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The life history of *Vegetia grimmia* (Geyer, 1832) (Saturniidae: Bunaeinae: Micragonini), with an account of its discovery, distribution and taxonomic distinction

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Abstract: The complete life history of *Vegetia grimmia* (Geyer, 1832), an uncommon species of Saturniidae restricted to the southwestern parts of the Western Cape province of South Africa, is described and illustrated for the first time. All immature stages of the species are described and illustrated, the larval host plants are recorded and a distribution map of the species based on all available records is compiled. The history of the scientific discovery of the species is summarised, and its distinction from similar species and its taxonomic status are clarified. Parasitism of its eggs by a parasitoid wasp in the genus *Anastatus* (Eupelmidae) is recorded and illustrated with high-resolution photographs, which are also available on www.waspweb.org.

Key words: larva, pupa, life cycle, *Eriocephalus*, *Cymbopappus*, *Vegetia ducalis*, *Vegetia dewitzi*, parasitoid, *Anastatus*.

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INTRODUCTION

Africa harbours a large fauna of Saturniidae, currently classified in six tribes, approximately 50 genera and more than 400 species. However, its taxonomy remains chaotic, with many taxa added in recent decades based on very scant morphological and genetic (“barcode”) evidence, usually without proper revisionary work (such as study of the types of older available names) and published without adequate (or any) peer review. Even though the actual diversity of the African Saturniidae is thus difficult to gauge, it is evident that the fauna is widely distributed over most of the continent, especially in savanna and forest regions but also in the more arid southwestern and northeastern areas. A noticeable exception to this pattern is the dearth of taxa in the extreme southwestern part of the continent, in particular in the area with cool-season rainfall recognised as the Greater Cape Floristic Region, which is in stark contrast to its high floristic diversity and endemism (e.g. Born *et al.*, 2006; Manning & Goldblatt, 2012; Colville *et al.*, 2014), suggesting that Saturniidae may have only intruded into this ecoregion sparingly and perhaps recently.

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There are two endemic saturniid genera in the southwestern part of Africa, *Eochroa* C. & R. Felder, 1874 and *Vegetia* Jordan, 1922, classified in the tribes Eochroini and Micragonini, respectively. *Eochroa* contains a single species, *E. trimenii* C. & R. Felder, 1874, and *Vegetia* four, *V. dewitzi* (Maassen, 1885)[1], *V. ducalis* Jordan, 1922, *V. grimmia* (Geyer, 1832) and *V. legraini* Bouyer, 2004. Single species of three genera of the tribe Bunaeini also extend into this region from the east, *Heniocha apollonia* (Cramer, 1779), *Gonimbrasia tyrrhea* (Cramer, 1775) and *Nudaurelia cytherea* (Fabricius, 1775), but these genera all contain several other species and occur widely throughout Africa. Of the four species of *Vegetia*, *V. dewitzi* and *V. legraini* inhabit the arid inland areas of the larger Cape region (the Karoo and southern Namibia, or the Nama-Karoo Biome), whereas *V. ducalis* and *V. grimmia* are restricted to the western and southwestern coastal areas of the Northern and Western Cape provinces. The genus most closely related to *Vegetia*, *Ludia* Wallengren, 1865, occurs north- and eastwards of the range of *Vegetia* throughout most of Africa, comprising approximately 15 species. Although the larvae of three of the species of *Vegetia* are now known (Pinhey, 1972; Oberprieler, 1995; Lampe, 2010; Staude *et al.*, 2016, 2020), their full life histories were not

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[1] The authorship of the name of this species is usually cited incorrectly in the literature. The name was coined by J. Peter Maassen only, as “**Ludia Dewitzi** Msssn. [*sic*] ♀ / Cap. Berl. Univ. Mus.”, not by him and August Weyding (who was the illustrator of the work in which the species was described). The correct full species name is therefore ‘*Vegetia dewitzi* (Maassen, 1885)’, and the bibliographic reference to the original name is ‘*Ludia dewitzi* Maassen in Maassen & Weyding, 1885: [1], figs. 90, 91’. This authorship (and concomitant mistakes in literature citations) applies to all other new species names published in this work (Maassen & Weyding, 1885).

yet described. *Vegetia grimmia* is the rarest of these species (only the Namibian *V. legraini* is rarer, known from only a single specimen) and also the one whose history is shrouded in the greatest mystery. In this paper we describe its life history, the first for any species of the genus, and provide a detailed account of its scientific discovery, its distribution and its distinction from the similar *V. ducalis*.

METHODS AND MATERIALS

History and distribution

All records of *V. grimmia* in the entomological literature were studied, and specimen records in all museums and some private collections in southern Africa and in some major overseas museums, gathered since the 1980s by R. Oberprieler, were used to collate the history of discovery of the species and to compile a first distribution map. Records of more recent discoveries by present-day collectors, many posted on the iNaturalist network (https://www.inaturalist.org), were verified and added to compile as comprehensive a distribution map as currently possible. The map was constructed using the software application ArcMap 10.8.1 (ArcGIS Desktop).

Rearing and documentation of life history

Larvae were collected in the wild in 1983 and 1989 by R. Oberprieler and in 2018, 2019 and 2020 by A. Morton and reared to pupation in captivity, following the method and protocol outlined by Joannou *et al*. (1992) and Oberprieler (1995). Observations of their behaviour and life cycle were made both in the field and in captivity. Photographs were taken of all immature stages (including all larval instars) as well as of their natural habitats. Some larvae of the 1983 and 1989 rearings were preserved in ethanol (in Collection R. Oberprieler), as were dried eggs, pupae and cocoons, and adults resulting from all broods were deposited in a number of collections. Parasitoid wasps that emerged from eggs collected in the wild were photographed, mounted and deposited in the Iziko South African Museum in Cape Town (SAMC).

RESULTS

History of discovery of *Vegetia grimmia*

Vegetia grimmia is the first-collected and first-described species of the genus, but its scientific discovery and region of occurrence remained enigmatic for a century and a half after its original description. It was named and illustrated by Peter Carl Friedrich Geyer (1802–1889), a German copper engraver who illustrated and published various supplements to Jacob Hübner's (1761–1826) works on Lepidoptera. The date of the name, which was originally coined as '*Heniocha Grimmia*', is generally stated incorrectly as 1837 (Kirby, 1892; Sonthonnax, 1904; Pinhey, 1972) or 1831 (Jordan, 1922; Schüssler, 1934; Bouvier, 1936; Bouyer, 1999; Lampe, 2010; d'Abrera, 2012), but Hemming (1937: xx–xxi) provided evidence that *Lieferung* 154.b. of Hübner's *Sammlung exotischer Schmetterlinge* Vol. 3, which comprises plate [44] with the illustration of the species, was published by Geyer between 20 July and 31 December 1832. The correct full name and authorship of the species is therefore *Vegetia grimmia* (Geyer, 1832).

The exact origin of the specimen on which Geyer's (1832) illustration is based appears unknown. He gave its provenance only as "Africa merid.", and this vague origin, or the English version "South Africa", was repeated in most subsequent literature (*e.g.*, Westwood, 1849; Kirby, 1892; Sonthonnax, 1904; Jordan, 1922). Only Gaede (1927) and Schüssler (1934) were somewhat more specific in writing "Capland" as distribution of the species. Most authors only knew *V. grimmia* from Geyer's illustration, Fawcett (1915) even stating that only "Hübner's" figure was known of it. However, Strand (1910) had reported examining a specimen in poor condition (forewing torn and covered in glue so that the venation could not be assessed) in the Museum für Naturkunde in Berlin, and Jordan (1922) later suspected this specimen to be Geyer's type, writing: "A specimen in the Staudinger collection (Mus. Berlin) from Herrich-Schäffer's collection. It agrees so well with Geyer's figure that one might be inclined to regard it as the specimen from which the figure was drawn". Comparison of Figs 1A and 1C shows that this is indeed the case. The specimen bears the labels 'Coll. H. Sch.', 'TYPE', 'grimmia H. Sch. Cap', 'Staudinger K 829' and 'Vegetia grimmia Geyer'. How it came into the collection of the German physician and entomologist Gottlieb August Wilhelm Herrich-Schäffer (1799–1874) is not recorded. Herrich-Schäffer's collection was purchased by the German natural-history dealer Otto Staudinger (1830–1900) and, after the latter's death, went to the Museum für Naturkunde in Berlin in 1907. It appears that no other specimens of *V. grimmia* were in existence in European collections until the late 1980s (see below).

