; Evans et al. 2000; Becerra and Venable 1990, 1999; Becerra et al. 2001; Becerra 2003, 2004a, b, 2007
Blepharida singularis Jacoby	*Bursera* Jacq. ex L.sp.	Furth 1998; Becerra 2004a
Blepharida sonorstriata Furth	*Bursera laxiflora* S. Watson	Furth 1998; Becerra 2004a, b, 2007
Blepharida sparsa (Clark)	*Bursera kerberi* Engl.	Becerra 1997; 2004a, b; Furth 1998; Evans et al. 2000; Becerra and Venable 1999; Becerra et al. 2001; Becerra 2003, 2007
	Bursera submoniliformis Engl.	Furth 1998; Becerra 2004a, b, 2007
	Bursera Jacq. ex L.sp.	Furth 1998
Blepharida unami Furth	*Bursera fagaroides* (H. B. K.) Engl.	Furth 1998; Becerra 2004a
	Bursera Jacq. ex L. sp.	Furth 1998
Blepharida variegatus Furth	*Bursera submoniliformis* Engl.	Furth 1998
Blepharida verdea Furth	*Bursera lancifolia* (Schlecht.) Engl.	Furth 1998; Becerra 2003, 2004a, b, 2007
	Bursera morelensis Ramirez	Furth 1998; Becerra and Venable 1999; Evans et al. 2000; Becerra et al. 2001; Becerra 2003, 2004a, b, 2007
	Bursera rzedowskii C. A.Toledo	Furth 1998; Becerra 2003, 2004a, b, 2007
Blepharida vittata Baly	*Rhus* L. sp.	Becerra 2004b

Species	Host plant	Reference
Blepharida xochipala Furth	*Bursera mirandae* C.A. Toledo	Furth 1998; Becerra 2004a, b, 2007
	Bursera Jacq. ex L.sp.	Furth 1998
Blepharida sp.	*Bursera cuneata* (Schlecht.) Engl.	Evans et al. 2000; Becerra et al. 2001
Blepharida sp.	*Bursera schlechtendalii* Engl.	Becerra and Venable 1990; Becerra 1994
Blepharida sp.	*Pseudoosmodingium perniciosum* (Kunth) Engl.	Furth 1999
Blepharida sp.1	*Bursera glabrifolia* Engl.	Becerra 2004b, 2007
Blepharia sp. 2	*Bursera chemapodicta* Rzed. & Ortiz	Becerra 2004b, 2007
Blepharida sp. 3	*Bursera vejar-vazquezii* Miranda	Becerra 2004b, 2007
Blepharida sp. 4	*Bursera biflora* (Rose) Standl.	Becerra 2004b, 2007
	Bursera longipes (Rose) Standl.	Becerrra 2004b, 2007
Blepharida sp. 5	*Bursera xochipalensis* Rzed.	Becerra 2004b, 2007
Blepharida sp. 1a	*Rhus* L. sp., *Commiphora* Jacq. sp.	Becerra 2004b
Blepharida sp. 2a	Bignoniaceae: *Rhizogum ebovatum?*	Becerra 2004b
Blepharida sp. 3a	*Commiphora mollis* (Oliv.) Engl.	Becerra 2004b
Blepharida sp. 6	*Bursera ribana* Rzed. & Calderón	Becerra 2007
Blepharida sp. 7	*Bursea suntui* C.A. Toledo	Becerra 2007
***Crimissa* Stål**	Anacardiaceae (?)	Furth and Lee 2000
	Anacardiaceae: *Anacardium* L.; *Mangifera* L.	Jolivet and Hawkeswood 1995
Crimissa cruralis Stål	*Anacardium occidentale* L.	Bastos 1975; Bastos 1977b; Bastos and Vieira 1977a, b; Santos and Vieira 1977; Sales and Pereira 1978; Bastos et al. 1979; Sales et al. 1981; Tandon and Verghese 1985; Marques et al. 1992
Crimissa sp.	*Anacardium occidentale* L.	Santos 1972
	Bignoniaceae	Jolivet and Hawkeswood 1995
***Diamphidia* Gerstaecker**	Burseraceae	Furth and Lee 2000
	Commiphora Jacq. sp.	Jolivet and Hawkeswood 1995; Furth 1998, 1999; Becerra 2003
Diamphidia femoralis Gerstaecker	*Commiphora* Jacq. sp.	Becerra 2004b; Chaboo et al. 2007
Diamphidia nigroornata Stål	*Commiphora* Jacq. sp.	Chaboo et al. 2007
	Commiphora africana (A. Rich.) Engl.	Becerra 2004b
	Commiphora angolensis Engl.	Neuwinger and Scherer 1976; Neuwinger 1996
	Commiphora glandulosa Schinz	Becerra 2004b
Diamphidia simplex Péringuey	*Commiphora africana* (A. Rich.) Engl.	Roodt 1993; Nonaka 1996
Diamphidia vittatipennis Baly	*Commiphora africana* (A. Rich.) Engl.	Neuwinger and Scherer 1976; Neuwinger 1996; Becerra 2004b
	Commiphora tenuipetiolata Engl.	Becerra 2004b

Species	Host plant	Reference
Diamphidia sp.	*Sclerocarya caffra* Sond.	Furth and Lee 2000
***Elithia* Chapuis**	Anacardiaceae	Furth and Lee 2000
	Burseraceae	Furth and Lee 2000
	Bursera Jacq. ex L. sp.	Furth 1998
	Bursera microphylla A. Gray	Becerra 2004a
Euplectroscelis xanti Crotch	*Bursera microphylla* A. Gray	Becerra 2004b, 2007
	Bursera odorata Brandegee	Furth and Lee 2000
***Notozona* Chevrolat**	Anacardiaceae (?)	Furth and Lee 2000
	Rhus L. sp. (?)	Furth 1998
	Burseraceae	Furth and Lee 2000
	Bursera Jacq. ex. L. sp.	Becerra 2004a
Notozona histrionica Chevrolat	*Bursera simaruba* (L.) Sarg.	Becerra 2004b, 2007
Notozona nicaraguensis Jaq.	*Bursera simaruba* (L.) Sarg.	Flowers and Janzen 1997
***Ophrida* Chapuis**	Anacardiaceae	Furth 1998; Furth and Lee 2000
	Apocynaceae	Jolivet and Hawkeswood 1995
	Burseraceae	Furth 1998; Furth and Lee 2000
	Boswellia Roxb. ex. Colebr., *Canarium* L., *Garuga* Roxb.	Jolivet and Hawkeswood 1995
Ophrida hirsuta Stebbing	*Boswellia serrata* Roxb.	Stebbing 1914; Beeson 1919, 1941; Takizawa 1978
Ophrida nigrovaria (MacLeay)	*Canarium australianum* F. Muell.	Furth 1998
Ophrida scaphoides (Baly)	Anacardiaceae: *Rhus succedanea* L.	Kimoto and Takizawa 1997
	Burseraceae: *Canarium* L.	Medvedev and Dap 1982
Ophrida spectabilis (Baly)	Anacardiaceae: *Rhus chinensis* Mill.; Gall nut, Sumac	Yang et al.1997; Bilun 1998a; Wang et al. 1998; Wu et al. 1999; Lee and Cheng 2007
	Rhus punjabensis J.L. Stewart	Wang et al. 1998
	Rhus trichocarpa Miq.	Zhang and Yang 2008
	Rhus verniciflua Stokes	Zhang and Yang 2008
Oprhida xanthospilota (Baly)	*Continus coggygria* Scop.	Zhao 1985; Furth 1998; Zhang and Yang 2008
***Podontia* Dalman**	Anacardiaceae	Furth 1998; Furth and Lee 2000
	Anacardiaceae: *Mangifera* L., *Rhus* L., *Spondias* L., *Toxicodendron* Mill.	Jolivet and Hawkeswood 1995
	Rhus L.	Becerra 2003
	Burseraceae	Furth 1998; Furth and Lee 2000
	Burseraceae: Canarium L.	Jolivet and Hawkeswood 1995
	Caesalpiniaceae (?)	Jolivet and Hawkeswood 1995
	Elaeocarpaceae: *Elaeocarpus* L. sp.	Jolivet and Hawkeswood 1995
	Moraceae: *Ficus* L. sp. (?)	Jolivet and Hawkeswood 1995
	Theaceae: *Thea* L. sp. (?)	Jolivet and Hawkeswood 1995

