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Monograph

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Revision of the enigmatic South African Cryptolaryngini (Coleoptera, Curculionidae), with description of a new genus and twenty-two new species

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Abstract. The weevil genus *Cryptolarynx* Van Schalkwyk, 1966 is endemic to the Northern and Western Cape provinces of South Africa. The two previously known species of the genus, *C. vitis* (Marshall, 1957) and *C. estriatus* (Marshall, 1957), have an aberrant globular body and head shape, which has made it difficult to place the genus into the classification systems of the Curculionoidea. This paper presents the description of 21 new species of *Cryptolarynx* from South Africa (*C. subglaber* Haran sp. nov., *C. squamulatus* Haran sp. nov., *C. muellerae* Haran sp. nov., *C. hirtulus* Haran sp. nov., *C. robustus* Haran sp. nov., *C. namaquanus* Haran sp. nov., *C. carinatus* Haran sp. nov., *C. variabilis* Haran sp. nov., *C. pyrophilus* Haran sp. nov., *C. pilipes* Haran sp. nov., *C. armatus* Haran sp. nov., *C. falciformis* Haran sp. nov., *C. oberprieleri* Haran sp. nov., *C. spinicornis* Haran sp. nov., *C. cederbergensis* Haran sp. nov., *C. homaroides* Haran sp. nov., *C. marshalli* Haran sp. nov., *C. endroedyi* Haran sp. nov., *C. oberlanderi* Haran sp. nov., *C. san* Haran sp. nov., and *C. luteipennis* Haran sp. nov.) and of one new genus and species, *Hadrocryptolarynx major* Haran gen. et sp. nov., also from South Africa. A redescription of the

genus *Cryptolarynx* is provided to incorporate the characters of the new species. The plant genus *Oxalis* (Oxalidaceae) is recorded as larval host for several species of *Cryptolarynx* and for *Hadrocryptolarynx* Haran gen. nov., as their larvae develop in the subterranean bulbs of members of the genus, and the egg, larva and pupa of *C. variabilis* are described. The characters of the *Cryptolarynx* larva confirm that Cryptolaryngini are an early-diverging group of Curculionidae, with a placement among taxa currently classified in the subfamily Brachycerinae sensu lato, and although their exact taxonomic position remains unresolved, some larval characters, and also pupal ones, suggest a close relationship between Cryptolaryngini and *Stenopelmus* Schoenherr. Potential use of species of *Cryptolarynx* in the biological control of weedy South African species of *Oxalis* is discussed.

Keywords. Brachycerinae, Southern Africa, new species, new genus, biocontrol.

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Introduction

In 1957, G.A.K. Marshall published the description of *Cryptopharynx*, a new weevil genus from the Northern and Western Cape provinces of the Republic of South Africa, and recognised two new species in it, *Cryptopharynx vitis* and *C. estriatus*. Marshall (1957) regarded the genus as aberrant in shape and characters and could not place it in any of the known weevil subfamilies because of its globular body shape, its head almost entirely retracted into the pronotum and its very short, muzzle-like rostrum undifferentiated from the head. He consequently erected a new subfamily of Curculionidae Latreille, 1802 for it, named Cryptopharynginae. Marshall (1957) further recorded the adults of *C. vitis* feeding on grapevine leaves in Stellenbosch. A few years later, Van Schalkwyk (1966) changed the name of the genus and subfamily to *Cryptolarynx* and Cryptolarynginae, respectively, as the name *Cryptopharynx* is preoccupied in Protozoa and the subfamily name therefore needed to be emended as well (Art. 39 of the ICZN).

Following these first publications, the position of *Cryptolarynx* in Curculionidae remained contentious and data on its life history very scarce. Van den Berg (1968) undertook a morphological study of *Cryptolarynx vitis* and agreed with Marshall that the genus could only be regarded as an aberrant member of Curculionidae, but he proposed it being related to the subfamily Scolytinae Latreille, 1807. In his important work on the morphology and classification of weevils, Thompson (1992) later elevated Cryptolarynginae to family rank, based on characters of the mouthparts, sternites and genital structures, which differ from those of the family Curculionidae in his restricted concept. He related Cryptolaryngidae to the family Brachyceridae Billberg, 1820 in his sense based on sternal structures, but he kept the two families apart due to differences in their maxillae (galea and lacinia differentiated in Cryptolaryngidae), and he expanded the composition of Cryptolaryngidae by including the similar Palaearctic genus *Perieges* Schoenherr, 1842 in it. Alonso-Zarazaga & Lyal (1999) retained this classification in their world catalogue of supraspecific taxa of Curculionoidea, as did Alonso-Zarazaga (2013) in the *Catalogue of*

Palaearctic Coleoptera. In contrast, Kuschel (1995), Oberprieler et al. (2007) and Oberprieler (2014) placed Cryptolaryngini Van Schalkwyk, 1966 as a tribe of Brachycerinae Billberg, 1820, the latter treated as a subfamily of Curculionidae. Morrone (1997) and Bouchard et al. (2011) adopted a different classification system again, placing Cryptolarynginae as a subfamily of Brachyceridae, but Alonso-Zarazaga et al. (2017), in an update of the Catalogue of Palaearctic Curculionoidea, accepted the Kuschel-Oberprieler classification, which is the one in current usage, in particular as recent molecular phylogenetic analyses (e.g., Mugu et al. 2018; Shin et al. 2018; Song et al. 2020) have confirmed the phylogenetic position of Brachycerinae as a basal lineage of Curculionidae vis-à-vis their sister group, the family Brentidae Billberg, 1820. Oberprieler et al. (2007) reported the existence of another 16 undescribed species of Cryptolarynx and adults having been found feeding on leaves of Moraea Mill. (Iridaceae) and provided a first colour photograph of a live specimen, and Oberprieler (2014) presented a comprehensive account of the morphological characters of Cryptolaryngini and a summary of the taxonomy, diversity and biology of the tribe.

More than a century after the collection of the first specimens (Marshall 1957), *Cryptolarynx* remained a mystery in many ways. Recent field sampling conducted in South Africa greatly increased the number of species and provided new insights into the life history of the genus. Based on this material, the objectives of this study are to i) describe new taxa, ii) redescribe the genus *Cryptolarynx* to account for the characters of the newly described species, iii) provide a description of the larval and pupal stages of the genus and iv) assess the position of the tribe Cryptolaryngini in the Curculionoidea in the light of all new evidence. In all, one new genus and 22 new species are described. The immature stages and life history of *Cryptolarynx* are described for the first time. Photographs of the habitus of the adult weevils and of the distinguishing characters of their male genitalia are presented. Mitochondrial DNA barcode and nuclear-gene sequences are provided for most species. The potential use of *Cryptolarynx* in the biological control of alien invasive species of *Oxalis* L. is briefly discussed.

Material and methods

Sampling

Field collecting was conducted in the Republic of South Africa from early 2018 to late 2019 at the localities of the two previously known species of *Cryptolarynx* as well as at other localities in the Western Cape and Northern Cape provinces, for a total of about 40 sites. Opportunistic sampling for Cryptolaryngini was also undertaken in the Eastern Cape and KwaZulu-Natal provinces. Specimens were obtained by beating and sweeping vegetation with an insect net and by visually searching for them on the ground. Plants found near specimens were sampled and plant tissues (flowers, fruits, stems, bulbs, root system) were dissected to search for immature stages. Plants were identified using field guides, and identifications were subsequently confirmed by plant taxonomists. The specific epithets of *Oxalis* host plants follow Salter (1944) and Manning & Goldblatt (2008). Weevil larvae were reared in vials with a sample of plant tissue or with soil collected on site. All specimens were collected directly into 96% ethanol and stored at room temperature. Dry pinned specimens in four collections (see depositories below) were borrowed and studied.

Preparation and taxonomic treatment

The abdomens of males were detached from the body and macerated in a 10% potassium hydroxide (KOH) solution to obtain clean preparations of genital structures. The habitus of adults and genitalia were photographed with a Keyence® VHX-5000 imaging system. Measurements were made with an ocular micrometer. Body length (L) of adults was measured as the distance from the pronotal apex to the elytral apex in dorsal view. Widths (W) were measured in dorsal view at the widest parts of the pronotum, the elytra and the body of the penis. Lengths were measured in dorsal view, along the

median line, of the pronotum from apex to base, of the elytra from the anterior margin of the scutellar shield to the elytral apex, of the penis from the base to the apex of the body of the penis (excluding the temones) (Fig. 8D, J). The width of the eyes was measured in facial (anterior) view. The terminology for the external and internal sclerites and structures of adults used mainly follows Lyal (2021). Deviations include the following: 'forehead' refers to the area between the eyes (Fig. 8A) and 'epifrons' to the dorsal surface of the rostrum between the anterior margins of the eyes posteriorly and the level of the antennal insertions anteriorly (Fig. 8A). The South African Cryptolaryngini exhibit significant intraspecific variation in body size and shape, in elytral colour patterns and in ratios of the dimensions of the antennal segments. Morphological characters that may distinguish species of Cryptolaryngini are mainly found on the ventrites and tibiae, in head ratios and in genital structures of the males. Females of most species exhibit few stable morphological interspecific differences, and females are therefore not considered in the species descriptions below.

About 500 specimens were examined for this study. Identifications of the previously described species were made by comparison with type specimens and study of the original descriptions. Label data of name-bearing types are reported verbatim, with consecutive lines separated by a slash and data from a single label enclosed by double quotation marks. Additional information and interpretations appear between square brackets. The format of the label data of other specimens is standardised.

Valuable additional bio-ecological information was obtained from the Coleoptera field collection books of the Ditsong National Museum of Natural History (the former Transvaal Museum) in Pretoria (TMSA). The handwritten entries in these books are numbered with the prefix 'E-Y', but they reference not only Sebastian Endrödy-Younga but all beetle collectors associated with the Ditsong Museum from 1973 to 2018. For approximately the three decades after about 1975, and sometimes until even more recently, South African insect collections (here SAMC, SANC and TMSA) formatted geographic coordinates according to the notation of the then *Times Atlas of the World*. As an example, the coordinates for Cape Town were accordingly rendered as "33.55S 18.25E". In recent years, an increasing number of authors treated these decimal-looking coordinates as decimal degrees, an error that may lead to considerable misinterpretation. The coordinates for Cape Town in degrees-minutes notation rightly are 33°55′ S, 18°25′ E and correspond to 33.92° S, 18.42° E in decimal-degree notation. We retained historic notations in label data citations of name-bearing types, but in all other cases we standardised such coordinates to the degrees-minutes notation.

Following Article 50.1 and Recommendation 50A of the Code (ICZN 1999), JMH is responsible for the new names introduced in this paper. The lectotype designation is in accordance with Article 74.1 (ICZN 1999).

Larvae and pupae used for morphological descriptions were preserved in 80% ethanol. Habitus photos of the larvae were taken with a JVC KY-F75U camera associated with a Leica MZ16f stereo microscope. The pupa was photographed with a Keyence® VHX-5000 imaging system. Larvae were dissected and slide-mounted for microscope study under high magnification, basically following the technique of May (1993, 1994). The larval head was extracted and the body was cut into two longitudinal halves and around the terminal abdominal segments (except for the smallest specimen). The dissected parts were cleared in 10% KOH, rinsed in distilled water and transferred to ethanol. After clearing, the mouthparts, head capsule and body cuticles were mounted in Euparal on permanent microscope slides. Illustrations of larval structures were made with the aid of a drawing tube attached to a Leitz Laborlux S compound microscope. The pupae were examined directly in ethanol under the stereo microscope. Terminology used for larval characters follows Marvaldi (1999), as also employed by Oberprieler *et al.* (2014).

Terminology for pupal characters follows May (1994). Setal numbers of bilateral structures are given for one side only.

Molecular analysis

For each species, when available, one or several specimens were sequenced for the standard DNA barcode region for invertebrates (mitochondrial cytochrome c oxidase subunit I: COI, Hebert et al. 2003) to test the interspecific boundaries identified from morphological examination. Because genetic divergences in maternally inherited mitochondrial DNA can be high in flightless insects and overestimate divergence between populations, we also sequenced the nuclear gene Elongation Factor 1 (EF1 α -F2, EF1) to cross-validate interspecific genetic divergences. DNA was extracted from whole specimens or a leg, using a DNeasy Blood & Tissue Kit (QIAGEN, Hilden, Germany). PCR amplification was carried out using a mix of primers for amplification of COI, and the primers described in Brady et al. (2006) were used for the amplification of EF1 (Appendix 1). PCR reactions were carried out in a Mastercycler® Nexus (Eppendorf, Hamburg, Germany) in a final volume of 10 μL containing 5 μl of Multiplex PCR Master Mix (QIAGEN, Hilden, Germany), 2 µM of each primer and 2 µl of DNA template. The PCR conditions were as follows: initial DNA denaturation at 94°C for 15 minutes, followed by 35 cycles of 30 s at 94°C, 1 min at 52°C and 1 min at 72°C, with a final extension of 15 min at 72°C. The PCR products were paired-end sequenced by Eurofins Genomics (http://www.eurofinsgenomics.eu). All voucher specimens were mounted, dried and deposited at CBGP, Montpellier, France, in the CIRAD collection (https://doi.org/10.15454/D6XAKL) or in the institutions listed in each Material examined section. Nucleotide sequences were aligned and manually checked using CodonCode Aligner ver. 3.7.1. (CodonCode Corporation, Centerville, MA, USA) to verify the absence of pseudogenes. Uncorrected p-distance values of pairwise genetic distances between species were computed with Mega 7 (Kumar et al. 2016). Reconstruction of phylogenetic trees was carried out with COI and EF1 sequences (658 and 517 base pairs, respectively) using PhyML (Guindon & Gascuel 2003) with 1000 bootstrap replicates. The trees were rooted with three species of two tribes of Brachycerinae sensu Oberprieler (2014), Brotheus crenelatus Marshall, 1907 (JHAR01250 0101), Synthocus hopei Boheman, 1842 (JHAR02578 0101) (both Brachycerini) and Ocladius baccicollis Boheman, 1838 (JHAR02406 0101) (Erirhinini), as well as with a species of the brentid genus Episus Billberg (JHAR02469 0101) (Microcerinae). These are all South African species. All sequences were deposited in GenBank (Appendix 2).

Abbreviations of depositories

FFWS

MLP

The specimens on which this study was based are lodged in the following institutions and specimen collections.

ANIC = Australian National Insect Collection, C.S.I.R.O., Canberra, A.C.T., Australia

CBGP = Continental Arthropod Collection, Centre de Biologie pour la Gestion des Populations, Montpellier, France

Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Prague,

Czech Republic

= Entomology Collection, Museo de La Plata, La Plata, Argentina

MNHN = Muséum national d'histoire naturelle, Paris, France

NHMUK = The Natural History Museum, London, United Kingdom SAMC = Iziko South African Museum, Cape Town, South Africa

SANC = South African National Collection of Insects, Pretoria, South Africa TMSA = Ditsong National Museum of Natural History, Pretoria, South Africa

Results

Taxonomy

Class Insecta Linnaeus, 1758 Order Coleoptera Linnaeus, 1758 Family Curculionidae Latreille, 1802 Subfamily Brachycerinae Billberg, 1820

Tribe Cryptolaryngini Van Schalkwyk, 1966

Cryptopharynginae Marshall, 1957: 18, not available (based on homonymic genus name). Type genus: *Cryptopharynx* Marshall, 1957 (unavailable, junior homonym).

Cryptolarynginae Van Schalkwyk, 1966: 745 (replacement name for Cryptopharynginae). Type genus: *Cryptolarynx* Van Schalkwyk, 1966 (replacement name for *Cryptopharynx* Marshall, 1957). Periegini Legalov, 2003: 68. Type genus: *Perieges* Schoenherr, 1842.

Cryptolaryngidae – Thompson 1992: 873, 877, 882. — Alonso-Zarazaga & Lyal 1999: 72. — Alonso-Zarazaga 2013: 497.

Cryptolaryngini – Kuschel 1995: 22. — Oberprieler *et al.* 2007: 506. — Alonso-Zarazaga 2013: 497. — Oberprieler 2014: 437–438. — Alonso-Zarazaga *et al.* 2017: 13, 112. — Legalov 2020: 320, 322. Periegini – Oberprieler 2014: 438. — Legalov 2020: 322.

Genus Cryptolarynx Van Schalkwyk, 1966

Cryptopharynx Marshall, 1957: 17, preoccupied by Cryptopharynx Kahl, 1928 in Ciliophora: Loxodida.Type species, by original designation: Cryptopharynx vitis Marshall, 1957.Cryptolarynx Van Schalkwyk, 1966: 745 (replacement name for Cryptopharynx Marshall, 1957).

Cryptolarynx – Van den Berg 1968: 183–221 (characters). — Thompson 1992: 842, 848, 876, 881–883 (characters, relationships). — Lyal 1995: 49–51 (ventral head structures). — Lyal & King 1996: 765 (elytral file absent). — Alonso-Zarazaga & Lyal 1999: 72 (catalogue). — Marvaldi & Morrone 2000: 48 (characters). — Oberprieler *et al.* 2007: 494–495, 505 (species numbers, photograph). — Oberprieler 2014: 425–426, 430, 437–439 (characters, classification, relationships, biology).

The description of *Cryptolarynx* by Marshall (1957) was based on the two species known at the time, *C. vitis* and *C. estriatus*. Van den Berg's (1968) detailed description supposedly applies to *C. vitis* as well, but this cannot be ascertained as several species of the genus occur in the area where he collected his material and no specific vouchers specimens were identified in the insect collection at Stellenbosch University. Several additional species were collected afterwards, Oberprieler *et al.* (2007) reporting at least another 16 species to occur in South Africa, but these were left undescribed until now, and the characteristics of Cryptolaryngini discussed by Oberprieler (2014) were also essentially based on *C. estriatus* and *C. vitis*.

Redescription (♂)

APPEARANCE AND MEASUREMENTS. Small to medium-sized weevils, body length 1.5–4.5 mm. Body in dorsal view stocky, subglobose, broadly ovate or somewhat elongate-ovate (Fig. 1). Pronotum in most species widest at base, elytral base then subequal in width; pronotum in some species widest at its middle, elytral base then as wide as widest part of pronotum. Elytra widest at or close to their middle. Body in lateral view (Fig. 3I–II) rather hunched, highest just behind elytral base to middle of elytral length; head almost hypognathous.

Colour and vestiture. Body integument black; antennae, tibiae and tarsi generally reddish. Dorsal vestiture (pronotum + elytra) consisting of short, recumbent clothing scales, these isodiametric to 2×10^{10} as long as wide, not aligned on interstriae, more or less concealing integument, colour ranging through black, dark brown to pale brown and grey to white, orange to yellow in one species; darker scales usually concentrated medially on pronotum and from there in broad stripe on elytral interstriae 1–3; paler scales concentrated at sides of dorsum or pale areas reduced to strips laterally on pronotum and along elytral interstriae 4; elytra with a pair of pale spots on interstriae 2–3 at apical $\frac{2}{3}$ of length, spots sometimes hardly discernible or confluent to form a pale transverse band that may further merge with pale areas laterally; scales arising from strial punctures suberect in some species and then up to 4×10^{10} as long as wide.

HEAD. Head capsule globose, in repose deeply retracted into prothorax, leaving only vertex and often eyes visible in dorsal view. Eyes subcircular or slightly oval, usually only slightly convex, situated dorsally or sublaterally, surrounded by a ring of mostly pale recumbent scales. Forehead flat, width ranging from less than to twice width of eye; fovea absent. Distance between eye and scrobe smaller than width of eye. Rostrum very short and broad, not differentiated from head; mandibles abutting anterior part of procoxae when head in repose. Epifrons short, width ³/₄× to subequal to width of forehead, medially deeply longitudinally depressed, epifrontal scales recumbent or suberect and orientated towards mouthparts. From largely indistinguishable but set off from epistome by slight carina, with 1 or more pairs of long setae laterally. Epistome crescentic, anterior margin medially notched, sometimes medially with single elongate seta about half as long as frontal setae. Mandibles beak-like, paucisetose (4–8 setae on each), with 2 setae long and erect and the others shorter; without scales. Maxillae with galea and lacinia separate, both bearing apical setae. Antennae inserted subdorsally at approximately midlength of rostrum; scapes slender, as long as or longer than width of epifrons between antennal insertions, regularly curved, clavate at apex and bearing erect setae, in repose folding into narrow scrobes extending onto underside of rostrum; funicles 7-segmented, longer than scape, segment 1 longer than wide, longer than or as long as 2, 1–4 flattened dorsoventrally, 2 and 4 or 2–4 angular or toothed ventrally, 5–7 globular or moderately elongate; funicles entirely hidden between head and pronotum when head in repose; clubs 4-segmented, fusiform, acuminate, shorter than funicle.

Thorax. Pronotum convex, at least moderately transverse, widest at base or near midlength, sides arcuate; integument finely and densely punctate, dull between punctures; anterior margin bisinuate, posterior margin more or less bisinuate, fitting closely to elytral bases up to level of elytral humeri. Prothorax anteriorly on each side produced into a large sharp-rimmed ventrolateral lamina extending from lower level of eye down to anterior edge of procoxa, concealing anterior prothoracic margin beneath it, rim of lamina asetose but anterior margin fringed with row of dense plumose scales, longer below eyes but shorter ventrally along prosternum. Prosternum broad, very short, depressed below anterior edge of procoxae, declivous, abutting rostrum when head in repose; procoxal cavities medially confluent, hypomeral lobes behind them short, suture of median junction faintly discernible. Mesoventrite deeply depressed, almost vertically declivous, intermesocoxal process subtuberculate; mesepimera narrowly triangular, fully separating mesanepisterna from elytral margin. Metaventrite narrower than width of metatarsus; metanepisterna fully fused to metaventrite, metanepisternal suture completely obliterated.

Scutellar shield not exposed.

ELYTRA. Globular to broadly ovate, sides convex, widest near or anterior of midlength; jointly rounded at apex; elytral base broadly concave, not marginate; integument flat, dull or shiny, 10-striate but striae generally indiscernible on outer surface, mixed with regular punctures and covered by scales.

METATHORACIC WINGS. Absent.

Legs. Slender. Procoxae subcontiguous, mesocoxae separated by $0.25 \times$ width of a mesocoxa. Trochanters with single long erect seta. Femora subcylindrical, unarmed; metafemora not reaching elytral apex. Tibiae straight, expanding slightly from base to apex, inner margin at least slightly bisinuate, protibiae crenulate in distal half, meso- and metatibiae unarmed; apex without spurs but with small stout mucro, this sometimes larger on metatibiae, meso- and metatibiae without corbels. Tarsi short or slender, segment 1 isodiametric or $2 \times$ as long as wide, longer than 2; 3 deeply bilobate; 5 about $2 \times$ as long as 3, gradually broadening apicad; claws paired, free, divaricate, simple with small basal lobe and long stiff ventrobasal seta.

ABDOMEN. Ventrites more or less concave medially, median impressions surrounded with cuticular ridges or not, surface more or less densely clothed with pale, recumbent scales, intermixed with suberect setae; ventrite 1 medially about twice as long as laterally, as long as or longer than each of ventrites 2–4, intercoxal process usually ogival in shape, with apex pointed or rounded, medially slightly concave to convex; ventrite 5 flat or medially slightly concave, apically devoid of scales.

MALE TERMINALIA. Body of penis elongate or moderately elongate (W:L ratio 0.25–0.6), 0.5– $2.0 \times$ as long as temones, acuminate at apex, moderately curved in profile; tectum narrow but distinct; endophallus with symmetrical copulatory sclerite, sometimes divided into two symmetrical structures, and with rows of cuticular denticles more or less visible between copulatory sclerite and base of penis body. Parameroid lobes of dorsal plate of tegmen separate, divided by median notch, not fused; apical setae always present but variable in length, number and arrangement. Spiculum gastrale asymmetrical; divergence of basal arms V- or U-shaped, right arm often angulate medially or bearing a tooth externally.

Female Terminalia. Gonocoxites (Fig. 8K) elongate, narrowly triangular, with only a few setae apically; styli inserted apicolaterally, 2× as long as wide, apices with 5–6 very short setae. Sternite VIII (Fig. 8L) with basal arms symmetrical, half the length of apodeme, angular at midlength. Spermatheca (Fig. 8M) stocky, cornu wide and slightly curved, nodulus rounded, collum and ramus not differentiated.