Geyer did not provide a derivation of the name *grimmia*, but the species is evidently named after a person with the surname Grimm. The species epithet *grimmia* is also contained in the scientific name of the Common Duiker, *Sylvicapra grimmia* (Linnaeus, 1758), which was named after the Swedish doctor and pharmacist Herman Niklas Grim (Hermann Nicolaus Grimm in German, latinised as Hermannus Nicolaus Grimmius) (1641–1711). Grimm (1686) had described this antelope species from an animal he observed at the Cape Town Castle, under the name "*Capra silvestri Africana*", but as the start date of zoological nomenclature is 1758, Grimm's name is not nomenclaturally available and Linnaeus' name is the valid one. Grimm worked as a doctor for the Dutch *Verenigde Oost-Indische Compagnie* (United East-India Company) in Batavia between 1665 and 1682 (Wikipedia, https://de.wikipedia.org/wiki/Herman_Niklas_Grim) and must have visited the former Dutch settlement at the Cape of Good Hope several times on his journeys between the Netherlands and Indonesia. He is not recorded as having collected natural history specimens around the settlement, but he probably explored the surrounding vegetation for medicinal plants, as he had done in Batavia, and may have encountered a specimen of *Vegetia grimmia* during such a venture. If so, it is, however, unlikely that he collected and brought it to Europe and that it would have remained there preserved in a collection but unstudied for about 150 years. If *V. grimmia* was indeed named after H. N. Grimm, he may not have known this species at all. From the labels on the type specimen in the Museum für Naturkunde in Berlin it seems more likely that the name *grimmia* was originally devised by Herrich-Schäffer and then adopted and published by Geyer. Herrich-Schäffer may have selected the name to honour either the (unknown) collector of the specimen or a contemporary scientific colleague, such as the German physician and botanist Johann Friedrich Carl Grimm (1737–1821), or some other member of the Grimm family, which, like the Schäffer family, was an eminent one in Regensburg in the 18th century and related to the Schäffers by marriage (Fürnrohr, 1963). The vernacular English name 'Grim Princeling' coined by Pinhey (1972) for *V. grimmia* is thus inapt; the species should be called 'Grimm's Princeling' instead.

A precise locality for *V. grimmia* was first published by Pinhey (1972), as "Cape L'Agulhas". Elliott Charles Gordon Pinhey (1910–1999) evidently did not know the species himself but obtained the place name from photographs of a specimen sent to him by the former Transvaal Museum in Pretoria, South Africa (now Ditsong National Museum of Natural History). The relevant specimen in that museum is a female collected by O. West at Cape Agulhas on 11 December 1911. Another female with the same collecting data is preserved in the Albany Museum in Grahamstown, and two females taken at Cape Agulhas in 1889 by W. E. Fry are in the SAMC (catalogue number SAM-LEP-A022996). In the SAMC there is also a male collected at Riversdale in 1901 by H. Fry (number SAM-LEP-A022997). The existence and locations of these five specimens taken around the beginning of the 20th century were evidently unknown to European authors, and it appears that the species was not seen again until the 1980s.

Vegetia grimmia was rediscovered at Struisbaai (near Cape Agulhas) in September 1983 by Rolf Oberprieler and Mark Williams, who had set out to find the larvae. The host plant was surmised to be a species of *Eriocephalus*, as *E. africanus* had been recorded as the host plant of *V. ducalis* by C. G. C. Dickson at Cape Town, Tygerberg and Malmesbury in 1946 and later (Dickson, 1965; as *E. umbellatus*), and this host plant was confirmed for *V. ducalis* by Oberprieler and Williams at Springbok and Nabapeep Poort in 1983 and later (Oberprieler, 1995; Staude *et al*., 2016). On 14 September 1983 about a dozen larvae of *V. grimmia* were found at Struisbaai feeding on *E. racemosus* bushes in the narrow strip of fynbos vegetation between the road and the beach, about 100 m from the shoreline (Figs 3A, 3B). Most larvae were in the fifth instar (L5) (Fig. 3E), but a few second-, third- (Fig. 3D) and fourth-instar larvae were also found, as were some clusters of empty ova (Fig. 3C). The larger larvae spun cocoons (Fig. 3H) and pupated at the end of September in captivity in Pretoria, but only one male successfully eclosed, in March 1984 (Fig. 1E). Oberprieler visited the same site again in September 1986 but found no larvae, but on 11 October 1989 he encountered 32 larvae at the site, again mostly in the fifth instar (Figs 3F, 3G). Several adults reared from these larvae eclosed in March 1990 (Figs 1D, 1F, 2A, 2B). Photos of these larvae were published by Lampe (2010) and Staude *et al*. (2016). Due to a lack of suitable host plants in Pretoria, it was not possible to rear a second generation of larvae in captivity and document also the earlier larval instars.

Subsequent to this rediscovery of *V. grimmia* and the first recording of its larva and host plant, the species was also recorded from the Gamkaberg Nature Reserve in April 1990, Riviersonderend in May 1999, the Haarwegskloof Nature Reserve in the Overberg region in September 2015 (Figs 6F, 6G), Montagu in May 2016 and 2018 (Figs 2G, 2H), McGregor in May 2017, the Cape of Good Hope Nature Reserve (on the Cape Peninsula) in October 2018 and subsequent years (Figs 4A–6E) (Staude *et al*., 2020) and the Eagle Rock Nature Reserve near Villiersdorp in May 2021. These records enabled an assessment of the broad distribution range of the species (Fig. 8). The discovery of the species in the Overberg region also revealed another host plant, *Cymbopappus adenosolen*, also a member of the Asteraceae and classified in the same tribe as *Eriocephalus*, and the successful recent rearing of several batches of larvae from the Cape Peninsula (where they were also found feeding on *E. africanus*) by A. Morton enabled the documentation of the entire life history. The discovery of *V. grimmia* on the Cape Peninsula also suggests that the type specimen, originally in the collection of Herrich-Schäffer and now in the Museum für Naturkunde in Berlin, may have been collected in that area rather than 220 km further east at Cape Agulhas, the next-oldest known locality (the lighthouse there was only built in 1848), and hence that the type locality of *V. grimmia* is probably somewhere on the Cape Peninsula.

Life history

Larval host plants

Three species of Asteraceae are so far known to serve as hosts for the larvae of *V. grimmia*: *Eriocephalus racemosus* (recorded at Struisbaai in 1983 and 1989, on the Cape Peninsula in 2018 and 2020), *E. africanus* (recorded on the Cape Peninsula in 2018 and 2019) and *Cymbopappus adenosolen* (recorded in the Haarwegskloof Nature Reserve in 2015 and 2016). *Eriocephalus* and *Cymbopappus* belong to the same tribe, Anthemideae, of the family Asteraceae and are South African endemics. *Eriocephalus racemosus* is an erect shrub of up to 1.5 m in height with silvery-grey, hairy, linear, densely grouped and highly aromatic leaves and creamy white flowers borne along the branches (Fig. 3B). The species occurs on sandy soils along and adjacent to the coast of the Western Cape province (Fig. 8). *Eriocephalus africanus* is a bushy green shrub up to 1.5 m in height with silvery-green leaves arranged in tufts along the branches and snow-white flowers covering the whole bush. It occurs on granite slopes of the western part of the Northern Cape and the southwestern parts of the Western and Eastern Cape provinces, and it is the main host plant of the closely related species *V. ducalis*. *Cymbopappus adenosolen* is a branched shrublet of 0.2–0.6 m height with a woody rootstock, smooth, linear, sometimes alternate leaves and small, white, yellow-centred flowerheads. It occurs in dry clay soils in Renosterveld habitats in the Overberg region and western Little Karoo (Fig. 8).

Ovum

Ova are ca. 1.4 × 1.8 mm in size, oval, slightly flattened. Initially they are irregularly patterned in brown, beige and cream colours, due to being covered by a liquid secreted from the female's abdomen to stick the ova together and onto the substrate (Oberprieler, 1995), but later they become plain white. They are laid in irregular clusters of up to 100 on thick stems and branches of the larval host plant (Figs 3C, 4A). They are prone to parasitism by eupelmid wasps (see below).