Species	Host plant	Reference
Podontia affinis (Gröndal)	Anacardiaceae: *Spondias* L. sp.	Kalshoven 1951
	Spondias dulcis Forster	Mohamedsaid 1989, 2004; Medvedev 1999
Podontia congregata Baly	Clusiaceae: *Garcinia gummi-gutta* (L.) N. Robson	**New Family Record, this paper**
Podontia dalmani Baly	Meliaceae: *Melia* L. sp.	Medvedev 1999
	Caesalpiniaceae	Medvedev and Dap 1982; Medvedev 1999
Podontia lutea (Olivier)	*Canarium* L. sp.	Medvedev and Dap 1982; Medvedev 1999
	Anacardiaceae: *Rhus* L. sp.	Hsu 1934a, b; Furth 1998; Medvedev 1999
	Rhus succedanea L.	Chujo 1935; Takizawa 1978; Kimoto and Takizawa 1997
	Toxicodendron Mill. sp.	Medvedev and Dap 1982; Medvedev 1999
Podontia quatuor-decimpunctata (L.)	Anacardiaceae: *Mangifera* L. sp.	Furth 1998
	Spondias L. sp.	Kalshoven 1951; Takizawa 1978; Medvedev 1999
	Spondias cyatherea Sonn.	Yunus and Hua 1980; Daulmerie 1994; Furth 1998
	Spondias dulcis Forster	Corbett and Yusope 1921; Maulik 1926; Bose 1953; Scherer 1969; Pramanik and Basu 1973; Mohamedsaid 1989, 2004; Singh and Misra 1989; Baksha 1997; Medvedev 1999
	Spondias pinnata (L.f.) Kurz (= *Spondias mangifera* Willd.)	Barlow 1900; Maxwell-Lefroy 1909; Stebbing 1914; Beeson 1919, 1941; Bose 1953; Scherer 1969; Pramanik and Basu 1973; Husain and Ahmad 1977; Sardar and Mondal 1983; Singh and Misra 1989; Howlader 1993; Baksha 1997; Deka and Kalita 1999, 2002a - d, 2003, 2004; Hossain et al. 2004
	Burseraceae: *Canarium* L.	Yunus and Hua 1980; Furth 1998
	Moraceae: *Ficus elastica* Roxb. ex Hornem.	Stebbing 1914; Beeson 1919, 1941; Scherer 1969; Baksha 1997; Singh and Misra 1989
	Ficus L.	Medvedev 1999
	"fruit trees" (native & imported)	Fletcher 1920, 1921; Susainathan 1923
	Lythraceae: *Duabanga grandiflora* Walp	Singh and Misra 1989; Baksha 1997
	Lythraceae: *Duabanga sonneratioides* Buch.	Ahmad 1939; Beeson 1941; Bose 1953
	Lythraceae: *Sonneratia apetala* Buch.-Ham.	http://banglapedia.search.com.bd/HT/B_0385.html
Podontia soriculata (Swartz)	*Thea boheae* (?)	Swartz 1808; Gressitt and Kimoto 1963
***Polyclada* Chevrolat**	Anacardiaceae	Roodt 1993; Jolivet and Hawkeswood 1995; Furth 1998; Furth and Lee 2000
	Pseudospondias Engl.	Jolivet and Hawkeswood 1995
	Rhus L.	Shaw et al. 1963
	Sclerocarya caffra Sond.	Jolivet and Hawkeswood 1995; Shaw et al. 1963

Species	Host plant	Reference
	Sclerocarya birrea (A.Richt.) Hochst.	Roodt 1993; Furth 1998; Chaboo et al. 2007
	Burseraceae: *Commiphora* Jacq.	Furth 1999
	Fabaceae: *Dalbergia* L. sp. (?)	Jolivet and Hawkeswood 1995
	Verbenaceae: *Clerodendrum* L. sp. (?)	Jolivet and Hawkeswood 1995
Polyclada flexuosa Baly	*Sclerocarya birrea* sub. sp. *caffra* Sonder	Shaw et al. 1963; Neuwinger and Scherer 1976; Neuwinger 1996
***Procalus* Clark**	Anacardiaceae	Jerez 1995; Furth and Lee 2000; Jolivet and Verma 2002
	Lithraea Miers ex Hook. & Arn., *Schinus* L.	Furth 1998
	Lithraea caustica (Molina) Hook. & Arn.	Jerez 1995, 1999; Jolivet and Hawkeswood 1995
	Schinus latifolius Engl.	Jerez 1995, 1999; Jolivet and Hawkeswood 1995
	Schinus montanus Engl.	Jerez 1995, 1999; Jolivet and Hawkeswood 1995
	Schinus patagonicus (Phil.) I.M. Johnst.	Jerez 1995, 1999
	Schinus polygamus (Cav.) Cabrera	Jerez 1992, 1995, 1999; Jolivet and Hawkeswood 1995
	Schinus velutinus (Turcz.) I.M. Johnst.	Jerez 1995; 1999
Procalus lenzi (Harold)	*Lithraea caustica* (Molina) Hook. & Arn.	Grez 1988; Jerez 1992
	Schinus polygamus (Cav.) Cabrera	Jerez 1992
Procalus malaisei Bechyné	*Lithraea caustica* (Molina) Hook. & Arn.	Etchegarray and Fuentes 1980; Fuentes et al. 1987; Poiani 1989; Grez 1988; Jerez 1992
Procalus mutans (Blanchard)	*Lithraea caustica* (Molina) Hook. & Arn.	Jerez 1992
	Schinus montanus Engl.	Jerez 1992
Procalus reduplicatus Bechyné	*Lithraea caustica* (Molina) Hook. & Arn.	Jerez 1992
Procalus silvai Jerez	*Schinus patagonicus* (Phil.) I.M. Johnst.	Jerez 1995
Procalus viridis (Philippi & Philippi)	*Lithraea caustica* (Molina) Hook. & Arn.	Fuentes et al. 1987; Poiani 1989
	Schinus latifolius Engl.	Krauss 1962, 1963; Jerez 1985, 1988, 1992; Poiani 1989
	Schinus montanus Engl.	Jerez 1992
	Schinus polygamus (Cav.) Cabrera	Philippi and Philippi 1864; Jerez 1985, 1992; Poiani 1989

Takizawa 1997). Immature stages are known for only *P. affinis* (Gröndal) (Fig. 7; Takizawa 1978; Furth and Lee 2000), *P. dalmani* Baly (Furth and Lee 2000), and *P. lutea* (Olivier) (Fig. 8; Takizawa 1978; Jolivet and Hawkeswood 1995; Kimoto and Takizawa 1997; Lee 1999; Furth and Lee 2000). With adults at ~2 cm long, *P. lutea,* the golden leaf beetle, is reputedly the largest flea beetle in the world (Fig. 8; Furth 1999).

Here, we review the biology of *Podontia* and other *Blepharida*-group genera and provide the first natural history account of *Podontia congregata* Baly, 1865. An endemic to the southern Western Ghats and adjoining areas, *P. congregata* is the largest flea beetle in southern India, ranging from 11.5 to 14.7 mm in length. Our study is based on both field and laboratory observations.

Natural History of *Podontia* Dalman, 1824

The biology for most *Podontia* species is unknown; however, host data on *P. affinis*, *P. lutea,* and *P. quatuordecimpunctata* (Linnaeus) indicate that these species severely defoliate anacardiaceous trees. For example, *P. affinis* (kedongdong spring-beetle) ranges from Indonesia to China and is a pest in Indonesia, where its larvae attack the foliage of *Spondias dulcis* Forster (Anacardiaceae; =*S. cytherea* Sonn., ambarella or kedongdong tree; Daulmerie 1994; Morton 1987). Female *P. affinis* live about 3 months, lay loose groups of eggs on the undersides of leaves and coat them with some substance (Kalshoven 1951). The larvae are parasitised by an encyrtid wasp, *Ooencyrtus podontiae* (Gahan) (Table 2; Gahan 1922; Kalshoven 1951).

The golden leaf beetle, *P. lutea* is large sized (~2 cm, Fig. 8) and its attractive coloration promotes its use in cheap Lucite jewelry. The limited available data indicates biology like other *Blepharida*-group members (Hsu 1934a, b; Lee 1999; Furth and Lee 2000). This beetle is a pest of the anacardiaceous shrub, *Toxicodendron vernicifluum* (Stokes) F. Barkley (=*Rhus verniciflua* Stokes) which is the source of the lacquer used in Asian furniture manufacturing (Li and Wang 1984a, b). The coccinellid beetle, *Aiolocaria mirabilis* (Motschulsky), has been studied as a biocontrol agent (Li and Wang 1984a, b).

