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**NATURAL HISTORY OF THE AUSTRALIAN TORTOISE BEETLE,
NOTOSACANTHA DORSALIS (WATERHOUSE, 1877) (COLEOPTERA:
CHRYSOMELIDAE: CASSIDINAE: NOTOSACANTHINI) WITH
SUMMARY OF THE GENUS IN AUSTRALIA**

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Abstract

The old-world tribe Notosacanthini is hypothesized as a transitional group between “hispine” leaf miners and exophagous tortoise beetles in the Cassidinae tree of life. Their biology, morphology, and genetics may help clarify evolution in the subfamily, yet few species have been studied deeply. Detailed field and rearing studies were conducted for *Notosacantha dorsalis* (Waterhouse) on the phyllodinous shrub, *Acacia crassa* Pedley (Fabaceae), in Queensland, Australia. Adults feed on phyllode tissue by biting linear, parallel grooves in the leaf-like phyllode surface. Solitary eggs are laid in short, shallow grooves bitten into the phyllode surface and coated with secretion then with faeces. Hatching larvae mine within the phyllode, depositing frass and larval exuviae near the hatched egg capsule. After consuming most resources of the initial phyllode, larvae cut their way out of the original mine (termed the primary mine) and re-enter a second phyllode, via an entry cut in the cuticle, to make a secondary mine. This entry cut serves to eject frass and exuviae. After a period of feeding, the secondary mine serves as the pupation chamber and the adult exits via the entry cut. We outline two processes for determining the number of instars for mining larvae which showed that *N. dorsalis* has four instars. Two hymenopteran parasites were collected. Museum specimens of Australian *Notosacantha* were examined to assess species and their distributions.

Key Words: *Acacia*, leaf-miner, Australia, endemic, life history, parasites, distribution

Introduction

Notosacanthini is a morphologically distinct tribe that is hypothesized as a transitional group between “hispine” leaf miners and exophagous tortoise beetles in the Cassidinae tree of life (Gressitt 1952; Gressitt and Kimoto 1963; Zaitsev and Medvedev 1982; Medvedev and Eroshkina 1988; Borowiec 1995; Staines 2002; Chaboo 2007). Inadequate knowledge of ecology, life cycles, and morphology of species of the following tribes—Aproidini, Basiprionotini, Cryptonychini, Delocraniini, Epistictini, Eurispini, Hemisphaerotini, Imatidiini, Leptispini, and Notosacanthini—leave many unanswered questions about their relations to each other and what could be evolutionary steps between the very different lifestyles, particularly of larvae, with leaf-mining and exposed leaf chewing and their correlated morphologies (Crowson 1955).

Notosacanthini comprises three extant genera, *Herminella* Spaeth, 1913 (4 spp.), the monotypic *Hermosacantha* Borowiec and Świętojańska, 2014a, and *Notosacantha* Chevrolat, 1837 as well as the extinct *Eosacantha* Chaboo and Engel, 2009. *Notosacantha* currently comprises 271 recognized species that

range from southern Africa and Madagascar to India and China, and through S.E. Asia, Philippines and Indonesia to New Guinea and Australia (Borowiec and Świętojańska 2012–2019). The adults have the pronotum and elytra explanate and with large punctures, the pronotal margin deeply indented exposing the head dorsally (as in the related tribe Hemisphaerotini), and the elytra with irregular raised costae and tubercles (Maulik 1919; Medvedev and Eroshkina 1988; Borowiec *et al.* 2013). Other diagnostic features are the vertex expanded anteriorly into plates that overlap the antennal bases (Gressitt 1952; Medvedev and Eroshkina 1988), the antenna short with an apical club comprised of antennomeres with single longitudinal grooves and striations (Chaboo 2007: 99, Fig. F), and the aedeagus with a pair of lateral lobes (Chaboo 2007: 143, Figs D–E). Borowiec and Takizawa (1991) suggested some species-groups based on patterns of costae and tubercles; they also pointed out a sexual dimorphism with females having 10 antennomeres and males 11.

Host plants have been documented for 14 species of *Notosacantha* (Borowiec and Świętojańska 2012–2019; Table 1). All known hosts are eudicotyledons. *Notosacantha* is unusual in having leaf-mining larvae in the very few species for which life history information is available. Both Chaboo (2007) and Świętojańska (2009) summarize the literature on cassidine immature stages, including four species of *Notosacantha*. Illustrated descriptions of juvenile stages are available for just two species: *Notosacantha vicaria* (Spaeth, 1913) based on larvae and pupa on *Carallia brachiata* (Lour.) Merr. (Rhizophoraceae) in India (Rane *et al.* 2000) and *Notosacantha siamensis* (Spaeth, 1933) based on larvae and pupae on *Phyllanthus emblica* L. (Euphorbiaceae) from Vietnam (Medvedev and Eroshkina 1988). Others report brief notes with line drawings: pupa of *N. sauteri* (Spaeth, 1914) (Kimoto and Takizawa 1997; Lee and Cheng 2007), larva of *N. siamensis* (Kimoto and Takizawa 1997), egg, larva and pupa of *Notosacantha castanea* (Spaeth, 1913), and photo of a larva of *Notosacantha ihai* Chûjô, 1958 (Borowiec and Świętojańska 2014b:207). These studies reveal that larvae of *Notosacantha* do not retain an exuvio-faecal shield, as is usual in tortoise beetles. The keys to larvae in Kimoto and Takizawa (1997) for *Notosacantha* are contradictory: p537, couplet 3(2) indicates “larvae bearing exuviae and excretions on caudal processes” but p546 has “leaf-miner lacking body processes.” Heron (2018) gives photographs of larval and pupal mines in South Africa for *Notosacantha badia* (Boheman, 1850) on leaves of *Gymnosporia nemorosa* (Eckl. & Zeyh.) Szyszyl. (Celastraceae) and of *Notosacantha laticollis* (Boheman, 1862) on *Canthium inerme* (L.f.) Kuntze (Rubiaceae). Monteith (1991a) briefly records and figures adult feeding, the egg capsule and larval leaf mining for the Australian *N. dorsalis* (Waterhouse, 1877) on *Acacia crassa* Pedley, 1974 (Fabaceae). The food plant was known from 1979–80 collections made by G.B. Monteith and the late M. DeBaar at Braemar State Forest and deposited in Brisbane museum collections. A colour photograph of *N. dorsalis* and adult feeding grooves on *A. crassa* at Barakula