Larva

The larva of *V. grimmia* is typical of the tribe Micragonini in having the 'pin-cushion' type of scolus, a low verruca studded with sharp, stiff, needle-like 'dry' bristles that administer a histamine-type of irritant (rather than a liquid, as occurs in the tribe Saturniini). This scolus type was termed *Stechborstenscolus* (stinging-bristle scolus) by Nässig (1989) and appears to constitute a synapomorphic character of the Micragonini (Oberprieler & Nässig, 1994; Oberprieler, 1997). Other micragonine characters present in the larva of *V. grimmia* are the finely plumose secondary hairs and the separate dorsal scoli of abdominal segment VIII (A-VIII) (fused in Bunaeini and most Urotini but also separate in Eochroini). Other salient characters of the larva of *V. grimmia* are: head dark with pale clypeus and pale adfrontal lines and lateral areas, 6 pairs of stemmata (each set arranged in a ring of 5 and a single one beneath the antenna); prothoracic shield short, anteriorly ridged with stinging bristles; 4 rows of segmental scoli on thorax (dorsal, dorsolateral, lateral, ventrolateral), abdomen without ventrolateral scolus row, dorsal scoli with 2–3 long white hairs at centre and ca. 40 pale-brown, black-tipped stinging bristles, dorsolateral and lateral scoli similar but with ca. 10–20 bristles and each row placed in pale lateral longitudinal stripe, ventrolateral scoli without bristles, only with hairs; anal shield (on segment A-X) short, strip-like; spiracles upright-oval, dark with pale outer ring; procoxae fully fused mesally, thoracic legs dark reddish-brown, abdominal prolegs dark with yellowish-brown outer lateral sclerite, anal claspers uniformly brown. There are five larval instars in both sexes, as in some other genera of Micragonini (*e.g., Ludia, Campimoptilum* Karsch, 1896 and *Decachorda* Aurivillius, 1898) but unlike as in *Holocerina* Pinhey, 1956, which has only four instars in the male.

1st instar (L1) (Figs 4B–D). Length ca. 2–10 mm; body uniformly jet-black, scoli with orange-brown, black-tipped bristles, longer non-stinging hairs only laterally; head black with pale clypeus, thoracic legs black, abdominal prolegs with black base and yellowish apex.

2nd instar (L2) (Figs 4E, 4F). Length ca. 10–20 mm; body black except for broken whitish lateral stripe beneath row of dorsolateral scoli and continuous whitish stripe along row of lateral scoli, scoli orange-yellow, elongate, with tufts of long white hairs, dorsal and dorsolateral scoli with 2– 3 long white hairs among shorter, brownish stinging bristles; segments dorsally each with 2 bands of dense white secondary setae directed mesad, one band before and the other behind scoli; head evenly dark brown except for pale clypeus and paler adfrontal lines.

3rd instar (L3) (Figs 3D, 4G, 4H). Length ca. 20–45 mm; similar to L2 but head with larger paler mottled area laterally (except around stemmata), body integument black except for numerous whitish setal bases, creating a speckled appearance; lateral stripes more pronounced and undulating, lateral scoli darker orange-brown, white setae on dorsal bands before and behind scoli even denser and more erect, long white setae on scoli longer and very pronounced; some larvae with brown lateral hairs between stripes, sometimes very dense and obscuring stripes.

4th instar (L4) (Figs 5A–D). Length ca. 45–65 mm; similar to L3 but integument more extensively black, lateral stripes thicker and more conspicuous, white dorsal hairs denser still; some larvae with more or less dense brown lateral hairs interrupting or obscuring white lateral stripes, scoli on these not orange-brown (Figs 5C, 5D).

5th instar (L5) (Figs 3E–G, 5E–H, 6A–D, 6F, 6G). Length ca. 65–80 mm; very similar to L4 but bulkier, especially females.

Variability Later-instar larvae (L4 and L5) are variable in coloration, three main colour forms being recognisable: a) white-and-black, with grey-and-black dorsal patches in front of scoli and orange-brown patches on lateral stripes, mainly around the scoli (Cape Peninsula; Figs 5A, 5B, 5E–G, 6C, 6D); b) reddish-brown, with orange-brown dorsal patches and reddish-brown lateral patches (Cape Agulhas and Overberg; Figs 3E–G, 6F); c) yellow/brown-and-black, with yellow to brown hairs laterally and sometimes dorsally and no coloured patches on lateral stripes (Cape Peninsula and Overberg; Figs 5C, 5D, 5H, 6A, 6B, 6G). The yellow/brown-and-black form occurs together with the white-and-black one in the Cape Peninsula and with the reddish-brown one in the Overberg region, but the latter two have thus far not been found together at the same localities.

Behaviour The larvae are semi-gregarious in L1, sitting and feeding together in small groups but without touching (Figs 4B, 4D), but less so in L2 and L3 and solitary in L4 and L5. The L1 larvae do not consume the eggshell after hatching. Feeding behaviour on plants is similar to that of other African saturniid larvae, in that the early-instar larvae feed more exposed at the tips of leaves and gradually strip them down from the tip in long downward movements of the head (Fig. 4D), whereas the larger, later-instar larvae feed further inside the bushes, hanging from twigs (as large caterpillars almost always do) and consuming entire leaves one after another (Figs 3E, 3F, 5E). Larger larvae tend to feed with the body inside the bush and the head pointing outwards, and they orientate towards the sun and move around the bush during the day to maintain exposure to the sun (presumably for warmth). In stable weather and when undisturbed (as in captivity), they can feed 24 hours a day, but in inclement weather (cold wind and rain) they stop feeding and retreat into the interior of the bushes. From a distance they are well camouflaged in the bushes, hanging beneath branches and their outline broken up by the long hairs and segmental colour pattern, but at close range their aposematic coloration is apparent, especially on their backs (Figs 3G, 6B, 6F), evidently serving as a warning of their urticating properties to vertebrate predators. When physically disturbed, they curl up the anterior part of the body, often around the twig (Fig. 6D), and fully expose the warning colour pattern and urticating bristles on their back. The bristles cause an intense burning sensation on human skin but no swelling and itch, and the pain subsides after approximately 15 minutes. On maturity the larvae empty their intestines and crawl down to the bottom of the bush and away from it, sometimes moving for about a day, until they find a suitable location on the ground among branches and detritus at the base of bushes, often at the main stem, where they spin a cocoon for pupation.

Pupa

The pupa (Fig. 7) is also typical of the tribe Micragonini in that it has a rough, wrinkled surface and is formed in a thin, parchment-like silken cocoon with a brittle, crumpling anterior end that enables the moth to eclose (Oberprieler, 1997). The cocoon is spun on the ground next to a stem or similar solid object and incorporates debris such as old leaves and sand grains (Figs 3H, 6E, 6H). The pupa is anchored in the cocoon by its stout cremaster hooking into a few silken strands at the posterior end. Its main features are: length ca. 20–25 mm in male, ca. 33–38 mm in female; dark brown in colour; integument matt, finely rugose to granulose, without any large calli; clypeolabrum strongly rugose; proboscis very short; forelegs broad, not reaching apices of wings; midlegs reaching to between wings, touching on midline; antennae short and broad, not touching on midline (in both sexes), segmentation faintly indicated; forewings broad, apices broadly touching on midline, hindwings not exposed; thoracic spiracles narrow, posterior (mesothoracic) surface slightly produced, flatly depressed with weak median ridge; abdominal segments IV to VI with broad posterior band of dense sharp asperities, A-X produced into cremaster with terminal rosette of ca. 8 to 14 short stout spines.

Life cycle

The life cycle of *V. grimmia* takes place mostly over winter, but it has only been recorded in detail for the Cape Peninsula population and partly for the Cape Agulhas one. The imagines (moths) hatch from the cocoons in about late March to early June, mainly in April and May. Eclosion occurs in the early morning, between approximately 8:00 and 9:00, but it can probably also happen later in cold weather (as observed in *V. ducalis*). The smaller males take to flight after their wings have expanded and hardened, flying fast and erratically, whereas the larger females remain stationary, hanging from a stem or similar object, and start emitting their sex pheromone when their wings are hard. The flight period of the males (and mating period) is in the early morning (between ca. 8:00 and 10:00) and again in the late afternoon (between ca. 16:00 and 18:00), whereas the females fly only after dark (around 20:00) to lay their eggs. A very similar pattern of eclosion and different flight periods of the sexes (the males being diurnal) occurs in other *Vegetia* species as well as in some *Ludia* species (Oberprieler, 1995), and it accounts for more females being present in collections as they are attracted to lights during their flight time. Copulation lasts several hours, sometimes for most of the day, and there can be competition between males for a ‘calling’ female (larger males dislodging smaller ones). Males can probably also mate with more than one female, as occurs in other *Vegetia* species and in *Ludia* (Oberprieler, 1995). Both sexes live for approximately three days.

The ova are laid in autumn (April to May). Those found on the Cape Peninsula took about 10 weeks to hatch, a very long period for a small saturniid species and longer than in *V. ducalis* (about four weeks) and in *V. dewitzi* (about ten days). Ova laid by wild-caught females in Montagu in May 2016 and 2017 also took four weeks to hatch (M. Maclean, pers. obs.), and this is likely to be the normal incubation period of the eggs. An incubation time of about 1–2 weeks is the rule in African Saturniidae (Oberprieler, 1995), but in species breeding during winter a longer period may occur due to lower temperatures or to coincide larval hatching with the appearance of fresh foliage of the host plants. The larval stage of *V. grimmia* is also considerably longer than is the norm in African Saturniidae (about six weeks; R. Oberprieler pers. obs.), lasting about five months (L1 feeding mainly in June, L2 in July, L3 in August, L4 in September and L5 in October). There may, however, be some variation between different locations and climates and between years. Pupation takes place approximately six days after completion of the cocoon, and the pupae estivate over mid-summer until eclosion of the imagines in late summer to autumn (in the following calendar year). There generally appears to be only one generation per season, but in Haarwegskloof Nature Reserve mature L5 larvae were already encountered and pupated in early June (Figs 6F–6H) and the species may thus be partly bivoltine in the Overberg region.