Sexual dimorphism

The sexes are distinguishable by their body shapes, males being smaller and globular and females larger and broadly ovate, and by the structure of the ventrite 1, in males centrally depressed but covered by plumose scales and in females flat.

Distribution

South Africa.

1. *Cryptolarynx vitis* (Marshall, 1957) Figs 1A, 2A, 3A, 4A, 5A, 6A–C, 8G

Cryptopharynx vitis Marshall, 1957: 18.

Cryptolarynx vitis – Van Schalkwyk 1966: 745 (implied new combination). — Van den Berg 1968: 189–204 (anatomy of adult). — Thompson 1992: 848 (figures of male abdominal ventrites, male sternite VIII). — Oberprieler 2014: 438 (biology).

Differential diagnosis

Cryptolarynx vitis is morphologically most similar to *C. subglaber* sp. nov. but differs in its denser vestiture (scattered in *C. subglaber*), only weakly contrasting white scales on the mes- and metanepisterna with those on the elytra (significantly different in *C. subglaber*) and its distinctly different copulatory sclerite. The two species differ genetically by uncorrected pairwise distances ranging from 15.1 to 22.1% for *COI* and from 1.1 to 2.7% for *EF1*.

Material examined

Lectotype

REPUBLIC OF SOUTH AFRICA • ♀; "Type [red label]" "Cape Prov. [REPUBLIC OF SOUTH AFRICA – **Western Cape**]. Stellenbosch; [33.93° S, 18.86° E]; On vine leaf. 1956" "*Cryptopharynx vitis*, Mshl. TYPE ♀" [Newly added label, red, printed:] "LECTOTYPE *Cryptopharynx vitis* Marshall, 1957 des. J. Haran 2023"; NHMUK.

Paralectotypes

All with original handwritten type labels: "*Cryptolarynx vitis* Mshl Cotypes ♂/♀". All with newly added labels, blue, printed: "PARALECTOTYPE *Cryptopharynx vitis* Marshall, 1957 des. J. Haran 2023".

Other material

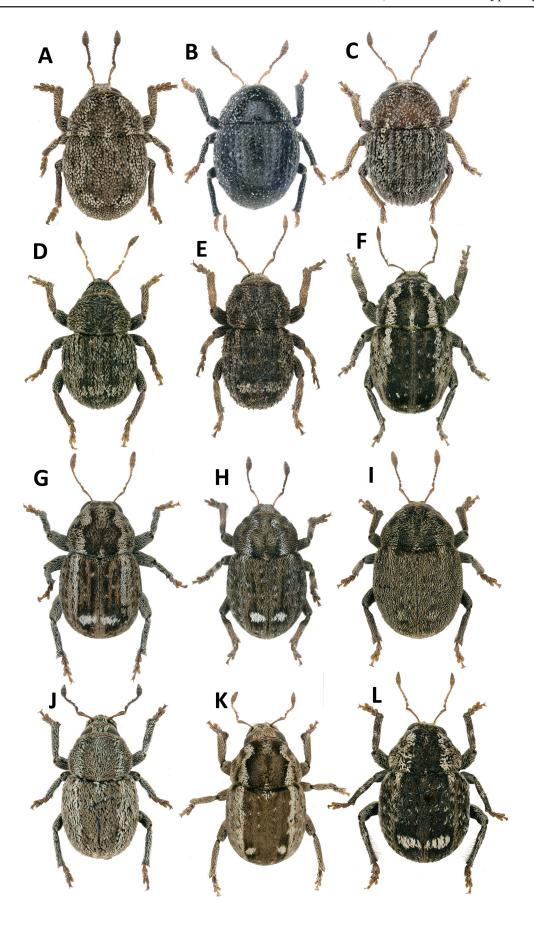
REPUBLIC OF SOUTH AFRICA – Western Cape • 1 \circlearrowleft , 4 \circlearrowleft 2; Stellenbosch; 33.930° S, 18.875° E; 6 Sep. 2018; J. Haran leg.; at base of Oxalis glabra; JHAR01484; CBGP • 1 \circlearrowleft , 14 specs (preserved in ethanol); Stellenbosch, Kylemore; 33.918° S, 18.956° E; 8 Sep. 2019; J. Haran leg.; at base of Oxalis glabra; JHAR01488; CBGP • 1 \circlearrowleft , 10 specs (preserved in ethanol); Malmesbury; 33.454° S, 18.743° E; 10 Sep. 2019; J. Haran leg.; at base of Oxalis spp.; JHAR02559; CBGP • 1 $\stackrel{\wedge}{\circ}$, 19 specs (preserved in ethanol); Cape Town, Tygerberg Nature Reserve; 33.875° S, 18.596° E; 20 Sep. 2019; J. Haran leg.; at base of Oxalis glabra; JHAR02568; CBGP • 1 spec. (preserved in ethanol); Pniel, Boschendal Estate; 33.873° S, 18.976° E; 16 Sep. 2019; J. Haran leg.; at base of *Oxalis* spp.; JHAR03198; CBGP • 5 specs (preserved in ethanol); Wellington 15 km WNW; 33.609° S, 18.849° E; 10 Sep. 2019; J. Haran leg.; at base of *Oxalis* spp.; JHAR03199; CBGP • 1 ♂, 1 ♀; Wellington; 33.64° S, 19.01° E; 1 Feb. 1955; G.D. Malan leg.; Ac. U.S. 708; SANC • 1 ♂, 1 ♀; same collection data as for preceding; NHMUK • 1 spec.; same collection data as for preceding; Jan.-Feb. 1955; G.D. Malan leg.; Ac. U.S. 708; SAM-COL-A045641; SAMC • 2 ♂♂, 1 ♀; Franskraal, Suikerbosrand Farm; 34.600° S, 19.400° E; 28 Sep. 1984; R. Müller leg.; sweeping; E-Y:2127; TMSA • 2 ♀♀; Cape Town, Cape Flats, Philippi, ca 3–4 mi E; 34.01° S, 18.62° E; elev. 180 ft; 7 Aug. 1954; J. Balfour-Browne leg.; with Hydrodictyon (algae) and Aponogeton; B.M. 1954-797, STN-347; NHMUK • 1 &; Cape Town, Cape Flats, Rapenburg; 33.95° S, 18.48° E; 1–14 Oct. 1920; R.E. Turner leg.; NHMUK • 1 ♂; Gansbaai, Grootbos Private Nature Reserve; 34.536° S, 19.416° E; 13 Oct. 2018; J. Haran leg.; on *Oxalis caprina*; JHAR01592; CBGP • 1 ♂, 1 ♀; Hottentots-Holland Nature Reserve, Nuweberg 10 km NE, Grabouw–Villiersdorp–Franschhoek junction; 34.027° S, 19.210° E; 13 Nov. 1973; S. Endrödy-Younga and J. Strydom leg.; in dam; E-Y:239; TMSA.

Redescription (♂)

Measurements. Body length 1.6–3.6 mm.

Colour and vestiture. Body integument black, scapes and tarsi reddish; vestiture of dorsum (pronotum \pm elytra) consisting of short, recumbent, subtriangular clothing scales, isodiametric or slightly longer than wide, partly concealing integument, overlapping or subcontiguous, and longer, suberect clothing scales at least $2 \times$ as long as wide in strial punctures; colour pattern highly variable, scale colours brown and

Fig. 1 (Part I) (next page). Habitus of males of species of *Cryptolarynx* Van Schalkwyk, 1966 (dorsal view). **A.** *C. vitis* (Marshall, 1957). **B.** *C. subglaber* Haran sp. nov. **C.** *C. squamulatus* Haran sp. nov. **D.** *C. muellerae* Haran sp. nov. **E.** *C. hirtulus* Haran sp. nov. **F.** *C. robustus* Haran sp. nov. **G.** *C. namaquanus* Haran sp. nov. **H.** *C. carinatus* Haran sp. nov. **I.** *C. variabilis* Haran sp. nov. **J.** *C. estriatus* (Marshall, 1957). **K.** *C. pyrophilus* Haran sp. nov. **L.** *C. pilipes* Haran sp. nov. Not to scale.



grey; grey scales usually condensed on pronotum at base and apex of median line, on two sublateral longitudinal stripes and on elytra on striae 4-5, usually forming a transverse band at apical $\frac{2}{3}$, sometimes divided into a pair of spots spanning interstriae 1-3.

HEAD. Forehead narrower than width of an eye, surface slightly concave. Eyes flat, in dorsal view only slightly exceeding outline of head, surrounded by a ring of short pale scales directed towards centre of eye; distance between eye and scrobe larger than width of antennal club. Epifrons narrow, distance between antennal insertions $0.5 \times$ length of scape, scales at least $3 \times$ as long as wide, suberect, overlapping. Frons with a single pair of long lateral setae. Epistome with single median seta. Antennae variable, with funicle segments 1 elongate, at least $2 \times$ as long as wide; 2–4 at least slightly longer than wide, compressed, on inside slightly angled; 5–7 isodiametric or wider than long, globular or slightly compressed.

Pronotum. Strongly transverse, nearly $2 \times$ as wide as long (W:L ratio 1.6–1.8), almost semicircular in dorsal view, widest at base, sides parallel or slightly arcuate in basal $\frac{1}{3}$, straight or slightly curved and converging in apical $\frac{2}{3}$; anteriorly $2 \times$ narrower than posteriorly.

ELYTRA. Globular, isodiametric (W:L ratio 1); sides convex, widest near midlength.

Legs. Tibiae with black apical mucro; protibiae with outer margin straight, inner margin with series of small black teeth in apical half; metatibiae bisinuate, distal side of mucro perpendicular to external margin of metatibiae. Tarsi short, segment 2 much wider than long (W:L ratio 1.7–2.0).

ABDOMEN. Ventrite 1 with distinct cuticular elevation reaching posterior suture, concave medially, forming a semicircular cavity, scales in impression plumose; ventrites 1–4 with overlapping white or pale brown scales; ventrite 5 with scattered suberect, elongate scales, partly concealing integument.

TERMINALIA. Body of penis elongate (W:L ratio 0.3), 0.6–1.0 × as long as temones, sides diverging apicad in basal ²/₃, converging in apical third; curvature in profile weak and regular, dorsoventrally strongly narrowed before apex. Copulatory sclerite slender, short. Parameroid lobes separate, divided by deep median notch, each lobe with anteapical constriction, bearing long marginal setae and shorter setae discally, all setae orientated centrifugally. Spiculum gastrale with basal arms regularly curved.

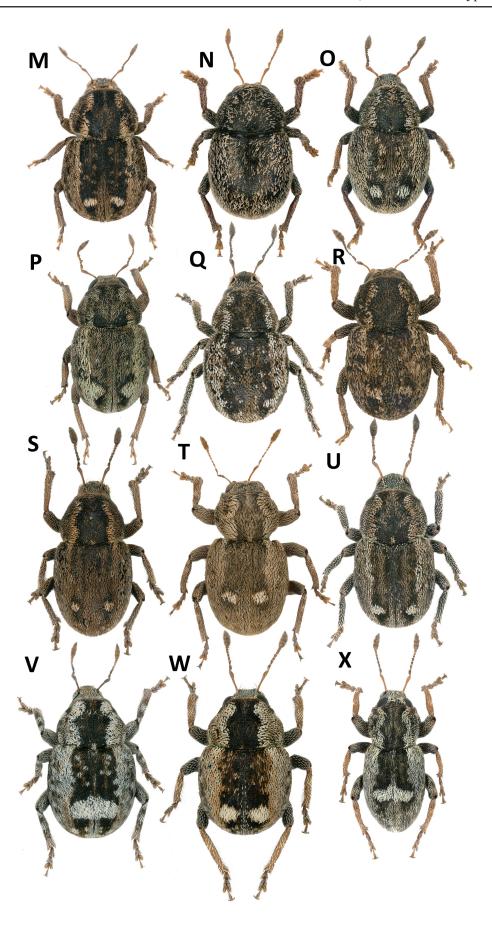
Sexual dimorphism

Males and females can be distinguished by their body shape (smaller and globular in male, larger and broadly ovate in female), the structure of the first ventrite (with a central cuticular depression concealed by plumose scales in male, flat in female) and the width of the forehead (at most slightly wider in male, $2 \times$ as wide as epifrons between antennal insertions in female).

Life history

Large numbers of specimens of *Cryptolarynx vitis* were collected in monospecific stands of *Oxalis glabra* Thunb. at various sites, but it was not reared from the bulbs of this plant species and its exact association with this species of *Oxalis* therefore needs verification. *Oxalis glabra* is a weedy species that forms dense covers in vineyards in winter. High population densities of *C. vitis* in these stands can lead to damage to vine leaves when adults emerge and undertake maturation feeding (Marshall 1957). In this study, adults of this species were mostly found between August and November but once, in a population

Fig. 1 (Part II) (next page). Habitus of males of species of *Cryptolarynx* Van Schalkwyk, 1966 and *Hadrocryptolarynx* Haran gen. nov. (dorsal view). **M**. *C. armatus* Haran sp. nov. **N**. *C. falciformis* Haran sp. nov. **O**. *C. oberprieleri* Haran sp. nov. **P**. *C. spinicornis* Haran sp. nov. **Q**. *C. cederbergensis* Haran sp. nov. **R**. *C. homaroides* Haran sp. nov. **S**. *C. marshalli* Haran sp. nov. **T**. *C. endroedyi* Haran sp. nov. **U**. *C. oberlanderi* Haran sp. nov. **V**. *C. san* Haran sp. nov. **W**. *C. luteipennis* Haran sp. nov. **X**. *Hadrocryptolarynx major* Haran gen. et sp. nov. Not to scale.



at Wellington, in January and February. The seasonal occurrence reported by Van den Berg (1968), if applicable to the same species, indicates an activity of adults from late September to early December, with a peak in mid-November.

Distribution

The species occurs in lowland valleys of the Cape Town area, from Cape Town to Malmesbury and Wellington in the north and to Gansbaai in the south-east, from sea level to 400 m in elevation (Fig. 13). The specimens from Ceres reported by Marshall (1957) could not be examined for this study and may represent a different species.

Remarks

A redescription of this species is provided to accommodate the variability in characters encountered in the wider geographical context than known to Marshall (1957) and Van den Berg (1968). Together with *C. hirtulus* sp. nov., *C. robustus* sp. nov., *C. squamulatus* sp. nov. and *C. subglaber* sp. nov., *C. vitis* forms a species group characterised mainly by a narrow forehead, slightly erect elytral scales and a narrow apex of the parameroid lobes. Preliminary reconstruction of the phylogenetic relationships between the species of *Cryptolarynx* also suggests that these species form a cluster distinct from the other species of the genus (Fig. 12). It should be noted that the weakly supported preliminary phylogenetic relationships in this species group were not fully resolved with *EF1* (Fig. 12). In *C. vitis*, intraspecific distances ranged up to 10.0% for *COI* and 2.5% for *EF1* between specimens from different localities. This species may comprise several genetic lineages in the process of speciation, but stable morphological differences could not be identified.

The description of *C. vitis* was based on 24 males and 24 females (Marshall 1957), of which 7 males and 10 females are preserved in the NHMUK and 2 males and 2 females in the SAMC. A female syntype in the NHMUK, bearing a type label in Marshall's hand, is here designated as the lectotype of *C. vitis* and was labelled accordingly (see above), and all other syntypes examined were labelled as paralectotypes.

2. *Cryptolarynx subglaber* Haran sp. nov. urn:lsid:zoobank.org:act:F2C57975-700A-4E2A-9378-87DCD314BFC6 Figs 1B, 2B, 3B, 4B, 5B

Differential diagnosis

Cryptolarynx subglaber sp. nov. is closely related to *C. vitis*, see the Differential diagnosis and Remarks sections under that species for diagnostic characters and genetic distances.

Etymology

This species is named in reference to the glabrous appearance of the integument, seemingly unique among known species of *Cryptolarynx*. The specific epithet is an adjective in the masculine form.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • & "REPUBLIC OF SOUTH AFRICA. Western Cape province, [Somerset West,] Helderberg NR [Nature Reserve]. 14.x.2019. J. Haran leg." "34.061° S 18.874° E, at base of *Oxalis* spp. JHAR02587_0101. Cirad-CBGP coll." "Holotype. *Cryptolarynx subglaber* Haran 2023"; SAMC.

Paratypes

REPUBLIC OF SOUTH AFRICA – **Western Cape** • 1 \circlearrowleft ; same collection data as for holotype; SAMC • 1 \circlearrowleft ; same collection data as for holotype; FFWS • 1 \circlearrowleft , 1 \hookrightarrow , same collection data as for holotype; CBGP • 1 \hookrightarrow ; Stellenbosch; 33.948° S, 18.879° E; 6 Aug. 2018; J. Haran leg.; *Oxalis lanata*; JHAR01235_0101; CBGP.

Description (♂)

Measurements. Body length 1.8–3.7 mm.

COLOUR AND VESTITURE. Body integument black, antennae and tarsi reddish; vestiture of dorsum (pronotum + elytra) consisting of short, recumbent, rounded or subtriangular clothing scales, isodiametric or slightly longer than wide, not contiguous, and longer, suberect scales, at least $2 \times$ as long as wide, brown or white, in each puncture of striae; scale colours brown and pale grey; grey scales usually condensed on two lateral stripes on pronotum and on transverse band on elytra at apical $\frac{2}{3}$ of length, sometimes divided into a pair of large spots on interstriae 1-3.

HEAD. Forehead at most slightly wider than epifrons near antennal insertions, narrower than width of an eye, scales not concealing integument. Eyes flat, in dorsal view only slightly exceeding outline of head, surrounded by a ring of short pale scales directed towards centre of eye; distance between eye and scrobe larger than width of antennal club. Epifrons narrow, distance between antennal insertions $0.5 \times length$ of scape, scales at least $3 \times as$ long as wide, erect, overlapping. Frons with a single pair of long lateral setae. Epistome with single median seta. Antennae variable, funicles with segment 1 elongate, at least $2 \times as$ long as wide; 2-4 at least slightly longer than wide, compressed, slightly angular on inside; 5-7 isodiametric or wider than long, globular or slightly compressed.

PRONOTUM. Strongly transverse, nearly $2 \times$ as wide as long (W:L ratio 1.7–2), almost semicircular in dorsal view, widest at base, sides parallel or slightly arcuate in basal $\frac{1}{3}$, straight or slightly emarginate and converging in apical $\frac{2}{3}$; apex $2 \times$ narrower than base.

ELYTRA. Globular, isodiametric or wider than long (W:L ratio 1–1.1), sides convex, widest before midlength.

Legs. Tibiae with black apical mucro; protibiae with outer margin straight, inner margin with series of small black teeth in apical half; metatibiae bisinuate, distal margin of mucro perpendicular to external margin of metatibia. Tarsi short, segment 2 much wider than long (W:L ratio 1.7–2.0).

ABDOMEN. Ventrite 1 with distinct cuticular elevation reaching posterior suture, concave medially, scales in impression plumose; ventrites 1–4 with overlapping white scales, partly concealing integument.

TERMINALIA. Body of penis elongate (W:L ratio 0.3–0.4), 0.6× as long as temones, sides subparallel, converging in apical quarter; curvature in profile weak and regular, dorsoventrally narrowed before apex. Copulatory sclerite short, shaped like an arrowhead. Parameroid lobes separate, divided by deep median notch, each lobe narrowing apicad, bearing long marginal setae and shorter setae discally, all setae orientated centrifugally. Spiculum gastrale with basal arms regularly curved.

Sexual dimorphism

The sexes can be distinguished by their body shape (globular in males (W:L ratio 0.7), broadly ovate in females (W:L ratio 0.6)) and by the cuticular elevation on ventrite 1 of males forming two ridges laterally (ventrite only slightly concave in females).

Life history

Specimens of *Cryptolarynx subglaber* sp. nov. were collected in mixed patches of species of *Oxalis* (*O. lanata* L. f., *O. glabra* and *O. purpurea* L.), and the exact host plant of the species is yet unknown. Adults were collected in August and October.

Distribution

The species occurs on western slopes of the Hottentots Holland Mountains, in Stellenbosch and the Helderberg Nature Reserve (elevation 130–170 m; Fig. 13).

3. *Cryptolarynx squamulatus* Haran sp. nov. urn:lsid:zoobank.org:act:F4FDD330-3922-4480-A93C-D830B3696A88 Figs 1C, 2C, 3C, 4C, 5C

Differential diagnosis

Cryptolarynx squamulatus sp. nov. belongs to the C. vitis group and in this group is most closely related to C. hirtulus sp. nov. These two species can be distinguished by their body shape, being globular in C. squamulatus and elongate in C. hirtulus, and their interspecific genetic distance was found to be 18.6% for COI and of 3.7% for EF1.

Etymology

This species is named in reference to the dense cover of suberect scales (squamae) on its elytra. The specific epithet is an adjective in the masculine form.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • & "REPUBLIC OF SOUTH AFRICA. Western Cape Province, West-coast NP [National Park], [Postberg Section,] 31.viii.2019, J. Haran leg." "33.105° S 18.004° E, at base of *Oxalis obtusa*, JHAR02555" "Holotype. *Cryptolarynx squamulatus* Haran 2023"; SAMC.

Paratypes

REPUBLIC OF SOUTH AFRICA – **Western Cape** • 1 \circlearrowleft ; same collection data as for holotype; CBGP • 1 \circlearrowleft ; same collection data as for holotype; SAMC.

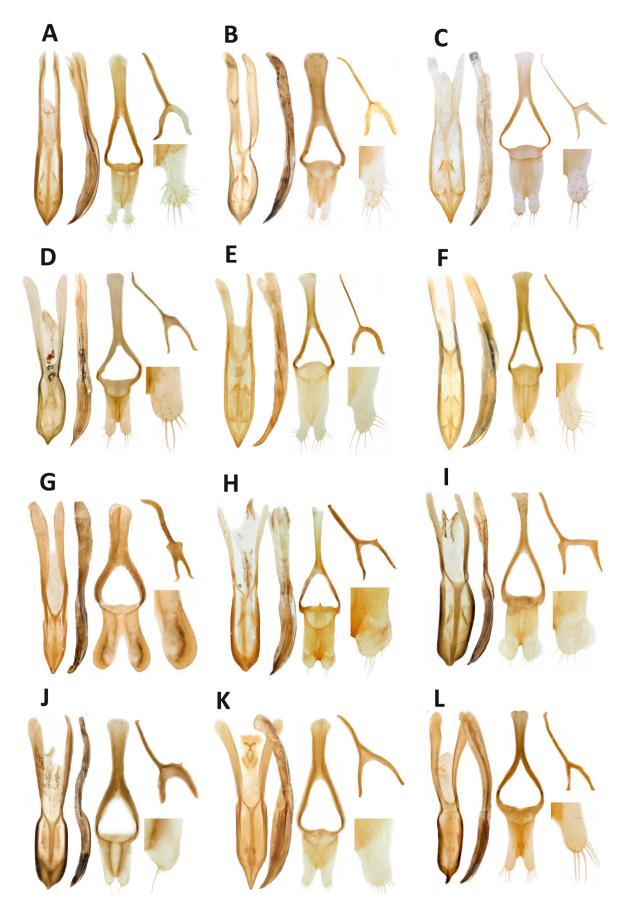
Description (♂)

MEASUREMENTS. Body length 1.9 mm.

COLOUR AND VESTITURE. Colour as in females (single known male teneral). Body integument black, antennae and tarsi reddish. Dorsal vestiture (pronotum + elytra) consisting of short, recumbent, subtriangular clothing scales, pearly grey, slightly longer than wide, subcontiguous on interstriae, and longer, suberect scales, at least $4 \times$ as long as wide, brown or white, in each strial puncture; pale scales usually concentrated at base of interstriae 4 and corresponding area at pronotal base as well as forming an ill-defined transverse band at apical $\frac{2}{3}$ of elytra.