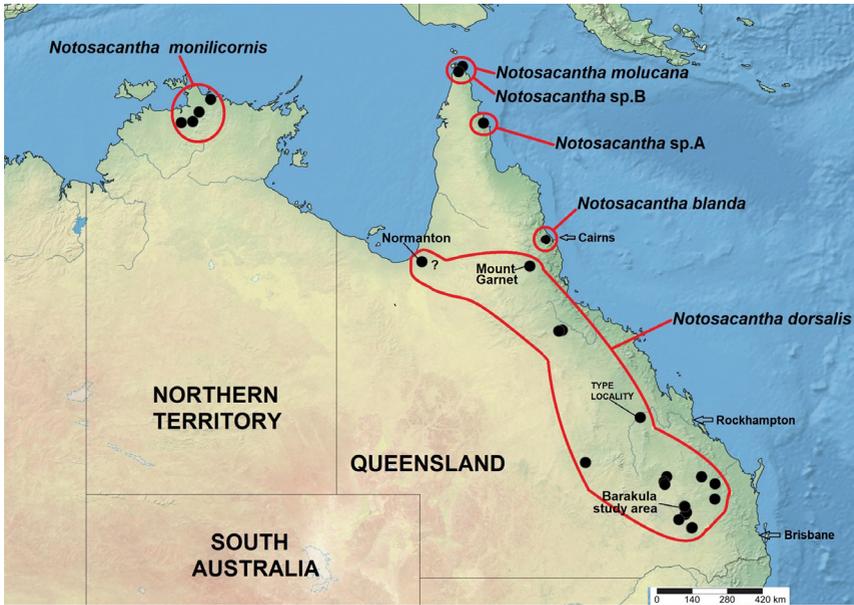


Fig. 1. Map of north-eastern Australia showing distribution of *Notosacantha* specimens in Australian museum collections. See text for explanation of species names used on the map.

State Forest, with speculative text, is given by Hawkeswood (1987, 1989) with corrections noted by Monteith (1991a) but repeated unchanged (Hawkeswood 1994, 2003; Jolivet and Hawkeswood 2005).

Four nominal species of *Notosacantha* are recorded in the literature from Australia (Borowiec and Świętojańska 2012–2019). Three of these were described from Australia, viz. *N. dorsalis* (Waterhouse, 1877), *N. monilicornis* Spaeth, 1913 and *N. blanda* (Spaeth, 1932). The fourth, *N. molucana* (Boheman, 1850), was described from Ambon in the Maluku Archipelago of Indonesia and subsequently recorded from New Guinea and from ‘Cap. York’ in Australia by Spaeth (1913). A preliminary review of the status of literature and museum records of the genus from Australia is given in the present paper.

This paper is the first step in a systematic study of Australian species of *Notosacantha*. It reports on the natural history and distribution of *N. dorsalis* based on field work, rearing of the life cycle, and on study of museum specimens by authors GM and VS over 2018–2021. Morphology of the immature stages will be presented in a subsequent paper.

Materials and Methods

This study was conducted under permit WIF418701617 issued by Queensland Department of Environment and Science to the Entomological Society of

Queensland (Principal Investigator: Christine Lambkin). Data and specimens were collected during ~18 months of field work, life cycle rearing, and study of museum specimens. Author initials are used below for specific research efforts.

Field study. Live populations of *N. dorsalis* were first discovered on the host plant, *Acacia crassa* (Fabaceae) by GM at two localities in 1979–80 in Braemar State Forest, Queensland. Some initial observations were made on their leaf mining and parasites then by GM and the late Murdoch De Baar of the Queensland Department of Forestry.

For the present comprehensive study, live populations were studied by GM and VS at AUSTRALIA: Queensland, Barakula State Forest (referred to as Barakula hereafter) on *Acacia crassa* (Figs 2–4). The locality is 300 km NW of Brisbane. Barakula comprises 283,000 ha of relatively undisturbed open forests and woodlands dominated by tree species of *Eucalyptus*, *Angophora*, *Corymbia* (Myrtaceae), *Allocasuarina* (Casuarinaceae) and *Callitris* (Cupressaceae) and with an understory of scattered shrubs which include many species of *Acacia*. The beetle occurs patchily on the host plant within Barakula. Most observations were made along Big Break Road, near the Forest Station, at -26.434°S X 150.507°E (elev. 340m), where beetles consistently occurred. At this site the vegetation type is classified as Regional Ecosystem 11.5.1 under the system developed for Queensland (Sattler and Williams, 1999) which is woodland on Caenozoic sand plains. Rainfall is around 550 mm per year with most rain in summer. The area is within the Brigalow Belt Biogeographic Region of Australia (Thackway and Cresswell, 1995).

The field site was visited six times during 2018–2021: 1–3 Oct. 2018, 19–20 Oct. 2018, 17–18 Dec. 2018, 27–28 Feb. 2019, 5–6 June 2019, and 4–5 Sept. 2021. Observations were made in the field and many specimens of all stages were taken to Brisbane for rearing and life cycle study.

Temperature range of study sites. As a rough guide to temperature range at the Barakula field study site and the Brisbane rearing site, the following summer and winter average maxima and minima are taken from the Bureau of Meteorology (2021) website: Brisbane: summer 20.4–29.2°C, winter 10.2–21.4°C; Barakula: summer 19.1–32.9°C, winter 4.5–20.2°C.

Life cycle study. Five young plants of *A. crassa* were transplanted from Barakula, potted, and grown in the Brisbane garden of author GM during October 2018 to February 2020. Plants were enclosed with large, suspended netting sleeves (Fig. 6) which could be easily lifted off for observations. Adult beetles collected from Barakula were released inside the cages and maintained for over a year on these potted plants where they completed two generations.

As the beetles laid eggs on the leaf-like phyllodes, we placed an ink numeral beside each egg. Plants were inspected semi-regularly to follow development of eggs and subsequent larvae. Larval mines were measured by recording



Figs 2–4. Habitat and host plant, *Acacia crassa* Pedley (Fabaceae), for *Notosacantha dorsalis* (Waterhouse, 1877) in Barakula State Forest, Queensland, Australia: (2) habitat showing open mixed-species vegetation with mature *A. crassa* tree on left; (3) young *A. crassa* plant; (4) phyllodes and inflorescence of *A. crassa*.

maximum length and width of each mine when examined. The silhouette of the larvae inside the mine could be seen by illuminating from behind by a hand-held light (Fig. 25). Length and often width of each larva were recorded when examined. Observations ceased when the larva died, was attacked by ants, or strayed when attempting to start a secondary mine. Development of 79 eggs was followed, at least partially. Some short-term observations were made on cut phyllodes held in water in the laboratory (Fig. 7).