Parasitoids

The only parasitoid of *V. grimmia* observed thus far is an egg parasitoid belonging to the eupelmid genus *Anastatus* Motschulsky, 1859. On the Cape Peninsula a female of a species of *Anastatus* (catalogue number SAM-HYM-P095121) was observed in May 2019 ovipositing into *V. grimmia* ova (Figs 10E, 10F), and two female (SAM-HYM-P095122, SAM-HYM-P095123) (Figs 9, 10A–D) and one male (SAM-HYM-P095124) (Fig. 11) wasps eclosed from these ova in captivity. Identification to species of these specimens is not possible without conducting a full taxonomic revision of the African fauna of the genus. There are many undescribed species present in South Africa, and some of the species currently only recorded from further north in Africa are also likely to occur in South Africa. These constraints, in combination with a lack of identification keys to the African species, mean that types of all described species will need to be examined to assess whether the species parasitising *V. grimmia* ova is undescribed or not.

The genus *Anastatus* is distributed worldwide and comprises 136 described species, 23 of them occurring in the Afrotropical region but only one, *A. capensis* Hedqvist, 1970, currently known from South Africa (Fusu *et al.*, 2015; van Noort, 2021). Species in this genus are predominantly primary endoparasitoids of the ova of several insect orders (Blattodea, Hemiptera, Lepidoptera, Mantodea, Neuroptera, Orthoptera, Phasmida), but some are hyperparasitoids of the ova of other primary parasitoid wasps (Ichneumonidae, Scelionidae) of Lepidoptera ova and a few have been recorded parasitising Coleoptera larvae and Diptera pupae (Gibson, 1995). Several *Anastatus* species are known to be egg parasitoids of Saturniidae and similar moths throughout the world (Gibson, 1995; Peigler, 1996). In Africa, *Anastatus* species have been recorded parasitising the ova of *Gonimbrasia belina* (Westwood, 1849) (van den Berg, 1971), *Nudaurelia clarki* Geertsema, 1971 (van den Berg, 1974a), *N. cytherea* (Geertsema, 1975; Prinsloo, 1980) and *Pseudobunaea natalensis* (Aurivillius, 1893) (van den Berg, 1974b). Although it is likely that species of this genus also parasitise the ova of many other saturniid species in Africa, none has so far been recorded doing so in a species of Micragonini. Saturniid ova are also commonly parasitised by species of the eupelmid genus *Mesocomys* Cameron, 1905, including in Africa (Gibson, 1995, 2020).

DISCUSSION

Although the larvae of several genera and species of Micragonini have been illustrated in the literature (Fawcett, 1901, 1903; Packard, 1914; Seydel, 1939; Rougeot, 1955, 1962; Pinhey, 1972; Oberprieler & Nässig, 1994; Oberprieler, 1995; Lampe, 2010; Staude *et al.*, 2016, 2020), the complete life history (including all immature stages) has been described for only two. Van den Berg (1975) provided a description (with colour illustrations) of the life cycle and all immature stages of *Holocerina smilax* (Westwood, 1849) from South Africa and Kohll (2013) a shorter one for a similar species of *Holocerina* from Tanzania. The description and illustration of the life cycle of *V. grimmia* in this paper adds not only another complete life history for the tribe Micragonini but also for one of its smallest genera and one of its rarest species. The photographs of the mature larva and live moths of *V. grimmia* published before (Lampe, 2010; Staude *et al.*, 2016, 2020) are from our rearings of the species as reported in full here.

The larvae of *V. grimmia* are most similar to those of the closely related *V. ducalis*, which differ in their smaller size, black head (only clypeus and labrum pale), lower scoli (especially the lateral thoracic ones), shorter urticating bristles, shorter and finer secondary hairs (hardly longer than the bristles) and those on the thorax dark (grey to black), only a single pale lateral stripe along the lateral scoli (a dorsolateral stripe only indicated and fragmented) and a less vivid dorsal pattern of black and white. The larvae of *V. ducalis* are, however, also quite variable in coloration, and a more comprehensive comparison of more material is required to fully assess the differences between the larvae of the two species.

The status of *V. grimmia* as a distinct species has been called into question by d'Abrera (2012), writing: "… but I suspect that this name possibly be only a local or seasonal form of either *dewitzi* or *ducalis*". He also regarded *V. ducalis* as "… I am sure, only a geographical or seasonal form of *dewitzi*". He admitted that he had not seen "sufficient material" nor been able to study the genitalia, but he cited Lampe's (2010) book, which features colour photographs of all three these species, and he should at least have been able to recognise that *V. dewitzi* is very different from *V. grimmia* and *V. ducalis* (or consulted Jordan (1922) and Oberprieler (1995) on the matter). His entire account of *Vegetia* is flawed in several ways: he omitted the fourth species (*V. legraini*), he gave incorrect authorships for *V. dewitzi* (two different ones!) and *V. grimmia*, he misrepresented their distributions (the "population" in the "extreme south" of South Africa is *V. grimmia*, not *V. ducalis*), he disregarded the priorities of the three names (*dewitzi* and *ducalis* can only be "forms" of *grimmia*, not the other way round) and his notes contradict the status that he afforded them (as distinct species).

Vegetia grimmia and *V. ducalis* are indeed quite similar and evidently constitute a closely related species pair, but there are several differences between them. In the imaginal stage, *V. grimmia* is considerably larger (wingspan in male 40–42 mm, in female 53–57 mm, vs. 31–36 mm and 42–46 mm in *V. ducalis*), the wings are speckled with white, the white antemedian band on the forewings is usually broken up into two large half-moons (a narrower continuous zigzag line in *V. ducalis*) and the hyaline mark on the forewings is more robust (the c-mark deeper, more closed, and the anterior bar shorter, thicker and externally indented) and lined with black and yellow (in *V. ducalis* thinner and longer, only thinly lined with black, rarely also thinly with yellow, the c-mark more open and the anterior bar longer and narrower, usually not indented). The clearest differences, however, occur in the male genitalia, the uncus in *V. grimmia* being much more bulbous and its apical prongs much shorter, broader and directed ventrad, the valves being higher (broader) and with a ventral subapical tooth and, most significantly, the gnathos being medially strongly produced, thick and heavily sclerotised. Together with the differences in the larva outlined above, there is therefore strong morphological evidence that *V. grimmia* and *V. ducalis* are distinct species. Molecular (mitogenome) characters also clearly distinguish the two species (Nethavhani *et al*. in press).

In addition to these morphological differences, *V. grimmia* and *V. ducalis* are also separated geographically and ecologically, in that they appear to be allopatric in their distribution and their larvae have different host plants. *Vegetia ducalis* occurs along the west coast of South Africa, recorded from the Springbok area of Namaqualand in the north southwards to the northern side of Cape Town (the Tygerberg Hills and Bellville), whereas *V. grimmia* occurs along the south coast and its hinterland, from the Cape Peninsula (south of Cape Town) westwards to about Mossel Bay (Figure 8). It is possible that the two species are (or were) sympatric or parapatric in the Cape Town area, but *V. ducalis* has not been recorded from south of Cape Town (the Cape Peninsula) and is apparently now extinct in the north of the city, as the fynbos habitats at Bellville and on the Tygerberg Hills, where Charlie Dickson found the larvae in the late 1940s, are now destroyed. The population of *V. grimmia* on the Cape Peninsula is evidently now separated from those further east (Figure 8), but the species is likely to have also occurred along the coast of the False Bay in the past and may have disappeared from there only after European settlement and destruction of native vegetation and habitats over the last few centuries. Together the distribution ranges of *V. grimmia* and *V. ducalis* conform with the Greater Cape Biochorion (the biogeographical area combining the Cape Floristic Region and the Succulent Karoo Region), whereas the range of *Vegetia* overall coincides with the broad western biogeographical division of South Africa as identifiable in plants and also in butterflies (Colville *et al.*, 2014).