HEAD. Forehead slightly wider than epifrons near antennal insertions, narrower than width of an eye, scales not concealing integument. Eyes flat, in dorsal view only slightly exceeding outline of head, surrounded by a ring of short pale scales directed towards centre of eye; distance between eye and scrobe larger than width of antennal club. Epifrons narrow, distance between antennal insertions $0.5 \times \text{length}$ of scape, scales at least $3 \times \text{as}$ long as wide, suberect, overlapping. Frons with single pair of long lateral setae. Epistome with single median seta. Antennal funicles with segment 1 elongate, $2 \times \text{as}$ long as wide; 2-4 slightly longer than wide, compressed, slightly angular on inside; 5-7 globular, slightly compressed.

Fig. 2 (Part I) (next page). Male genitalia of species of *Cryptolarynx* Van Schalkwyk, 1966. Penis in dorsal and lateral view (left), tegmen in dorsal view (middle) and details of apex of a parameroid lobe and spiculum gastrale in dorsal view (right). **A.** *C. vitis* (Marshall, 1957). **B.** *C. subglaber* Haran sp. nov. **C.** *C. squamulatus* Haran sp. nov. **D.** *C. muellerae* Haran sp. nov. **E.** *C. hirtulus* Haran sp. nov. **F.** *C. robustus* Haran sp. nov. **G.** *C. namaquanus* Haran sp. nov. **H.** *C. carinatus* Haran sp. nov. **I.** *C. variabilis* Haran sp. nov. **J.** *C. estriatus* (Marshall, 1957). **K.** *C. pyrophilus* Haran sp. nov. **L.** *C. pilipes* Haran sp. nov. Not to scale.



PRONOTUM. Strongly transverse (W:L ratio 1.6), almost semicircular in dorsal view, widest at base, sides arcuate in basal ½, almost straight and converging in apical ½; apex 1.5 × narrower than base.

ELYTRA. Globular, slightly wider than long (W:L ratio 1.1), sides convex, widest before midlength.

Legs. Tibiae with black apical mucro; protibiae with outer margin straight; metatibiae with inner margin bisinuate, distal margin of mucro perpendicular to external margin of metatibia. Tarsi short, segment 2 much wider than long (W:L ratio 1.7).

ABDOMEN. Ventrite 1 slightly concave; ventrites 1–4 with overlapping white scales, partly concealing integument.

TERMINALIA. Body of penis elongate (W:L ratio 0.3), twice as long as temones, sides straight, diverging from base to apical ¾, converging in apical quarter; curvature in profile weak and regular, dorsoventrally narrowed before apex. Copulatory sclerite weakly sclerotised (or not discerned in single examined specimen). Parameroid lobes separate, divided by deep median notch, each lobe narrowed before apex, spatulate, bearing long marginal setae and shorter setae discally, all setae orientated centrifugally. Spiculum gastrale with basal arms regularly curved, right arm with lateral tooth.

Sexual dimorphism

The sexes can be distinguished by their body shape (more globular in male, broadly ovate in female).

Life history

Specimens of *Cryptolarynx squamulatus* sp. nov. were collected in a patch of *Oxalis obtusa* Jacq., but the exact host association of the species was not verified. Freshly emerged adults were found in October.

Distribution

The species occurs in the West Coast National Park, Postberg Section (elevation 170 m; Fig. 13).

4. *Cryptolarynx muellerae* Haran sp. nov. urn:lsid:zoobank.org:act:0650659E-5354-4EA3-A832-2E093387BCE8 Figs 1D, 2D, 3D, 4D, 5D

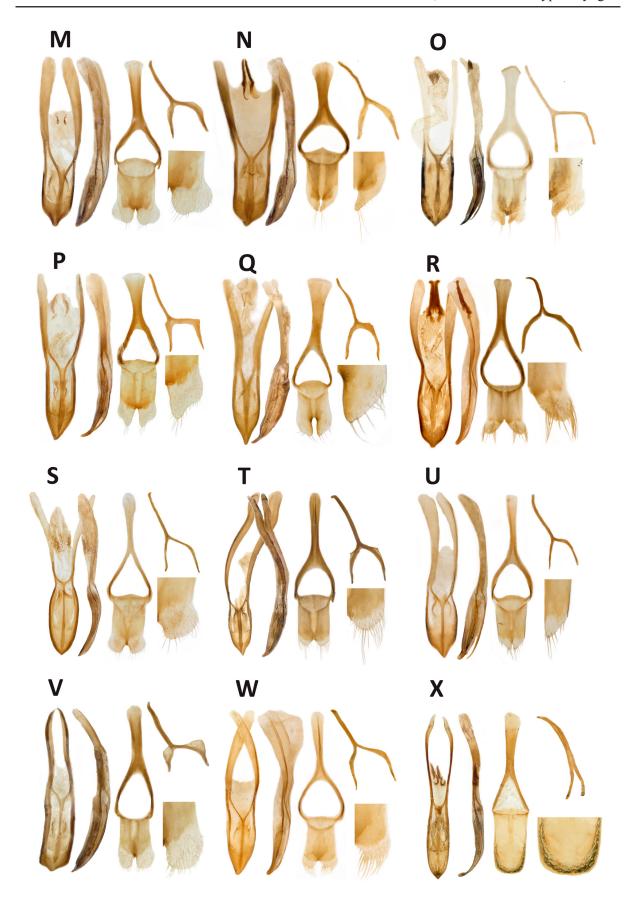
Differential diagnosis

Cryptolarynx muellerae sp. nov. has the general appearance of the species in the C. vitis group, but the male can be distinguished from these by its wider forehead, the absence of a mucro on the metatibiae and its non-constricted parameroid lobes. Among other species of the genus, it is the only species with long metatibial setae that has a body length of less than 2.5 mm.

Etymology

Cryptolarynx muellerae sp. nov. is dedicated to our colleague Ruth Müller, entomologist and collection manager at the Ditsong National Museum of Natural History in Pretoria, who provided substantial

Fig. 2 (Part II) (next page). Male genitalia of species of *Cryptolarynx* Van Schalkwyk, 1966 and *Hadrocryptolarynx* Haran gen. nov. Penis in dorsal and lateral view (left), tegmen in dorsal view (middle) and details of apex of a parameroid lobe and spiculum gastrale in dorsal view (right). **M.** *C. armatus* Haran sp. nov. **N.** *C. falciformis* Haran sp. nov. **O.** *C. oberprieleri* Haran sp. nov. **P.** *C. spinicornis* Haran sp. nov. **Q.** *C. cederbergensis* Haran sp. nov. **R.** *C. homaroides* Haran sp. nov. **S.** *C. marshalli* Haran sp. nov. **T.** *C. endroedyi* Haran sp. nov. **U.** *C. oberlanderi* Haran sp. nov. **V.** *C. san* Haran sp. nov. **W.** *C. luteipennis* Haran sp. nov. **X.** *Hadrocryptolarynx major* Haran gen. et sp. nov. Not to scale.



support in accessing the collection under her care and for the loan of specimens that have made this study possible. The specific epithet is a noun in the genitive case.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • &; "S. Afr., W. Cape Prov. [REPUBLIC OF SOUTH AFRICA – Western Cape], [Vanrhynsdorp S], Wiedouw farm. 31.43S - 18.43E [31.717° S, 18.717° E]" "18.8.1983; E-Y:1942. grassnetting [sweeping]. leg. Endrödy[-Younga] & Penrith" "Holotype. *Cryptolarynx muellerae* Haran 2023"; TMSA.

Paratypes

REPUBLIC OF SOUTH AFRICA – **Western Cape** • 1 ♂; same collection data as for holotype; CBGP • 1 ♀; same collection data as for holotype; TMSA • 1 ♀; same collection data as for holotype; SANC.

Description (♂)

Measurements. Body length 2–2.2 mm.

COLOUR AND VESTITURE. Body integument black, antennae, tibiae and tarsi reddish. Dorsal vestiture (pronotum + elytra) consisting of short, recumbent, subtriangular clothing scales, $2 \times$ as long as wide, subcontiguous on elytral interstriae, and longer, suberect scales, at least $4 \times$ as long as wide, in each strial puncture; scales creamy-white and brown; pale scales usually concentrated laterally on pronotum and elytra and on transverse band at apical $\frac{2}{3}$ of elytra.

HEAD. Forehead wider than epifrons near antennal insertions, as wide as width of an eye, scales not concealing integument. Eyes flat, in dorsal view only slightly exceeding outline of head, surrounded by a ring of short pale scales, those on forehead directed towards occiput; distance between eye and scrobe as large as width of antennal club. Epifrons narrow, distance between antennal insertions $0.5 \times length$ of scape, scales at least $3 \times as$ long as wide, suberect, overlapping. Frons with single pair of long lateral setae. Epistome without single median seta. Antennal funicles with segments 1-2 elongate, $2 \times as$ long as wide; 3-4 slightly longer than wide, compressed, slightly angular on inside; 5-6 globular; 7 transverse.

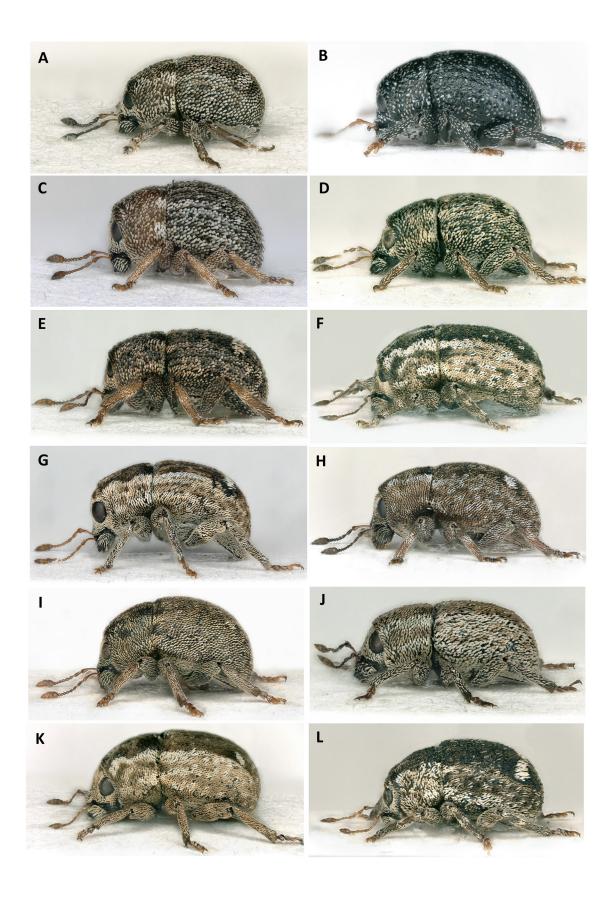
Pronotum. Strongly transverse (W:L ratio 1.4), almost semicircular in dorsal view, widest near midlength, sides arcuate; width of apex 0.7 × width of base.

ELYTRA. Globular to broadly ovate, isodiametric to slightly longer than wide (W:L ratio 1.0–0.9), sides convex, widest near midlength.

Legs. Tibiae with black apical mucro; protibiae with both outer and inner margins straight; metatibiae with inner fringe of long setae, the setae longer than segment 5 of metatarsus. Tarsi with segment 2 isodiametric or slightly wider than long.

ABDOMEN. Ventrite 1 slightly concave, bearing plumose scales in impression; other surfaces with overlapping creamy-white scales, partly concealing integument.

Fig. 3 (Part I) (next page). Habitus of males of species of *Cryptolarynx* Van Schalkwyk, 1966 (lateral view). **A**. *C. vitis* (Marshall, 1957). **B**. *C. subglaber* Haran sp. nov. **C**. *C. squamulatus* Haran sp. nov. **D**. *C. muellerae* Haran sp. nov. **E**. *C. hirtulus* Haran sp. nov. **F**. *C. robustus* Haran sp. nov. **G**. *C. namaquanus* Haran sp. nov. **H**. *C. carinatus* Haran sp. nov. **I**. *C. variabilis* Haran sp. nov. **J**. *C. estriatus* (Marshall, 1957). **K**. *C. pyrophilus* Haran sp. nov. **L**. *C. pilipes* Haran sp. nov. Not to scale.



TERMINALIA. Body of penis moderately elongate (W:L ratio 0.4), 0.7× as long as temones, sides straight, subparallel, converging abruptly near apex; curvature in profile weak and regular, dorsoventrally narrowed before apex. Copulatory sclerite weakly sclerotised or not discerned in examined specimens. Parameroid lobes separate, divided by a deep median notch, each lobe parallel-sided, rounded at apex; distal margin setose, two setae long, exceeding length of others. Spiculum gastrale with basal arms regularly curved, right arm laterally angulate.

Sexual dimorphism

The sexes can be distinguished by their body shape (more globular in male, more broadly ovate in female) and the width of the forehead (slightly wider than epifrons in male, nearly $2 \times$ wider in female).

Life history

Unknown. All known specimens of this new species were collected by sweeping vegetation.

Distribution

The species is only known from the type locality, near Vanrhynsdorp in the Western Cape Province (Fig. 13).

5. *Cryptolarynx hirtulus* Haran sp. nov. urn:lsid:zoobank.org:act:0CC60E56-F3AF-42E8-924C-97CBB58B6D15 Figs 1E, 2E, 3E, 4E, 5E, 6D–F

Differential diagnosis

Cryptolarynx hirtulus sp. nov. belongs to the *C. vitis* species group, see the Remarks section under that species for details. In this group it is most closely related to *C. squamulatus* sp. nov., see the Differential diagnosis section under that species for diagnostic characters and genetic distances.

Etymology

The species name is derived from the Latin adjective 'hirtus', meaning 'hairy', and refers to the suberect scales in the strial punctures, which give the species a slightly hairy appearance. The specific epithet is an adjective in the masculine form.

Material examined

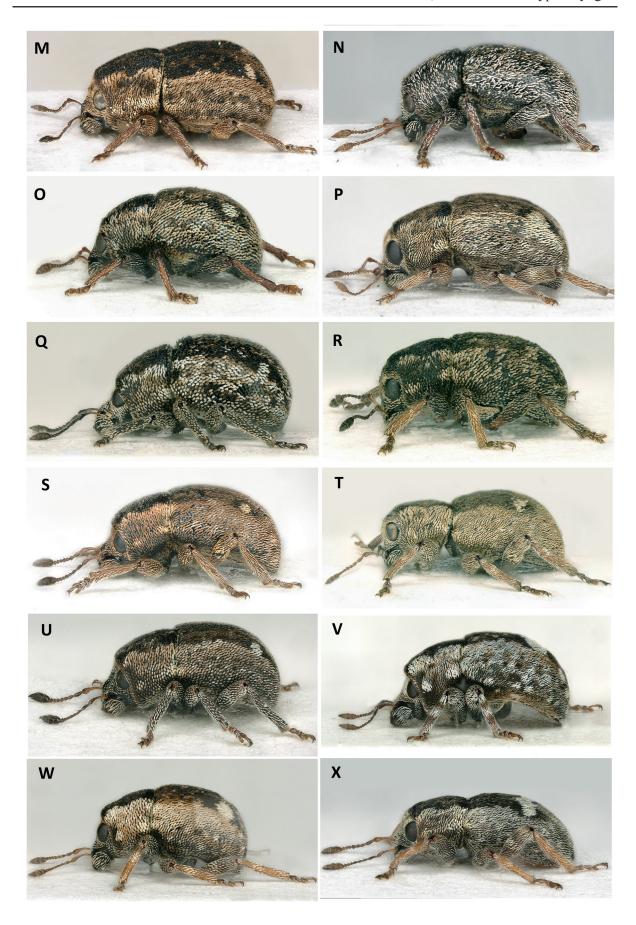
Holotype

REPUBLIC OF SOUTH AFRICA • & "REPUBLIC OF SOUTH AFRICA. Western Cape Province, Worcester. 29.viii.2019. J. Haran leg." "33.623° S 19.472° E. Near *Oxalis* spp. JHAR02356_0101. Cirad-CBGP coll." "Holotype. *Cryptolarynx hirtulus*. Haran 2023"; SAMC.

Paratypes

REPUBLIC OF SOUTH AFRICA – **Western Cape** • 1 \circlearrowleft , 2 \hookrightarrow \circlearrowleft (preserved in ethanol); same collection data as for holotype; CBGP • 1 \hookrightarrow ; Clanwilliam 29 km N, flat valley-bottom; 31.950° S, 18.717° E; 29 Aug. 1989; S. Endrödy-Younga and J. Klimaszewski leg.; ground and vegetation; E-Y:2675; TMSA • 1 \hookrightarrow ; Clanwilliam N, Olifants River ca 500 m W, roadside cut with boulders; 32.150° S, 18.883° E;

Fig. 3 (Part II) (next page). Habitus of males of species of *Cryptolarynx* Van Schalkwyk, 1966 and *Hadrocryptolarynx* Haran gen. nov. (lateral view). **M**. *C. armatus* Haran sp. nov. **N**. *C. falciformis* Haran sp. nov. **O**. *C. oberprieleri* Haran sp. nov. **P**. *C. spinicornis* Haran sp. nov. **Q**. *C. cederbergensis* Haran sp. nov. **R**. *C. homaroides* Haran sp. nov. **S**. *C. marshalli* Haran sp. nov. **T**. *C. endroedyi* Haran sp. nov. **U**. *C. oberlanderi* Haran sp. nov. **V**. *C. san* Haran sp. nov. **W**. *C. luteipennis* Haran sp. nov. **X**. *Hadrocryptolarynx major* Haran gen. et sp. nov. Not to scale.



29 Aug. 1989; S. Endrödy-Younga and J. Klimaszewski leg.; flowering vegetation; E-Y:2674; TMSA • 2 ♂♂; Malmesbury; 33.454° S, 18.743° E; 10 Sep. 2019; J. Haran leg.; at base of *Oxalis* spp.; JHAR02561; CBGP • 1 ♀; Touws River 16 km SW; 33.402° S, 19.886° E; 23 Jul. 2019; J. Haran leg.; emerged from bulbs of *Oxalis obtusa*; JHAR02444; CBGP. – **Northern Cape** • 1 ♂; Wupperthal area, Botterkloof Pass 5 km from top; 31.783° S, 19.267° E; 17 Jul. 1995; S. Neser leg.; feeding on leaves of *Homeria* [now *Moraea*] sp. (Iridaceae) growing in road verge; SANC • 1 ♀; Calvinia N, Hantamsberg; 31.352° S, 19.803° E; 1544 m; 9 Nov. 2018; R. Borovec leg.; FFWS • 1 ♂; Nieuwoudtville 8–12 km SE; 31.467° S, 19.300 °E; 18 Sep. 1986; R. Oberprieler leg.; on *Galenia africana* [now *Aizoon africanum* (L.) Klak, Aizoaceae]; SANC • 1 ♂; Vanrhyns Pass, stony mountainside; 31.383° S, 19.033° E; 18 Aug. 1983; S. Endrödy-Younga and M-L. Penrith leg.; pitfall traps 78 days with meat bait; E-Y:1940; TMSA • 1 ♀; Vanrhyns Pass, E base; 31.367° S, 19.033° E; 25 Sep. 1994; C.L. Bellamy leg.; on flowers and vegetation; shrub vegetation on coarse sand; E-Y:3044; TMSA.

Description (♂)

Measurements. Body length 2–2.6 mm.

Colour and vestiture. Body integument black, antennae, tarsi and sometimes tibiae reddish. Dorsal vestiture (pronotum + elytra) consisting of short, recumbent, subtriangular clothing scales, $1.2-2 \times$ as long as wide, subcontiguous on interstriae, and longer, suberect scales, at least $4 \times$ as long as wide, in each strial puncture, visible in lateral view; scales creamy-white, brown and black; pale scales usually concentrated in two longitudinal stripes on pronotum and on elytral interstriae 4 and forming a pair of pale spots surrounded by black scales on interstriae 1-4 at apical $\frac{2}{3}$ of elytra.

HEAD. Forehead as wide as epifrons near antennal insertions, narrower than width of an eye, scales not entirely concealing integument. Eyes moderately convex, in dorsal view only slightly exceeding outline of head, surrounded by a ring of short pale scales directed towards centre of eye; distance between eye and scrobe larger than width of antennal club. Epifrons narrow, distance between antennal insertions $0.5 \times \text{length}$ of scape, scales at least $3 \times \text{as}$ long as wide, suberect, overlapping. Frons with single pair of long lateral setae. Epistome without single median seta. Antennal funicles with segments 1–2 elongate, $2.5 \times \text{as}$ long as wide; 3–4 slightly longer than wide, compressed, slightly angular on inside; 5–6 globular; 7 transverse.

Pronotum. Strongly transverse (W:L ratio 1.4), widest near midlength, sides arcuate; apex and base subequal in width.

ELYTRA. Broadly ovate, slightly longer than wide (W:L ratio 0.9), sides convex, widest near midlength.

Legs. Tibiae with black apical mucro; protibiae with outer margin straight, inner margin bisinuate; metatibiae with inner setal fringe, the setae shorter than segment 5 of metatarsus. Tarsi with segment 2 isodiametric or slightly wider than long.

ABDOMEN. Ventrite 1 flat or slightly concave, bearing plumose scales in impression; other surfaces with overlapping creamy-white scales, partly concealing integument.

Terminalia. Body of penis elongate (W:L ratio 0.25), $1.5-2.0 \times$ as long as temones, sides moderately convex, widest near midlength; curvature in profile weak and regular, dorsoventrally slightly narrowed before apex. Copulatory sclerite weakly sclerotised or not discerned in examined specimens. Parameroid lobes separate, divided by deep median notch, each lobe narrowed anteapically and rounded at apex, bearing long setae marginally and discally, all setae orientated centrifugally. Spiculum gastrale with basal arms regularly curved.

Sexual dimorphism

The sexes can be distinguished by the width of the forehead (as wide as epifrons in male, distinctly wider in female), and females also lack the metatibial mucro and plumose scales on ventrite 1.

Life history

Adults of *C. hirtulus* sp. nov. were found at several localities in homogenous stands of *Oxalis obtusa*. Some were extracted from galleries in the soil, emerging from the bulbs of *O. obtusa* (JHAR02444, Fig. 6E–F). Adults were collected between July and September, with freshly emerged specimens encountered in July and August (JHAR02356; JHAR02444).

Distribution

Cryptolarynx hirtulus sp. nov. occurs at various localities in the southern and northern parts of the Cederberg mountain range and in the area of Malmesbury (Fig. 13). Specimens were collected from 120 to 1544 m above sea level.

Remarks

The amplification of *COI* sequences from several populations of this species failed repeatedly, probably due to mismatches in the primer sequences. At intraspecific level, genetic distances between distant populations were found to be up to 1.3% in *EF1* (JHAR02356; JHAR02561), suggesting that several lineages may exist in the species as described here. It should be noted that the preliminary phylogenetic relationships were not fully resolved for *EF1* between this species and *C. robustus* sp. nov. (Fig. 12).

6. *Cryptolarynx robustus* Haran sp. nov. urn:lsid:zoobank.org:act:1907FA04-FD58-4E1E-AAC1-83CE5225B449 Figs 1F, 2F, 3F, 4F, 5F

Differential diagnosis

Cryptolarynx robustus sp. nov. belongs to the C. vitis species group, see Remarks section under that species for details. In this group it is distinguishable from C. hirtulus sp. nov. by the width of its forehead being greater than the width of an eye (narrower in C. hirtulus). Uncorrected p-distances between C. robustus (JHAR02560) and C. hirtulus (JHAR02561) were found to be 17.4% for COI and 1.7% for EFI (Supp. file 1).

Etymology

The species name is derived from the Latin adjective '*robustus*' and refers to the stocky appearance of the species. The specific epithet is an adjective in the masculine form.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • &; "REPUBLIC OF SOUTH AFRICA. Western Cape Province, Malmesbury. 10.ix.2019. J. Haran leg." "33.454° S 18.743° E, at base of *Oxalis* spp. JHAR02560_0101. Cirad-CBGP coll." "Holotype. *Cryptolarynx robustus* Haran 2023"; SAMC.

Paratypes

REPUBLIC OF SOUTH AFRICA – **Western Cape** • 1 \circlearrowleft ; same collection data as for holotype; SAMC • 1 \circlearrowleft (preserved in ethanol); same collection data as for holotype; CBGP.

Description (\bigcirc)

Measurements. Body length 4.5–5 mm.