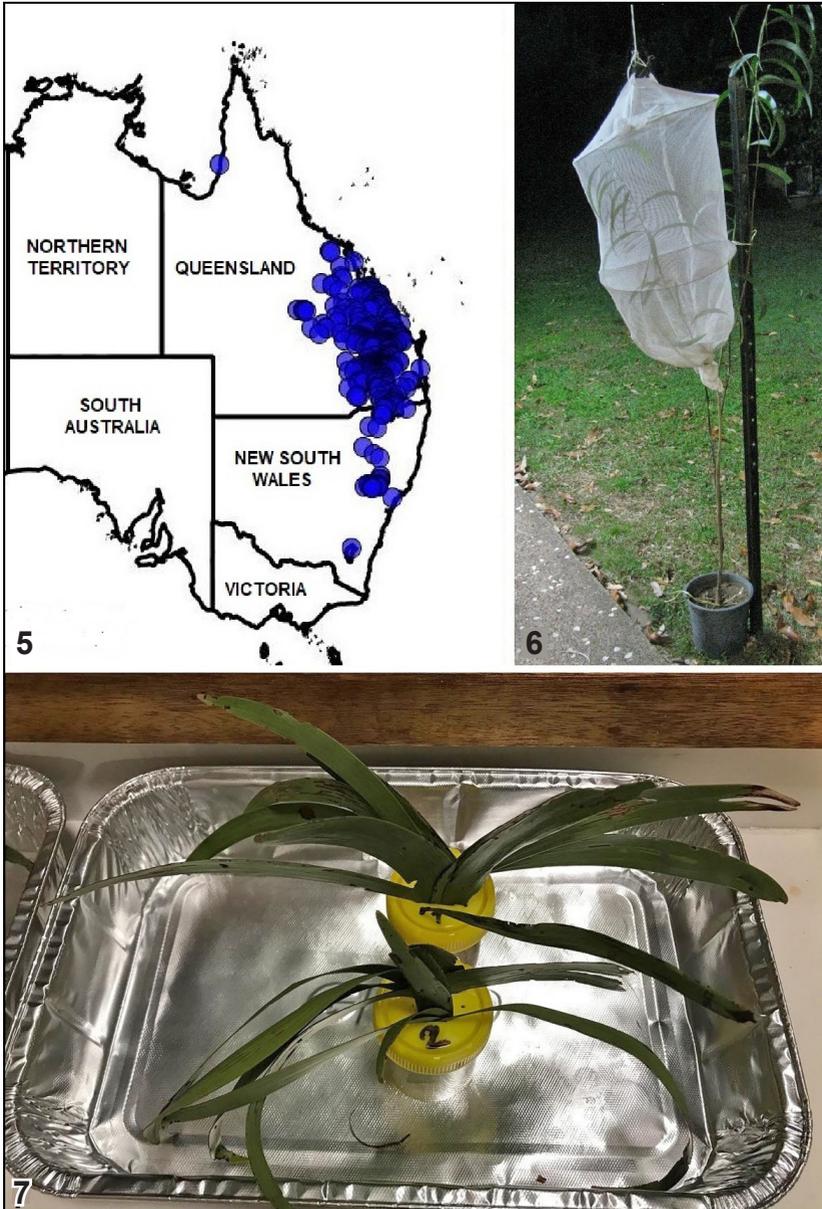
Specimens studied. Vouchers of all life history stages of *N. dorsalis* from the present study are deposited in the Queensland Museum, Brisbane, Queensland (QM) and in the University of Nebraska State Museum, Lincoln, Nebraska, USA (UNSM). Vouchers of Hymenoptera parasites are lodged in QM. A pressed voucher of *Acacia crassa* from Barakula is lodged in the Queensland Herbarium, Brisbane (BRI). Museum specimens of Australian *Notosacantha* were examined and listed by GM and VS from: Queensland Museum (132); the Australian National Insect Collection, Canberra (ANIC) (31); the Australian Museum, Sydney (AM) (4); the Museum of Victoria (MV) (1); the Queensland Dept of Agriculture and Fisheries Collection (QDAF) (12); the Museum and Art Gallery of Northern Territory, Darwin (MAGNT) (1); and the CSIRO Darwin collection, Berrimah (NTCSIRO) (2).

RESULTS

Notosacantha in Australia—species and distributions.

A summary is given here of the *Notosacantha* species recorded from Australia, based on examination of 183 specimens in Australian collections plus the few published localities in the literature indicated in our introduction. These records for the genus are mapped (Fig. 1) and show the genus is confined to Queensland and Northern Territory in the north-east sector of the continent. Clearly, formal taxonomic study is required, but there appear to be at least three, and perhaps as many as six species, in Australia. The four nominal described species below are figured in colour in the online catalog of Borowiec and Świętojańska (2012–2019).

1. *Notosacantha dorsalis* (Waterhouse, 1877) (Figs 1, 8–11). Most examined specimens (176 of 183) of Australian *Notosacantha* belong to this species. Published records in addition to the ‘Mackenzie River’ type locality are by Spaeth (1913) for ‘Gayndah’, ‘Gawler’ and ‘Normantown’, all of which he gives as in Queensland. Gayndah is confirmed by modern records. ‘Normantown’ may be an error for Normanton on the Gulf of Carpentaria beyond the known range, but it coincides with an outlier herbarium record for the foodplant (Fig. 5) and may be correct but needs confirmation. The only Australian ‘Gawler’ place name is in South Australia, well beyond the possible range, so we do not accept this record. The overall distribution of *N. dorsalis* is close to that of its confirmed foodplant *A. crassa* (Fig. 5). Reliable modern specimen records for *N. dorsalis* near Mt. Garnet and Charters Towers



Figs 5–7. *Acacia crassa* Pedley: (5) map of distribution in Australia downloaded from Australian Virtual Herbarium website; (6) transplanted, potted plant in Brisbane with breeding beetles in netting bag; (7) cut phyllodes in water for short-term observations. Larvae lived for some time in such phyllodes.

are beyond the plant's range and *N. dorsalis* may have a different food plant at these places.

2. *Notosacantha monilicornis* (Spaeth, 1913) (Fig. 1) was described with the locality unspecified, simply 'Austral. boreal.' (=northern Australia). Only four specimens are in Australian museums. The locality from King River, on the northern coast of the Northern Territory, of a 1916 specimen in MV by a reliable collector, is supported by three modern specimens in MAGNT and NTCSIRO from nearby Kakadu National Park. It differs from *N. dorsalis* in having lower elytral tubercles and only one pair of radial bars extending to margin of elytra.

3. *Notosacantha blanda* (Spaeth, 1932) (Fig. 1) was described from 'Kuranda, Queensland' and resembles *N. monilicornis*. Kuranda is now well collected, but specimens of this species have not been recollected there. Much insect material was sold to European collectors and museums by F.P. Dodd who lived in Kuranda from 1904 to 1936. He and his sons collected widely across tropical Australia and New Guinea; it is known that specimens from elsewhere often became labelled 'Kuranda, Queensland' (Monteith, 1991b). The status of this species remains in doubt, and it may be the same as *N. monilicornis* and/or *Notosacantha* sp. B (see below).

4. *Notosacantha molucana* (Boheman, 1850) (Fig. 1) is a uniformly black species described from Maluku in Indonesia and is also recorded from New Guinea and 'Cap. York' by Spaeth (1913). It has not been retaken in Australia. Cape York (-10.690°S X 142.532°E) is the northern tip of Australia, only 150 km from New Guinea. In the late 1800s there was an early settlement near Cape York from which early explorers and collectors visited New Guinea. Many shipments of New Guinea specimens were consigned to Europe from there and were often given the provenance of 'Cape York' (Monteith and Dewhurst 2011). There are several other uniformly black species known from New Guinea (Borowiec and Świętojańska 2012–2019). Until confirmed by further collecting, *N. molucana* remains doubtfully Australian.