The larvae of *V. ducalis* feed mainly on *E. africanus* but in Namaqualand also on *E. ericoides* and *E. microcephalus* (Oberprieler, 1995), whereas those of *V. grimmia* feed on *E. racemosus* (along the coast) and *Cymbopappus adenosolen* (further inland) but on the Cape Peninsula also on *E. africanus*. Larvae of *V. grimmia* from Struisbaai offered *E. africanus* in captivity accepted it only hesitantly and clearly preferred *E. racemosus* (R. Oberprieler, pers. obs. 1983, 1989), but those on the Cape Peninsula readily feed on both *E. africanus* and *E. racemosus* in the wild and can easily be switched between them in captivity. L1 larvae hatched in Montagu did not accept *E. ericoides* or *Pentzia incana* or *Elytropappus* as food and died (M. Maclean, pers. obs. 2016). From the distribution ranges of *V. grimmia* and its main two larval host plants (Figure 8) it appears that *Cymbopappus adenosolen* may be its main host plant (in most of its range) and *E. racemosus* only a less utilised, secondary one (along the coast), a pattern supported by the fact that *V. grimmia* does not occur in the western and northern range of *E. racemosus* along the west coast of the Western Cape province. It is, however, also possible that the larvae of *V. grimmia* feed on yet other plants in parts of its range. Considerable further fieldwork is required to properly understand the pattern of host utilisation of *V. grimmia*.

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Figure 1 – *Vegetia grimmia*, pinned imagines. A. Female, dorsal view; illustration by Geyer (1832, plate [44]). B. Female, ventral view; illustration by Geyer (1832, plate [44]). C. Female, holotype; Museum für Naturkunde, Berlin, Germany (photo C. Lemaire, 1990). D. Female; red form, Struisbaai, Western Cape province, *ab larva* on *Eriocephalus racemosus*, 28.vi.1990 (R. Oberprieler). E. Male; Struisbaai, *ab larva* on *E. racemosus*, 13.iii.1984 (R. Oberprieler). F. Female, grey form; Struisbaai, *ab larva* on *E. racemosus*, 30.iii.1990 (R. Oberprieler). G. Male; Cape of Good Hope Nature Reserve, Western Cape province, *ab larva* on *E. racemosus*, 17.xi.2020 (A. Morton). H. Female; Cape of Good Hope Nature Reserve, *ab larva* on *E. racemosus*, 17.xi.2020 (A. Morton). Scale bars 10 mm.

Figure 2 – *Vegetia grimmia*, live imagines. A. Male; Struisbaai, Western Cape province, *ab larva* on *Eriocephalus racemosus*, 19.iii.1990 (R. Oberprieler). B. Female, red form; Struisbaai, *ab larva* on *E. racemosus*, 08.iii.1990 (R. Oberprieler). C. Female in resting position; Cape of Good Hope Nature Reserve, Western Cape province, *ab ovo* on *E. africanus*, 11.iv.2019 (A. Morton). D. Female hardening wings after eclosion; Cape of Good Hope Nature Reserve, *ab ovo* on *E. africanus*, 08.iv.2019 (A. Morton). E. Male; Haarwegskloof Nature Reserve, Western Cape province, *ab larva* on *Cymbopappus adenosolen*, 21.v.2017 (J. Groenewald). F. Female; Haarwegskloof Nature Reserve, *ab larva* on *C. adenosolen*, 14.iv.2016 (J. Groenewald). G. Female; Montagu, Western Cape province, 25.iv.2016 (M. Maclean). H. Female; Montagu, 01.v.2018 (M. Maclean).

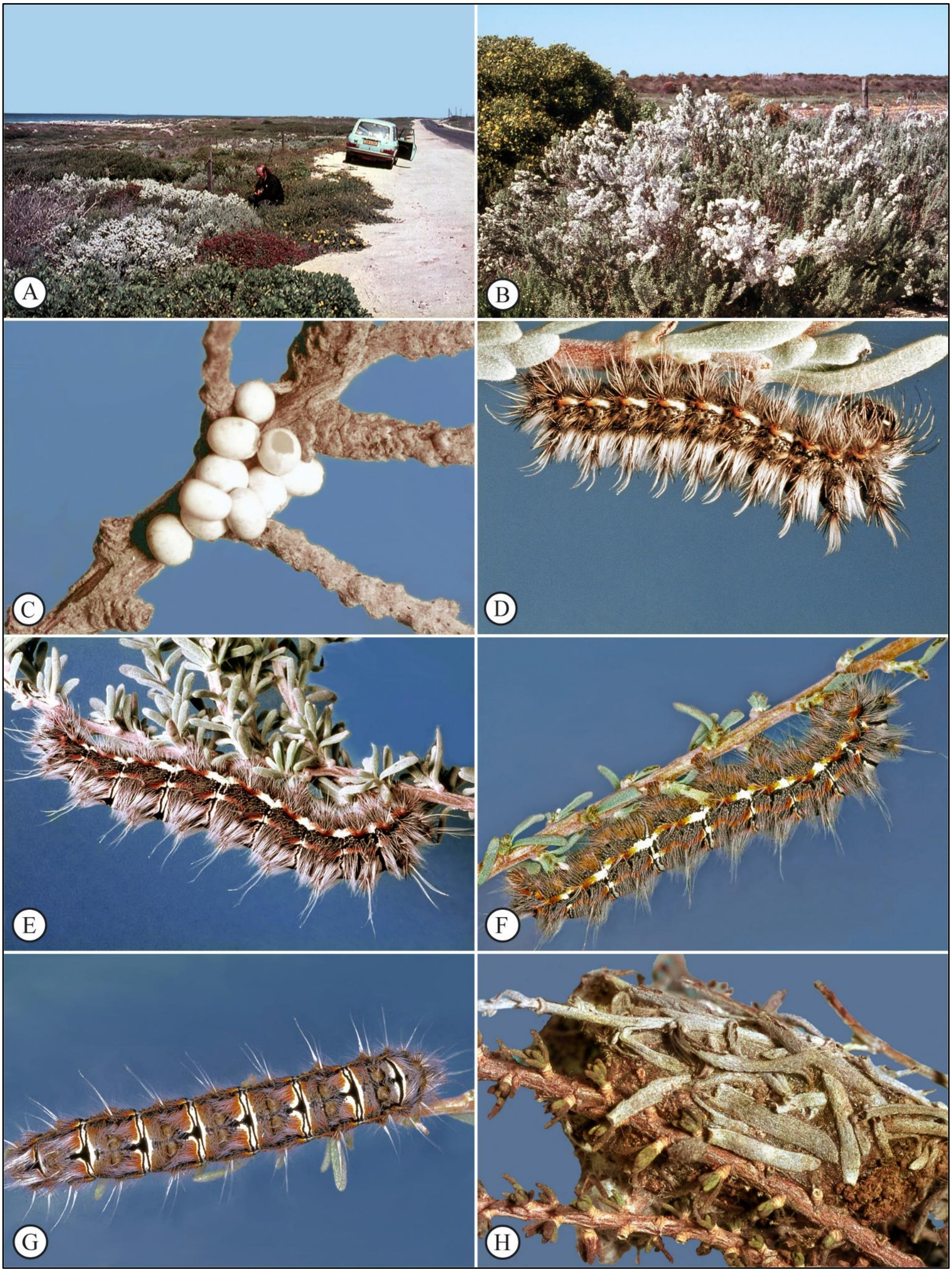


Figure 3 – *Vegetia grimmia*, habitat and immature stages; Struisbaai, Western Cape province (all R. Oberprieler). A. Habitat at roadside along coast, 14.ix.1983. B. Larval host plant (*Eriocephalus racemosus*) in habitat, 14.ix.1983. C. Ova cluster on host plant in habitat, 14.ix.1983. D. Larva L3, lateral view, 16.ix.1983. E. Larva L5, lateral view, 30.ix.1983. F. Larva L5, lateral view, 11.x.1989. G. Larva L5, ventral view, 11.x.1989. H. Cocoon among twigs and leaves of host plant, 05.x.1983.