COLOUR AND VESTITURE. Body integument black, antennae, tarsi and sometimes tibiae reddish. Dorsal vestiture (pronotum + elytra) consisting of short, overlapping, recumbent, subtriangular clothing scales, $1.2-2\times$ as long as wide, subcontiguous on interstriae, and longer, slightly suberect scales, at least $3\times$ as long as wide, in each strial puncture, visible in lateral view on elytral declivity; scales creamy-white, brown and black; pale scales usually concentrated in two longitudinal stripes on pronotum and on elytral interstria 4, black scales forming spots on interstriae 1-4 at apical $\frac{2}{3}$ of elytral length.

HEAD. Forehead slightly wider than epifrons near antennal insertions, wider than width of an eye, scales suberect, not entirely concealing integument. Eyes flat, in dorsal view only slightly exceeding outline of head, surrounded by a ring of short pale scales directed towards centre of eye; distance between eye and scrobe larger than width of antennal club. Epifrons narrow, distance between antennal insertions 0.5×10^{12} length of scape, scales at least 3×10^{12} as long as wide, suberect, overlapping. Frons with single pair of long lateral setae. Epistome with two median setae arising from same puncture. Antennal funicles with segments 1–2 elongate, subequal, about 3×10^{12} as long as wide; 3–4 slightly longer than wide, compressed, slightly angular on inside; 5–7 globular, isodiametric.

Pronotum. Transverse (W:L ratio 1.3), almost semicircular in dorsal view, widest near midlength, sides arcuate; width of apex 0.67 × width of base.

ELYTRA. Broadly ovate, slightly longer than wide (W:L ratio 0.9), sides convex, widest near midlength.

Legs. Protibiae with outer margin straight, inner margin slightly bisinuate; metatibiae with black apical mucro and inner setal fringe, the setae shorter than segment 5 of metatarsus. Tarsi with segment 2 slightly wider than long.

ABDOMEN. Ventrite 1 slightly concave; ventrites 1–2 with plumose scales medially; other surfaces with overlapping creamy-white scales, partly concealing integument.

TERMINALIA. Body of penis elongate (W:L ratio 0.3), 1.5–1.7× as long as temones, sides moderately convex, widest near midlength; curvature in profile weak and regular, dorsoventrally slightly narrowed before apex. Copulatory sclerite weakly sclerotised or not discerned in examined specimen. Parameroid lobes separate, divided by deep median notch, each lobe narrow, narrowed anteapically and rounded at apex, bearing long setae marginally and discally, all setae oriented centrifugally. Spiculum gastrale with basal arms regularly curved.

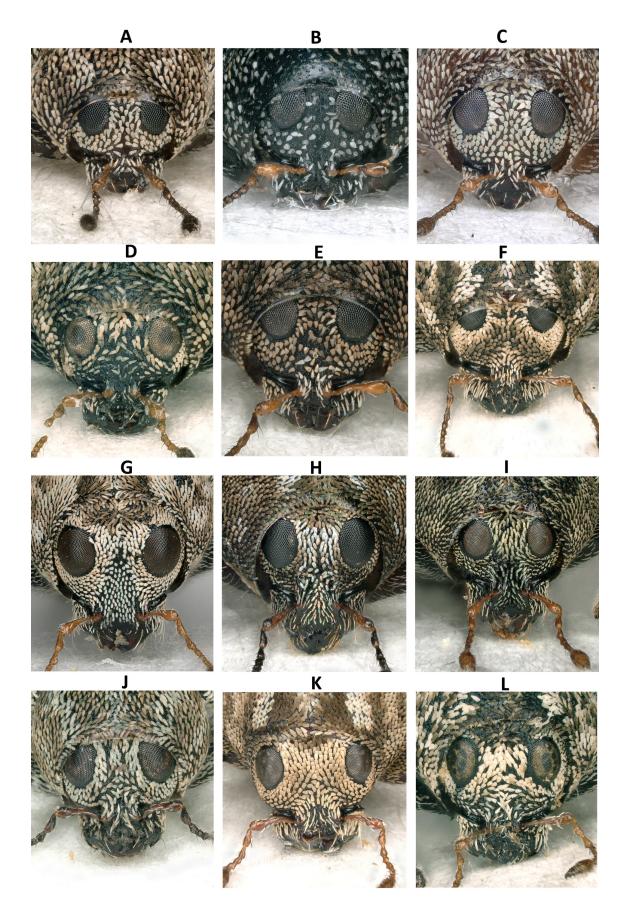
Sexual dimorphism

Males can be distinguished from females by the width of their forehead (as wide as epifrons in male, distinctly wider in female), and females also lack a mucro on the metatibiae and plumose scales on ventrite 1.

Life history

Adults of *C. robustus* sp. nov. were collected in September, at the bases of plants of *Oxalis* cf. *purpurea* in patches of Renosterveld.

Fig. 4 (Part I) (next page). Head of males of species of *Cryptolarynx* Van Schalkwyk, 1966. **A.** *C. vitis* (Marshall, 1957). **B.** *C. subglaber* Haran sp. nov. **C.** *C. squamulatus* Haran sp. nov. **D.** *C. muellerae* Haran sp. nov. **E.** *C. hirtulus* Haran sp. nov. **F.** *C. robustus* Haran sp. nov. **G.** *C. namaquanus* Haran sp. nov. **H.** *C. carinatus* Haran sp. nov. **I.** *C. variabilis* Haran sp. nov. **J.** *C. estriatus* (Marshall, 1957). **K.** *C. pyrophilus* Haran sp. nov. **L.** *C. pilipes* Haran sp. nov. Not to scale.



Distribution

The species was only found at the type locality in the Western Cape province (Fig. 13).

Remarks

Cryptolarynx robustus sp. nov. and *C. hirtulus* sp. nov. have a similar general appearance and can be found in sympatry at the same localities.

7. *Cryptolarynx namaquanus* Haran sp. nov. urn:lsid:zoobank.org:act:F889226B-4182-43BB-A918-3DE821DEC07E Figs 1G, 2G, 3G, 4G, 5G, 8D

Differential diagnosis

Cryptolarynx namaquanus sp. nov. can be distinguished from other species of Cryptolarynx by its wide epifrons (subequal to length of scapes), its narrow forehead (narrower than width of eyes) and its proximally cylindrical metatibiae. Its broad parameroid lobes of the male genitalia, bearing only very short setae, and the shape of the spiculum are also unique among the species of the genus. Cryptolarynx namaquanus is most similar to C. variabilis sp. nov. and C. carinatus sp. nov., but in the male it can be easily distinguished from these by its proximally cylindrical metatibiae (bearing an inner carina in C. variabilis and C. carinatus) and the conformations of its male genitalia. Uncorrected p-distances between C. namaquanus and these two species were found to span 12.8–15.1% for COI and 3.7–4.2% for EFI with C. variabilis and 9.3–10.4% for COI and 3.4% for EFI with C. carinatus (Supp. file 1).

Etymology

The species name *namaquanus* refers to the area where this species was found, the Namaqualand region of the Northern Cape province and part of the traditional home of the Nama people (Namaqua). The specific epithet is an adjective in the masculine form.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • &; "REPUBLIC OF SOUTH AFRICA. **Northern Cape Province**, Kamieskroon [15 km NW, Namaqua National Park, Skilpad Flower Camp]. 29.viii.2019. J. Haran leg." "30.170° S 17.793° E at base of *Oxalis obtusa*. JHAR02535_0101. Cirad-CBGP coll." "Holotype. *Cryptolarynx namaquanus*. Haran 2023"; SAMC.

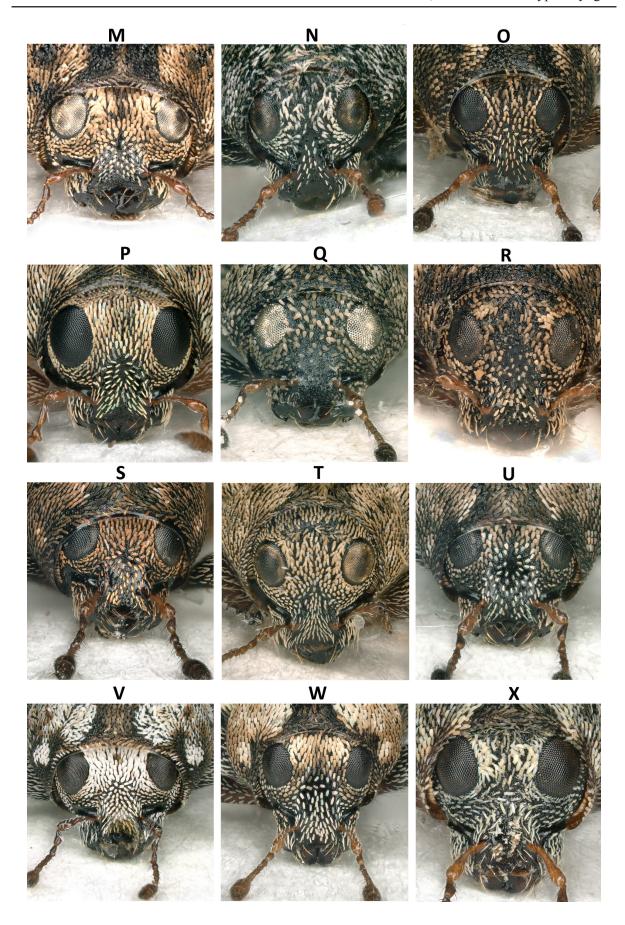
Paratypes

REPUBLIC OF SOUTH AFRICA – **Northern Cape** • 1 \circlearrowleft , 1 \circlearrowleft ; same collection data as for holotype; SAMC • 1 \circlearrowleft , 9 specs (preserved in ethanol); same collection data as for holotype; CBGP.

Description (\circlearrowleft)

Measurements. Body length 2–3 mm.

Fig. 4 (Part II) (next page). Head of males of species of *Cryptolarynx* Van Schalkwyk, 1966 and *Hadrocryptolarynx* Haran gen. nov. **M**. *C. armatus* Haran sp. nov. **N**. *C. falciformis* Haran sp. nov. **O**. *C. oberprieleri* Haran sp. nov. **P**. *C. spinicornis* Haran sp. nov. **Q**. *C. cederbergensis* Haran sp. nov. **R**. *C. homaroides* Haran sp. nov. **S**. *C. marshalli* Haran sp. nov. **T**. *C. endroedyi* Haran sp. nov. **U**. *C. oberlanderi* Haran sp. nov. **V**. *C. san* Haran sp. nov. **W**. *C. luteipennis* Haran sp. nov. **X**. *Hadrocryptolarynx major* Haran gen. et sp. nov. Not to scale.



COLOUR AND VESTITURE. Body integument black, antennae and tarsi reddish. Dorsal vestiture (pronotum + elytra) consisting of overlapping, recumbent, parallel-sided clothing scales, 2× as long as wide, truncate at apex; colour of scales varying from evenly greyish or creamy-white to brown or black; pale scales concentrated in two longitudinal stripes on pronotum and on elytral interstriae 4 as well as forming a pair of whitish spots surrounded by black scales at apical ½ of elytra; scales on interstriae recumbent, in lateral view not distinct from rest of vestiture.

HEAD. Forehead as wide as epifrons near antennal insertions, slightly narrower than width of an eye, scales recumbent. Eyes convex, in dorsal view exceeding outline of head, surrounded by a ring of short pale scales, on forehead directed towards occiput; distance between eye and scrobe as large as or slightly smaller than width of antennal club. Epifrons wide, distance between antennal insertions as large as length of scape, scales at most $2 \times$ as long as wide, recumbent, subcontiguous. Frons with pairs of erect lateral setae. Epistome without median seta. Antennal funicles with segments 1–2 elongate, subequal, about $3 \times$ as long as wide; 3–4 as long as wide, compressed, slightly angular on inside; 5–7 globular, isodiametric; 7 sometimes wider than long.

Pronotum. Transverse (W:L ratio 1.1–1.2), widest near midlength, sides arcuate; apex and base subequal in width.

ELYTRA. Broadly ovate, isodiametric (W:L ratio 1), sides convex, widest near midlength.

Legs. Protibiae with outer margin straight, inner margin slightly bisinuate; metatibiae with apical mucro and inner setal fringe, setae shorter than segment 5 of metatarsus. Tarsi with segment 2 isodiametric.

Abdomen. Ventrites 1 and 5 slightly concave medially; ventrites 1–4 with creamy-white plumose scales, almost concealing integument, intermixed with long suberect setae, each apically bifid.

TERMINALIA. Body of penis moderately elongate (W:L ratio 0.5), 2 × as short as temones, sides subparallel in basal half, converging in distal half; curvature in profile weak and regular, dorsoventrally slightly thickened at apex. Copulatory sclerite weakly sclerotised or not discerned in examined specimens. Parameroid lobes separate, divided by very deep median notch, each lobe broad, rounded at apex, bearing a series of very short setae. Spiculum gastrale with basal arms short and feebly curved.

Sexual dimorphism

Males can be distinguished from females by the shape of ventrites 1 and 5 (concave in male, flat or slightly convex in female).

Life history

Adults of *C. namaquanus* sp. nov. were found in monospecific stands of *Oxalis obtusa*, in the month of August.

Distribution

All specimens collected were found at the type locality, the only one thus far known for the species (Fig. 13).

8. *Cryptolarynx carinatus* Haran sp. nov. urn:lsid:zoobank.org:act:D16B89D2-B0A2-4FA8-951C-04D8EC14AD97 Figs 1H, 2H, 3H, 4H, 5H, 6G–H, 8E

Differential diagnosis

Cryptolarynx carinatus sp. nov. is most similar to C. variabilis sp. nov. but distinguishable from it by the inner carina on the metatibiae, whose proximal edge forms a smaller angle with the tibial axis than

in *C. variabilis* (Fig. 8E). The copulatory sclerite of the penis is divided into two blocks in *C. carinatus*, whereas it forms an entire sclerite in *C. variabilis*. Genetic distances between these two species were found to range between 10.5% and 17.4% for *COI* and 3.1% and 3.6% for *EF1*. They were also not found in sympatry, *C. carinatus* apparently restricted to the eastern slopes of Table Mountain and *C. variabilis* only found at several localities on the western slopes of the Hottentots Holland Mountains.

Etymology

The species name *carinatus* refers to the distinct proximal inner carina of the metatibiae in this species. The specific epithet is an adjective in the masculine form.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • & "REPUBLIC OF SOUTH AFRICA. Western Cape Province, [Cape Town,] Rondebosch Com. [Common] 26.vi.2019. J. Haran leg." "S33°57'10, E18°29'5, at base of *Oxalis purpurea*. JHAR02336_0101. Cirad-CBGP coll." "Holotype. *Cryptolarynx carinatus*. Haran 2023"; SAMC.

Paratypes

REPUBLIC OF SOUTH AFRICA – **Western Cape •** 1 \circlearrowleft , 3 specs (preserved in ethanol); same collection data as for holotype; CBGP • 4 specs; Cape Town, Constantia; [34.025° S, 18.423° E]; Sep. 1885; "*Cryptolarynx* nr. *vitis* (Marshall) det. R. Oberprieler, 1988"; SAM-COL-A052010; SAMC.

Description (♂)

Measurements. Body length 2.7–3 mm.

Colour and vestiture. Body integument black, scapes and tarsi reddish. Dorsal vestiture (pronotum + elytra) consisting of overlapping, recumbent, parallel-sided clothing scales, $2-3 \times$ as long as wide, truncate or rounded at apex; colour of scales varying from greyish to pale brown to black; pale scales concentrated in two longitudinal stripes on pronotum and at base of elytral interstriae 4, white scales forming a pair of spots surrounded by black scales at apical $\frac{2}{3}$ of elytra; scales of interstriae recumbent, in lateral view not distinct from rest of vestiture.

HEAD. Forehead as wide as epifrons near antennal insertions, as wide as width of an eye, scales recumbent. Eyes convex, in dorsal view slightly exceeding outline of head, surrounded by a ring of short pale scales, on forehead directed towards occiput; distance between eye and scrobe slightly smaller than width of antennal club. Epifrons with distance between antennal insertions $0.67 \times length$ of scape, scales at least $2 \times as$ long as wide, recumbent, subcontiguous. Frons with pairs of erect lateral setae. Epsitome without median setae. Antennal funicles with segment 1 elongate; 2 half as long as 1, at most $2 \times as$ long as wide; 3–4 globular, isodiametric, compressed, slightly angular on inside; 5–7 globular, isodiametric; 7 sometimes wider than long.

PRONOTUM. Transverse (W:L ratio 1.4–1.5), widest near midlength, sides arcuate; width of apex 0.67× width of base.

ELYTRA. Broadly ovate, slightly wider than long (W:L ratio 1.1), sides convex, widest near midlength.

Legs. Protibiae with outer margin straight, inner margin slightly bisinuate; metatibiae with apical mucro and inner setal fringe, setae shorter than segment 5 of metatarsus; metatibiae proximally with inner carina set off at 45° angle to outer margin. Tarsi with segment 2 wider than long.

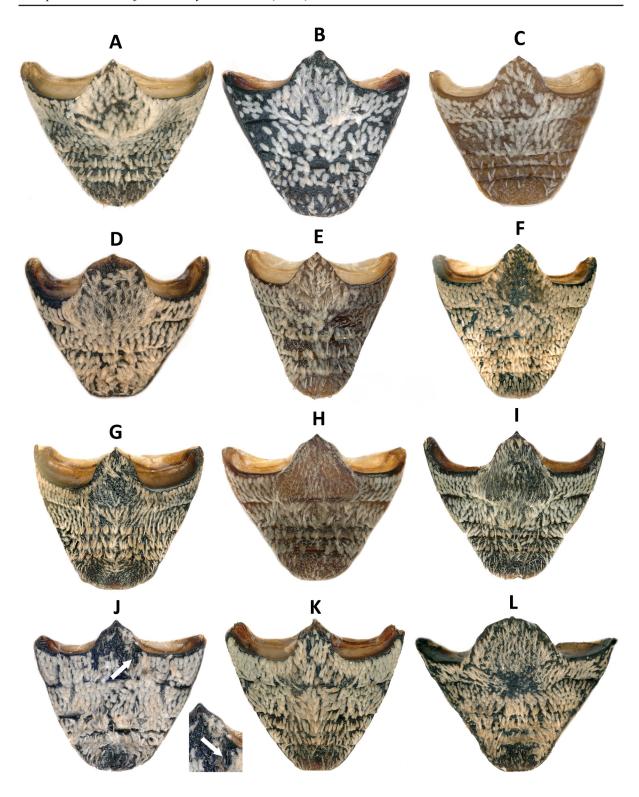


Fig. 5 (Part I). Ventrites of males of species of *Cryptolarynx* Van Schalkwyk, 1966. **A.** *C. vitis* (Marshall, 1957). **B.** *C. subglaber* Haran sp. nov. **C.** *C. squamulatus* Haran sp. nov. **D.** *C. muellerae* Haran sp. nov. **E.** *C. hirtulus* Haran sp. nov. **F.** *C. robustus* Haran sp. nov. **G.** *C. namaquanus* Haran sp. nov. **H.** *C. carinatus* Haran sp. nov. **I.** *C. variabilis* Haran sp. nov. **J.** *C. estriatus* (Marshall, 1957), with details of a cuticular carina (white arrows). **K.** *C. pyrophilus* Haran sp. nov. **L.** *C. pilipes* Haran sp. nov. Not to scale.



Fig. 5 (Part II) (next page). Ventrites of males of species of *Cryptolarynx* Van Schalkwyk, 1966 and *Hadrocrypto-larynx* Haran gen. nov. M. *C. armatus* Haran sp. nov. N. *C. falciformis* Haran sp. nov. O. *C. oberprieleri* Haran sp. nov. P.C. spinicornis Haran sp. nov. Q. *C. cederbergensis* Haran sp. nov. R. *C. homaroides* Haran sp. nov. S. *C. marshalli* Haran sp. nov. T. *C. endroedyi* Haran sp. nov. U. *C. oberlanderi* Haran sp. nov. V. *C. san* Haran sp. nov. W. *C. luteipennis* Haran sp. nov. X. *Hadrocryptolarynx major* Haran gen. et sp. nov. Not to scale.

ABDOMEN. Ventrite 1 concave medially, impression devoid of scales, with long setae only; ventrites 1–4 with creamy-white or greyish plumose scales, not concealing integument, intermixed with long suberect setae, each apically bifid.

TERMINALIA. Body of penis moderately elongate (W:L ratio 0.4), as long as temones, sides subparallel, converging near apex; curvature in profile weak and regular, dorsoventrally narrowed before apex. Copulatory sclerite serrate, divided into two sections, a long part near body of penis and a second, shorter part near apices of temones. Parameroid lobes separate, divided by moderate median notch, each lobe broad, bearing a series of long setae directed apicad. Spiculum gastrale with basal arms long and regularly curved.

Sexual dimorphism

Female unknown.

Life history

All specimens of *C. carinatus* sp. nov. were collected at the base of *Oxalis purpurea* L. plants, in the month of June.

Distribution

The species in only known to occur in the Rondebosch Common and at Constantia in Cape Town (Fig. 13).

9. *Cryptolarynx variabilis* Haran sp. nov. urn:lsid:zoobank.org:act:CABBADE9-B99D-481E-A5EE-ACFA0FF97187 Figs 1I, 2I, 3I, 4I, 5I, 6I–N, 8E

Differential diagnosis

Cryptolarynx variabilis sp. nov. is most similar to *C. carinatus* sp. nov., see the Differential diagnosis and Remarks sections under that species for diagnostic characters and genetic distances.

Etymology

The species name *variabilis* refers to the substantial morphological variation encountered in this species in terms of size, body ratios and elytral pattern. The specific epithet is an adjective in the masculine form.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • & "REPUBLIC OF SOUTH AFRICA. Western Cape Province, Stellenbosch. 20.vii.2018. J. Haran leg." "33.949° S 18.876° E, sweeping of *Oxalis pes-caprae*. JHAR01185 0101. Cirad-CBGP coll." "Holotype. *Cryptolarynx variabilis*. Haran 2023"; SAMC.

Paratypes

REPUBLIC OF SOUTH AFRICA – **Western Cape** • 2 \$\pi\$; same collection data as for holotype; SAMC • 3 \$\frac{1}{10}\$, 2 \$\pi\$; same collection data as for holotype; MLP • 3 \$\frac{1}{10}\$, 2 \$\pi\$\$, 10 specs (preserved in ethanol); same collection data as for holotype; CBGP • 1 \$\frac{1}{10}\$, 1 \$\pi\$, 3 specs (preserved in ethanol); Stellenbosch, Paradyskloof; 33.965° S, 18.877° E; 26 Jul. 2018; J. Haran leg.; at base of *Oxalis purpurea*; JHAR01215; CBGP • 1 \$\frac{1}{10}\$; Stellenbosch; 33.948° S, 18.879° E; 6 Aug. 2018; J. Haran leg.; *Oxalis lanata*; JHAR01235-0102; CBGP • 1 \$\pi\$; Stellenbosch, Jan Marais Nature Reserve; 33.931° S, 18.877° E; 15 Oct. 2019; R. Borovec leg.; sifting under *Oxalis* sp. in forest margin; FFWS • 1 \$\frac{1}{10}\$; Stellenbosch area, Koopmanskloof Nature Reserve; 33.897° S, 18.769° E; Jul. 2014; A. Stander leg.; D-vac sampling;

JHAR01245; CBGP • 1 Å, 3 specs (preserved in ethanol); Stellenbosch; 33.942° S, 18.873° E; 9 Aug. 2018; J. Haran leg.; *Oxalis lanata*; JHAR01247; CBGP • 4 specs (preserved in ethanol); Stellenbosch; 33.941° S, 18.872° E; 17 Aug. 2018; J. Haran leg.; *Oxalis lanata*; JHAR01363; CBGP • 1 Å, 17 specs (preserved in ethanol); Stellenbosch; 33.949° S, 18.876° E; 3 Sep. 2018; J. Haran leg.; *Oxalis pescaprae*; JHAR01479; CBGP • 1 Å, 7 specs (preserved in ethanol); Stellenbosch, Jan Marais Nature Reserve; 33.930° S, 18.875° E; 13 Sep. 2018; J. Haran leg.; at base of *Oxalis purpurea*; JHAR01497; CBGP • 1 Å, 2 specs (preserved in ethanol); Franschhoek Pass; 33.904° S, 19.157° E; 15 Sep. 2018; J. Haran leg.; JHAR01499; CBGP • 2 specs (preserved in ethanol); Pniel, Boschendal Estate; 33.891° S, 18.980° E; 16 Aug. 2019; J. Haran leg.; at base of *Oxalis* spp.; JHAR02564; CBGP • 4 specs (preserved in ethanol); Somerset West, Helderberg Nature Reserve; 34.061° S, 18.874° E; 14 Oct. 2019; J. Haran leg.; at base of *Oxalis purpurea*; JHAR02586; CBGP • 3 specs (preserved in ethanol); same collection data as for preceding; at base of *Oxalis lanata*; JHAR02588; CBGP • 1 Å; Somerset West; [34.07° S, 18.84° E]; Nov.–Dec. 1927; A.J. Hesse; SAM-COL-A051992; SAMC.