Podontia quatuordecimpunctata is the best-known *Podontia* species because both adults and larvae defoliate the tree *S. dulcis*. This tree, commonly known as the mak-ok, hog plum, or golden apple tree, is cultivated for its edible fruits in Indonesia, Malaysia, India, Thailand, and the Caribbean (Figs 11–15; Table 1 and references therein). Pramanik and Basu (1973) first described the *P. quatuordecimpunctata* life cycle (See also Singh and Misra 1989). Like *P. affinis*, this species' pest status has led to the use of a vernacular name, "kadondong beetle" (alternate spelling "kedongdong"; Corbett and Yusope 1921), which resembles that for *P. affinis* (Morton 1987). The colorful orange-pink adults are active from June to October, and form pairs that copulate multiple times (Fig. 12). [Additional images of live stages can be viewed at: http://greeneyesth.multiply.com/photos/album/33/Podontia_quatuordecimpunctata]. Females oviposit 20–60 eggs in clusters on the leaf surface; eggs are bright yellow, naked and are arranged in multiple

layers, usually two. Hatching occurs within 7–8 days and the yellow-brown larval instars feed gregariously and prefer younger leaves (Singh and Misra 1989). Barlow (1900) indicated that all five larval stages retain a fecal coat (Figs 13–14), possibly mimicing bird droppings (Barlow 1900; Stebbing 1914; Baksha 1997). The final instar descends the plant, enters the soil, and forms an earthen cell in which it pupates. The yellow-brown pupae last 14–29 days. Adults hibernate in soil or under leaves. Insect (e.g., Fig. 15), nematode, and fungal enemies are documented (Table 2; Singh and Misra 1989). Foliar sprays of cypermethrin (Baksha 1997), metathion (Sardar and Mondal 1983), and carbaryl (Singh and Misra 1989) have been recommended as effective controls.

Natural history of other *Blepharida*-group genera

Asiophrida Medvedev comprises 20 species in three subgenera (Medvedev 1999; Zhang and Yang, 2008; Mohammedsaid 2004). One of us (KDP) recently discovered populations of *Asiophrida marmorea* (Wiedemann) on one known host, *Garuga pinnata* Roxb. (Burseraceae; Table 1) at Vellanikkara, Kerala, southern India (Fig. 1). Larvae are naked, not retaining fecal coverings; field study is underway.

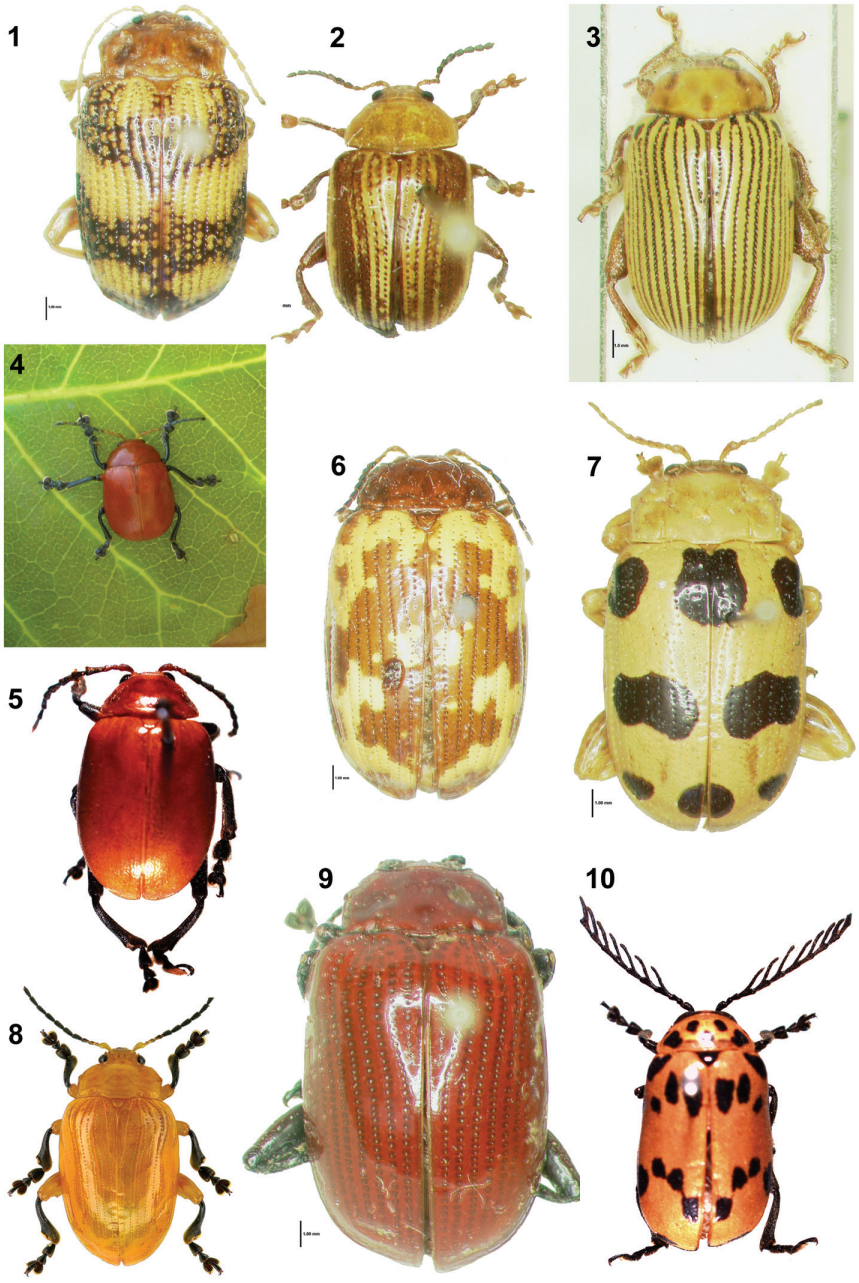
The biology of *Blepharida*, with 55 species, is currently the best known among *Blepharida*-group genera. Life cycle data have been published for *Blepharida rhois* (Forster) (as *B. dorothea* Mignot) (Frost 1972). *Blepharida evanida* (Baly) is reported as a source of arrow poison used by Kalahari San Bushmen (Lewin 1912, 1923). Furth (1982, 1985) summarized the biology of *B. sacra* (Weise), the sacred sumac flea beetle. Generally, *Blepharida* adults lay clusters of eggs on branches and cover them with fecal material. The slug-like larvae retain soft feces, or long fecal threads or pellets under drier conditions. The prepupal and pupal phases are underground in earthen cells and can last over 7 months. Eggs are parasitized by the eulophid wasp, *Tetrastichus* sp., while larvae are attacked by the fly parasitoid, *Meigenia mutabilis* Fallen (Diptera: Tachninidae; Furth 1985).

Crimissa cruralis Stål, the red cashew beetle, is a major pest of cultivated cashew in Brazil, *Anacardium occidentale* L. (Fig. 4; Pereira et al. 1975; Bastos 1975, 1977a; Bastos and Vieira 1977a, b; Bastos et al. 1979). Eggs are deposited on the trees, larvae eat from leaves, and adults rasp and leave characteristic lesions on leaf surfaces (Pereira et al. 1975). Pupation is underground in soil-based cocoons near the base of the trunk (Santos 1972; Bastos 1977b; Santos and Vieira 1977; Sales and Pereira 1978). Morphology of the immature stages is apparently undescribed. Various chemicals (Bastos 1975; Bastos and Veira 1977a, b; Bastos et al. 1979) and cashew gum exudates (Marques et al. 1992) have been tested to control this pest.