5. *Notosacantha* sp. A. (Fig. 1). In ANIC are two adult specimens collected at Mt Tozer, Iron Range (-12.725°S X 143.284°E) in July 1986 by reliable coleopterists, T. Weir and A. Calder. Adults are distinct, pale with a crescentic dark band across the posterior half of the elytra, and do not resemble any of the many species illustrated by Borowiec and Świętojańska (2012–2019); they are likely to represent a new species.

6. *Notosacantha* sp. B. (Fig. 1). The QM collection has a single adult specimen collected at Bamaga (-10.886°S X 142.329°E) in January 1984 by the reliable collector, J. Sedlacek. The specimen closely resembles *N. blanda* and *N. monilicornis* and suggests that there is perhaps just a single species shared across the northern part of Northern Territory and Cape York Peninsula. If this is so, then the name, *Notosacantha monilicornis*, would take priority.



Figs 8–11. Adults of *Notoscantha dorsalis*: (8) linear grooves made by feeding adult with ootheca in centre of phyllode at top; (9) detail of adult with feeding grooves placed between parallel veins of phyllode; (10) oblique view of adult showing elytral tubercles; (11) mating pair.

Natural history of *Notoscantha dorsalis* (Waterhouse, 1877)

Host plant (Figs 2–6). Beside our main study sites near the Barakula Forest Station, other sites where the beetle has been taken on *Acacia crassa*, as sightings or specimen records in QM, are: Braemar State Forest, -27.188°S X 150.785°E, GM, 4.iv.1996 & 15.iii.1980; Braemar SF, -27.204°S X 150.766°E, GM, 15–19.x.1979; Rockwood Station, -26.714°S X 150.534°E, GM, 18.viii.1984; Barakula, -26.433°S X 150.504°E, GM & VS, 2018; VS, 5.ix.2021; Barakula, -26.435°S X 150.521°E, GM & VS, 2018; Waterton State Forest, -25.370°S X 149.869°E, GM & VS, 2019; Condamine State Forest, -26.903°S X 150.305°E, GM & VS, Oct, 2019.

The QDAF collection has six adults from Calderdale, -24.860°S X 146.950°E, 8.vi.2000, G. Pegg & D. Spolc, with label data “*Acacia bancroftiorum* Maiden”. The ANIC has a very old specimen with the label “collected on *Acacia penninervis*” and no locality. Both these *Acacia* species occur at Barakula, but we did not observe the beetle on them. Both are phyllodinous species (Lithgow 1997) but are not closely related to *A. crassa* and their phyllodes have very different venation and texture from that of *A. crassa*. These putative hosts both need confirmation as a host plant that supports breeding in *Notoscantha*.

Acacia crassa is native to inland, eastern Australia where it occupies a range which is roughly concordant with the Brigalow Belt Biogeographic Region (Thackway

and Creswell 1995) though it reaches the coast in the northern part of its range. Its distribution is shown here from the Australian Virtual Herbarium data (Fig. 5). It grows as a small tree reaching about 10 m. Seedlings germinate readily in disturbed areas. At Barakula it is a common understory tree on sandy soils and young plants are numerous as roadside regrowth (Figs 2–4). It is phyllodinous, as apparent leaves are expanded leaf-like petioles known as phyllodes (Figs 4, 7). Developing phyllodes at apex of branchlets have apical and basal nectary glands (Lithgow 1997) which attract ants during early phyllode development. Mature phyllodes are crescentic and average about 15 cm by 2 cm in size; each surface of the phyllode is identical. Their lamina is comparatively thick (hence the name *crassa*) with tough parallel veins within the tissue spaced about 0.5 mm apart. Usually, three of the veins are thicker than the others (Figs 18, 19). *Notosacantha dorsalis* favours juvenile plants and was rarely seen on plants taller than 3 m.

The distribution of *A. crassa* is roughly the same as that of *Notosacantha dorsalis* in the southern part of the beetle's range. However, the plant does not extend north to the Charters Towers and Mount Garnet region where we have recent records for the beetle (cf. Figs 1, 5); thus, we predict the beetle has another host plant there.

Adults and adult feeding (Figs 8–11). Adults can be found on the foliage almost year-round, except though the second half of winter (July–August) which is also the driest part of the year. We presume adults overwinter in concealed sites such as under bark and in litter during this period. During rearing in Brisbane pupae and eggs did not overwinter which supports the idea that adults are the usual over-wintering stage. Mating takes place on the phyllode surface (Fig. 11) and is facilitated by the adults' ability to cling very strongly to the surface with their expanded tarsi.

Adults of *N. dorsalis* have lengths of 4.2–5.0 mm and widths of 3.3–3.8 mm and cling tightly to the phyllode surface when disturbed. They resemble discoloured patches on the phyllodes, which are often caused by their own larval mining. Males and females are similar in appearance and there is no obvious morphological difference which allows easy sexing of adults, however, males are normally a little smaller than females. Both males and females have 11-segmented antennae, contrary to that observed in other species which usually have 10 segments in the female (Borowiec and Takizawa 1991).

Adults feed on surface of the phyllodes by taking bites of the surface cuticle and the underlying juicy epidermal and mesophyll cells with their sharp, straight-edged mandibles as they move slowly forward or backward. Bites are made between the hard parallel veins; this progressively produces a straight, shallow, linear groove in the phyllode surface which may extend for 10–20 mm in a straight line (Figs 8, 9). The feeding beetle then reverses direction and makes a new feeding groove between an adjacent pair of veins. This process results in irregular patches of several closely parallel feeding grooves. The grooves soon turn brown on the



Figs 12–17. Oothecae of *Notosacantha dorsalis* and egg parasitoid, *Asecodes* sp (Eulophidae): (12) freshly deposited faecal ootheca on centre of phyllode; (13) detail of ootheca showing fragments of undigested cuticle; (14) ootheca lifted off egg, showing collateral gland sheath deposited over egg before faecal layer added; (15) incipient mine beside ootheca opened to show newly hatched larva; (16) ootheca lifted and egg removed to show collateral gland sheath above and below egg position; (17) egg parasitoid pupa removed from inverted ootheca. Key to lettering: **a**, cavity chewed in leaf surface by female for reception of ootheca; **b**, lifted and inverted faecal ootheca case; **c**, collateral gland sheath deposited over egg; **d**, remains of egg shell left by parasitoid; **e**, egg; **f**, pupa of egg parasitoid, *Asecodes* sp.

green background resulting in a distinctive appearance (Fig. 20) which is good indication that beetles are present on a plant. Adult feeding penetrates less than half the depth of the phyllode, so it is possible for adult feeding to take place on the opposite phyllode surface to areas that have already been browsed. Adult feeding inhibits later larval feeding mines from extending inside the leaf through

the same area (Fig. 20). Adult feeding is usually concentrated into patches of closely adjacent grooves, which seems to leave much of the phyllode available for subsequent larval mines.

Eggs and egg-laying (Figs 12–19). Eggs are elongate-ovate, pale yellow in colour and measure about 1.5 x 0.7 mm (Fig. 14). These are laid singly on the phyllode and always close to its centre (Fig. 12). The eggs may be laid on both sides of one phyllode, but it is rare for more than two eggs to be laid on any one side. We noted one example of four eggs on one phyllode, all being separated by at least 20 mm.