Description (♂)

Measurements. Body length 2.2–4.0 mm.

Colour and vestiture. Body integument black, scapes and tarsi reddish. Dorsal vestiture (pronotum + elytra) consisting of overlapping, recumbent, parallel-sided clothing scales, $2-3 \times$ as long as wide, truncate or rounded at apex; colour of scales varying from greyish to pale brown to black; pale scales concentrated in two longitudinal stripes on pronotum and on elytral interstriae 4, white scales forming a pair of spots surrounded by black scales at apical $\frac{2}{3}$ of elytra; scales of striae recumbent, in lateral view not distinct from rest of vestiture.

HEAD. Forehead as wide as epifrons near antennal insertions, as wide as width of an eye, scales recumbent. Eyes convex, in dorsal view slightly exceeding outline of head, surrounded by a ring of short pale scales, on forehead directed towards occiput; distance between eye and scrobe slightly smaller than width of antennal club. Epifrons with distance between antennal insertions 0.75×10^{10} length of scape, scales at least 2×10^{10} as long as wide, recumbent, not contiguous. Frons with pairs of erect setae laterally. Epistome without median seta. Antennal funicles with segment 1 elongate; 2 half as long as 1, at most 2×10^{10} as wide; 3–4 globular, isodiametric, compressed, slightly angular on inside; 5–7 globular, isodiametric; 7 sometimes wider than long.

PRONOTUM. Transverse (W:L ratio 1.5–1.7), widest near midlength, sides arcuate; width of apex $\frac{2}{3}$ width of base.

ELYTRA. Broadly ovate, slightly wider than long (W:L ratio 1.1), sides convex, widest near midlength.

Legs. Protibiae with outer margin straight, inner margin almost straight; metatibiae with apical mucro and inner setal fringe, setae shorter than segment 5 of metatarsus; metatibiae proximally with inner carina set off at an angle of ca 20° to outer margin. Tarsi with segment 2 wider than long.

ABDOMEN. Ventrite 1 concave medially, impression with long setae and little scale cover; ventrites 1–4 with creamy-white or greyish plumose scales, not concealing integument, intermixed with long suberect setae, each apically bifid.

TERMINALIA. Body of penis elongate (W:L ratio 0.4), as long as temones, sides subparallel, converging close to apex; curvature in profile weak and regular, dorsoventrally narrowed before apex. Copulatory sclerite serrate. Parameroid lobes separate, divided by modest median notch, each lobe broad, bearing a series of long setae directed apicad. Spiculum gastrale with basal arms long, right arm angled in midlength.

Sexual dimorphism

The sexes can be distinguished by the shape of ventrite 1 (in males concave with long setae divided from their bases, in females flat or slightly convex with short setae not or only slightly divided at their apices).

Life history

The larvae of *C. variabilis* sp. nov. develop in the bulbs of various species of *Oxalis* (*O. pes-caprae* L., *O. purpurea* and *O. lanata*); see Life history and Morphology of immature stages subsections of the Results section for details. Adults of the species were collected between July and October. The heat tolerance of this species was assessed in a comparative study of weevils associated with fire-prone ecosystems (Javal *et al.* 2022). Adults of *C. variabilis* were found to survive temperatures above 50°C, which is rare for arthropods, especially in small insects. This tolerance was hypothesized to be an adaptation for the survival of the larvae and teneral adults when enclosed in the bulbs during summer, a few centimetres below the surface of the ground.

Distribution

Based on the samples examined, *C. variabilis* sp. nov. seems to be restricted to the western slope of the Hottentots Holland Mountains range, from the Franschhoek Pass to Somerset West (Fig. 13).

Remarks

Intraspecific genetic distances among *C. variabilis* sp. nov. specimens were found to span up to 7.0% for *COI* (JHAR02563 / JHAR02586) and 1.9% for *EFI* (JHAR01499 / JHAR01235), suggesting that several lineages in the process of differentiation may exist in the species as treated here.

10. *Cryptolarynx estriatus* (Marshall, 1957) Figs 1J, 2J, 3J, 4J, 5J

Cryptopharynx estriatus Marshall, 1957: 19

Cryptolarynx estriatus – Van Schalkwyk 1966: 745 (implied new combination). — Oberprieler et al. 2007: 505, fig. 17 (colour photograph).

Differential diagnosis

Cryptolarynx estriatus can be distinguished from all other species of the genus by its suberect scales on epifrons, the two short carinae on ventrite 1 of the male and the unique long seta on the parameroid lobes.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • & "Type" "S Africa. Cape Province [REPUBLIC OF SOUTH AFRICA – **Northern Cape**]. Nieuwoudtville [31.38° S, 19.11° E]. 18-22 xi 1931" "Miss A. Mackie" "*Cryptopharynx. estriatus*. Mshl. TYPE" "G.A.K. Marshall. Coll. B.M.1950-255"; NHMUK.

Other material

Redescription (♂)

Measurements. Body length 1.75–2.5 mm.

COLOUR AND VESTITURE. Body integument black, scapes and tarsi reddish; vestiture of dorsum (pronotum + elytra) consisting of short, appressed, narrowly elliptical clothing scales partly concealing integument, slightly overlapping or subcontiguous, and longer, suberect clothing scales at least 2× as long as wide on strial punctures; colour pattern consisting of broad median stripe of pearly brown scales on pronotum and elytra, flanked on either side by narrower stripe of white scales, laterally with paler brown scales intermixed with sparser white scales, without distinct white spots on elytral declivity.

HEAD. Forehead narrower than width of an eye, surface flat. Eyes flat, in dorsal view only slightly exceeding outline of head, surrounded by a ring of short pale scales directed towards centre of eye except mesal ones directed posteriad; distance between eye and scrobe as wide as antennal club. Epifrons narrow, distance between antennal insertions 0.5×10^{10} length of scape, scales narrow, 3×10^{10} as long as wide, suberect. Frons with double pair of long lateral setae. Epistome with single median seta ca half as long as frontal setae. Antennae with funicle segment 1 and 2 elongate, more than 2×10^{10} as long as wide; 3-4 slightly longer than wide, slightly compressed, slightly angulate on inside, 2 and 4 on inside slightly angled; 5-7 isodiametric, subglobular.

Pronotum. Strongly transverse, nearly $1.5 \times$ as wide as long (W:L ratio 1.4–1.5), subcircular in dorsal view, widest just behind middle of length, sides strongly arcuate in basal half, straight and converging in apical half; anteriorly $2 \times$ narrower than posteriorly.

ELYTRA. Globular, isodiametric (W:L ratio 1); sides convex, widest near midlength.

Legs. Tibiae with black apical mucro; protibiae with outer margin straight, inner margin with series of small black teeth in apical half; metatibiae with outer and inner margins faintly sinuate, mucro subperpendicular to external margin. Tarsi short, segment 2 wider than long (W:L ratio 1.4).

ABDOMEN. Ventrites with creamy-white to pale brown plumose scales almost concealing integument, medially intermixed with long suberect setae; ventrite 1 concave medially, flanked on either side by a short but high, flat, black peg midway between anterior margin at metacoxae and posterior margin.

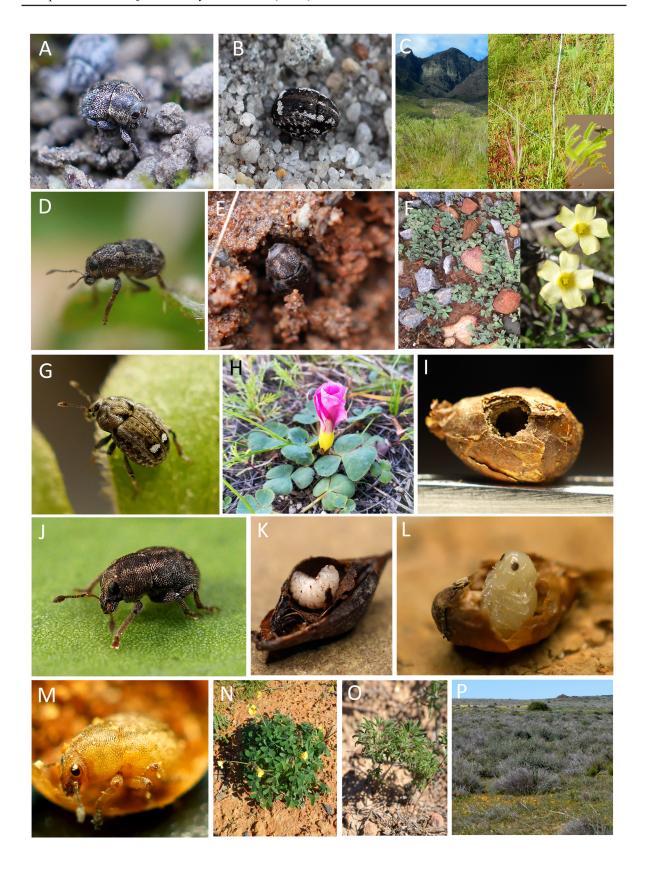
Terminalia. Body of penis elongate (W:L ratio 0.45), 0.9 × as long as temones, sides subparallel, strongly rounded inwards distally, apex subacuminate; curvature in profile weak and regular, dorsoventrally strongly flattened before apex. Copulatory sclerite indistinct, consisting of short, very thin, outwardly curved sclerotised rods at apices of longer and thicker crescentic fields of very fine asperities. Parameroid lobes separate, divided by deep median notch, each with anteapical constriction, bearing long marginal setae and shorter setae discally, all setae orientated centrifugally. Spiculum gastrale with basal arms regularly curved.

Sexual dimorphism

The sexes can be distinguished foremost by the conspicuous pair of flat black pegs on ventrite 1 in the male (absent in the female).

Life history

Specimens of *C. estriatus* were found on the ground or feeding on vegetation, but no precise data of its host plants are known. A series of adults was found feeding on leaves of *Moraea* by S. Neser near Nieuwoudtville in 1995, and they also fed on this plant in captivity (Oberprieler *et al.* 2007: fig. 17), but, in view of the wide use of *Oxalis* as larval host in *Cryptolarynx*, the larvae of *C. estriatus* probably also develop in bulbs of an *Oxalis* species rather than on *Moraea*. Adults were collected in July, September and November.



Distribution

Most specimens were collected in the Nieuwoudtville area, on the escarpment (Fig. 13).

Remarks

Marshall described this species based on a single female, but examination of the genitalia of ts specimen showed that it is actually a male. No fresh material of this species could be obtained.

11. *Cryptolarynx pyrophilus* Haran sp. nov. urn:lsid:zoobank.org:act:93795B58-0E02-4471-8486-42670DD6458A Figs 1K, 2K, 3K, 4K, 5K, 7C, 8B–C

Differential diagnosis

Cryptolarynx pyrophilus sp. nov. can be distinguished from other species of the genus by its very wide forehead ($2 \times$ as wide as width of an eye) and by the suberect scales on the epifrons. It is most similar to C. cederbergensis sp. nov., the two species showing interspecific genetic distances ranging from 20.9% to 23.3% for COI and 5.2 % for EF1 among the specimens available for study.

Etymology

The species was named in reference to the migration of specimens towards recently burnt areas observed in this species, formed from combining the Greek nouns 'pyr' ('fire') and 'philia' ('affection'). The specific epithet is an adjective in the masculine form.

Material examined

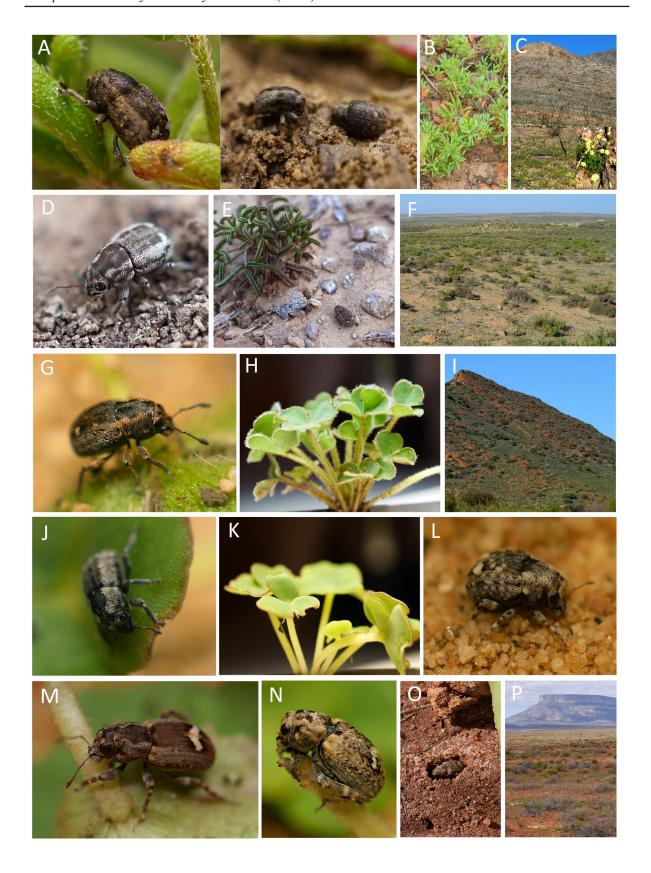
Holotype

REPUBLIC OF SOUTH AFRICA • & "REPUBLIC OF SOUTH AFRICA. Western Cape Province, Montagu [4 km SE]. 23.ix.2018. J. Haran leg." "33.814° S 20.151° E, *Oxalis* spp. JHAR01528_0101. Cirad-CBGP coll." "Holotype. *Cryptolarynx pyrophilus*. Haran 2023"; SAMC.

Paratypes

REPUBLIC OF SOUTH AFRICA – **Western Cape •** 2 ♂♂, 17 specs (preserved in ethanol); same collection data as for holotype; CBGP • 1 ♀; Montagu; [33.79° S, 20.12° E]; 1–24 Oct. 1924; R.E. Turner leg.; 466; NHMUK • 1 ♀; Hex River Valley; [ca 33.43° S, 19.72° E]; Jun. 1883; SANC.

Fig. 6 (preceding page). Habitus in natura, host plants and biotopes of species of *Cryptolarynx* Van Schalkwyk, 1966 (part 1). A. C. vitis (Marshall, 1957), Tygerberg Nature Reserve (JHAR02568). B. Dark variants of *C. vitis*, Grootbos Private Nature Reserve (JHAR01592). C. Biotope and stands of *Oxalis glabra* Thunb. hosting *C. vitis* (JHAR01488). D. Habitus of *C. hirtulus* Haran sp. nov., Worcester (JHAR02356). E. Adult of *C. hirtulus* Haran sp. nov. under a stone, in its gallery after emergence from a bulb of *Oxalis obtusa* Jacq., near Touwsrivier (JHAR02444). F. Biotope of *C. hirtulus* Haran sp. nov. with stands of *Oxalis obtusa*, near Touwsrivier. G. Habitus of *C. carinatus* Haran sp. nov., Rondebosch Common (JHAR02336). H. *Oxalis purpurea* L., host of *C. carinatus* Haran sp. nov., Rondebosch Common. I. Corm of *Oxalis pes-caprae* L. with emergence hole of *C. variabilis* Haran sp. nov. J. Habitus of *C. variabilis* Haran sp. nov., Stellenbosch (JHAR01185). K. Larva of *C. variabilis* Haran sp. nov. in bulb of *Oxalis purpurea*, Stellenbosch (JHAR01215). L. Pupa of *C. variabilis* Haran sp. nov. in bulb of *Oxalis pes-caprae*, Stellenbosch (JHAR01247). M. Teneral adult of *C. variabilis* Haran sp. nov. in bulb of *Oxalis pes-caprae*, Stellenbosch (JHAR01185). N. *Oxalis pes-caprae*, host of *C. variabilis* Haran sp. nov., Stellenbosch. O–P. *Oxalis* sp. host and biotope of *C. armatus* Haran sp. nov., near Nieuwoudtville (JHAR02519).



Description (♂)

Measurements. Body length 1.5–4.5 mm.

COLOUR AND VESTITURE. Body integument black, antennae and tarsi reddish. Dorsal vestiture (pronotum + elytra) consisting of overlapping, recumbent, parallel-sided clothing scales, 2–3× as long as wide, truncate or rounded at apex; colour of scales varying from creamy-white to pale brown to dark brown; white scales concentrated in two longitudinal stripes laterally on pronotum and on elytral interstriae 4, creating a broad, dark medial stripe on pronotum and basal ½ of elytra; white scales forming a pair of spots surrounded by black scales on interstriae 3 at apical ½ of elytral length; scales of striae recumbent, in lateral view not distinct from rest of vestiture.

HEAD. Forehead very wide, $1.3 \times$ as wide as epifrons near antennal insertions, $2 \times$ as wide as width of an eye, scales recumbent. Eyes convex, in dorsal view slightly exceeding outline of head, surrounded by a ring of short pale scales, on forehead directed towards occiput; distance between eye and scrobe as large as width of antennal club. Epifrons with distance between antennal insertions $0.75 \times$ length of scape, scales at least $2 \times$ as long as wide, suberect, contiguous. Frons with a single pair of erect lateral setae. Epistome with single elongate median seta. Antennal funicles with segment 1 elongate; 2 shorter, at most $1.5 \times$ as long as wide; 3–4 globular, isodiametric, compressed, slightly angular on inside; 5–6 globular, isodiametric; 7 wider than long.

PRONOTUM. Transverse (W:L ratio 1.4), widest near midlength, sides arcuate; apex slightly narrower than base.

ELYTRA. Broadly ovate, slightly wider than long (W:L ratio 1.1), sides convex, widest near midlength.

Legs. Tibiae with apical mucro; protibiae with outer margin straight, inner margin bisinuate; metatibiae with inner setal fringe, the setae shorter than segment 5 of metatarsus. Tarsi with segment 2 wider than long.

ABDOMEN. Ventrite 1 concave medially; ventrites 1–4 with creamy-white plumose scales, almost concealing integument, intermixed with long suberect scales; ventrite 5 devoid of scales in apical half, there bearing only erect setae.

Fig. 7 (previous page). Habitus in natura, host plants and biotopes of species of Cryptolarynx Van Schalkwyk, 1966 Cryptolarynx and Hadrocryptolarynx Haran gen. nov. (part 2). A. Habitus of C. oberprieleri Haran sp. nov. on and at base of Oxalis glabra Thunb., Stellenbosch (JHAR01201). **B.** Patch of O. glabra, biotope of C. oberprieleri Haran sp. nov., Stellenbosch (JHAR01485). C. Burnt area near Montagu with patches of Oxalis pes-caprae L. resprouting; biotope of C. pyrophilus Haran sp. nov. (JHAR01528). D-F. Habitus, Oxalis cf. odorata J.C.Manning & Goldblatt, host and biotope of C. spinicornis Haran sp. nov., Sutherland (JHAR02512). G. Habitus of C. marshalli Haran sp. nov., near Worcester (JHAR02355). H. Oxalis imbricata Eckl. & Zeyh., hosting adults of C. marshalli Haran sp. nov., near Worcester. I. Shale Renosterveld vegetation type on hillsides at Worcester, biotope of C. marshalli Haran sp. nov. (JHAR02355). J. Habitus of C. oberlanderi Haran sp. nov., near Worcester (JHAR02353). K. Oxalis depressa Eckl. & Zeyh., hosting adults of C. oberlanderi Haran sp. nov., near Worcester. L. Habitus of C. san Haran sp. nov., Langebaan Dune Strandveld vegetation type near West Coast National Park (JHAR02484). M. Habitus of male of *Hadrocryptolarynx major* Haran gen. et sp. nov., Klawer (JHAR02464). N. Habitus of female of Hadrocryptolarynx major Haran gen. et sp. nov., Klawer. O. Gallery formed by Hadrocryptolarynx major Haran gen. et sp. nov. under a leaf of Amaryllidaceae J.St.-Hil. P. Vanrhynsdorp Gannabosveld vegetation type near Vanrhynsdorp, biotope of *Hadrocryptolarynx major* Haran gen. et sp. nov.

TERMINALIA. Body of penis elongate (W:L ratio 0.3–0.4), as long as temones, sides subparallel, converging in apical third; curvature in profile weak and regular, dorsoventrally narrowed before apex. Copulatory sclerite shaped like a reversed plunger. Parameroid lobes separate, divided by deep median notch, each lobe broad, bearing a series of long setae directed apicad. Spiculum gastrale with basal arms long, regularly curved.

Sexual dimorphism

The sexes can be distinguished by the shape of the elytra (wider than long in male, longer than wide, more broadly ovate in female), and females also have a wider forehead and smaller metatibial mucrones.

Life history

Large numbers of adults of *C. pyrophilus* sp. nov. were collected in and close to a recently burnt area (seven months prior to sampling), at the bases of emerging *Oxalis pes-caprae* L. plants; see the subsection Behaviour below for details. The heat tolerance of this species was assessed in a comparative study of weevils associated with fire-prone ecosystems, but the adults showed a lower tolerance to heat than those of *C. variabilis* sp. nov. (Javal *et al.* 2022). Adults were collected in September and October.

Distribution

The species occurs in the inland valleys of Montagu and the Hex River (Fig. 13).

12. *Cryptolarynx pilipes* Haran sp. nov. urn:lsid:zoobank.org:act:065BA1C5-F34E-472F-8C2F-675C2DF5820E Figs 1L, 2L, 3L, 4L, 5L

Differential diagnosis

Cryptolarynx pilipes sp. nov. can be distinguished from other species of the genus by the combination of the inner fringe of elongate setae on the metatibiae and the suberect scales on the epifrons.

Etymology

The species name *pilipes* is derived from the Latin nouns '*pilus*' ('hair') and '*pes*' ('foot') and refers to the fringe of long setae on the metatibiae of the species. The specific epithet is a noun in apposition.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • &; "S. Africa. W. Cape. [REPUBLIC OF SOUTH AFRICA – Western Cape], Clanwilliam. 32.10S 18.52E [32.167° S, 18.867° E]. 10.x.1986 M. Way" "CSIRO Entomology. Survey of weed. Biocontrol agents; in South Africa." "visiting. Arctotheca calendula" "National Coll. [Collection] of Insects. Pretoria, South Africa. Ex CSIRO / UCT, 2003" "Holotype. Cryptolarynx pilipes. Haran 2023"; SANC.

Paratype

REPUBLIC OF SOUTH AFRICA – Western Cape • 1 3; same collection data as for holotype; SANC.

Description (♂)

Measurements. Body length 3.4–3.7 mm.

Colour and vestiture. Body integument black, antennae and tarsi reddish. Dorsal vestiture (pronotum + elytra) consisting of overlapping, recumbent, parallel-sided clothing scales, at least $2 \times$ as long as wide, truncate or rounded at apex; colour of scales varying from white to pale brown to dark brown, white

scales concentrated laterally on pronotum and at base of elytral interstriae 4 and forming a pair of subcontiguous white spots surrounded by dark scales at apical ½ of interstriae 1–4; scales of striae recumbent, in lateral view not distinct from rest of vestiture.

HEAD. Forehead wide, $1.5 \times$ wider than epifrons near antennal insertions, $1.25 \times$ as wide as width of an eye, scales suberect. Eyes convex, in dorsal view slightly exceeding outline of head, surrounded by a ring of short pale scales, on the forehead directed towards occiput; distance between eye and scrobe as large as width of antennal club. Epifrons with distance between antennal insertions $0.5 \times$ length of scape, scales at least $2 \times$ as long as wide, suberect, contiguous. Frons with single pair of erect lateral setae. Epistome without median seta. Antennae with funicle segment 1 elongate; 2 slightly shorter, at most $2 \times$ as long as wide; 3–5 longer than wide, compressed; 6–7 globular, isodiametric.