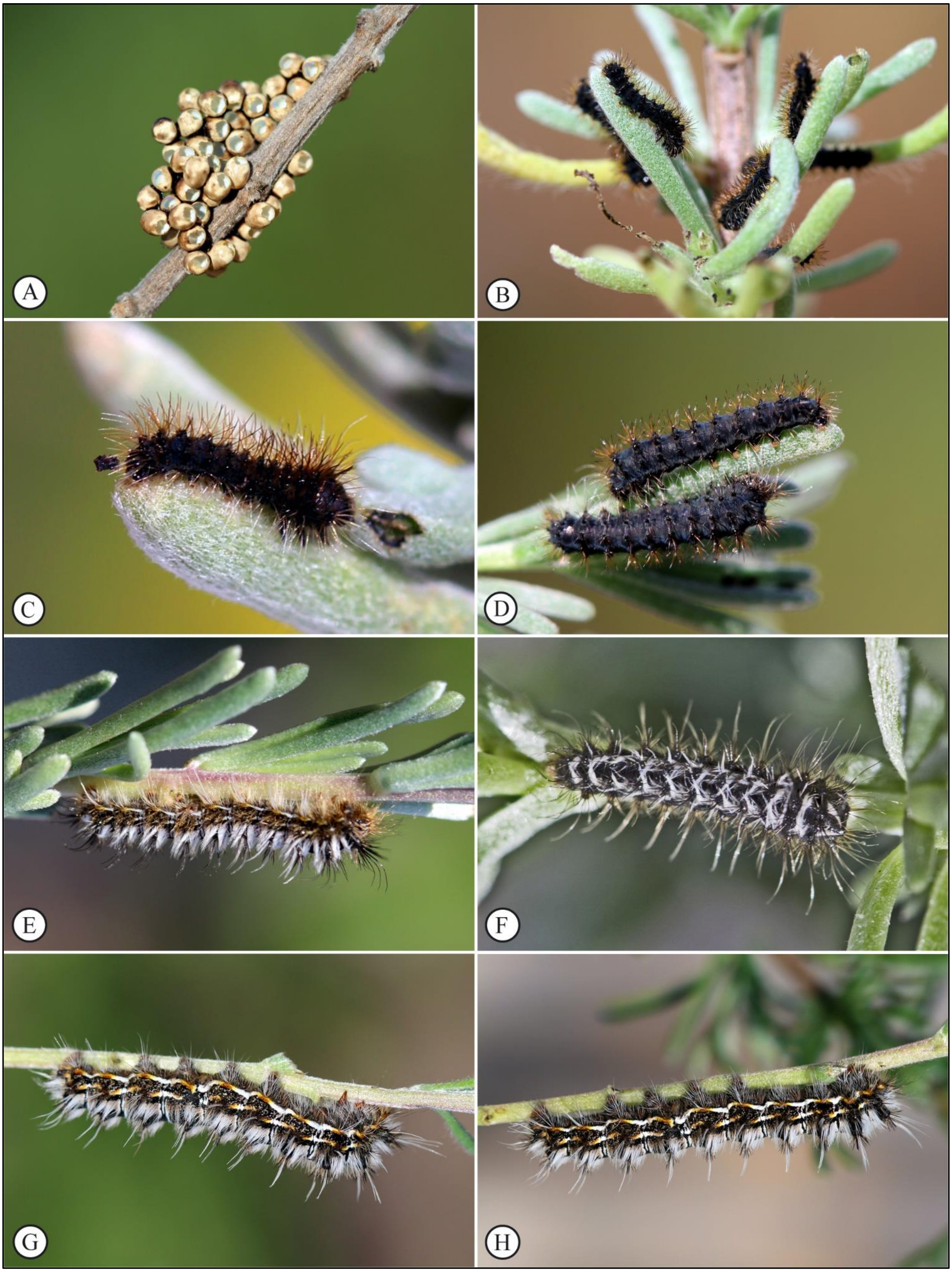


Figure 4 – *Vegetia grimmia*, immature stages on *Eriocephalus africanus*; Cape of Good Hope Nature Reserve, Western Cape province (all A. Morton). A. Ova cluster on host plant in habitat, 04.ix.2019. B. Larvae early L1, 29.vi.2019. C. Larva early L1, lateral view, 29.vi.2019. D. Larvae late L1, lateral and ventral view, 12.vii.2019. E. Larva L2, lateral view, 03.ix.2019. F. Larva L2, ventral view, 20.vii.2019.G. Larva L3, lateral view, 03.ix.2019. H. Larva L3, lateral view, 03.ix.2019.

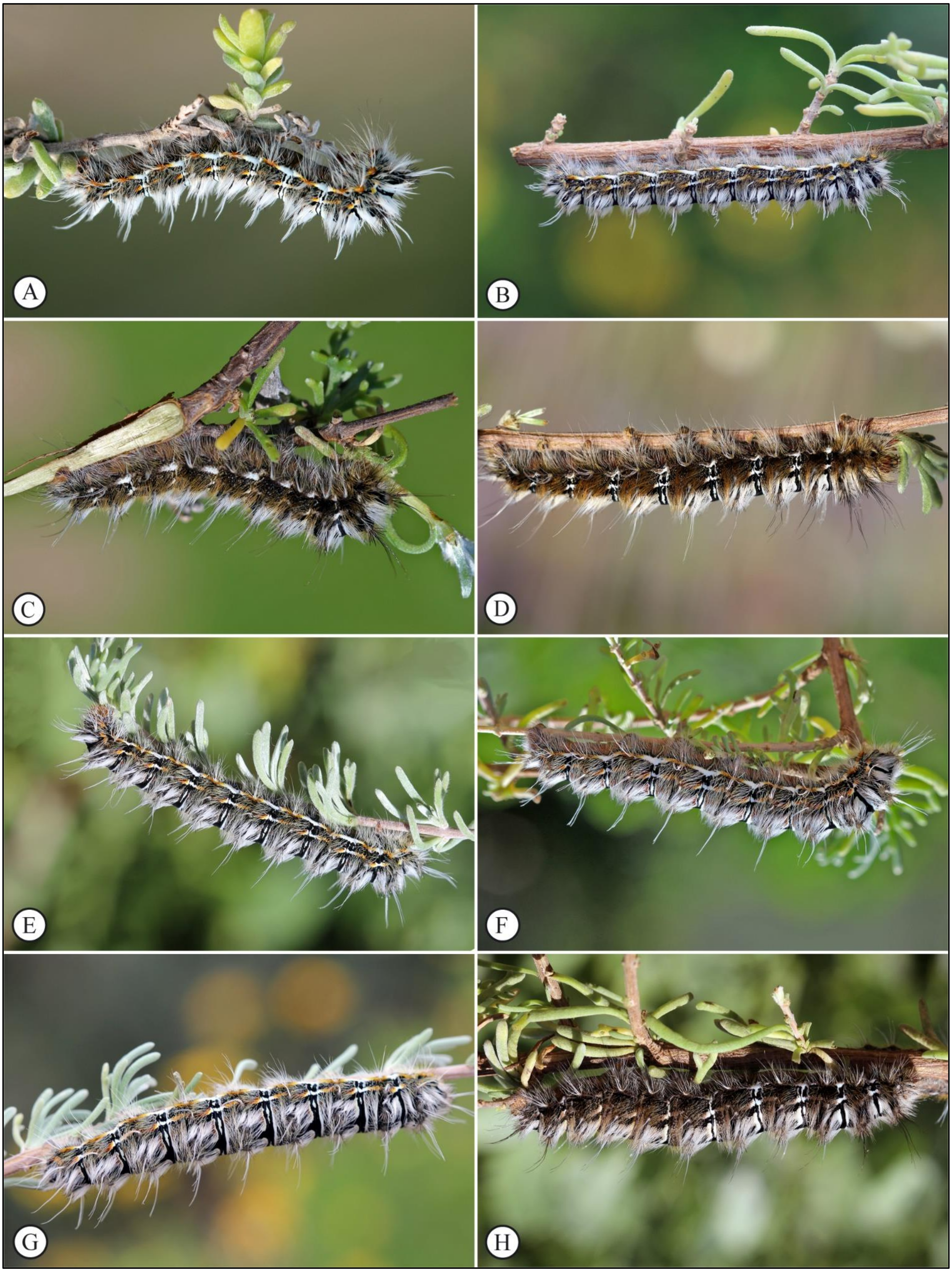


Figure 5 – *Vegetia grimmia*, immature stages on *Eriocephalus africanus*; Cape of Good Hope Nature Reserve, Western Cape province (all A. Morton). A. Larva L4, lateral view, 04.ix.2019. B. Larva L4, lateral view, 18.ix.2019. C. Larva L4, dark form, lateral view, 08.ix.2018. D. Larva L4, dark form, ventrolateral view, 27.ix.2019. E. Larva L5, lateral view, 13.x.2018. F. Larva L5, lateral view, 13.x.2018. G. Larva L5, ventrolateral view, 02.x.2019. H. Larva L5, dark form, lateral view, 13.x.2018.

Figure 6 – *Vegetia grimmia*, immature stages; Cape of Good Hope Nature Reserve (A–E, A. Morton) and Haarwegskloof Nature Reserve (F–H, J. Groenewald), Western Cape province. A. Larva L5, dark form, lateral view; 08.x.2018. B. Larva L5, dark form, ventral view; 13.x.2018. C. Larva L5 on host plant, ventral view; 18.x.2018. D. Larva L5 in defensive posture on host plant; 18.x.2018. E. Cocoon among leaves of host plant; 16.iv.2019. F. Larva L5, brown form, ventrolateral view; 05.vi.2016. G. Larva L5, dark form, ventrolateral view; 05.vi.2016. H. Cocoon; 05.vi.2016.