Before ovipositing, the female bites a short, deep cavity ca. 2.0 x 1.5 mm into the phyllode surface (Figs 14, 16, 17). She then deposits a single egg into the cavity and covers it with a thick, opaque sheath, presumably a secretion of the collateral glands. The sheath material seals to the edge of cavity all around but does not adhere to the egg surface (Figs 14, 16, 17). Occasionally the sheath material extends beneath the egg (Fig. 16). The female then deposits a pile of faeces that covers and surrounds the egg cavity and adheres to the glandular sheath. The female then presses her abdomen to flatten the faecal deposit. The final composite structure is termed an ootheca.

Microscopic examination of the surface shows that the faecal mass is composed of numerous squares of un-digested leaf cuticle, each representing a feeding 'bite' by the adult (Fig. 13). These cuticle pieces are embedded in a hard black material and often form a 'tiled' surface to the ootheca. The faecal material dehydrates to a hard, tough protective capsule for the egg. The long axis of the ootheca is always parallel to the long axis of the leaf (Fig. 12). Oothecae are about 2.5 mm long and 1.5 mm wide. Attachment of oothecae to the phyllode is very strong and these remain in place, even after hatching, for the life of the phyllode.

Egg duration, hatching and mine initiation (Figs 15, 18, 19). We followed the fate of 38 eggs which hatched and determined the average duration of egg stage to be 13.4 days (range 9–24 days). The egg is not visible, so hatching was determined as when the larva commenced a visible mine beside the egg capsule. Sometimes this may postdate actual hatching by a few days. We saw no evidence of delayed hatching as a hibernation device.

Since the egg is sunken in the leaf cavity made by the female in the phyllode tissue, the neonate larva can feed its way directly ahead, exit the egg chamber below the level of the hard faecal deposit, and enter the subsurface phyllode parenchyma tissue beneath the tough cuticle which remains intact as a transparent roof over the nascent mine chamber (Figs 15, 18). The mine chamber is connected to the empty oothecal chamber but not to the outside environment. This mine is rapidly enlarged by feeding in one direction, away from the empty ootheca which remains contiguous with the mine perimeter. Within a few days, the new larval mine may have a diameter of 3–5 mm. We term this first larval mine the 'primary mine', as defined below.



Figs 18–21. Primary larval mines of *Notosacantha dorsalis*: (18) newly hatched ootheca with small initial mine made by first instar emanating from capsule. Note early mine does not cross major veins; (19) same mine as in 18 opened to show first instar larva; (20) large primary mine emanating from ootheca at left. Note mine crosses major and minor veins but does not cross old adult feeding groves; (21) opened primary mine to show frass heap of faecal pellets (f) and exuviae (e) deposited by larva adjacent to ootheca (o). Note raised ribs of veins across floor of mine exposed by larval feeding.

Primary mines (Figs 15, 18–21). The primary mine is that made by the neonate larva once it ecloses. This mine is roofed by the transparent cuticle, has no opening to the exterior (it is closed) and has the hatched ootheca contiguous at one side. The cuticle bulges upward a little, giving the larva room to move freely within the mine. The larva extends the mine by feeding on sub-cuticular tissues at the edges of the mine. This is done by pushing and biting under the edge of the cuticle with its flat wedge-shaped head and prognathous mandibles (Fig. 26). The mine is extended in random directions across and along the phyllode, often towards both apex and base of the phyllode from the initial egg hatching site.

Mines never extend beneath previous feeding marks of adults on the phyllode surface (Fig. 20). We measured many mines and found the largest mines to have maximum length 100mm and maximum width of 20 mm. If two eggs are laid on one phyllode surface, then the two separate mines that develop from them sometimes merge; a merged mine may thus be occupied for a short time by two larvae. This is the only time we observed interactions between these solitary larvae. Two such larvae in one merged mine were never seen to both reach maturity suggesting some aggression/predation between the two larvae within such merged mines.

Rarely, the larva grows to full size and eventually pupates inside the primary mine.

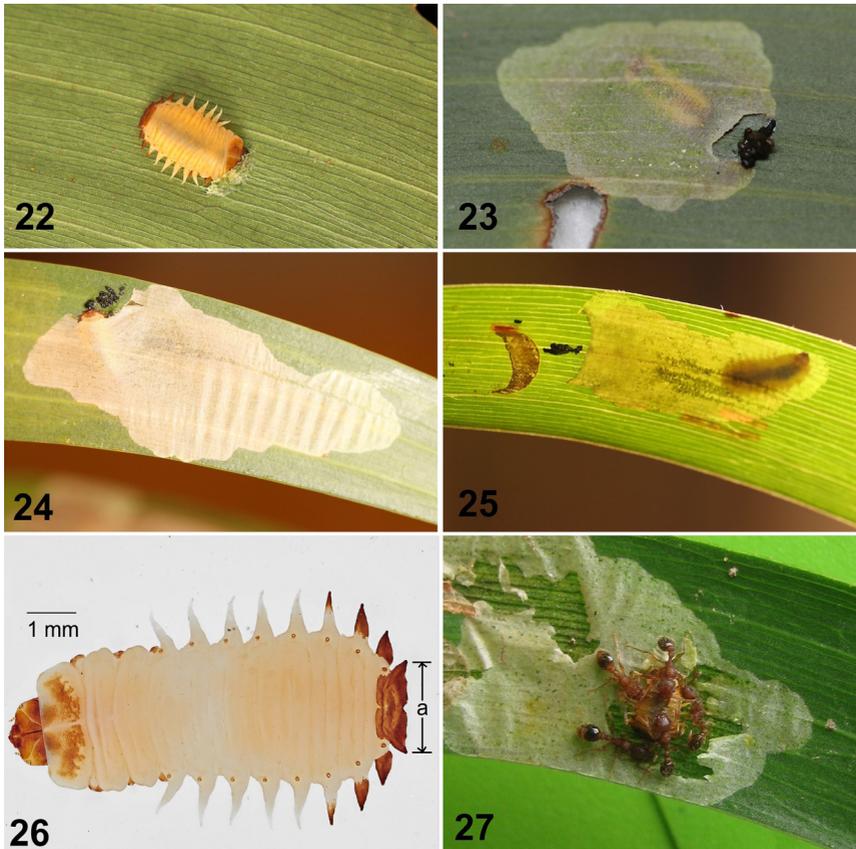
More commonly, the III–IV instars exit the primary mine and constructs what we term a ‘secondary mine’ as defined below.

Secondary mines (Figs 22–25, 28, 29). When the larva in a primary mine has exhausted areas of the original phyllode into which it can extend that mine, it exits the mine by cutting a slit in the cuticle, travels along the phyllode and stem surface, and then enters another phyllode surface. This may be on the opposite side of the original phyllode, on an adjacent phyllode, or sometimes several phyllodes further along the same stem. Such new mines have a permanent, crescentic opening and are termed ‘secondary mines’.