PRONOTUM. Transverse (W:L ratio 1.5), widest near midlength, sides arcuate; width of apex ²/₃ × width of base.

ELYTRA. Globular, slightly wider than long (W:L ratio 1.1), sides convex, widest near midlength.

Legs. Protibiae with both outer and inner margins straight; pro- and mesotibiae with small apical mucro, metatibiae amucronate; metatibiae with inner fringe of setae as long as segment 5 of metatarsus. Tarsi with segment 2 wider than long.

ABDOMEN. Ventrite 1 medially with broad, semicircular concavity with deeply divided, plumose scales; ventrites 2–4 with creamy-white plumose scales, partly concealing integument, intermixed with long suberect scales; ventrite 5 with erect setae.

TERMINALIA. Body of penis elongate (W:L ratio 0.3), slightly shorter than temones, sides subparallel, converging strongly near apex; curvature in profile weak and regular, dorsoventrally narrowed at apex. Copulatory sclerite weakly sclerotised or not discerned in examined specimens. Parameroid lobes separate, divided by deep median notch, each lobe broad, rounded at apex, bearing a series of long setae directed apicad, setae as long as depth of median notch. Spiculum gastrale with basal arms short, regularly and moderately curved, laterally slightly angulate.

Sexual dimorphism

Female unknown.

Life history

Adults of *C. pilipes* sp. nov. were collected in October, from *Arctotheca calendula* (L.) (Asteraceae).

Distribution

The species was found only at the type locality, Clanwilliam in the Western Cape province (Fig. 13).

13. *Cryptolarynx armatus* Haran sp. nov. urn:lsid:zoobank.org:act:0694E5BE-EBA9-4DDE-8647-ECBE6A5A47F7 Figs 1M, 2M, 3M, 4M, 5M, 6O–P, 8I

Differential diagnosis

Cryptolarynx armatus sp. nov. is most similar to C. falciformis sp. nov. and C. oberprieleri sp. nov., in possessing apically thickened protibiae in the male. In addition to their distinct copulatory sclerites of the endophallus, these species can also be distinguished by the setae on the ventrites (simple in

C. armatus, bifid at least apically in C. falciformis and C. oberprieleri). Genetically, C. armatus is closest to C. spinicornis sp. nov., the distance between their EF1 sequences found to be 1.6%.

Etymology

The species name *armatus* refers to the apical cuticular expansion of the protibiae of the males, forming together with the mucro two strong teeth. The specific epithet is an adjective in the masculine form.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • \circlearrowleft ; "REPUBLIC OF SOUTH AFRICA. **Northern Cape Province**, Nieuwoudtville. 20.viii.2019. J. Haran leg." "31.384° S 19.140° E at base of *Oxalis obtusa*. JHAR02519 0101. Cirad-CBGP coll." "Holotype. *Cryptolarynx armatus*. Haran 2023"; SAMC.

Paratypes

REPUBLIC OF SOUTH AFRICA – **Northern Cape** • 1 \circlearrowleft ; same collection data as for holotype; SAMC • 1 \circlearrowleft , 15 specs (preserved in ethanol); same collection data as for holotype; CBGP.

Description (♂)

Measurements. Body length 1.5–3.5 mm.

COLOUR AND VESTITURE. Body integument black, scapes, tibiae and tarsi reddish in fully sclerotised specimens. Dorsal vestiture (pronotum + elytra) consisting of overlapping, recumbent, parallel-sided clothing scales, 2–2.5 × as long as wide, truncate at apex; colour of scales varying from pale brown to dark brown; pale scales concentrated in two longitudinal bands laterally on pronotum as well as broadly on elytral interstriae 4, creating a broad, dark medial stripe on pronotum and basal ½ of elytra; pale scales forming a pair of spots surrounded by black scales on interstriae 3 at apical ½ of elytral length; scales of striae recumbent, in lateral view not distinct from rest of vestiture.

HEAD. Forehead wide, slightly wider than epifrons near antennal insertions, almost $2 \times$ as wide as width of an eye, scales recumbent. Eyes convex, in dorsal view slightly exceeding outline of head, surrounded by a ring of short pale scales, on forehead directed towards occiput; distance between eye and scrobe as large as width of antennal club. Epifrons with distance between antennal insertions as large as length of scape, scales in middle of epifrons at most $2 \times$ as long as wide, recumbent, not contiguous. Frons with a pair of long erect lateral setae. Epistome without median seta. Antennal funicles with segment 1 elongate, $2 \times$ as long as wide; 2 shorter, at most $1.5 \times$ as long as wide; 3-5 isodiametric, compressed, 4 slightly angular on inside; 6-7 wider than long.

Pronotum. Transverse (W:L ratio 1.3–1.4), widest near midlength, sides arcuate; apex slightly narrower than base.

ELYTRA. Globular, slightly wider than long (W:L ratio 1.1), sides convex, widest near midlength.

Legs. Protibiae with outer margin straight and inner margin bisinuate, expanded proximally of apical mucro; meso- and metatibiae with small apical mucro, metatibiae with inner setal fringe, setae shorter than segment 5 of metatarsus. Tarsi with segment 2 isodiametric or wider than long.

ABDOMEN. Ventrites with creamy-white plumose scales partly concealing integument, with long, suberect, undivided setae concentrated medially; ventrite 1 slightly concave medially, ventrite 5 devoid of scales in apical 3/4, there bearing only erect setae.

TERMINALIA. Body of penis moderately elongate (W:L ratio 0.4), almost 2× as short as temones, sides subparallel, converging in apical quarter; in profile almost straight, dorsoventrally narrowed close to apex. Copulatory sclerite small, comma-shaped. Parameroid lobes separate, divided by modest median notch, each lobe broad, bearing a series of setae directed apicad, the longest setae located closer to middle. Spiculum gastrale with basal arms long, regularly curved.

Sexual dimorphism

The sexes can be distinguished by the shape of the elytra (wider than long in male, longer than wide, more broadly ovate in female) and by the inner expansion of the apex of the protibiae (present in male, absent in female).

Life history

Adult specimens of *C. armatus* were collected in August, in stands of *Oxalis obtusa* and *O.* cf. *suteroides* T.M. Salter.

Distribution

All specimens were collected at the type locality near Nieuwoudtville (Fig. 13).

Remarks

Mitochondrial barcode sequences could not be obtained for this species, probably due to a mismatch in primer sequences.

14. *Cryptolarynx falciformis* Haran sp. nov. urn:lsid:zoobank.org:act:6A1E6036-9863-440A-B4AF-CD8AD094AABA Figs 1N, 2N, 3N, 4N, 5N

Differential diagnosis

Cryptolarynx falciformis sp. nov. is most similar to *C. oberprieleri* sp. nov.; see Differential diagnosis section under that species for details.

Etymology

The species name *falciformis* refers to the falcate (sickle-shaped) copulatory sclerite in the endophallus of this species. The specific epithet is an adjective in the masculine form.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • &; "South Africa. [REPUBLIC OF SOUTH AFRICA – Western Cape], Tulbagh [33.28° S, 19.14° E]. Nov. 1952. J.G. Theron" "Holotype. *Cryptolarynx falciformis*. Haran 2023"; SAMC.

Description (♂)

MEASURMENTS. Body length 3.2 mm.

Colour and vestiture. Body integument black, antennae and tarsi reddish. Dorsal vestiture (pronotum + elytra) consisting of overlapping, recumbent, parallel-sided clothing scales, $2-3 \times$ as long as wide, rounded or truncate at apex; colour of scales greyish and pale brown; greyish scales concentrated laterally of elytral interstriae 4 and in two ill-defined pale spots at apical $\frac{2}{3}$ of interstriae 3; scales of striae recumbent, in lateral view not distinct from rest of vestiture.

HEAD. Forehead wide, slightly wider than epifrons near antennal insertions, almost $2 \times$ as wide as width of an eye, scales recumbent. Eyes convex, in dorsal view slightly exceeding outline of head, surrounded by a ring of short pale scales, on forehead directed towards occiput; distance between eye and scrobe smaller than width of antennal club. Epifrons with distance between antennal insertions as large as length of scape, scales in middle of epifrons at most $2 \times$ as long as wide, recumbent, not contiguous. Frons with a pair of long erect lateral setae. Epistome without median seta. Antennal funicles with segments 1–2 elongate, subequal; 3–6 isodiametric, 4 slightly angular ventrally; 7 wider than long.

PRONOTUM. Transverse (W:L ratio 1.4), widest anteriorly of midlength, sides arcuate; apex slightly narrower than base.

ELYTRA. Broadly ovate, isodiametric (W:L ratio 1), sides convex, widest near midlength.

Legs. Protibiae with outer margin straight and inner margin bisinuate, expanded proximally of apical mucro; meso- and metatibiae with apical mucro; metatibiae with inner setal fringe, setae shorter than segment 5 of metatarsus and with small ventral carina near base. Tarsi with segment 2 wider than long.

ABDOMEN. Ventrites with creamy-white, rounded, plumose scales not concealing integument; with long suberect deeply divided setae concentrated medially; ventrite 1 slightly concave medially; ventrite 5 devoid of scales in apical 3/4, there bearing only erect setae.

Terminalia. Body of penis moderately elongate (W:L ratio 0.5), almost $1.5 \times$ as short as temones, sides subparallel, converging in apical quarter; in profile almost straight, dorsoventrally narrowed before apex. Copulatory sclerite shaped like a pair of sickles. Parameroid lobes separate, divided by modest median notch, each lobe narrowing apicad, bearing two long setae apically. Spiculum gastrale with basal arms long, regularly curved.

Sexual dimorphism

Female unknown.

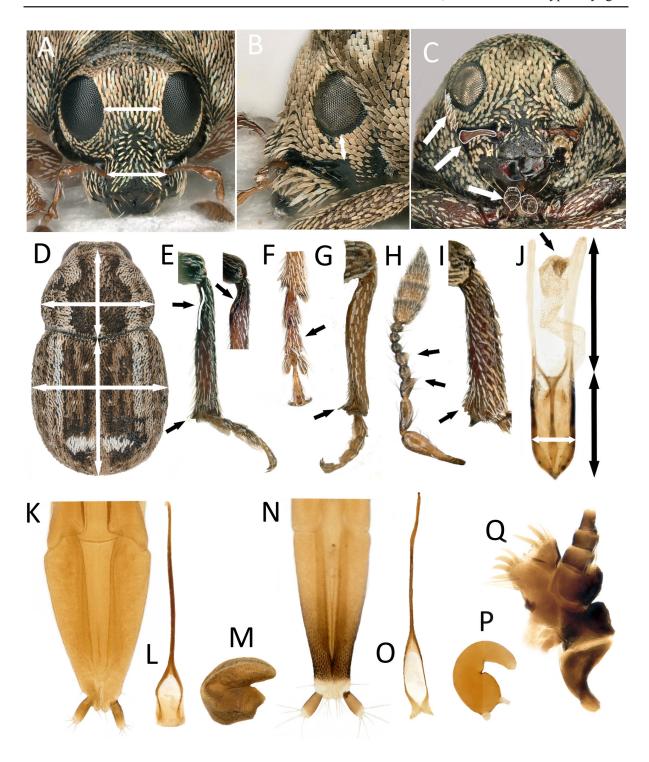
Life history

No data on host plants are available. The single known specimen was collected in November.

Distribution

The species was only found at the type locality, Tulbagh in the Western Cape province (Fig. 13).

Fig. 8 (next page). Structural details and measurements of Cryptolaryngini Van Schalkwyk, 1966. **A**. *Cryptolarynx spinicornis* Haran sp. nov., cephalic view, arrows indicating width of forehead (top) and of epifrons (bottom). **B**. Head of *C. pyrophilus* Haran sp. nov., lateral view, arrows indicating distance between eye and scrobe. **C**. Head of *C. pyrophilus* Haran sp. nov., in cephalic view, arrows showing prothoracic scales near eyes (top), position of scape when antennae in repose (middle) and position of clubs near procoxae when in repose (bottom). **D**. *C. namaquanus* Haran sp. nov., dorsal view, arrows indicate length and width dimensions of pronotum and elytra as measured. **E**. Metafemora and metatarsus of *C. variabilis* Haran sp. nov. (left) and *C. carinatus* Haran sp. nov. (right), arrows indicating position of proximal inner carina in latter species (highlighted with a white line in *C. variabilis* Haran sp. nov.) and short apical mucro. **F**. Metatarsus of *Hadrocryptolarynx major* Haran gen. et sp. nov., arrow indicating elongate segment 2 (longer than wide). **G**. Hindleg of *C. vitis* (Marshall, 1957), arrow indicating apical mucro. **H**. Antenna of *C. spinicornis* Haran sp. nov., arrows pointing at inner tooth of funicle segments 2



and 4. I. Protibia of *C. armatus* Haran sp. nov., arrow pointing at inner preapical expansion proximally of mucro. J. Penis of *C. oberprieleri* Haran sp. nov., dorsal view, black arrows indicating length of penis body and temones and white arrows indicating width of penis body as measured; bottom arrow indicating copulatory sclerite. K. Ovipositor, *Crypolarynx variabilis* Haran sp. nov. L. Sternite VIII, same species. M. Spermatheca, same species. N. Ovipositor, *Hadrocryptolarynx major* Haran gen. et sp. nov. O. Sternite VIII, same species. P. Spermatheca, same species. Q. Right maxilla, same species. Not to scale.

15. *Cryptolarynx oberprieleri* Haran sp. nov. urn:lsid:zoobank.org:act:92F63525-1018-4C50-BA14-3284DCFAC09A Figs 10, 20, 30, 40, 50, 7A–C, 8J

Differential diagnosis

Cryptolarynx oberprieleri sp. nov. can be distinguished from other species of the genus by the combination, in males, of apically expanded protibiae, deeply divided setae on ventrite 1 and arrowhead-shaped copulatory sclerite. It differs from the most similar congener, *C. falciformis* sp. nov., by the structure of the apex of the parameroid lobes and the copulatory sclerite in the endophallus (Fig. 2O). Among the species for which fresh tissue was obtained, *C. oberprieleri* was found to be genetically closest to *C. marshalli* sp. nov., the two species showing uncorrected p-distances ranging from 19.8% to 22.1% for *COI* and from 3.4% to 3.6% for *EF1*, whereas intraspecific distances were up to 3.5% for *COI* (JHAR01246; JHAR02585) and 0.6% for *EF1* (JHAR02340; JHAR02585) (Supp. file 1).

Etymology

Cryptolarynx oberprieleri sp. nov. is dedicated to Rolf G. Oberprieler for his substantial contribution to weevil taxonomy and classification, not least regarding the South African fauna. The specific epithet is a noun in the genitive case.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • &; "REPUBLIC OF SOUTH AFRICA. Western Cape Province, Stellenbosch [Paradyskloof]. 26.vii.2018. J. Haran leg." "33.964° S 18.876° E. at base of *Oxalis glabra*. J. Haran leg., JHAR01201_0101. Cirad-CBGP coll." "Holotype. *Cryptolarynx oberprieleri*. Haran 2023"; SAMC.

Paratypes

REPUBLIC OF SOUTH AFRICA – **Western Cape •** 2 & &, 17 specs (preserved in ethanol); same collection data as for holotype; CBGP • 1 &, 19 specs (preserved in ethanol); Stellenbosch, Jan Marais Nature Reserve; 33.931° S, 18.875° E; 27 Jun. 2019; J. Haran leg.; at base of *Oxalis glabra*; JHAR02340; CBGP • 1 &; same collection data as for preceding; 33.930° S, 18.875° E; 6 Sep. 2018; J. Haran leg.; at base of *Oxalis glabra*; JHAR01485; SAMC • 1 &, 1 &, 20 specs (preserved in ethanol); same collection data as for preceding; CBGP • 1 &, 3 specs (preserved in ethanol); Stellenbosch, Coetzenburg; 33.9416° S, 18.8722° E; 9 Aug. 2018; J. Haran leg.; at base of *Oxalis* spp.; JHAR01246; CBGP • 1 &, 4 specs (preserved in ethanol); Somerset West, Helderberg Nature Reserve; 34.061° S, 18.874° E; 14 Oct. 2019; J. Haran leg.; at base of *Oxalis glabra*; JHAR02585; CBGP • 1 &, 5 specs (preserved in ethanol); Klipheuwel 3 km E; 33.725° S, 18.739° E; 10 Sep. 2019; J. Haran leg.; at base of *Oxalis glabra*; JHAR02558; CBGP • 1 &, 5 specs (preserved in ethanol); J. Haran leg.; at base of *Oxalis glabra*; JHAR0250; CBGP • 1 &, Kogel Bay; 34.212° S, 18.835° E; 5 Aug. 2018; J. Haran leg.; at base of *Oxalis glabra*; JHAR01230; CBGP • 1 &, Kogel Bay; 34.212° S, 18.835° E; 5 Aug. 2018; J. Haran leg.; at base of *Oxalis livida*; JHAR01230; CBGP • 1 &; De Hoop Nature Reserve, western side; 34.496° S, 20.420° E; 29 Oct. 2019; R. Borovec leg; sweeping low vegetation in coastal sand dunes; FFWS.

Description (\bigcirc)

Measurements. Body length 1.9–3.2 mm.

Colour and vestiture. Body integument black, scapes and tarsi reddish in fully sclerotised specimens. Dorsal vestiture (pronotum + elytra) consisting of overlapping, recumbent, parallel-sided clothing scales, $2-3 \times as$ long as wide, rounded or truncate at apex; colour of scales pale to dark brown; pale scales concentrated in two lateral stripes on pronotum and on elytra from interstriae 4 laterad, as well as

forming a pair of white spots surrounded by darker scales at apical ²/₃ of interstriae 2–3; scales of striae recumbent, in lateral view not distinct from rest of vestiture.

HEAD. Forehead slightly wider than epifrons near antennal insertions, as wide as an eye, scales recumbent. Eyes convex, in dorsal view slightly exceeding outline of head, surrounded by a ring of short pale scales, on forehead directed towards occiput; distance between eye and scrobe smaller than width of antennal club. Epifrons with distance between antennal insertions slightly smaller than length of scape, scales in middle of epifrons at least $3 \times$ as long as wide, recumbent, not contiguous. Frons with a pair of long erect lateral setae. Epistome without median seta. Antennal funicles with segments 1–2 moderately elongate, subequal in length, $1.5-1.8 \times$ as long as wide; 3 isodiametric; 4 slightly angular ventrally; 5–7 globular, isodiametric.

PRONOTUM. Transverse (W:L ratio 1.3–1.4), widest near midlength, sides arcuate; apex slightly narrower than base.

ELYTRA. Broadly ovate or bullet-shaped, wider than long (W:L ratio 1.1), sides convex, widest near or anterior of midlength.

Legs. Protibiae with outer margin straight and inner margin slightly bisinuate, with small expansion proximally of apical mucro; meso- and metatibiae with small apical mucro, metatibiae with inner setal fringe, setae shorter than segment 5 of metatarsus, and with small inner carina near base. Tarsi with segment 2 wider than long.

ABDOMEN. Ventrites with creamy-white plumose scales, partly concealing integument; with long suberect setae and elongate scales concentrated medially; ventrite 1 slightly concave medially; ventrite 5 devoid of scales in apical ³/₄, there bearing only erect setae.

Terminalia. Body of penis moderately elongate (W:L ratio 0.45), slightly shorter than temones, sides subparallel, converging in apical quarter; curvature in profile moderate and regular, dorsoventrally narrowed at apex. Copulatory sclerite sagittate. Parameroid lobes separate, divided by modest median notch, each lobe bilobate, with median sublobes bearing two long setae apically. Spiculum gastrale with basal arms long, right arm angulate at its midlength.

Sexual dimorphism

The sexes can be distinguished by the shape of the elytra (wider than long in male, longer than wide and more broadly ovate in female), by the shape of ventrite 1 (medially concave in male, convex in female) and by the protibiae (with small expansion near mucro in male).

Life history

Specimens of *C. oberprieleri* sp. nov. were collected at several localities in monospecific stands of *Oxalis glabra* and, at one location, at the base of a plant of *O. livida* Jacq. Larvae and teneral adults were found inside bulbs of *O. glabra*. Adults were collected between late June and late October, found to be active during the day at the base of their host plant but at sunset retreating into small holes in the soil, which they formed under debris and under the leaves of Iridaceae.

Distribution

This species was found on the western slopes of the Hottentots Holland Mountain range and adjacent valleys, from Stellenbosch and Klipheuwel in the north to Kogel Bay beach in the south. A single specimen was discovered in the De Hoop Nature Reserve (Fig. 13).

16. *Cryptolarynx spinicornis* Haran sp. nov. urn:lsid:zoobank.org:act:73337A01-7C56-441F-8DDF-E100910E5B7A Figs 1P, 2P, 3P, 4P, 5P, 7D–F, 8A, H

Differential diagnosis

Cryptolarynx spinicornis sp. nov. differs from all other species of the genus by its enlarged funicle segments 2 and 4, bearing an inner tooth (Fig. 8H). A mitochondrial barcode fragment could not be obtained for it, probably due to mismatch in the primers sequences. Uncorrected p-distances of EF1 show that this species is closest to C. san sp. nov. but distant from it by 1.1% (Supp. file 1).

Etymology

The species name *spinicornis* is derived from the Latin nouns '*spina*' ('spine') and '*cornu*' ('horn', 'antenna') and refers to the teeth on funicle segments 2 and 4 in this species. The specific epithet is an adjective in the masculine form.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • & "REPUBLIC OF SOUTH AFRICA. Western Cape Province, Klawer [13 km S]. 26.vii.2019. J. Haran leg." "31.902° S 18.630° E, at base of *Oxalis cf. luteola*. JHAR02465_0101. Cirad-CBGP coll." "Holotype. *Cryptolarynx spinicornis*. Haran 2023"; SAMC.

Paratypes

REPUBLIC OF SOUTH AFRICA – **Western Cape •** 1 \circlearrowleft , 2 specs (preserved in ethanol); same collection data as for holotype; CBGP. – **Northern Cape •** 2 \circlearrowleft \circlearrowleft , 18 specs (preserved in ethanol); Sutherland 21 km SW, Blesfontein Farm; 32.462° S, 20.436° E; 18 Aug. 2019; J. Haran leg.; at base of *Oxalis* cf. *odorata*; JHAR02512; CBGP.

Description (\bigcirc)

Measurements. Body length 1.7–3.0 mm.

COLOUR AND VESTITURE. Body integument black, antennae, tarsi and sometimes tibiae reddish. Dorsal vestiture (pronotum + elytra) consisting of overlapping, recumbent, parallel-sided clothing scales, 3 × as long as wide, truncate at apex; colour of scales pale to dark brown; pale scales generally concentrated in two lateral bands on pronotum and on elytral interstriae 4 as well as forming a pair of white spots surrounded by darker scales at apical ½ of interstriae 2–3; dark scales concentrated in a pair of spots at base of pronotum near scutellar shield; scales of striae recumbent, in lateral view not distinct from rest of vestiture.

HEAD. Forehead slightly wider than epifrons near antennal insertions, slightly wider than width of an eye, scales recumbent. Eyes convex, in dorsal view slightly exceeding outline of head, surrounded by a ring of short pale scales, on forehead directed towards occiput; distance between eye and scrobe smaller than width of antennal club. Epifrons with distance between antennal insertions as large as length of scape, scales in middle of epifrons at least $3 \times$ as long as wide, recumbent, not contiguous. Frons with 3 pairs of erect lateral setae. Epistome without median seta. Antennal funicles with segment 1 very elongate, $2 \times$ as long as 2; 2 and 4 compressed, strongly angular, toothed on inside; 3 isodiametric or slightly longer than wide; 5-7 globular, isodiametric.

PRONOTUM. Transverse (W:L ratio 1.4), widest anteriorly of midlength, sides arcuate; apex slightly narrower than base.

ELYTRA. Bullet-shaped, longer than wide (W:L ratio 0.9), sides convex, widest anteriorly of midlength.