Figure 7 – *Vegetia grimmia*, pupa (Struisbaai, Western Cape province, 30.iii.1990) (R. Oberprieler). **A**. Male pupa, ventral view. **B**. Male pupa, left lateral view. **C**. Male pupa, dorsal view. **D**. Female pupa, ventral view. **E**. Female pupa, left lateral view. **F**. Female pupa, dorsal view. Scale bars 10 mm.

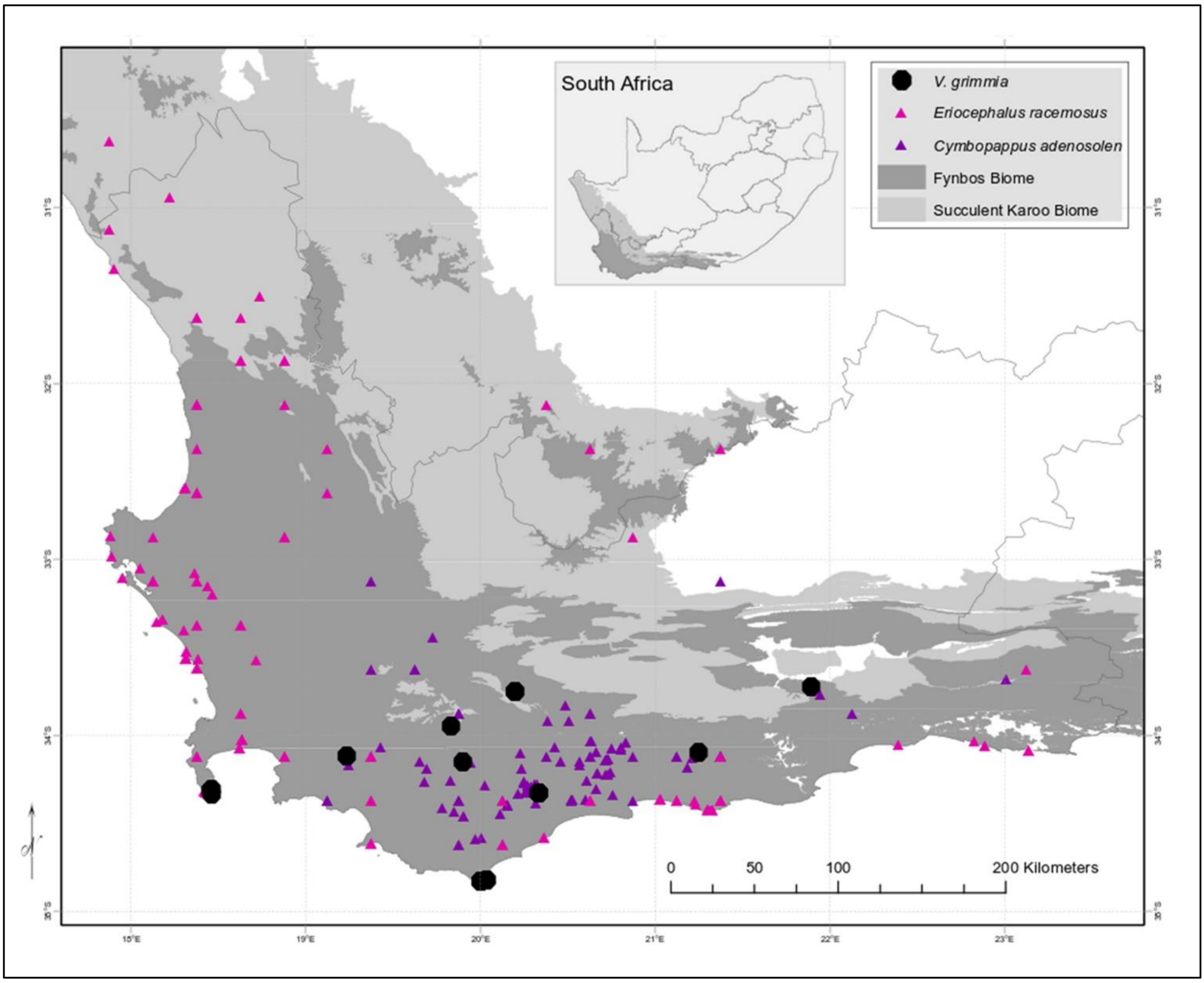
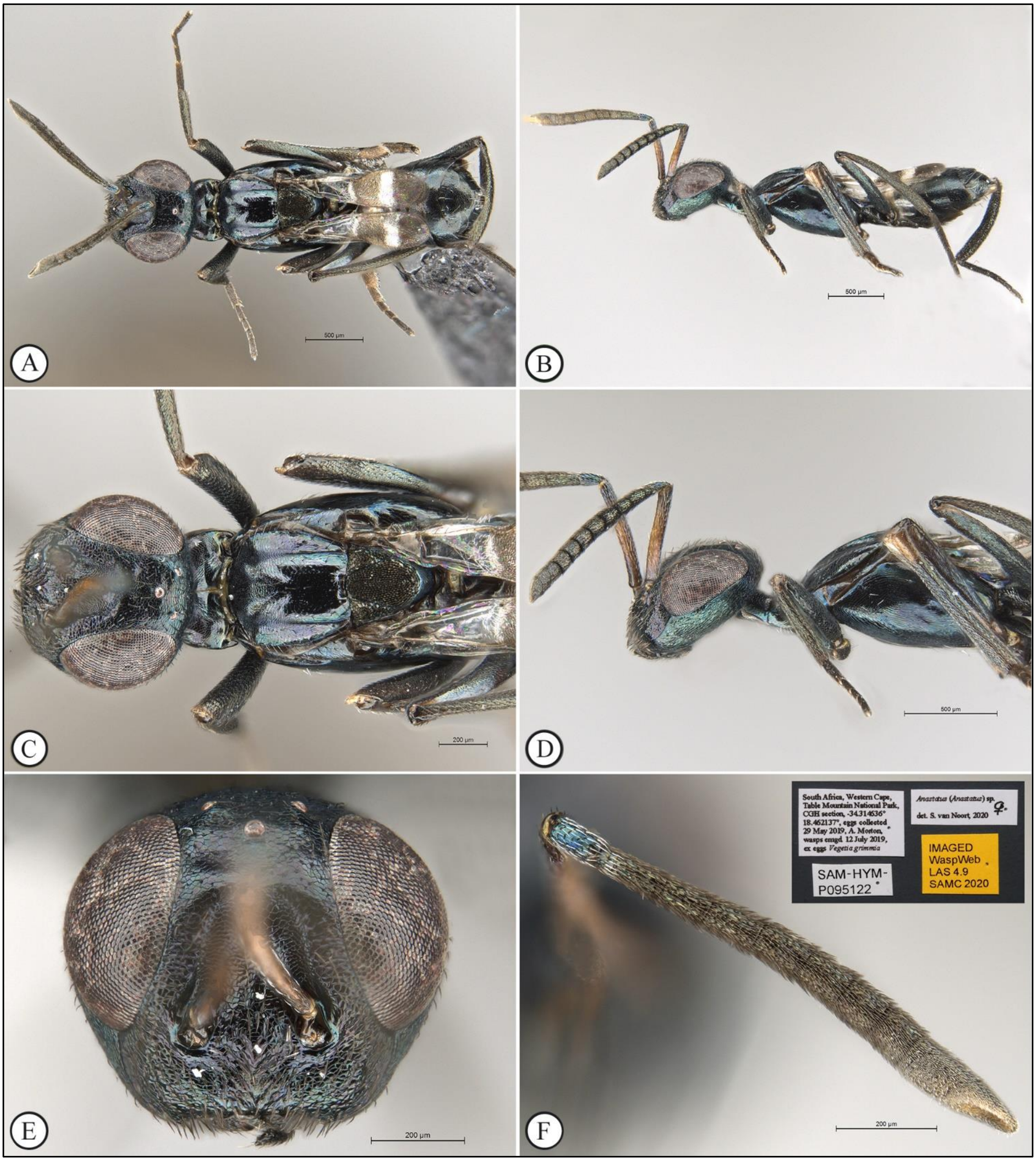


Figure 8 – Map of southwestern region of Western Cape province, South Africa, showing known locality records of *V. grimmia* and its larval host plants *Eriocephalus racemosus* and *Cymbopappus adenosolen*, superimposed on region of the Fynbos and Succulent Karoo Biomes.



South Africa, Western Cape,
Table Mountain National Park,
CGH section, -34.314636°
18.462137°, eggs collected
29 May 2019, A. Morton,
wasps emgd 12 July 2019,
ex eggs *Vegetia grimmia*

Anastatus (*Anastatus*) sp. ♀.
det. S. van Noort, 2020

SAM-HYM-
P095122

IMAGED
WaspWeb
LAS 4.9
SAMC 2020

Figure 9 – *Anastatus* species, female (SAMC; SAM-HYM-P095122). A. Habitus, dorsal view. B. Habitus, lateral view. C. Head and mesosoma, dorsal view. D. Head and mesosoma, lateral view. E. Head, anterior view. F. Antennal pedicel and flagellum, dorsal view (inset: data labels).