In our observations, secondary mines were always initiated at night when we presume the exposed, travelling larva was safer from predation (this was also presumed for other night-time crossing larvae in Ford and Cavey (1985)). We tested this ability to make new mines by removing several late-stage larvae from existing mines (in our garden plants) and enclosing them with cut phyllodes in petri dishes where they made new mines within about 30 minutes. The larva initiates the secondary mine by gripping the phyllode surface with tarsal claws, then swinging the head in a short arc from one side to the other, biting a curved incision 4–5mm long into the cuticle as it does so (Fig. 22). It then repeats the movement, biting into the epidermal cells beneath the cuticle and pushing further under the cuticle with its flat, wedge-shaped head. As this is repeated the cuticle progressively lifts and the larva pushes further and further under the cuticle until it is completely within an incipient mine with the distinctive arc-shaped entrance (Figs 23–25) that is characteristic of a secondary mine. The larva then continues to feed on the soft tissue and enlarges the mine as it did earlier in the primary mine.

In some cases, in our reared stock on potted plants, we observed larvae making a second secondary mine after they had exhausted available feeding area in the first mine. In one case, a single larva made three secondary mines in sequence, on three different leaves.

Larval behaviour within the mine: feeding, defaecation and moulting (Figs 21, 23–25). Within the mine the larva cuts through the upper part of the hard veins, freeing the cuticle above so that it lifts above the tissue surface. The larva then feeds on the soft tissue between the closely spaced, hard veins beneath it. This gradually exposes the veins as a series of raised ridges across the floor of the mine (Fig. 21). However, the mandibles functionally can only reach a short distance into the cleft between the veins, so only the upper layer of soft-tissue cells is consumed. Feeding is so shallow that two larvae can form separate mines on opposite sides of the same portion of a phyllode without the two mines becoming connected, while the stiff veins maintain the structural shape of the phyllode.



Figs 22–27. *Notosacantha* mature larva in secondary mines: (22) late instar larva commencing a secondary mine; (23) secondary mine showing wide, arc-shaped entrance where larva entered. Larva visible through cuticle roof of mine. Note larval faeces deposited outside entrance of secondary mines; (24) secondary mine with larva protruding rear end out entrance to deposit faeces; (25) backlit feeding larva in secondary mine, with faeces outside arc-shaped entrance. Larval gut is full and evacuated before pupation. Note on left abandoned first attempt by larva to commence mine; (26) last instar larva showing measurement of anal plate used for instar determination, photo © Queensland Museum; (27) *Tetramorium bicarinatum* ants killing a larva after tearing open the mine.

Young larvae in primary mines, during instars I–II, always deposit their faecal pellets by pushing them into a compact deposit against the opening into the empty ootheca (Fig. 21). This dries to a hard, black, shiny deposit. When the larva begins to moult, exuviae I and II are also pushed into this refuse pile and become covered by subsequent faecal deposits. From instar III onwards the faeces and exuviae are usually just deposited in the centre of the closed primary mine.

After the larva leaves the primary mine and enters a secondary mine, it then always deposits faeces and exuviae on the phyllode surface outside the opening of the secondary mine (Figs 23–25).

Duration of larval life. During breeding on potted plants in Brisbane we recorded four larvae which grew from egg hatching to pupation. The growth periods from egg hatching to pupation were 20 (26 Nov.–15 Dec.), 24 (13 Dec.–16 Jan.), 35 (5 Dec.–9 Jan.), and 36 days (5 Jan.–10 Feb.). These give an average of 29 days (range of 20–36 days). All occurred during the Australian mid-summer. We observed breeding well into early winter in the field, but we have no data on the larval durations at that time.

Pupation (Figs 28, 29). The prepupal larva is instar IV (see determination of instar number below). In secondary mines it always adopted a quiescent position just inside the arc-shaped mine entrance, with the head of the larva directed towards the entrance. During this period of a few days, the dark stomach contents, which could be seen at the centre of the larva by using a backlight (Fig. 25), were evacuated. Shortly afterwards, the pupal moult occurred; as the moult ended, twitching forward and backward pupal movements always ejected exuviae IV through the mine entrance. In our garden cultures, the pupal period, from moult to adult emergence ranged from 8–15 days in 8 observed individuals and averaged 12 days. There was no evidence of delayed adult emergence as an overwintering strategy. In early spring (5 Sept 2021) author VS found mature adults feeding, mating and laying eggs on foliage, with no sign of recent pupal mines on leaves. It is assumed these adults had spent winter in concealed hibernation.

Adult emergence (Fig. 29). The pupa rests inside the secondary mine with head towards the mine entrance. As the adult beetle emerges from the pupa it drags itself outside the entrance of the mine and the pupal exuviae is usually finally shed on the surface of the leaf, falling away. Only rarely does the pupal exuviae remain inside the mine. This is unlike some other hispines where the teneral adult remains in the mine, avoiding predators while the body hardens (Ford and Cavey 1985). The adult begins to feed on the leaf surface within 1–2 days of emergence.

Number of instars (Figs 26, 30). Since *Notosacantha* larvae live in a mine it is not possible to directly observe moulting. We determined the number of instars in *N. dorsalis* by two indirect methods: (1) measurement frequency of a standard body part, and (2) counting of exuviae discarded in mines.

(1) *Measurement frequency.* Head width is usually used for plotting a measurement frequency to determine larval number in insects under the Brooks-Dyar Rule (e.g., Floater 1996) and was applied for *Pentispa* (Cassidinae: Chalepini; Boldt and Staines 1993). We did not have a large enough sample of all instars of whole larvae to undertake this, so we used measurements of the maximum width of the heavily sclerotized last (ninth) abdominal tergum (anal plate) instead (Fig. 26). The anal plate is preserved intact in larval exuviae, of which we were able to obtain many from inside mines (Fig. 21). The width distribution of the 128



Figs 28, 29. Pupation and adult emergence of *Notosacantha dorsalis*: (28) opened secondary mine showing pupa shedding larval exuviae near mine entrance; (29) adult beetle shortly after emerging from the pupal exuviae outside the arc-shaped entrance of its secondary larval mine.

individual measurements obtained is shown in Fig. 30 where each bar represents the number of individuals which fall within an 0.04 mm size class. This clearly shows four size groups corresponding to instars. Figures indicate that ~95% of larvae fall into one of the following anal plate size classes: instar I (0.34–0.42 mm), instar II (0.60–0.70 mm), instar III (1.00–1.10 mm), instar IV (1.60–1.80 mm). This simple measurement provides some confidence to determine the instar of larvae.

(2) *Exuvial number.* Since exuviae of larvae in primary mines remain in the closed mine, usually embedded in the faecal mass, it was possible to carefully extract them from the faecal pile (Fig. 21) and arrange in sequence of size. We were never able to find more than three exuviae in the primary mine. We carefully observed the large larvae in their secondary mines. Those that had vacated their primary mine, leaving three exuviae behind, never moulted again more than once in their secondary mine. From this we arrived at the number of four larval stadia which accords with the results obtained from anal plate frequency measurement.