Legs. All tibiae with small apical mucro; protibiae with outer margin straight, inner margin slightly bisinuate; metatibiae with inner setal fringe, setae shorter than segment 5 of metatarsus. Tarsi with segment 2 wider than long on forelegs and longer than wide on hindlegs.

ABDOMEN. Ventrites with creamy-white plumose scales partly concealing integument, with long suberect setae not or only slightly bifid at apex, concentrated medially; ventrite 1 slightly concave medially, impression devoid of scales; ventrite 5 with scales concentrated laterally, medially bare.

TERMINALIA. Body of penis moderately elongate (W:L ratio 0.4), slightly shorter than temones, sides subparallel in basal ²/₃, converging in apical third; curvature in profile moderate and regular, more strongly downcurved near apex, dorsoventrally narrowed before apex. Copulatory sclerite shaped like a pair of sickles. Parameroid lobes separate, divided by deep median notch, each lobe slightly bilobate, with median sublobes bearing several long setae apically. Spiculum gastrale with basal arms long, right arm angulate at its midlength.

Sexual dimorphism

The sexes can be distinguished by the shape of the elytra (shorter in male than in female) and the forehead (narrower in male than in female).

Life history

Specimens of *Cryptolarynx spinicornis* sp. nov. were found at the bases of plants of *Oxalis* cf. *luteola* Jacq. and *O.* cf. *odorata* J.C. Manning & Goldblatt at sites where *O. obtusa* was also present.

Distribution

The species occurs in the Vanrhynsdorp area and up to 1500 m above sea level on the Great Escarpment near Sutherland (Fig. 13).

Remarks

Mitochondrial barcode sequences could not be obtained for this species, probably due to a mismatch in the primer sequences.

17. *Cryptolarynx cederbergensis* Haran sp. nov. urn:lsid:zoobank.org:act:1F91C372-DB13-4390-8130-02F8B37A4FE2 Figs 1Q, 2Q, 3Q, 4Q, 5Q

Differential diagnosis

Cryptolarynx cederbergensis sp. nov. is most similar to C. pyrophilus sp. nov. but can be distinguished from it by the width of its forehead, which is less than twice the width of an eye (equal to twice width in C. pyrophilus), and by the arrangement of setae at the apex of the parameroid lobes (Fig. 2Q). The two species were found to have interspecific uncorrected p-distances ranging from 20.9% to 23.3% for COI and 5.2% for EF1 (Supp. file 1).

Etymology

The species name *cederbergensis* refers to the origin of this species, the Cederberg mountains in the Western Cape province. The specific epithet is an adjective in the masculine form.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • & "REPUBLIC OF SOUTH AFRICA. Western Cape Province, [Cederberg Wilderness Area;] Algeria [Forest Station] ca. 20 km S. 23.viii.2018. J. Haran leg." "32.469° S 19.206° E, at base of *Oxalis obtusa*. JHAR01422_0101. Cirad-CBGP coll." "Holotype. *Cryptolarynx cederbergensis*. Haran 2023"; SAMC.

Paratypes

REPUBLIC OF SOUTH AFRICA – Western Cape • 1 \circlearrowleft , 2 \circlearrowleft \circlearrowleft ; same collection data as for holotype; CBGP.

Description (♂)

Measurements. Body length 1.9–2.2 mm.

Colour and vestiture. Body integument black, basal half of scapes reddish in mature specimens. Dorsal vestiture (pronotum + elytra) consisting of overlapping, recumbent, parallel-sided clothing scales, 2×10^{10} as long as wide, mostly rounded at apex; colour of scales white or pale brown to dark brown; white scales usually concentrated in a pair of longitudinal lateral stripes on pronotum and elytral interstriae 4, creating a broad darker stripe medially on pronotum and basal $\frac{2}{3}$ of elytra; white scales also concentrated in a pair of ill-defined pale spots surrounded by black scales at apical $\frac{2}{3}$ of interstria 3; scales of striae recumbent, in lateral view not or only very slightly distinct from rest of vestiture.

HEAD. Forehead very wide, slightly wider than epifrons near antennal insertions, ca $2 \times$ as wide as width of an eye, scales suberect. Eyes convex, in dorsal view slightly exceeding outline of head, surrounded by a ring of short pale scales, on forehead directed towards occiput; distance between eye and scrobe as large as width of antennal club. Epifrons with distance between antennal insertions $0.8 \times$ length of scape, scales at least $3 \times$ as long as wide, suberect, contiguous. Frons with a pair of long erect lateral setae. Epistome with one or two elongate median setae. Antennal funicles with segment 1 elongate; 2 shorter, at most $1.5 \times$ as long as wide; 3 longer than wide; 4 globular, isodiametric, compressed, slightly angular on inside; 5–7 globular, isodiametric.

PRONOTUM. Transverse (W:L ratio 1.6), widest posteriorly of midlength, sides arcuate; apex and base subequal in width.

ELYTRA. Broadly ovate, isodiametric (W:L ratio 1), sides convex, widest near midlength.

Legs. Tibiae with apical mucro; protibiae with both outer and inner margins straight; metatibiae with inner setal fringe, the setae shorter than segment 5 of metatarsus. Tarsi with segment 2 slightly longer than wide.

Abdomen. Ventrites with creamy-white plumose scales not concealing integument; ventrites 1–4 with long suberect scales; ventrite 5 devoid of scales in apical half, there bearing only erect setae.

TERMINALIA. Body of penis elongate (W:L ratio 0.3–0.4), as long as temones, sides subparallel, converging in apical third; curvature in profile weak and regular, dorsoventrally narrowed before apex. Copulatory sclerite forming a reversed V. Parameroid lobes separate, divided by deep median notch, each lobe broad, bearing a series of long setae directed apicad. Spiculum gastrale with basal arms long, regularly curved, right arm angulate near its base.

Sexual dimorphism

The sexes can be distinguished by the width of the forehead (as wide as or narrower than width of an eye in male, wider in female).

Life history

Specimens of *C. cederbergensis* sp. nov. were collected in monospecific stands of *Oxalis obtusa*, in the month of August.

Distribution

The species was found only at the type locality (Fig. 13).

18. *Cryptolarynx homaroides* Haran sp. nov. urn:lsid:zoobank.org:act:B52976BC-5840-45EC-9813-C4BB817C0056 Figs 1R, 2R, 3R, 4R, 5R

Differential diagnosis

Cryptolarynx homaroides sp. nov. is most similar to *C. marshalli* sp. nov., but the body of the latter species is distinctly more elongate and lacks the distinct lobster-like copulatory sclerite of *C. homaroides*.

Etymology

The species name *homaroides* is derived from the genus name of the European Lobster (*Homarus gammarus* Linnaeus) and refers to the remarkably similar shape of copulatory sclerite in the endophallus of this species. The specific epithet is an adjective with immutable ending.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • &: "S. Afr. [REPUBLIC OF SOUTH AFRICA – Northern Cape], Namaquald [Namaqualand]. Springbok–Mesklip. 29.49S–17.52E [29.817° S, 17.867° E]" "30.8.1976; E-Y:1186. From under stones. [coarse sandy neck of rocky hills] leg. Endrödy-Younga" "Holotype. Cryptolarynx homaroides. Haran 2023"; TMSA.

Description (\circlearrowleft)

MEASUREMENTS. Body length 2.3 mm.

COLOUR AND VESTITURE. Body integument black, scapes at their bases, tibiae and tarsi reddish. Dorsal vestiture (pronotum + elytra) consisting of overlapping, recumbent, parallel-sided or subtriangular clothing scales, 1.5–2 × as long as wide, truncate or rounded at apex; colour of scales pale to dark brown; pale scales generally concentrated in two lateral bands on pronotum and at base of elytral interstriae 4, creating irregular shades on elytra, and concentrated in a pair of pale spots surrounded by darker scales at apical ½ of interstriae 2–3; scales of striae recumbent, in lateral view not distinct from rest of vestiture.

HEAD. Forehead as wide as epifrons near antennal insertions, scales recumbent. Eyes convex, in dorsal view slightly exceeding outline of head, surrounded by a ring of short pale scales, on forehead directed towards occiput; distance between eye and scrobe smaller than width of antennal club. Epifrons with distance between antennal insertions as large as length of scape, scales in middle of epifrons at most $2 \times$ as long as wide, recumbent, not contiguous. Frons with 3 pairs of long erect lateral setae. Epistome without median seta. Antennal funicles with segment 1 moderately elongate, $1.5 \times$ as long as wide; 2-4 longer than wide, compressed; 5-6 globular, isodiametric; 7 wider than long.

PRONOTUM. Transverse (W:L ratio 1.3), widest near midlength, sides arcuate; apex and base subequal in width.

ELYTRA. Broadly ovate, slightly longer than wide (W:L ratio 0.9), sides convex, widest near midlength.

Legs. All tibiae with small apical mucro; protibiae with outer margin straight, inner margin slightly bisinuate; metatibiae with inner setal fringe, the setae shorter than segment 5 of metatarsus. Tarsi with segment 2 wider than long.

ABDOMEN. Ventrites with creamy-white plumose scales, partly concealing integument, and long suberect setae or setiform scales, each apically truncate or slightly bifid, concentrated medially; ventrite 1 slightly concave medially; ventrite 5 with scales concentrated in basal half.

TERMINALIA. Body of penis moderately elongate (W:L ratio 0.45), slightly shorter than temones, sides convex; in profile straight, slightly downcurved and dorsoventrally slightly narrowed near apex. Copulatory sclerite in dorsal view shaped like a lobster. Parameroid lobes separate, divided by deep median notch; each lobe bearing two brushes of erect setae. Spiculum gastrale with basal arms long, longer than ventral strut, right arm regularly curved.

Sexual dimorphism

Female unknown.

Life history

Unknown. The single known specimen of *C. homaroides* sp. nov. was collected under stones.

Distribution

The species was only found at the type locality, the Springbok area in the Northern Cape province (Fig. 13).

19. *Cryptolarynx marshalli* Haran sp. nov. urn:lsid:zoobank.org:act:B4281E9A-F0FF-42D4-8099-9ADA5005C6E5 Figs 1S, 2S, 3S, 4S, 5S, 7G–I

Differential diagnosis

Cryptolarynx marshalli sp. nov. is closely related to *C. oberprieleri* sp. nov. but distinctly more elongate, and the apex of its parameroid lobes is also distinct (Fig. 2O–S). See Differential diagnosis section under species *C. oberprieleri* for the genetic distances between these species.

Etymology

This species is dedicated to the late weevil expert Sir Guy A.K. Marshall, who described the genus and its original two species and discussed its unique characters among known weevils. The specific epithet is a noun in the genitive case.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • &; "REPUBLIC OF SOUTH AFRICA. **Western Cape Province**, Worcester. 3.vii.2019. J. Haran leg." "33.613° S 19.447° E. at base of *Oxalis imbricata*. JHAR02355_0101. Cirad-CBGP coll." "Holotype. *Cryptolarynx marshalli*. Haran 2023"; SAMC.

Paratypes

REPUBLIC OF SOUTH AFRICA – **Western Cape •** 1 \circlearrowleft , 2 specs; same collection data as for holotype; CBGP.

Description (♂)

Measurements. Body length 2.5–2.9 mm.

COLOUR AND VESTITURE. Body integument black, antennae, tibiae and tarsi reddish. Dorsal vestiture (pronotum + elytra) consisting of overlapping, recumbent, parallel-sided clothing scales, 3 × as long as wide, truncate at apex; colour of scales mostly brown, white scales interspersed with pale brown scales concentrated in two longitudinal bands on pronotum, at base of elytral interstriae 4, and in a pair of pale spots surrounded by black scales at apical ½ of interstriae 3; scales of striae recumbent, in lateral view not or only very slightly distinct from rest of vestiture.

HEAD. Forehead wide, slightly wider than epifrons near antennal insertions, scales suberect. Eyes convex, in dorsal view slightly exceeding outline of head, surrounded by a ring of short scales, on forehead directed towards occiput; distance between eye and scrobe smaller than width of antennal club. Epifrons with distance between antennal insertions slightly smaller than length of scape, scales at least $2 \times$ as long as wide, recumbent, mostly non-contiguous. Frons with 3 pairs of erect lateral setae. Epistome without median seta. Antennal funicles with segment 1 moderately elongate, 1.5 longer than wide; 2 subequal in length to 1; 2 and 4 compressed, slightly angular on inside; 5–7 globular, isodiametric or wider than long.

PRONOTUM. Moderately transverse (W:L ratio 1.2), widest near midlength, sides arcuate; apex and base subequal in width.

ELYTRA. Bullet-shaped, longer than wide (W:L ratio 0.85), sides convex, widest anteriorly of midlength.

Legs. Slender. Tibiae with apical mucro; protibiae with outer margin straight, inner margin slightly bisinuate; metatibiae with inner setal fringe, setae shorter than segment 5 of metatarsus. Tarsi with segment 2 wider than long.

ABDOMEN. Ventrite with creamy-white plumose scales not fully concealing integument, scales on ventrites 2–5 medially intermixed with long suberect setae, apically bifid or not; ventrite 1 slightly concave medially, impression covered with long setae deeply divided from their bases; ventrite 5 with scales concentrated laterally and on basal third.

TERMINALIA. Body of penis moderately elongate (W:L ratio 0.45), slightly shorter than temones, sides convex; curvature in profile weak, stronger in basal half, not dorsoventrally narrowed at apex. Copulatory sclerite weakly sclerotised or not discerned in examined specimens. Parameroid lobes separate, divided by modest median notch, each lobe broad, bearing a series of setae directed apicad, median setae longer. Spiculum gastrale with basal arms long, right arm slightly angulate at its midlength.

Sexual dimorphism

The sexes can be distinguished by the elytra (shorter in male) and by ventrite 1 in the female lacking the long, deeply divided setae.

Life history

All specimens of this species were collected in July at the base of Oxalis imbricata Eckl. & Zeyh. plants.

Distribution

The species is only known from the type locality (Fig. 13).

20. *Cryptolarynx endroedyi* Haran sp. nov. urn:lsid:zoobank.org:act:76B9D666-207A-4BC2-A344-844400B78F98 Figs 1T, 2T, 3T, 4T, 5T

Differential diagnosis

Cryptolarynx endroedyi sp. nov. differs from all other known species of the genus by its distinctly elongate body and by the following two features (in the male): the presence of depressions on the pronotum and elytra and the temones of the penis being almost twice as long as the penis body.

Etymology

We dedicate this species to the late Sebastian Endrödy-Younga, coleopterist at the Ditsong National Museum of Natural History (formerly the Transvaal Museum) from 1973 to 1999. The extent of his field collecting in South Africa and Namibia exceeds imagination with respect to the large numbers of species and of specimens he collected and the significant number of localities he surveyed. He also collected many of the specimens of *Cryptolarynx* and *Hadrocryptolarynx* gen. nov. reported in this study. The specific epithet is a noun in the genitive case.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • ♂; "S. Africa. SW. Cape. Prov. [REPUBLIC OF SOUTH AFRICA – **Western Cape**], Clanwilliam, 29 km N [flat valley bottom]. 31.47S - 18.43E [recte 31°57′S, 18°43′E]" "29.viii.1989; E-Y:2675. Flowering meadow. Endrödy[-Younga] & Klimaszew[ski]" "Holotype. *Cryptolarynx endroedyi*. Haran 2023"; TMSA.

Paratypes

REPUBLIC OF SOUTH AFRICA – **Western Cape** • 2 \circlearrowleft ; same collection data as for holotype; TMSA • 1 \circlearrowleft ; same collection data as for holotype; CBGP.

Description (\circlearrowleft)

Measurements. Body length 3.6 mm.

COLOUR AND VESTITURE. Body integument black, antennae, tibiae and tarsi reddish. Dorsal vestiture (pronotum + elytra) consisting of overlapping, recumbent, parallel-sided clothing scales, 3–4× as long as wide, mostly truncate at apex; colour of scales mostly brown; whitish scales interspersed with pale brown scales concentrated laterally on pronotum and on elytra laterally from interstriae 4, white scales forming a pair of pale spots surrounded by dark scales at apical ½ of elytral interstriae 2–3; scales of striae recumbent, in lateral view not distinct from rest of vestiture.

HEAD. Forehead slightly wider than epifrons near antennal insertions, scales suberect. Eyes convex, in dorsal view distinctly exceeding outline of head, surrounded by a ring of short pale scales, on forehead directed towards occiput; distance between eye and scrobe slightly smaller than width of antennal club. Epifrons with distance between antennal insertions $0.33 \times \text{length}$ of scape, scales at least $2 \times \text{as}$ long as wide, recumbent, subcontiguous. Frons with 3 pairs of long erect lateral setae. Epistome without median seta. Antennal funicles with segments 1–2 elongate, subequal in length; 3–4 longer than wide; 5–6 globular; 7 wider than long.

PRONOTUM. Transverse (W:L ratio 1.35), widest near midlength, sides arcuate; apex and base subequal in width; with a depression at midlength on either side of dark median longitudinal stripe.

ELYTRA. Broadly ovate, longer than wide (W:L ratio 0.9), sides convex, widest anteriorly of midlength; with a slight depression on basal half of interstriae 1–2.

Legs. Slender. Tibiae with apical mucro; protibiae with outer margin straight, inner margin slightly bisinuate; metatibiae with inner setal fringe, the setae shorter than segment 5 of metatarsus. Tarsi with segment 2 isodiametric.

ABDOMEN. Ventrites with creamy-white plumose scales not concealing integument; scales on ventrites 2–5 medially intermixed with long suberect setae, bifid or not at the apex; ventrite 1 slightly concave medially, impression covered with long setae deeply divided from their bases; ventrite 5 with scales concentrated in basal quarter.

TERMINALIA. Body of penis moderately elongate (W:L ratio 0.5), $2 \times$ as short as temones, sides convex; in profile straight, downcurved near apex, dorsoventrally narrowed at apex. Copulatory sclerite weakly sclerotised or not discerned in examined specimen. Parameroid lobes separate, divided by modest median notch, each lobe broad, bearing a series of setae directed apicad. Spiculum gastrale with basal arms long, regularly curved.

Sexual dimorphism

The sexes can be distinguished by the shape of the elytra (shorter in the male) and by ventrite 1 lacking the long and deeply divided setae in the female.

Life history

Specimens of *Cryptolarynx endroedyi* sp. nov. were collected in a flowering meadow. No data about any host plant association of the species are available.

Distribution

The species was only found at the type locality, the Clanwilliam area in the Western Cape province (Fig. 13).

21. *Cryptolarynx oberlanderi* Haran sp. nov. urn:lsid:zoobank.org:act:4AD62755-5B76-406D-84AC-D5A8C49EE048 Figs 1U, 2U, 3U, 4U, 5U, 7J–K

Differential diagnosis

Cryptolarynx oberlanderi sp. nov. is very similar to *C. san* sp. nov. and *C. luteipennis* sp. nov. but distinguishable from these by its narrower forehead and non-overlapping scales on the epifrons, and the apex of its parameroid lobes is also distinct among these species. *Cryptolarynx oberlanderi* was found to be genetically distinct from *C. luteipennis* and *C. san* by 8.1% and 15.1% for *COI* and by 3.7% and 4.0% for *EF1*, respectively.

Etymology

This species is dedicated to our colleague Kenneth Oberlander, specialist of the taxonomy of the genus *Oxalis*. Thanks to his substantial help with the location and identification of species of this genus, numerous new species of *Cryptolarynx* were discovered, including this one. The specific epithet is a noun in the genitive case.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • & "REPUBLIC OF SOUTH AFRICA. Western Cape Province. Worcester. 3.vii.2019. J. Haran leg." "33.639° S 19.391° E, at base of *Oxalis depressa*. JHAR02353_0101. Cirad-CBGP coll." "Holotype. *Cryptolarynx oberlanderi*. Haran 2023"; SAMC.

Paratypes

REPUBLIC OF SOUTH AFRICA – **Western Cape •** 1 ♀; same collection data as for holotype; SAMC • 1 ♂, 7 specs (preserved in ethanol); same collection data as for holotype; CBGP • 1 ♂, 1 spec.; Hex River Valley, Kanetvlei, GG Camp Sandhill; 33.509° S, 19.574° E; 3 Jul. 2019; J. Haran leg.; at base of *Oxalis depressa*; JHAR03227; CBGP.

Description (♂)

MEASUREMENTS. Body length 2.1–3.0 mm.

COLOUR AND VESTITURE. Body integument black, scapes and tarsi reddish. Dorsal vestiture (pronotum + elytra) consisting of overlapping, recumbent, parallel-sided or subtriangular clothing scales, isodiametric to 3 × as long as wide, truncate at apex; colour of scales brown; dark brown scales forming a longitudinal stripe medially on pronotum and elytral interstriae 1–3, pale brown scales concentrated laterally on pronotum and on elytra laterally of interstria 4; white scales surrounded by black scales forming a pair of pale spots on elytral interstriae 2–3 at apical ¾ of elytral length; scales of striae recumbent, in lateral view not distinct from the of vestiture.

HEAD. Forehead wide, slightly wider than epifrons near antennal insertions, scales recumbent, not concealing integument. Eyes convex, in dorsal view slightly exceeding outline of head, surrounded by a ring of short scales, on forehead directed towards occiput; distance between eye and scrobe smaller than width of antennal club. Epifrons with distance between antennal insertions as large as length of scape, scales in middle of epifrons at most $2 \times$ as long as wide, recumbent, non-contiguous. Frons with 3 pairs of long erect lateral setae. Epistome without median seta. Antennal funicles with segment 1 moderately elongate, $1.5 \times$ as long as; 2 slightly shorter, 2 and 4 compressed, slightly angular on inside; 5–7 globular, isodiametric.

PRONOTUM. Moderately transverse (W:L ratio 1.25), widest near midlength, sides arcuate; apex slightly narrower than base.

ELYTRA. Broadly ovate, slightly longer than wide (W:L ratio 0.9), sides convex, widest anterior of midlength.

Legs. Tibiae with apical mucro; protibiae with outer margin straight, inner margin slightly bisinuate; metatibiae with inner setal fringe, setae shorter than segment 5 of metatarsus. Tarsi with segment 2 of protarsus transverse, of meso- and metatarsus isodiametric.

ABDOMEN. Ventrite with creamy-white plumose scales not concealing integument, scales on ventrites 2–5 medially intermixed with long suberect setae, apically bifid or not; ventrite 1 slightly concave medially, impression covered with long setae deeply divided from their bases; ventrite 5 almost completely devoid of scales except for a series of small scales along suture, medially with a smooth area without setae or punctures.

Terminalia. Body of penis moderately elongate (W:L ratio 0.6), $2 \times$ as short as temones, sides slightly convex, converging in apical quarter; in profile straight, weakly downcurved and dorsoventrally narrowed

at apex. Copulatory sclerite weakly sclerotised or not discerned in examined specimens. Parameroid lobes separate, divided by modest median notch, each bearing a series of setae directed apicad, longer medially, longest setae longer than depth of median notch. Spiculum gastrale with basal arms long, right arm slightly angulate near midlength.

Sexual dimorphism

The sexes can be distinguished by the elytra (longer in the female) and by abdominal ventrite 1 lacking long, deeply divided setae in the female.

Life history

The known specimens of *C. oberlanderi* sp. nov. were all found in July, at the base of plants of *Oxalis depressa* Eckl. & Zeyh.

Distribution

The species is only known from the Hex River valley and the Worcester area (Fig. 13).

22. *Cryptolarynx san* Haran sp. nov. urn:lsid:zoobank.org:act:C211DB32-D638-459F-BFBE-EB80EB647535 Figs 1V, 2V, 3V, 4V, 5V, 7L

Differential diagnosis

This species is most similar to *C. luteipennis* sp. nov. but distinguishable by the setae on ventrite 2 of the male (bifid from the base in *C. san* sp. nov.; entire or only bifid near apex in *C. luteipennis*). The shape of the body of the penis and the conformation of the apical setae on the parameroid lobes are also different between these species (Fig. 2V). Uncorrected genetic distances between them were found to be 16.3% for *COI* and between 3.5% and 4.1% for *EF1*.