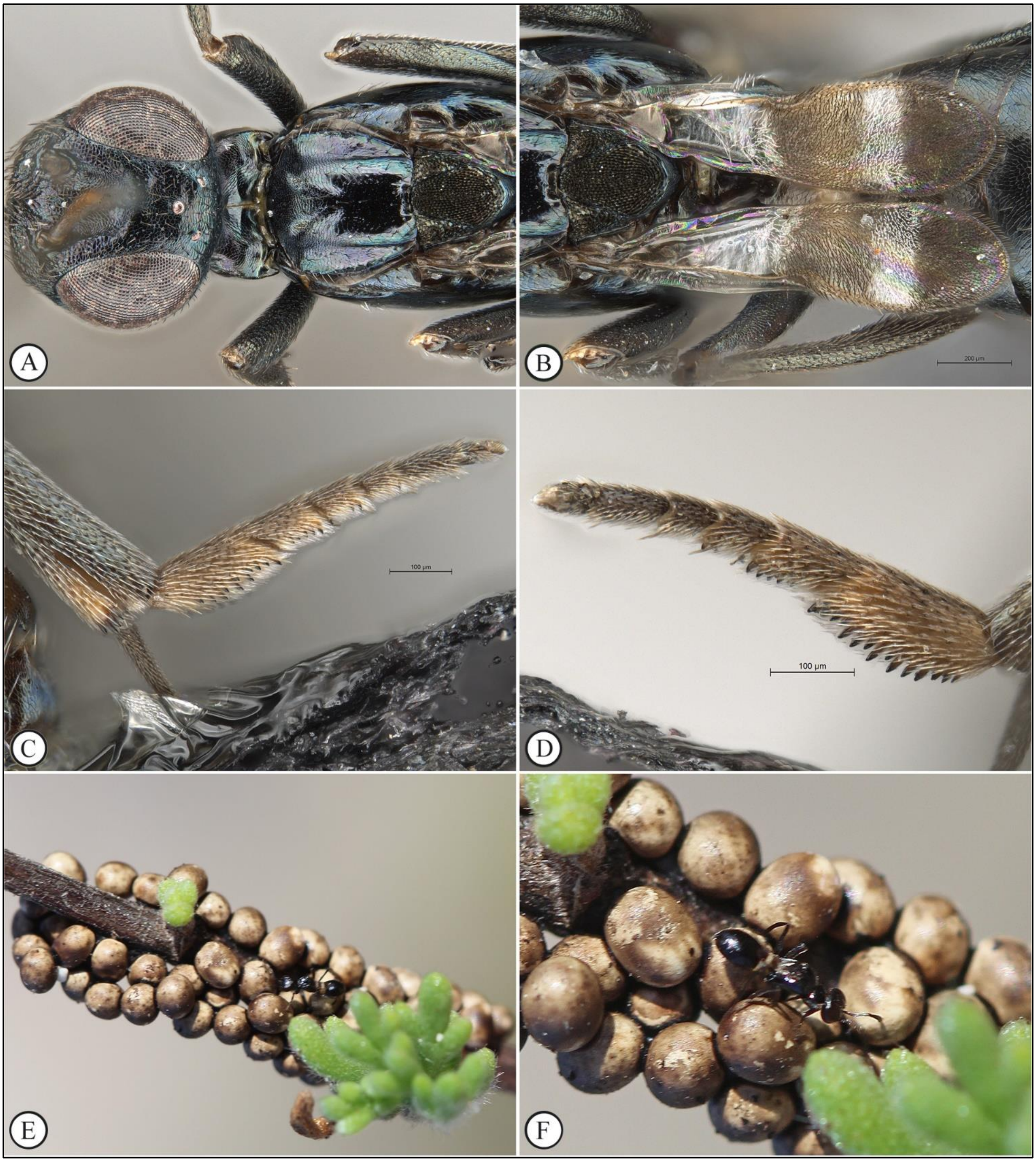


Figure 10 – *Anastatus* species, female (SAMC; A–D: SAM-HYM-P095122, E–F: SAM-HYM-P095121). A. Head and mesosoma, dorsal view. B. Wings, dorsal view. C. Metatibia, antaxial lateral view. D. Metatibia, axial lateral view. E. Female inspecting cluster of *Vegetia grimmia* ova, Cape of Good Hope Nature Reserve, Western Cape province. F. Ditto, enlarged view.

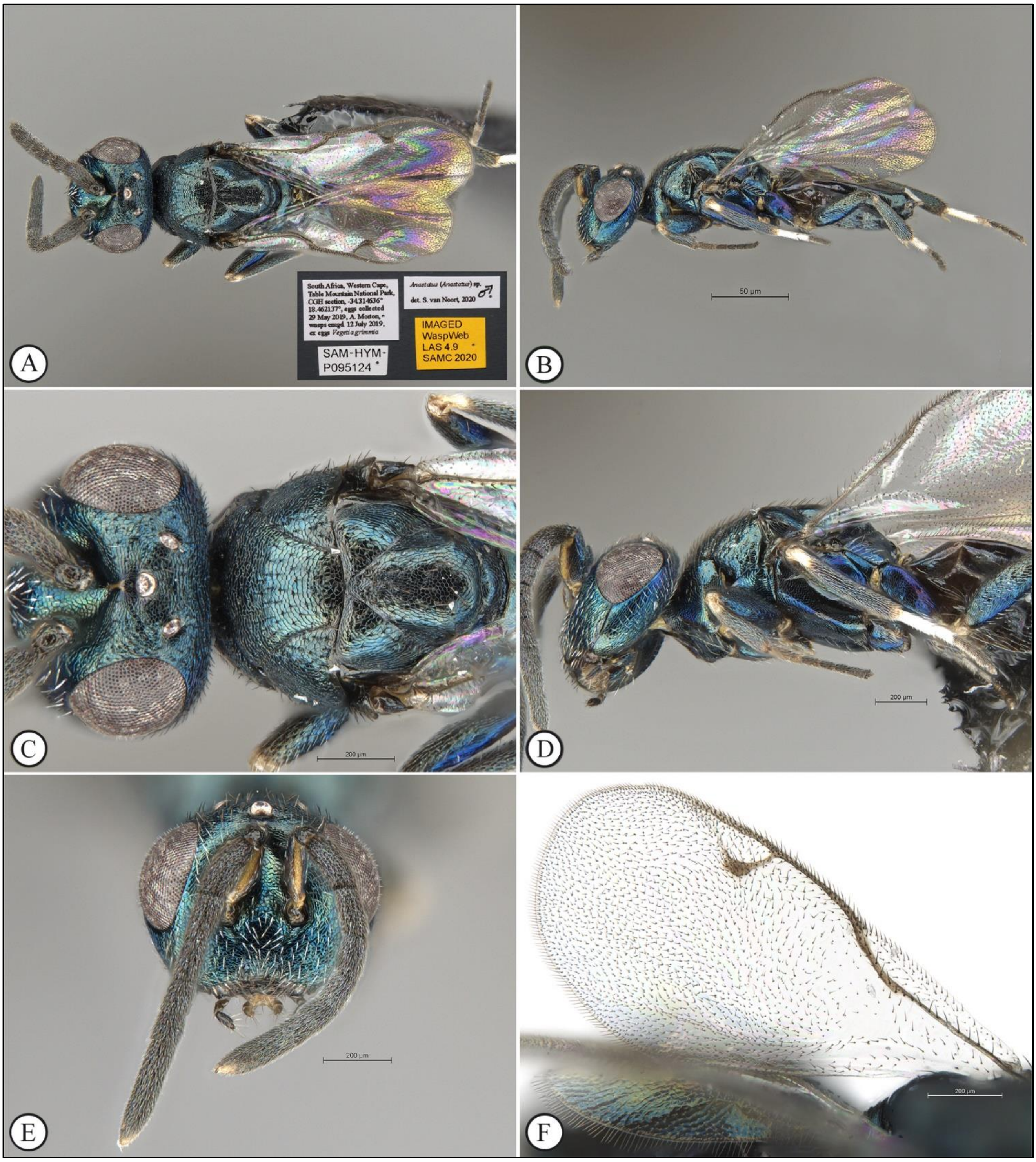


Figure 11 – *Anastatus* species, male (SAMC; SAM-HYM-P095124). A. Habitus, dorsal view (inset: data labels). B. Habitus, lateral view. C. Head and mesosoma, dorsal view. D. Head and mesosoma, lateral view. E. Head, anterior view. F. Wings, dorsal view.