Predators of *Notosacantha dorsalis* (Fig. 27). During rearing of *N. dorsalis* in Brisbane, larvae and pupae inside the mines were often attacked and killed by the introduced ant *Tetramorium bicarinatum* (Nylander, 1846). This ant is a soil-nesting, semi-cosmopolitan, stinging species that has been introduced to Australia from its original distribution in S. E. Asia (Burwell, 2007). The ants tore open the surface membrane of the mine (Fig. 27), envenomated the larva or pupa, dismembered the body and carried it off. Although this ant is not established in natural environments in Australia, we assume that other native predatory ants may attack *Notosacantha* mines in the field, though we did not observe this.

Parasitoids of *Notosacantha dorsalis* (Figs 16, 17). Hymenopteran parasites of both egg and larval stage were detected in *N. dorsalis*. A larval parasite was taken on only one occasion, but in numbers, and the specimens have been identified as an undescribed species of *Notanisomorphella* Girault, 1913 (Hymenoptera: Eulophidae; Chris Burwell, *pers. comm.*). Thirty-one primary larval mines were collected by GM at Braemar State Forest, 15 March 1980. When opened, 15 of

the mines contained dead beetle larvae plus pupae, pupal exuviae and/or adults of the wasp parasitoid. The parasitoid larvae had emerged from a single hole in the venter of the beetle larvae and numbered from 1–6 (mean 2.4) per host larva. The parasite larvae pupate free in the mine with the pupa connected by its shed exuviae to a congealed drop of prepupal faeces on the floor of the mine. Where the emerged wasps had exited the mine, there was a circular chewed hole in the roof of the mine. Nine male and 20 female adult wasps were recovered from the mines. Since they were all closed primary mines it is assumed that female wasps oviposited into the beetle larva through the roof membrane of the mine.

The egg parasite was detected twice. Of 11 egg oothecae collected at Barakula by GM on 10 June 2018, six contained viable eggs while five had remains of the pupae of an unknown microhymenopteran (Hymenoptera) which had consumed the egg. Very recently VS collected 20 egg oothecae at Barakula on 5 Sept 2021. Six of these contained pupae of the same parasitoid (Fig. 17), two of which hatched on 20 and 21 September to a 1.0 mm slender metallic green wasp now identified as a species of *Asecodes* Förster, 1856 (Eulophidae: Entedontinae) by Dr Chris Burwell. He advises that the biology of the species in the genus is varied, with hosts including Diptera (especially Agromyzidae), Lepidoptera and Coleoptera. They are parasitoids of egg, larvae and pupae; some are parasitoids of Chrysomelidae eggs, including hispines (Burwell, *pers. comm.*). It is difficult to conceive such a small wasp, lacking a long ovipositor, penetrating the oothecal defence of the *Notosacantha* egg. Being very small, it may oviposit by stealth during the actual egg laying process.

The field infestation rate for both the above parasitoids was quite high in the collected field samples. Neither was encountered in two years of rearing *Notosacantha dorsalis* in open situations in Brisbane which is outside the natural range of the beetle. Ant predators and Hymenoptera parasitoids are common enemies of Cassidinae (Cox 1994, 1996).

Discussion

Our study of *N. dorsalis* revealed many features relevant to species variations in *Notosacantha* and to broader patterns, including existing and potential character hypotheses, that could strengthen the systematics of the genus and tribe within Cassidinae. We discuss some of these below, with potential information for phylogenetic characters in Chaboo (2007: Appendix 4) for Cassidinae and in wider Chrysomelidae (Reid 1995).

Notosacantha species show a wide choice of host plants (Table 1: 12 different families to date) and it is difficult to discern any phylogenetic and or chemistry patterns across these choices. A single *Notosacantha* species can use phylogenetically diverse hosts, e.g., Sekerka (2009) reported *N. molucana* on three confirmed, unrelated hosts. Ghate *et al.* (2003) remarked “Both the species of *Notosacantha* prefer plants with somewhat thicker, smooth surface leaves.” Our observations concur with selection of thicker, smooth leaves.

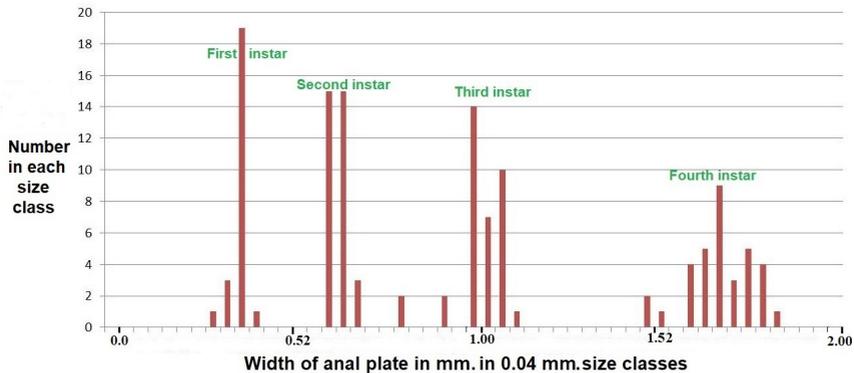


Fig. 30. Plot of size frequency of widths of measured anal plates of 128 larvae of *Notosacantha dorsalis* used to determine number of instars. Each bar represents number of anal plate widths in that size class.

Our observations revealed solitary, sessile eggs attached within a groove chewed out by the female (Characters 0–1 of Chaboo 2007; Character 48 of Reid 1995). This maternal behaviour of preparing the groove is similar to that reported for *N. siamensis* (Medvedev and Eroskhini (1988) and resembles reports for cassidine genera (e.g., Chalepini: *Pentispa* Chapuis, 1875 by Boldt and Staines 1993; Coelaenomenoderini: *Javeta* Baly, 1858 by Shameem *et al.* 2016; Hispini: *Platypria* Guérin-Méneville, 1840 by Ranade *et al.* 2021). It may be widespread in Cassidinae and could offer a novel phylogenetic character. Another potentially novel character is the maternal behavior of covering the egg, resembling that in some other cassidines (e.g., Chalepini by Boldt and Staines 1993; Promecothechini by Taylor 1937). The female's effort to cover and flatten the faecal pile is reminiscent even of Camptosomata leaf beetles whose females may spend up to one hour carefully creating the protective coating of single eggs (Brown and Funk 2005). The material covering the egg is significant since some females of mining Cassidinae secrete a fluid that hardens into an ootheca (e.g., *Javeta*, *Platypria*) whereas others regurgitate leaf fibres (*Coelaenomenodera* Blanchard, 1853) (Shameem *et al.* 2016). Multi-layered membranous oothecal coverings also occur in some tortoise beetles (e.g., *Aspidomorpha miliaris* (Fabricius, 1775) produces very complex ootheca; Maulik 1919). Some elaborate oothecae may be further covered with faecal deposits (Verma and Kailachelvan 2004). Thus, there is rich diversity in Cassidinae maternal behaviors at oviposition.