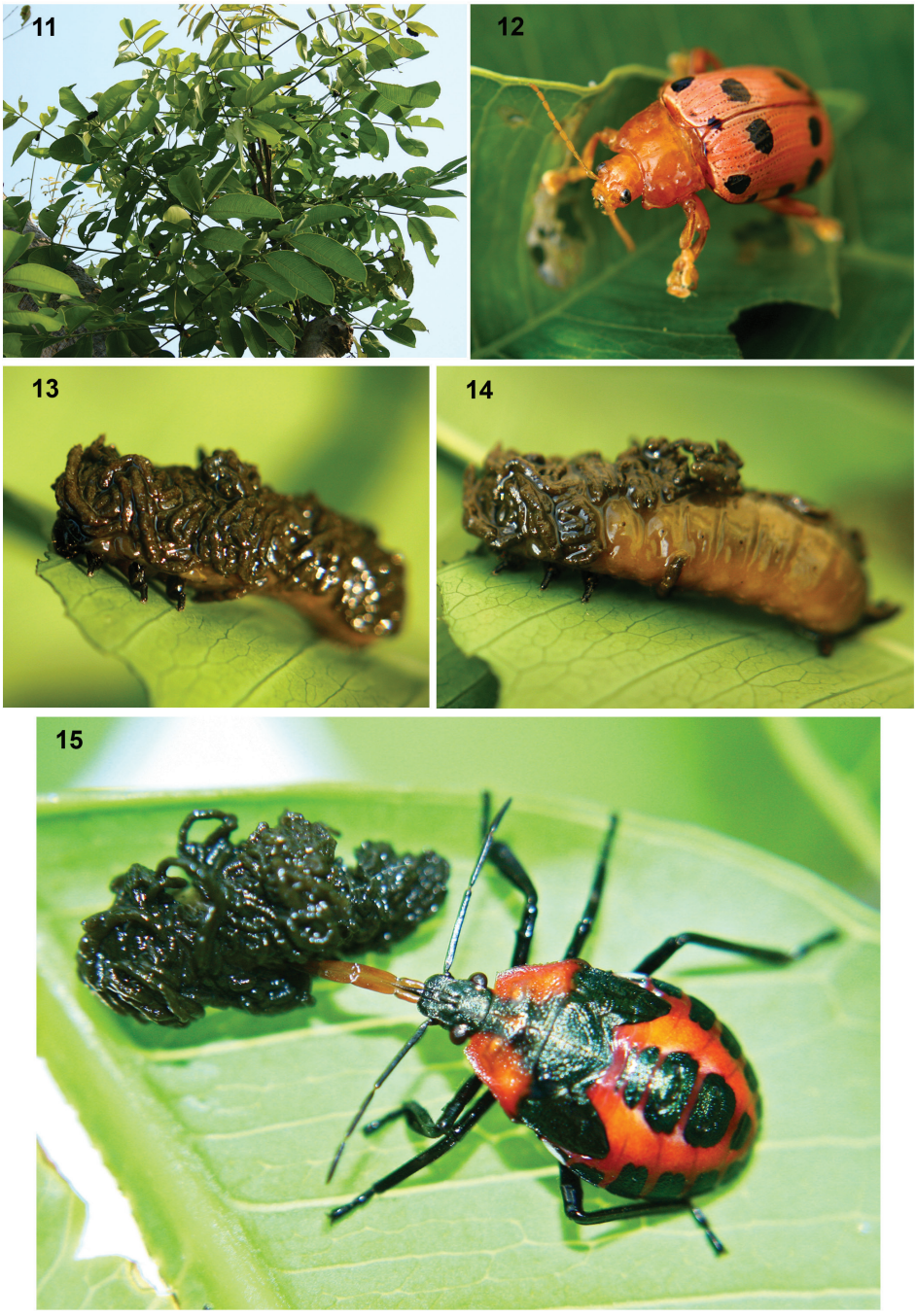
The nine known species of *Diamphidia* are distributed along the eastern coast from Ethiopia to South Africa and into Namibia (Fig. 5; Baly 1865; Heikertinger and Csiki 1940). Several species of *Diamphidia* are implicated as sources of the Kalahari San arrow poison (Lewin 1923; Roodt 1993; Neuwinger 1996). *Diamphidia* biology is similar to that of other *Blepharida*-group members with the exception that most spe-

Table 2. Documented enemies of *Podontia* species.

Species	Life stage	Enemy	Source
Podontia	Egg, larva	Coleoptera: Coccinellidae: *Aiolocaria* Crotch sp.	Li and Wang 1984a, b; Cox 1994, 1996
Podontia affinis (Gröndal)	Not indicated	Hymenoptera: Encyrtidae: *Ooencyrtus podontiae* (Gahan)	Gahan 1922
	Egg	Hymenoptera: Encyrtidae: *Ooencyrtus podontiae* (Gahan)	Kalshoven 1951
	Not indicated	Nematoda: Mermithidae: *Mermis* Dujardin sp.	Daulmerie 1994
	Not indicated	Sphaeriales: Hypocreaceae: *Cephalosporium* Corda sp.	Daulmerie 1994
Podontia congregata Baly	Egg	Hymenoptera: Encyrtidae: *Ooencyrtus keralensis* Hayat & Prathapan	Hayat and Prathapan 2010
	Larva	Heteroptera: Pentatomidae: *Eucanthecona parva* (Distant)	This paper (Figs 22, 23)
Podontia lutea (Olivier)	Egg, larva	Coleoptera: Coccinellidae: *Aiolocaria mirabilis* (Motschulsky)	Li and Wang 1984a, b
		Fungi: Laboulbeniales: *Laboulbenia podontiae* Thaxter	Thaxter 1914
Podontia quatuordecimpunctata (Linnaeus)	Adult	Arachnida: Lynx spider	Deka and Kalita 2003, 2004
	Adult	Aves: *Corvus splendens* Vieillot; *Acridotheres tristis* (L.)	Deka and Kalita 2003, 2004
	Egg, larva	Mantodea	Deka and Kalita 2003, 2004
	Egg	Hymenoptera: Braconidae: *Apanteles* Foerster, *Meteorus* Haliday; Trichogrammatidae: *Trichogramma* Westwood	Deka and Kalita 2003, 2004
	Egg	Hymenoptera: Chalcididae	Corbett and Yusope 1921
	Egg	Hymenoptera: Eulophidae: *Pediobius* Walker sp.	Baksha 1977
	Egg	Hymenoptera: Encyrtidae: *Ooencyrtus corbetti* Ferr.	Corbett and Miller 1933; Singh and Misra 1989; Baksha 1997
	Larva	Heteroptera: Pentatomidae	This paper (Fig. 15)
	Larva	Nematoda: Mermithidae: *Mermis* Dujardin sp.	Singh and Misra 1989; Daulmerie 1994; Baksha 1997
	Larva	Fungi: Laboulbeniales: *Laboulbenia podontiae* Thaxter	Thaxter 1914
	Larva	Fungi: Sphaeriales: Hypocreaceae: *Cephalosporium* Corda sp.	Singh and Misra 1989; Daulmerie 1994; Baksha 1997



Figures 1–10. Habitus of adults of *Blepharida*-group genera, size <2 cm long. 1. *Asiophrida marmorea* (Wiedemann) (photo by C.-w. Shin). 2. *Blepharida rhois* (Forster) (photo by C.-w. Shin). 3. *Blepharida vittata* Baly (photo by C.-w. Shin). 4. *Crimissa cruralis* Stål (Photo by M. Tavares). 5. *Diamphidia femoralis* Gerstaecker (photo by C.S. Chaboo). 6. *Ophrida spectabilis* (Baly) (photo by C.-w. Shin). 7. *Podontia affinis* (Gröndal) (photo by C.-w. Shin). 8. *Podontia lutea* (Olivier) (photo by C.-F. Lee). 9. *Podontia rufocastanea* Baly (photo by C.-w. Shin). 10. *Polyclada flexuosa* Baly (photo by C.S. Chaboo).



Figures 11–15. *Podontia quatuordecimpunctata* on the host tree, *Spondias dulcis Forster* (Anacardiaceae; mak-ok, ambarella, kedongdong) in Thailand **11** Host plant **12** The colorful adult, ~ 2 cm long **13** A larva completely covered by feces **14** Larva, partially covered by feces **15** A juvenile pentatomid bug (Heteroptera: Pentatomidae) attacking a fecal-covered larva, with the beak inserted through the fecal cover. (Photos by S. Damrongsiri).

cies have woody hosts in Burseraceae (*Commiphora* Jacq.) or Anacardiaceae (*Sclerocarya* Hochst.) (Table 1; Chaboo et al. 2007).

The austral-oriental genus *Ophrida* Chapuis consists of four or five species (Medvedev 1999; Zhang and Yang 2008). Immature biology is known for *Ophrida scaphoides* (Baly) (Kimoto and Takizawa 1997), *O. spectabilis* (Baly) (Bilun 1998a; Park and Lee 2001; Lee and Cheng 2007), and *O. xanthospilota* (Baly) (Bai and Zhang 1990; Zhang and Yang 2008). There appears to be one generation per year, with eggs overwintering in slits of host twigs (Park and Lee 2001) or on host trunks (Bilun 1998a, b). The three larval instars are gregarious and retain fecal coverings. Mature larvae descend the plant and construct earthen cocoons underground, at about 20 cm deep; pupation takes about two months (Bilun 1998a). *Ophrida spectabilis* specializes on *Rhus* Linnaeus (Park and Lee 2001) and is a pest of *R. chinensis* Mill. (Bilun 1998a; Yang et al. 1997) and *R. punjabensis* J. L. Stewart (Wang et al. 1998). *R. chinensis*, or Chinese sumac, is the source of gallnuts (or nutgalls); these "nuts" are extruded tannins that harden and are used in traditional Chinese medicine (Bilun 1998a, b). The plant's medical value has led to the development of chemical and biocontrol measures that include egg and larval removal from the host (Bilun 1998b), powder applications containing *Beauveria bassiana* (Bals.-Criv.) Vuill. (Fungi: Clavicipitaceae) (Yang et al. 1997; Wu et al. 1999), and propagation of an egg-parasitoid wasp, *Trichogramma* Westwood (Hymenoptera: Trichogrammatidae; Yang et al. 1997; Bilun 1998a, b; Wang et al. 1998). In China, *O. xanthospilota* is a pest of the anacard *Cotinus coggygria* Scop. (Bai and Zhang 1990).

The 12 species of *Polyclada* Chevrolat are distributed along east Africa, from South Africa to the Arabian Peninsula (Heikertinger and Csiki 1940; Bryant 1942; Chaboo in review). Oddly, some species are also reported from Senegal, which suggests a wider distribution of species, misidentifications, or possibly an inaccurate application of generic concepts. So far as is known, all larvae retain feces (Chaboo et al. 2007). Late 4th instar larvae of some species are dug up, crushed, and their hemolymph is applied to hunting arrows by the San (Bushmen) in Namibia and Botswana (Neuwinger and Scherer 1976; Roodt 1993; Chaboo et al. 2007; Chaboo 2011).

The South American genus *Procalus* Clark comprises nine species that are associated with Anacardiaceae (Table 1; Jerez 1992, 1995, 1999). Two species are significant defoliators of economically important plants in the sub-Andean "matorral" habitat (Mediterranean shrubland) (Fuentes et al. 1987). In Hawaii, *P. mutans* (Blanchard) was introduced as a biocontrol agent for Christmas berry, the weed *Schinus terebinthifolius* Raddi (Anacardiaceae) (Krauss 1962, 1963). Viviane Jerez has described the biology of *P. artigasi* Jerez (Jerez 2003), *P. mutans* (Jerez 1999, 2003), *P. ortizi* Jerez (Jerez 2003), *P. reduplicatus* Bechyné (Jerez 2003), *P. viridis* (Philippi and Philippi) (Jerez 1985, 1988), and *P. silvai* Jerez (Jerez 1995, 2003). Adults become active in early spring; by late spring (October) the females attach groups of cylindrical eggs to leaves and cover them with a secretion. The life cycle includes three larval instars. Third instar larvae construct underground cocoons of sand grains and overwinter for up to nine months. Cocoons are

found about 3 cm underground at the base of the host plant. Larvae of *P. viridis* and *P. mutans* retain fecal shields (Jerez 1985, 1999). Mermithid nematodes are known to be larval parasites (Jerez and Centella 1996).

Immature stages of *Euplectroscelis* Crotch, *Furthia* Medvedev, *Neoblepharella* (Medvedev) [=*Blepharella* Medvedev, which was previously occupied as a genus of tachinid flies (Özdikmen 2008)], and *Notozona* Chevrolat are unknown (Medvedev 1999).

Materials and Methods

One of us (KDP) studied natural populations of *Podontia congregata* on its host tree, *Garcinia gummi-gutta,* under field conditions during several visits in 2008–2010 in Vallamkulam, Pathanamthitta, Kerala, India. We also reared beetles in cages for laboratory observations. We examined beetle specimens obtained from the Department of Entomology, College of Horticulture, Mudigere, India (see Fig. 16).

Cage-reared beetle populations were maintained under ambient conditions at Vellayani, Trivandrum, Kerala, India. Individuals from these cage-reared populations were introduced onto field plants of the host for observations. Although *P. congregata* is absent in Vellayani, the host tree grows naturally on the banks of Vellayani Lake.

Habitat 1. India: Kerala State: Pathanamthitta District, Vallamkulum (76º36'18.4" E, 9º22'29.5" N; 12 - 20 m above msl). This is a typical urbanized village in Kerala, where the majority of the agricultural holdings are below 0.5 ha. Homestead farming, a hallmark of the settlement pattern in Kerala, comprises a diverse assortment of crop trees (e.g., *G. gummi-gutta*), shrubs and herbs, which enhances biodiversity conservation in this densely populated village. This rather hot and humid locality is endowed with a few rivulets to the extent that rice fields can remain submerged during the rainy season. Mature *G. gummi-gutta* trees are common on the banks of paddy fields and rivulets.

Habitat 2. India: Kerala State: Trivandrum District, Vellayani (76º59'8.3" E, 8º25'47.5" N; 18 m above msl). This is a watershed bordered by small hillocks that drain into Vellayani Lake, which is the second largest freshwater lake in Kerala. Banana and vegetable cultivation dominate the low-lying paddy fields, while a coconut-based cropping system is practiced on the hillocks. Perhaps because it is not preferred for culinary purposes in southern Kerala, *G. gummi-gutta* is generally uncommon in southern Kerala homesteads and particularly so in Trivandrum. A local preference for dried tamarind fruit (Fabaceae: *Tamarindus indica* Linnaeus) may explain the low abundance of the host plant here.

Habitat 3. India: Kerala State: Alappuzha District: Pandanad (76º35'0.7" E, 9º19'15.1" N; 12 m above msl), located ~8 km south of Vallamkulam. This is an urbanized village similar to Habitat 1.

Habitat 4. India: Kerala State: Trivandrum District: Ponmudi (77° 06' 43.7" E, 8° 45' 19.9" N; 872 m above msl), a hill station, near the southern end of the Western Ghats mountains. A century ago Ponmudi was covered with pristine wet ever green

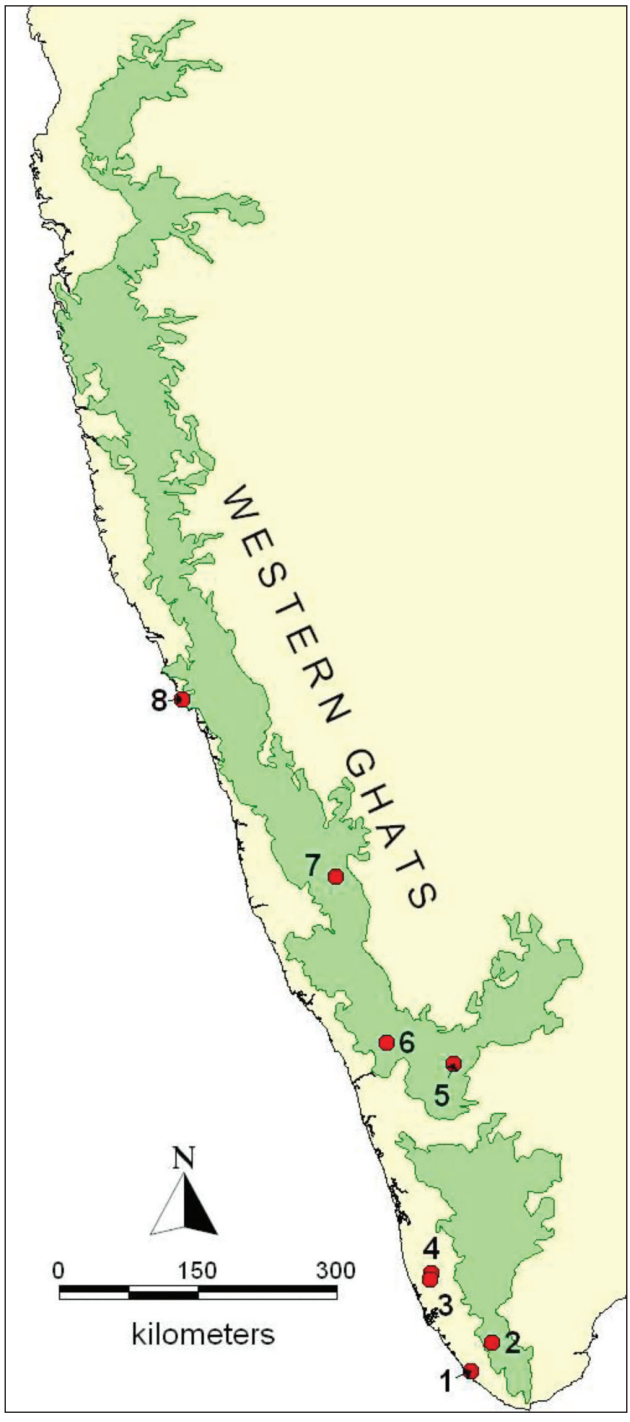


Figure 16. The Western Ghats Mountains in south India with the localities Vellayani (1), Pomudi (2), Pandanad (3), Vallamkulam (4), Conoor (5), Meppadi (6), Mudigere (7) and Karwar (8) where *Podontia congregata* has been recorded in the present study and in Maulik (1926).