Cassidinae larvae display a remarkable variation in the number of instars, ranging from two in *Promecothecha cumingii* Baly, 1858 (Maulik 1919) to nine in *Alurnus humeralis* Rosenberg, 1898 (Villacis Santos 1968). Our determination of the number of four instars may be the most comprehensive done for any Cassidinae. This may be the norm in Notosacanthini, Coelaenomenoderini, Hispoleptini, and

Table 1: Recorded foodplants of *Notosacantha* (see Borowiec and Świętojańska 2012–2019 for original sources) updated with additional records (marked by *) from Borowiec and Takizawa (1991) and this paper.

NOTOSACANTHA SPECIES	PLANT SPECIES	PLANT FAMILY	REGION
<i>Notosacantha badia</i> (Boheman, 1850)	<i>Gymnosporia mossambicensis</i> (Klotsch) Loes.	Celastraceae	South Africa
<i>Notosacantha calligera</i> (Spaeth, 1921)	<i>Gironiera</i> sp. <i>Knema</i> sp.	Myrsinaceae	Borneo
<i>Notosacantha dammaropsi</i> Sekerka, 2009	<i>Ficus dammaropsis</i> Diels	Moraceae	New Guinea
<i>Notosacantha diabolica</i> Świętojańska, 2001	<i>Ardisia</i> sp. <i>Embelia</i> sp.	Myrsinaceae	Borneo
<i>Notosacantha dorsalis</i> (Waterhouse, 1877)	<i>Acacia crassa</i> Pedley ? <i>A. bancroftiorum</i> Maiden ? <i>A. penninervis</i> DC	Fabaceae	Australia
<i>Notosacantha junodi</i> (Spaeth, 1913)	<i>Tarenna pavettooides</i> (Harv.) Sim	Rubiaceae	South Africa
<i>Notosacantha laticollis</i> (Boheman, 1862)	<i>Canthium inerme</i> (L.P.) Kuntze	Rubiaceae	South Africa
* <i>Notosacantha maculipennis</i> (Boheman, 1850)	<i>Alnus</i> sp.	Betulaceae	India
<i>Notosacantha molucana</i> (Boheman, 1850)	<i>Decalobanthus peltatus</i> (L.) Simoes and Staples <i>Pterocarpus indicus</i> Willd. <i>Ficus variegata</i> Blume	Convolvulaceae Fabaceae Moraceae	Ambon, New Guinea Australia?
* <i>Notosacantha nepalensis</i> Borowiec and Takizawa, 1991	<i>Cleyera japonica</i> Thunb.	Theaceae	India
<i>Notosacantha pakistanica</i> Sultan <i>et al</i> , 2008	<i>Alnus nitida</i> (Spach) Endl.	Betulaceae	Pakistan
<i>Notosacantha quadra</i> (Spaeth, 1915)	<i>Ardisia elliptica</i> Thunb.	Myrsinaceae	Borneo
<i>Notosacantha severini</i> (Spaeth, 1913)	<i>Carissa carandas</i> L.	Apocynaceae	India, Thailand
<i>Notosacantha siamensis</i> (Spaeth, 1933)	<i>Phyllanthus emblica</i> L.	Euphorbiaceae	Thailand Vietnam
<i>Notosacantha tenuicula</i> (Spaeth, 1913)	<i>Cleyera japonica</i> Thunb.	Theaceae	India, Nepal
<i>Notosacantha vicaria</i> (Spaeth, 1913)	<i>Glochidion ellipticum</i> Wight <i>Carallia brachiata</i> (Lour.) Merr.	Euphorbiaceae Rhizophoraceae	India Sri Lanka

some Hispini (see Chaboo 2007:45). It is unclear if contracting and speeding the life cycle avoids enemy pressure.

Taylor (1937), using the synonym *Promecotheca reichei* Baly, 1869 for *Promecotheca caeruleipennis* Blanchard, 1853, pointed out that the mining neonate larva chews forward from the egg, so the leaf in front of the egg must be long enough to accommodate larval consumption and growth. Our observations confirm that the neonate *Notosacantha* initially chew forwards from the egg, but since the egg is always placed in the centre of the leaf, and since an irregular blotch mine is formed, there is always room for the mine to later expand in any direction.

The ability of the *N. dorsalis* leaf-mining larva to exit the initial mine and to re-enter the leaf at a different site has been documented for other *Notosacantha* species in India (Rane *et al.* 2000; Ghate *et al.* 2003; Ghate 2004), South Africa (Heron 2018), and Vietnam (Medvedev and Eroshkina 1988). Medvedev and Eroshkina (1988) termed the initial mine a ‘trophic mine’. In those other *Notosacantha* species, the secondary mine or ‘pupal mine’ is made only at the end of larval life; no substantial feeding takes place in the new mine and it is made just big enough to accommodate the pupa. In *N. dorsalis*, however, the first secondary mine is usually made well before the end of larval growth, may be enlarged considerably by feeding to become as large as the primary mine, and this enlarged secondary mine serves for pupation.

Of the larval exit from a primary mine, Medvedev and Eroshkina (1988) write (translation): ‘So they cut at one end, and crawl out backwards. The end is obviously cut by the posterior shovel, but we did not observe it.’ By ‘posterior shovel’ they refer to the sclerotized and toothed anal plate (Fig. 26). Our breeding larvae often exited primary mines through a cut slit, always at night, and we also did not observe this process. However, we often observed larvae cutting slits for entry into new mines (Fig. 22) and their chisel-shaped head and cutting mandibles are the efficient tools used in this process. We suggest that it is not necessary to speculate that the anal plate is used to make exit slits when the mandibles are available. From our observations we believe the sclerotized and toothed structures at the anal end of the larvae function to grip the surface of the substrate to aid in pushing the body forward during forward locomotion, especially when inside the mine.

Chrysomelid larval morphology strongly reflects their life as leaf miners, cryptic feeders, or open feeders (Reid 1995) and this applies to *Notosacantha* larvae with their dorso-ventral flattening and wedge-shaped, knife-edged head. We will address specific features, patterns and characters in a future study on morphology of mining larvae.

Few characters have been developed and tested for chrysomelid pupae (Reid 1995). Chaboo (2007) offered just two characters for Cassidinae and López-Pérez *et al.* (2021) proposed 10 new ones. Nevertheless, as more Cassidinae pupae are

being collected and described, this life stage could potentially offer a novel suite of characters to inform phylogeny resolution. The pupation site and morphology of *Notosacantha* pupae are promising avenues for future exploration.

Conclusions. Not long ago, Borowiec and Świętojańska (2014b:199) considered “Life cycles of Cassidinae are generally poorly known and concern mostly Holarctic species.” As more species are studied world-wide, particularly those with leaf mining life cycles, we are uncovering rich information to determine novel patterns, unique traits, and new character hypotheses for taxonomic and evolutionary assessment. Our study of museum specimens here suggests more diversity in the adults of *Notosacantha* in Australia so clearly more collecting and morphological study are needed. These species will be examined further as we focus next on the morphology of the life stages of *N. dorsalis*. Our study converges with the review of Bornean *Notosacantha* (Borowiec *et al.* 2013) and of Indian *Notosacantha* (Hari and Prathapan, unpublished data) and altogether will unravel further the biology and systematics of this ancient and evolutionarily enigmatic tribe of Cassidinae.

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