forests and is a hot spot of biodiversity in peninsular India. However, agricultural plantations, tourism, and commercial tree felling has altered the landscape significantly.

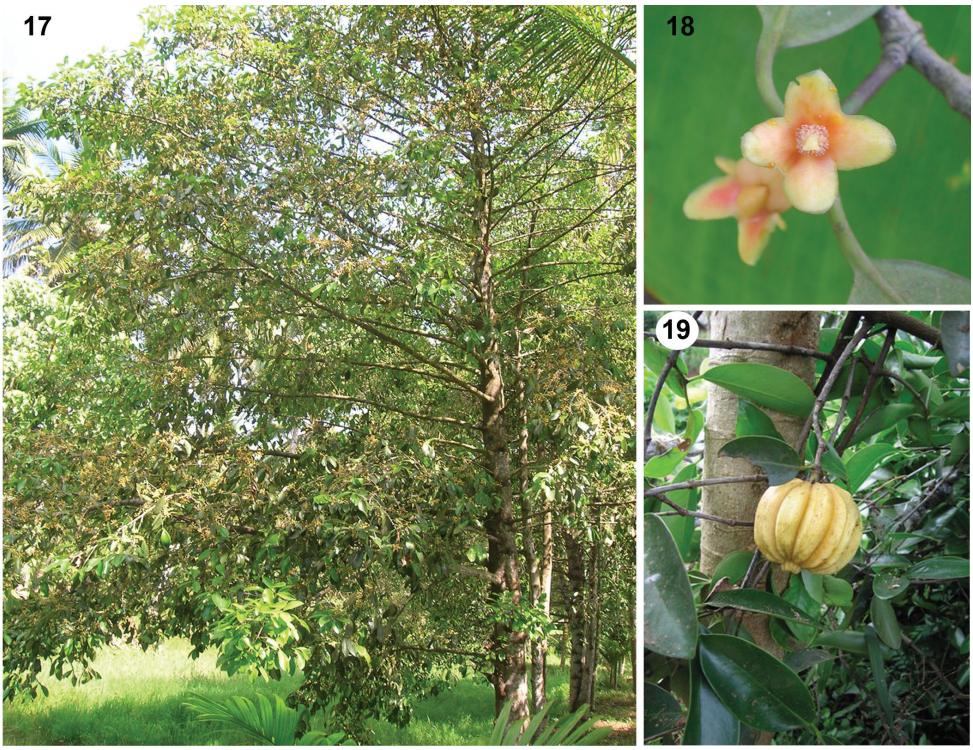
Laboratory conditions. Laboratory culture of *Podontia congregata* was started at Vellayani from nearly half a dozen adults and several larvae collected at Vallamkulam. Adults were confined in a cage of 30 cm^3. We offered food and oviposition sites by supplying branches of the host plant, with the cut end placed in water in a glass bottle. Leaves with eggs were transferred to Petri dishes. Larvae were reared on branches in cages or plastic containers, as well as in Petri dishes. Wet soil was provided for pupation. Rearing was carried out at an ambient temperature of about 22–32°C. About two dozen laboratory reared adults and larvae were introduced onto a naturally growing *G. gummi-gutta* tree at Vellayani during October–December, 2008, and the different life stages were observed.

Natural history of the host plant. Garcinia gummi-gutta (Figs 17–19) grows well in the high rainfall areas of the southern Western Ghats Mountains, India. This medium-sized tree (Fig. 17), locally known as *kodampuli*, is found naturally along banks of rivers, lakes and inundated paddy fields, and is common in Kerala's homestead gardens, as the fruits (Fig. 19) are used in various ways (Manomohandas et al. 2001). The rind is sun-dried for 3–5 days and smoked, and is used as a prized condiment, for curing fish, and as medicine for humans and cattle (Gupta 2002). The acidic pulp covering the seeds is also edible. The thick fleshy rind of ripe fruits is a rich source of hydroxy citric acid (HCA); its derivatives are unique metabolic regulators of obesity (George 2005). Other uses include coagulating rubber latex and polishing gold and silver (Manomohandas et al. 2001). The wood is used as firewood but not valued as timber (Verghese 1991; Geetha 1994; Manomohandas et al. 2001). The tree yields a translucent yellow resin, which does not form an emulsion with water. It is soluble in turpentine and gives a yellow varnish (Sastri 1956).

Study of fecal coat formation. Nine laboratory-reared second and third instar larvae were washed under a very light stream of tap water and lightly brushed with a soft camel-hair brush to remove the fecal cover. Larvae thus cleaned were observed for the formation of a new fecal cover. The fecal thread was removed from the live animal and immersed in water on a slide for microscopic examination.

Tables 1 and 2. For host plants of the *Blepharida*-group taxa (Table 1) we incorporated many little-known articles from Indian journals and assembled host records from an extensive primary literature to collate a list that could be most valuable to the widest community of users. We assembled data on enemies for *Podontia* only, to aid agriculturists dealing with the defoliating effects of these species in Asia. We suspect that there may be obscure agricultural records for other *Blepharida*-group taxa where they are pests (e.g., *Crimissa* is a pest of cashew in Brazil) but such a literature survey will need collaborators involved at the local level.

Specimens. The identity of *P. congregata* was determined by examining the holotype deposited in the Natural History Museum, London, UK, with four labels: Type HT, Baly coll., *Podontia congregata* Baly, examined K. Prathapan, 2005. Specimen vouch-



Figures 17–19. The host plant, *Garcinia gummi-gutta* (L.) N. Robson (Clusiaceae; kodampuli) in India. 17. Tree. 18. Flower. 19. Fruit. (Photos by D. Prathapan).

ers of our study are deposited in the Travancore Insect Collection, Kerala Agricultural University, Vellayani, India, and in the Snow Entomology Collection (SEMC), University of Kansas, Lawrence, U.S.A. (Voucher codes IMcsc00385–IMcsc00390). Vouchers of the bug predator, *Eucanthecona parva* (Distant) (Heteroptera: Pentatomidae), are deposited in the University of Agricultural Sciences, Bangalore, India, and in SEMC. Vouchers of *Ooencyrtus* are deposited in the Aligarh Muslim University, India, and in SEMC. Plant vouchers are deposited in the Calicut University Herbarium, Calicut, India (Accession no. 6394).

Results

Eggs of *P. congregata* are deposited in masses (Fig. 20), usually laid in two layers at Vellayani, egg masses were observed in the field on both abaxial and adaxial surfaces of leaves. In the laboratory, the egg masses comprise 4–20 eggs, and were attached mostly on the adaxial surface. Each orange-yellow egg is oriented vertically. Eggs measure

1.82–1.92 mm long and 0.94–1.03 mm wide. About 6–7 days after oviposition, the egg coloration changes to grey brown just before hatching.

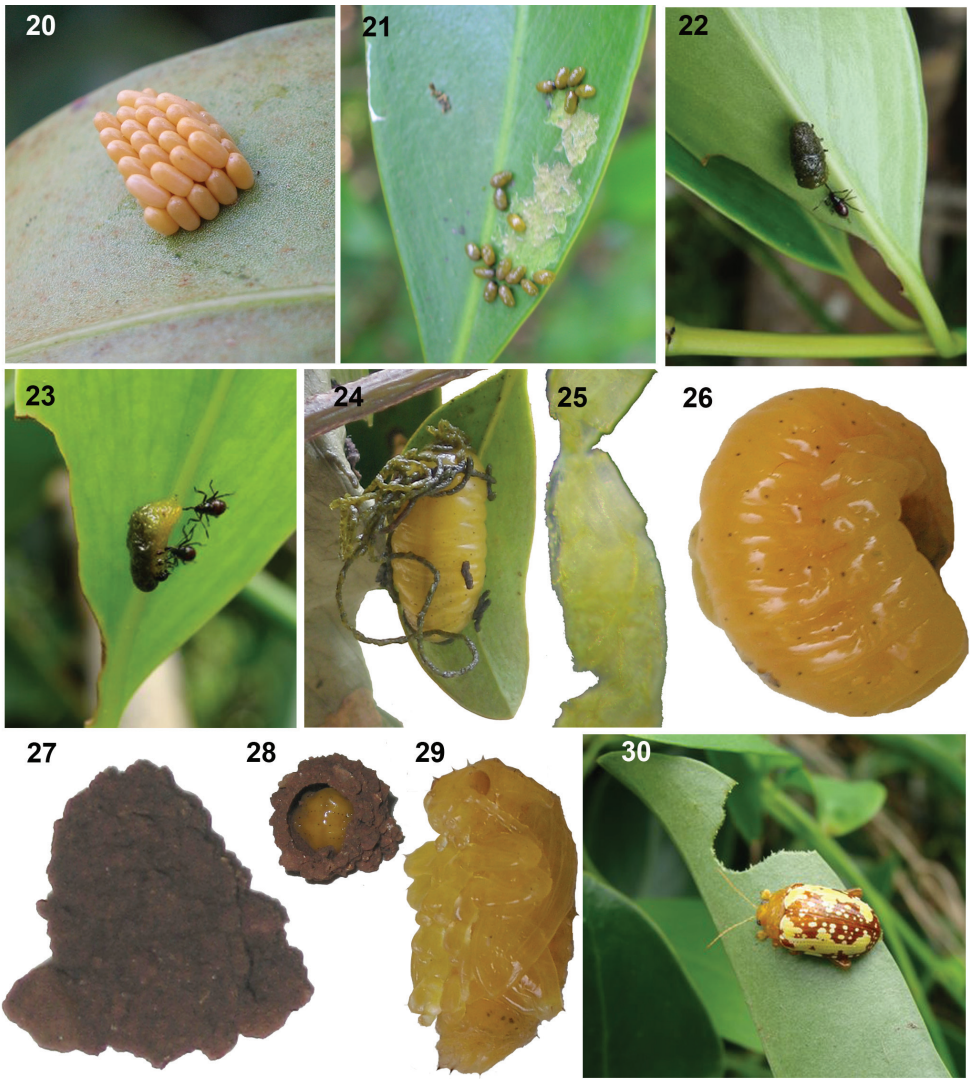
The neonate larva (Fig. 21) is lemon yellow with a dark head. Young larvae feed by scraping on the adaxial surface of the lamina (Fig. 21). Older larvae feed by cutting the leaf lamina while positioning themselves on the abaxial side of the leaf. Older larvae were observed singly on leaves, indicating a solitary nature (Figs 22–24). Larvae that are old enough to cut the leaf tend to remain on the abaxial side of the leaf. The larva with its fecal coat resembles bird droppings (Figs 22–23). The larval period varied from 18–25 days.

The larval fecal coat is formed with feces being excreted as a single thread, which is then transversely folded over the back to cover the dorsum of each larva (Fig. 25). Convulsive movements of the dorsum move it forward. The fecal thread is extruded with a glue-like, transparent material that binds the particles together (Fig. 25). When the fecal coats were removed, larvae took about 6–8.5 hours to refurbish a new coat. The coat color depends on the maturity of the leaf eaten by the larva; larvae feeding on tender leaves have a light colored, wet fecal cover, while those feeding on mature leaves have a rather dark green, apparently drier fecal coat.

Formation of pupae (Figs 27–29) was observed in the laboratory. Full fed final instar larvae shed the fecal coat and remained motionless for about 1–2 days and then assumed a C-shape with concave venter. Prior to pupation, they wriggle on wet soil that was provided in the rearing cage, creating a small depression on the surface and then gathering soil particles from around the body and manipulating these with the legs and mouthparts to form a layer covering the body. Ultimately this layer becomes an earthen cocoon roughly globular in shape (Figs 27–28). The larva never dug into soil, but always constructed the cocoon on the surface.

The adult emerged through a nearly circular exit hole. Construction of the cocoon to adult emergence took 21–24 days. The total life cycle was completed in 49–53 days. Adults (Fig. 30) lived in captivity for about 3–4 months. They feed by cutting the leaf lamina. Adults feign death and fall down (= thanatosis) or reluctantly jump when disturbed. Laboratory-reared adults released on naturally growing host plants at Vellayani were found to be less mobile. Some adults remained on the same branch for weeks and oviposited. The color pattern of adults appears to mimic bird droppings. Like larvae, adults too preferred to remain on the abaxial side of leaves.

At Vallamkulam, the insect was active throughout the year except during the dry summer months. Adult and larval presence was noticed after the onset of monsoon rains in May-June in 2008, and larvae were observed until early January 2009. Neither larvae nor adults were observed during the harsh, dry, summer months. Vellayani received the first summer rain of 9.8 mm on 13 March in 2009, and a single newly emerged adult was noticed on 15 March in the field. Two third instar larvae were observed on 11 April indicating sustenance and possible establishment of *P. congregata* at Vellayani where it was newly introduced. Six adults and several larvae were noticed on this tree during the last week of May, 2009. Two adults and three final instar larvae could be spotted after thorough checking of 14 host trees on 14 April at two spots in Vallamkulam. This indicates a similar seasonality and pre-monsoon buildup of the



Figures 20-30. Life stages of *Podontia congregata* Baly in India. 20. Egg mass. 21. Gregarious instar I larva scraping leaf. 22. Instar II covered with green fecal pellets, being attacked by a juvenile predatory bug, *Eucanthecona parva* (Distant) (Heteroptera: Pentatomidae: Asopini). 23. Instar III larva with incomplete fecal cover and under attack by the juvenile bugs. 24. Mature larva with long fecal strands. 25. Fecal strand, immersed in water. 26. Mature larva, prior to construction of pupation chamber. 27. Pupation chamber. 28. Prepupa within pupation chamber. 29. Pupa. 30. Adult and chewing damage on leaf. (Beetle adult < 2 cm long; Photos by D. Prathapan, N. Anith).

population in both the localities. Interestingly, the introduced *P. congregata* at Vellayani was confined to the single tree on which it was introduced, till the last quarter of 2009. There are 11 other host trees in its vicinity, with the nearest one at a distance of 19 m. Grown-up larvae were observed during December, 2009 on a second tree about 22 m

away from the tree on which the beetle was first introduced. This indicates extremely slow dispersal of the insect.

At Vellayani, in 2010, the host trees put forth new flushes during the harsh summer, and all stages of the insect were active throughout the summer, without a break in activity. Diapause in *P. congregata* is probably correlated with flushing of the host tree rather than the harsh dry summer. However, the entire population mysteriously disappeared in May, indicating a probable local extinction of the species.

Nymphs of a pentatomid, *Eucanthecona parva* (Distant) (Heteroptera), were observed feeding on the larvae of *P. congregata*. A parasitoid was reared from the beetle eggs at Vellayani and is described as a new species, *Ooencyrtus keralensis* Hayat and Prathapan (Hymenoptera: Encyrtidae; Hayat and Prathapan 2010).

Discussion

The occurrence of *Podontia congregata* at Vallamkulam and Pandanad extends its range beyond the Western Ghats Mountains to the southwest plains. The absence of *P. congregata* at Vellayani in Trivandrum District, in spite of the presence of the host plant, is curious. Vellayani is only at a linear distance of about 37 km away from Ponmudi, the nearest locality where *P. congregata* was collected. There is no significant difference in altitude, vegetation, or climate between Vellayani and Pandanad or Vallamkulam, except that the rainfall is low at Vellayani (average annual rainfall of about 1833 mm) compared to Vallamkulam (average annual rainfall recorded at Thiruvalla, about 4 km north of Vallamkulam, is 2912 mm) (M. C. Kiran, pers. comm.). Low rainfall, low abundance of the host plant population, competition or poor rate of dispersal could probably explain its past absence in Vellayani.

Members of the *Blepharida*-group have been reported on many plant families (Table 1), but some records are questionable as they are singleton reports lacking further confirmation. For example, Stebbing's (1914) report of *Podontia quatuordecimpunctata* on *Ficus elastica* Roxb. ex Hornem is that of adult feeding; this may be accidental, as is common in flea beetles, and does not necessarily indicate true trophic relationships. Anacardiaceae and Burseraceae are the unequivocally proven host plant families of *Blepharida*-group species. This has been confirmed by multiple observations and reports of natural history. These two plant families are closely related; Anacardiaceae, Burseraceae, and Sapindaceae belong to the Order Sapindales of Malvids, but Clusiaceae is phylogenetically distant from Malvids, being situated within the Order Malpighiales of Fabids (Judd et al. 2008). Our novel discovery of a Clusiaceae as host for a *Blepharida*-group taxon is intriguing. Other chrysomelid genera on Clusiaceae include *Nodina* Motschulsky, *Homoschema* Blake, and *Megistops* Boheman (Jolivet and Hawkeswood 1995). There is also a report of larvae of an unnamed beetle defoliating *Garcinia gummi-gutta* from India (Anonymous 2003), which is probably *P. congregata*. Despite being phylogenetically distant, it is possible that *G. gummi-gutta* is chemically similar to Anacardiaceae and Burseraceae and it produces resinous gum like most

Anacardiaceae. Interestingly, a similar pattern of host selection exists with leafhoppers (Hemiptera: Cicadellidae); Anacardiaceae are common host plants of Oriental Idiocerinae leafhoppers with ten species documented on mango, *Mangifera indica* L., alone (Viraktamath and Viraktamath 1985). Two species of the idiocerine genus *Busoniomimus* Maldonado Capriles occur in India (Viraktamath and Murphy 1980; Viraktamath and Viraktamath 1985); *Busoniomimus mudigarensis* (Viraktamath) feeds on *Buchanania angustifolia* Roxb. (Anacardiaceae) in south India (Viraktamath and Murphy 1980). The second species, *Busoniomimus manjunathi* Viraktamath and Viraktamath, feeds on mango (Viraktamath and Viraktamath 1985) and *G. gummi-gutta* in Kerala (Mathew et al. 2002; KDP personal observations), showing a similar host plant selection to *P. congregata.*

At least three *Podontia* species are regarded as serious pests— *P. affinis* on *S. dulcis* in Indonesia, *P. lutea* on *T. vernicifluum* in China, and *P. quatuordecimpunctata* on *Spondias* spp. At this time, *P. congregata* is a minor pest of *G. gummi-gutta*, causing damage of little economic significance. The large size and fecundity of these species may contribute to their defoliating impacts. Documenting natural enemies as in Table 2 may be useful in finding biocontrol agents.

Species in six *Blepharida*-group genera are now documented with fecal retention— *Blepharida* (Becerra et al. 2001), *Diamphidia* and *Polyclada* (Chaboo et al. 2007), *Ophrida* (Lee and Cheng 2007), and *Podontia* (Barlow 1900; Corbett and Yusope 1921; Pramanik and Basu 1973; Takizawa 1978; Singh and Misra 1989). Both Pramanik and Basu (1973) and Singh and Misra (1989) mention an exudate covering the feces of *Podontia quatuordecimpunctata*. No such exudate was observed in *P. congregata*. Cast exuvial skins are retained in the larval fecal covering of *P. lutea* and *Blepharida nigrotesselata* Baly, but such inclusions have not been reported in other *Blepharida*-group species (Paterson 1943; Takizawa 1978). Among chrysomelids that retain a fecal covering, exuvial skin inclusions in larval and pupal fecal shields is a widespread and significant structural feature only in Cassidinae (Chaboo 2007 and citations therein). The gum-like substance covering the fecal thread, revealed through microscopic examination, probably acts as a binding material to create a single, unbroken thread that forms the fecal shield (Fig. 25).

Larvae may reduce enemy attack in several ways. Larvae which are large enough to feed by cutting the lamina position themselves on the abaxial side of the leaf and thus probably evade pouring rains as well as secure some cover from natural enemies. Young larvae prefer to feed on young, tender leaves. Older larvae feed on both light green tender leaves as well as tougher, darker green mature leaves. Fecal cover of larvae feeding on tender leaves is light green while that of those feeding on tougher mature leaves is dark green-grey, which may enhance any background camouflage effect. The fecal coats may further act as physical barriers against some predators and parasitoids. However, bugs may be specialist predators by virtue of their propensity to insert their beaks into the vulnerable ventro-lateral area of the body not covered by the fecal coat (Figs 15, 23). Host specific parasitoids, like *Ooencyrtus podontiae,* are also known to attack *Podontia affinis* (Gahan 1922).

Pupation within hard earthen cocoons is widespread among flea beetles and may reduce vulnerability to predators and parasites. Bose (1953) reported leaf inclusions in these cocoons. Such constructions may minimize desiccation, particularly in the drier habitats where many *Blepharida*-group species occur. Most pupation is underground which further enhances protection, but surface pupation occurs in *P. congregata.* Reports for *P. quatuordecimpunctata* are contradictory, indicating underground pupation (Corbett and Yusope 1921; Pramanik and Basu 1973; Sardar and Mondal 1983; Singh and Misra 1989; Baksha 1997; Deka and Kalita 1999) and surface pupation (Bose 1953; Singh and Misra1989; Baksha 1997).

Podontia adults escape by thanatosis, whereby they fall from the foliage, remain motionless and thus disappear into the undergrowth. This defensive tactic is a widespread escape response among Chrysomelidae. Larvae appear to use an "anal extremity" to adhere to leaves (Pramanik and Basu 1973); this may be referring to the adhesive anal disc of the pygopods in some chrysomelids which acts as a holdfast organ, minimizing the risk of falling off hosts (Gustafson and Chaboo 2009).

Chrysomelids are well known for their chemical defenses (e.g., Pasteels et al. 1989, 1994) and *Blepharida*-group species have intimate ecological and evolutionary relationships with their host plants, and which appear to be chiefly driven by a chemical arms race based on host secondary metabolites (e.g., Becerra 2003). *Blepharida*-group species present two different strategies of chemical defense: (1) the sequestration of host plant chemicals for incorporation into their fecal defenses, and (2) an apparent synthesis of toxins by the beetle itself like in southern African taxa. As an example of the first strategy, chemical analyses of the feces of *B. rhois* larvae (Morton 1997; Vencl and Morton 1998, 1999) revealed a mix of fatty acids, tannins, and phytol derived from its host plant, *Rhus glabra* Linnaeus, which function as deterrents to ant attack. As an example of the second strategy, diamphotoxin, a relatively small hemolytic and neurotoxic protein, has been isolated from larvae of *D. nigroornata*, one of the beetles used by southern African Kalahari San as a source of their arrow poisons (Koch 1958; Mebs et al. 1982; Woollard et al. 1984). It is unclear if this protein occurs in other species of *Diamphidia*, *Polyclada*, and *Blepharida* which are also suspected sources of arrow poison.

The monophyly of the *Blepharida*-group is supported by characters from host plants, beetle morphology, and behavior of all life stages (Takizawa 1978; Furth and Lee 2000; Chaboo et al. 2007). Takizawa's (2005) *Podontia*-group was based on eggs being deposited in rows; however Hsu (1934b) illustrates eggs of *P. lutea* clustered at the apex of a leaf. Farrell (1998) identified the relationship *Podontia* + (*Orthocrepsis* + *Nisotra*) based on = 18S ribosomal sequence (entire). Becerra (2004a, and subsequent studies) has focused on *Blepharida* and its co-evolutionary association with *Bursera*, but the similar host plant choices of *Blepharida*-group species suggest that Becerrra's coevolutionary model may be extrapolated to the entire *Blepharida*-group.

The host plant choices of *Blepharida*-group species are interesting to agriculturists, foresters, anthropologists, and chemists. In Brazil, India and Thailand, the pest species on economically important plants attract agricultural interests. In China, forestry officials are concerned about damage to forests and trees used in traditional medicine.

Southern African species are the source of the San's indigenous arrow poisons. The *Blepharida*-group is a model for research on diverse questions.

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