Etymology

This species is dedicated to the San people, the first inhabitants of southern Africa. This hunter-gatherer people left important traces of their activities (debris of bones, shells) on the coasts of the Western Cape province. The specific epithet is a noun in apposition.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • & "REPUBLIC OF SOUTH AFRICA. Western Cape Province, [Jacobs Bay,] Bokpunt. 21.ix.2018. J. Haran leg." "33.522° S 18.324° E. at base of *Oxalis luteola*. JHAR01514_0101. Cirad-CBGP coll." "Holotype. *Cryptolarynx san*. Haran 2023"; SAMC.

Paratypes

REPUBLIC OF SOUTH AFRICA – **Western Cape** • 1 \circlearrowleft ; same collection data as for holotype; at base of *Oxalis* cf. *hirta*; JHAR01515; SAMC • 7 specs (preserved in ethanol); same collection data as for preceding; CBGP • 1 \circlearrowleft , 2 specs; West Coast National Park, near southern entrance; 33.243° S, 18.204° E; 27 Jul. 2019; J. Haran leg.; near *Oxalis obtusa*; JHAR02484; CBGP.

Description (♂)

Measurements. Body length 2.7–3.6 mm.

COLOUR AND VESTITURE. Body integument black, antennae, tibiae and tarsi reddish. Dorsal vestiture (pronotum + elytra) consisting of overlapping, recumbent, parallel-sided clothing scales, 2–3 × as long

as wide, truncate at apex; colour of scales black, pale brown or white; black scales forming a medial longitudinal stripe over pronotum and on basal half of elytral interstriae 1–3; pale brown and white scales concentrated laterally on pronotum and on elytra laterally from interstriae 4; white scales forming a pair of pale spots on elytral interstriae 2–3 at apical ³/₄ of elytral length, these spots sometimes contiguous, confluent and merged with pale areas laterally; scales of striae recumbent, in lateral view not distinct from rest of vestiture.

HEAD. Forehead wide, distinctly wider than epifrons near antennal insertions, scales suberect, almost concealing integument. Eyes convex, in dorsal view slightly exceeding outline of head, surrounded by a ring of short pale scales, on forehead directed towards occiput; distance between eye and scrobe smaller than width of antennal club. Epifrons with distance between antennal insertions $0.33 \times length$ of scape, scales in middle of epifrons at least $2 \times as$ long as wide, recumbent, non-contiguous. Frons with 3 pairs of long erect lateral setae. Epistome without median seta. Antennal funicles with segment 1 elongate, $2 \times as$ long as wide; 2 slightly shorter; 2 and 4 compressed, slightly angular on inside; 5–7 globular, isodiametric.

Pronotum. Transverse (W:L ratio 1.35), widest near midlength, sides arcuate; width of apex 0.67× width of base

ELYTRA. Broadly ovate or globular, isodiametric (W:L ratio 1), sides convex, widest anteriorly of midlength.

Legs. Tibiae with apical mucro; protibiae with outer margin straight, inner margin bisinuate; metatibiae with inner setal fringe, setae shorter than segment 5 of metatarsus. Tarsi with segment 2 of protarsus transverse, of meso- and metatarsus isodiametric.

ABDOMEN. Ventrites with creamy-white plumose scales almost concealing integument, scales on ventrites 2–5 medially intermixed with long suberect setae, each mostly bifid apically; ventrite 1 slightly concave medially, devoid of scales; ventrite 5 almost devoid of scales except for a few scales along lateral margins.

TERMINALIA. Body of penis elongate (W:L ratio 0.35), as long as temones, sides subparallel, slightly divergent from base to apex, strongly converging at apex; curvature in profile weak and regular, dorsoventrally narrowed at apex. Copulatory sclerite weakly sclerotised or not discerned in examined specimens. Parameroid lobes separate, divided by modest median notch, each lobe bearing a series of setae directed apicad, longer medially, longest setae shorter than depth of median notch. Spiculum gastrale with basal arms moderately and regularly curved, each arm bearing a wide cuticular expansion.

Sexual dimorphism

The sexes can be distinguished by the elytra (longer in females) and by the centre of ventrite 1 (lacking long deeply divided setae in females).

Life history

Adults of *C. san* sp. nov. were collected in the vicinity of stands of various species of *Oxalis* (*O. obtusa*, *O. luteola* and *O. hirta* L.), but the exact host plant could not be confirmed. Specimens were collected in July and September. The scales on the elytra can be white or pale brown, and their colour corresponds well with that of the soil where particular specimens were found. Compared with the other species of the genus, the adults of *C. san* can move very fast on the ground.

Distribution

The species occurs at various locations of the West Coast, in Bokpunt and near the West Coast National Park (Fig. 13).

23. *Cryptolarynx luteipennis* Haran sp. nov. urn:lsid:zoobank.org:act:EF56A88D-DBE8-4B40-8627-DF0E55A8E965

Figs 1W, 2W, 3W, 4W, 5W

Differential diagnosis

This species is most similar to *C. san* sp. nov.; see Differential diagnosis section under that species for diagnostic characters and genetic distances.

Etymology

The species name *luteipennis* refers to the orange or yellowish shades on elytra on many specimens of this species. These colours are seemingly unique to this species and provide an efficient camouflage of adults on the pinkish-orange sand on which they were found near Graafwater. The specific epithet is an adjective in the masculine form.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • & "REPUBLIC OF SOUTH AFRICA. Western Cape Province, Graafwater [7 km N]. 26.vii.2019. J. Haran leg." "32.091° S 18.590° E, at base of *Oxalis* spp. JHAR02468_0101. Cirad-CBGP coll." "Holotype. *Cryptolarynx luteipennis*. Haran 2023"; SAMC.

Paratypes

REPUBLIC OF SOUTH AFRICA – **Western Cape** • 1 \circlearrowleft , 1 \circlearrowleft , 13 specs; same collection data as for holotype; CBGP • 1 \circlearrowleft , 9 specs; same collection data as for holotype; JHAR02471; CBGP • 2 \circlearrowleft \circlearrowleft , 2 \circlearrowleft \circlearrowleft ; Velddrif 13 km E, Doornfontein Farm; 32.800° S, 18.300° E; 31 Aug. 1981; S. Endrödy-Younga leg.; pitfall traps 59 days baited with banana; yellowish sands; E-Y:1871; TMSA • 1 \circlearrowleft , 1 \circlearrowleft ; same collection data as for preceding; SANC • 1 \circlearrowleft ; Redelinghuys 20 km SW, Saamstaan Farm; 32.583° S, 18.367° E; 30 Aug. 1981; S. Endrödy-Younga leg.; pitfall traps 60 days baited with faeces; vegetated white dunes behind coastal dunes; E-Y:1866; TMSA • 1 \circlearrowleft ; Velddrif 3 km E; 32.767° S, 18.233° E; 31 Aug. 1981; S. Endrödy-Younga leg.; pitfall traps 59 days baited with banana; densely vegetated reddish sand; E-Y:1870; TMSA.

Description (♂)

Measurements. Body length 1.8–2.6 mm.

COLOUR AND VESTITURE. Body integument black, antennae, tibiae and tarsi reddish. Dorsal vestiture (pronotum + elytra) consisting of overlapping, recumbent, parallel-sided clothing scales, 1.5–2 × as long as wide, truncate at apex; colour of scales black, dark brown to pale brown and yellow or orange; darkest scales forming medial longitudinal stripe over pronotum and on basal ½ of elytral interstriae 1–3; paler scales concentrated laterally on pronotum and on elytra from interstriae 4 laterad; white scales forming a pair of pale spots on elytral interstriae 2–3 at apical ¾ of elytral length; scales of striae recumbent, in lateral view not distinct from rest of vestiture.

HEAD. Forehead wide, slightly wider than epifrons near antennal insertions, scales suberect, almost concealing integument. Eyes strongly convex, in dorsal view distinctly exceeding outline of head, surrounded by a ring of short scales, on forehead directed towards occiput; distance between eye and scrobe smaller than width of antennal club. Epifrons with distance between antennal insertions 0.33×10^{12} length of scape, scales at least 2×10^{12} as long as wide in middle, recumbent, non-contiguous. Frons with 3 pairs of erect lateral setae. Epistome without median seta. Antennal funicles with segment 1 elongate,

2× as long as wide; 2 slightly shorter than 1; 2 and 4 compressed, slightly angular on inside; 5–6 globular, isodiametric; 7 wider than long.

Pronotum. Transverse (W:L ratio 1.45), widest near midlength, sides arcuate; apex slightly narrower than base.

ELYTRA. Globular, slightly wider than long (W:L ratio 1.1), sides convex, widest near midlength.

Legs. Tibiae with apical mucro; protibiae with outer margin straight, inner margin bisinuate; metatibiae with inner setal fringe, setae shorter than segment 5 of metatarsus. Tarsi with segment 2 of protarsus transverse, of meso- and metatarsus isodiametric.

ABDOMEN. Ventrites with creamy-white plumose scales not concealing integument, scales on ventrites 2–5 intermixed mostly medially with long suberect setae, bifid from midlength or at least at apex; ventrite 1 slightly concave medially, devoid of scales, impression covered with long setae, deeply divided from their bases; ventrite 5 devoid of scales, bearing only erect setae.

TERMINALIA. Body of penis moderately elongate (W:L ratio 0.5), $0.66 \times$ length of temones, sides convex; curvature in profile weak, more strongly downcurved near apex, not dorsoventrally narrowed at apex. Copulatory sclerite weakly sclerotised or not discerned in examined specimens. Parameroid lobes separate, divided by modest median notch, each lobe bearing a series of setae directed apicad and converging. Spiculum gastrale with basal arms moderately curved, bearing a tooth near midlength.

Sexual dimorphism

The sexes can be distinguished by the shape of ventrite 1 (convex with deeply divided setae in male, concave with undivided setae in female).

Life history

Adults of *C. luteipennis* sp. nov. were collected in the vicinity of stands of various species of *Oxalis* (including *O. obtusa*), but the exact host plant of the species has not been identified. All specimens were collected in July and August.

Distribution

The species occurs on the West Coast between Velddrif and the Clanwilliam area (Fig. 13).

Key to the species of Cryptolarynx Van Schalkwyk, 1966 (males)

- 2. Pale scales on forehead adjacent to eyes directed towards centre of eyes (Fig. 4A–C, E–F). Metatibial mucrones strongly developed, almost perpendicular to external margin of metatibiae (Fig. 8G).

_	Apical half of metatibiae medially with setae shorter than segment 5 of metatarsi. Parameroid lobes laterally narrowed before apex (Fig. 2A–C, E–F)
3.	Body globular (Fig. 1A–C). Elytra isodiametric or wider than long (W:L ratio 1.0–1.1)
4. -	Elytral scales distinctly suberect on entire elytral surface, at angle of 45° with cuticle (Fig. 3C). Abdominal ventrite 1 flat, not raised in middle (Fig. 5C)
5.	Appressed scales on dorsum dense, concealing integument; elytral scales imbricate, contiguous or subcontiguous (Fig. 1A). Scale covering of mes- and metanepisterna similar to that on lateral elytral interstriae. Copulatory sclerites of penis shaped like a tilted "E" (Fig. 2A)
_	Appressed scales on dorsum sparse, not concealing integument; elytral scales distinctly non-contiguous (Fig. 1B). Scale covering mes- and metanepisterna white and dense, contrasting with glabrous appearance of lateral elytral interstriae (Fig. 3B). Copulatory sclerites of penis sagittate (Fig. 2B)
6.	Forehead narrow, interocular distance smaller than or subequal to width of an eye (Fig. 4E)
_	Forehead wider, interocular distance greater than width of an eye (Fig. 4F)
7.	Forehead narrow, as wide as or slightly narrower than distance between antennal insertions (Fig. 4G–I). Ventral prothoracic scales near eyes (Fig. 8C) not visible, in lateral view not exceeding anterior margin of pronotum
_	Forehead wide, at least slightly wider than distance between antennal insertions, if equally wide (<i>C. homaroides</i> sp. nov.) then copulatory sclerites of penis shaped like a lobster (Fig. 2R). Ventral prothoracic scales near eyes (Fig. 8C) generally visible, in lateral view exceeding anterior margin of pronotum
8.	Metatibiae proximally simply cylindrical, without carina. Eyes large, width greater than length of antennal clubs. Abdominal ventrite 1 medially with erect setae as long as scales on ventrites; surface of ventrite 5 with longitudinal impression at approximately midlength (Fig. 5G). Apices of
_	parameroid lobes with minute setae (Fig. 2G)
9.	Subbasal inner carina of metatibiae forming distinct angle with long axis of metatibia (Fig. 8E, right). Copulatory sclerite of penis consisting of two parts, a longer apical part and a shorter basal part (Fig. 2H)

_	Subbasal inner carina of metatibiae not forming notable angle with long axis of metatibia (Fig. 8E, left). Copulatory sclerites of penis basal, each serrate medially (Fig. 2I)
	9. <i>C. variabilis</i> Haran sp. nov.
10.	Scales on epifrons suberect, visible in lateral view, their apices raised from integument (Fig. 4J–L). Distance between eye and scrobe subequal to or greater than width of antennal club (Fig. 3J–L)
_	Scales on epifrons recumbent, not visible in lateral view, their apices indiscernibly raised from integument (Fig. 4N–W). Distance between eye and scrobe generally smaller than width of antennal club (Fig. 3P)
11.	Abdominal ventrite 1 with a short but high flat longitudinal peg on either side of midline (Fig. 5J). Parameroid lobes rounded at apex, bearing a single long, erect seta (Fig. 2J)
_	Abdominal ventrite 1 medially flat to slightly concave, lacking peg (Fig. 5K–L). Parameroid lobes bluntly truncate or rounded at apex, bearing multiple erect setae (Fig. 2K–L)
12.	Forehead wide, interocular distance significantly greater than width of an eye (Fig. 4K). Median impression of abdominal ventrite 1 concealed by scales similar to those on rest of ventrites (Fig. 5K). Metatibiae with apical mucro, apical half with inner fringe of setae as long as those on protibiae. Parameroid lobes with apical setae shorter than length of lobes (Fig. 2K)
_	Forehead narrower, interocular distance subequal to width of an eye (Fig. 4L). Median impression of abdominal ventrite 1 concealed by plumose scales different from those on rest of ventrites (Fig. 5L). Metatibiae without mucro, apical half with inner fringe of setae twice as long as those on protibiae. Parameroid lobes with apical setae almost as long as lobes (Fig. 2L) 12. <i>C. pilipes</i> Haran sp. nov.
13. -	Apex of protibiae expanded on inside near mucro, sometimes bearing teeth (Fig. 8I)
14.	Erect setae medially on ventrite 1 simple, not bifid at their apices (Fig. 5M). Copulatory sclerites of penis in form of small bars (Fig. 2M)
15. _	Copulatory sclerites of penis elongate and sickle-shaped (Fig. 2N). Funicles with segment 2 as long as 1
	shorter than 1
16.	Funicles with segment 2 with a distinct inner tooth directed anteriad (Fig. 8H), segment apically distinctly wider than apical width of segment 1
- 17.	Abdominal ventrite 1 medially with intermingled recumbent scales and erect setae, integument more
_	or less concealed by scales (Fig. 5Q–S)

19. Body short, stocky; elytra isodiametric (W:L ratio 1) (Fig. 1R). Parameroid lobes apically with two brushes of elongate setae; copulatory sclerites of penis together shaped like a lobster (Fig. 2R) Body elongate; elytra longer than wide (W:L ratio 0.8) (Fig. 1S). Parameroid lobes apically with erect setae, the median ones longest; copulatory sclerites of penis weakly sclerotised, consisting of 20. Pronotum with small cuticular depression on either side of midline. Body slender, pronotum and elytra moderately imbricate (W:L ratio of body < 0.55) (Fig. 1T)20. *C. endroedyi* Haran sp. nov. Pronotal surface regular, without cuticular depressions. Pronotum and elytra tightly fitting onto 21. Forehead as wide as width of an eye (Fig. 4U). Forehead and epifrons with sparse cover of scales, on epifrons mostly not contiguous, at centre of forehead leaving a bare area (Fig. 4U) Forehead 1.2–1.4× as wide as width of an eye (Fig. 4V–W). Epifrons medially with overlapping 22. Abdominal ventrite 2 with at least 20% of the erect setae bifid from base or from midlength (Fig. 5V). Parameroid lobes with apical setae shorter than incision between lobes (Fig. 2V); body of penis Abdominal ventrite 2 with erect setae either not bifid or bifid only apically (Fig. 5W). Parameroid lobes with apical setae longer than incision between lobes (Fig. 2W); body of penis with sides sinuate, gradually converging from midlength to apex (Fig. 2W) 23. *C. luteipennis* Haran sp. nov.

24. Undescribed species of Cryptolarynx Van Schalkwyk, 1966 left in abeyance

Among the specimens of *Cryptolarynx* recently collected or located in museums, six additional putative undescribed species were found, as based on morphological differences and/or genetic distance. These species are not described here as they were only represented by female specimens or because longer series are needed to identify reliable morphological features to distinguish them from similar species. To facilitate future research on this genus, the label data of these specimens, their depositories are reported here and links to their DNA sequences data in Appendix 2.

Cryptolarynx sp. 1

REPUBLIC OF SOUTH AFRICA – **Western Cape** • 2 \circlearrowleft ; Cederberg Mountains, Gecko Creek Wilderness Lodge, campsite; 32.396° S, 18.987° E; 22 Aug. 2018; J. Haran leg.; near stands of *Oxalis obtusa*; JHAR01387; CBGP.

Cryptolarynx sp. 2

REPUBLIC OF SOUTH AFRICA – **Western Cape** • 3 \(\text{?} \); Swellendam 36 km E, Honeywood Farm; 34.007° S, 20.826° E; 24 Aug. 2018; J. Haran leg.; at base of *Oxalis* cf. *purpurea*; JHAR01435; CBGP.

Cryptolarynx sp. 3

REPUBLIC OF SOUTH AFRICA – **Northern Cape** • 1 \circlearrowleft , 1 \circlearrowleft ; Nieuwoudtville; 31.389° S, 19.135° E; 20 Aug. 2019; J. Haran leg.; in stands of *Oxalis obtusa*; JHAR03268; CBGP.

Cryptolarynx sp. 4

REPUBLIC OF SOUTH AFRICA – **Northern Cape** • 1 \circlearrowleft ; Calvinia 16 km N, Groot Toren Farm; 31.333° S, 19.733° E; 14 Sep. 1994; S. Endrödy-Younga & C.L. Bellamy leg.; "ground and vegetation"; bushy vegetation, sandy/stony soil; E-Y:3003; TMSA.

Cryptolarynx sp. 5

REPUBLIC OF SOUTH AFRICA – **Western Cape** • 1 \circlearrowleft , 1 \circlearrowleft ; West Coast National Park, Postberg Section; 33.105° S, 18.003° E; 31 Aug. 2019; J. Haran leg.; at base of *Oxalis obtusa*; JHAR03236; CBGP. *EF1* with 0.7% divergence from *C. spinicornis* sp. nov. (JHAR02465).

Cryptolarynx sp. 6 (near C. hirtulus sp. nov.)

REPUBLIC OF SOUTH AFRICA – **Northern Cape •** 1 \circlearrowleft , 1 \circlearrowleft ; Calvinia N, Hantamsberg; 31.352° S, 19.803 °E; elevation 1544 m; 9 Nov. 2018; R. Borovec leg.; FFWS.

Genus *Hadrocryptolarynx* Haran gen. nov. urn:lsid:zoobank.org:act:1983869F-4CDD-43AD-A2B0-CAEC1CED873B

Type species

Hadrocryptolarynx major Haran gen. et sp. nov., by present designation.

Differential diagnosis

Among the specimens of, or similar to, Cryptolarynx available for study, a series was found that differ from all species of Cryptolarynx in having a larger body size (length ca 6.0 mm; only ca 4.5 mm in the largest Cryptolarynx), a more elongate shape in the male (more or less globular in Cryptolarynx), elongate metatarsi with segment 2 at least $1.5 \times$ as long as wide (shorter in Cryptolarynx) and apically fused and glabrous parameroid lobes of the aedeagus (divided and setiferous in Cryptolarynx). As already suggested by Oberprieler (2014), these differences are deemed significant to assign these specimens to a different genus.

Etymology

This genus is named in reference to the remarkably larger size and bulk of its type species compared to that of species of *Cryptolarynx*. The name is a noun in the nominative singular case and its gender is masculine.

Description (\circlearrowleft)

MEASUREMENTS. Medium-sized, body length 2.0–6.0 mm. Body shape elongate in dorsal view, elytra and pronotum subequal in width. Pronotum widest at or slightly anteriorly of midlength; base narrower than elytra at humeri. Elytra widest near midlength. Body in lateral view (Fig. 3X) slightly hunched, highest just behind elytral base to middle of elytral length; head almost hypognathous.

COLOUR AND VESTITURE. Body integument black; antennae, tibiae and tarsi generally reddish. Dorsal vestiture (pronotum + elytra) consisting of short, recumbent clothing scales $2-5 \times$ as long as wide, not aligned on interstriae, more or less concealing integument, colour ranging through black, dark brown to

pale brown and grey to white; darker scales usually concentrated medially on pronotum and from there in broad median stripe along elytral interstriae 1–3; paler scales concentrated on a spot near middle of elytral interstriae 1–4.

HEAD. Head capsule globose, in repose deeply retracted into prothorax, leaving only vertex and eyes visible in dorsal view. Eyes subcircular or slightly oval, convex, situated sublaterally, surrounded by a ring of pale recumbent scales. Forehead flat, slightly narrower than width of an eye; median fovea absent. Rostrum very short and broad, not differentiated from head, dorsal surface perpendicular to longitudinal axis of prothorax when head in repose. Epifrons flat, as wide as forehead, epifrontal scales subcrect and orientated laterad, towards scrobes. Mandibles beak-like, densely setose (ca 20 setae each), with a pair of longer erect setae arising medio-laterally. Maxillae with galea and lacinia separate, both bearing apical setae (Fig. 8Q). Antennae inserted subdorsally at approximately middle of rostrum; scapes slender, as long as width of epifrons between antennal insertions, regularly and moderately curved, apically clavate and bearing erect setae, in repose folding into narrow scrobes extending onto underside of rostrum; funicles 7-segmented, longer than scapes, segment 1 elongate, funicles entirely hidden between head and cuticular anteroventral expansion of prothorax when head in repose; clubs 4-segmented, fusiform, acuminate, shorter than funicles.

THORAX. Pronotum moderately transverse; integument densely punctate, narrow spaces between punctures dull; anterior margin bisinuate, posterior margin arcuate, fitting closely to elytral bases up to level of humeri. Prothorax anteriorly on each side produced into a large sharp-rimmed ventrolateral lamina extending from lower level of eye down to anterior edge of procoxa, concealing anterior prothoracic margin beneath it, rim of lamina asetose but anterior margin fringed with row of dense plumose scales, longer below eyes but shorter ventrally along prosternum. Prosternum broad, short, depressed below anterior edge of procoxae, declivous, abutting rostrum when head in repose; procoxal cavities medially confluent, hypomeral lobes behind them short, suture of median junction obscure. Mesoventrite deeply depressed, almost vertically declivous, intermesocoxal process subtuberculate; mesepimera broadly separating mesanepisterna from elytral margin. Metaventrite between metacoxae as wide as metatarsus; metanepisterna fully fused to metaventrite, metanepisternal suture completely obliterated.

Scutellar shield very small, indistinct.

ELYTRA. Broadly ovate, longer than wide; jointly rounded at apex; elytral base broadly concave, not marginate; integument flat, shiny, 10-striate but striae indiscernible on outer surface, mixed with regular punctures.

METATHORACIC WINGS. Absent.

Legs. Slender. Procoxae subcontiguous, distance between mesocoxae equal to width of segment 5 of mesotarsus. Trochanters with single long erect seta. Femora subcylindrical, unarmed; metafemora not reaching elytral apex. Tibiae cylindrical, inner margin entire, without teeth; apex without spurs but with small stout mucro; pro- and mesotibiae curved in distal half, narrowing from base to apex; metatibiae slightly curved laterally, without corbels. Tarsi flattened; protarsi short, segments 1 and 2 isodiametric; metatarsi slender, segment 1 2 × as long as wide, as long as 2, 3 deeply bilobate, shorter than 2, 5 clavate, longer than 3; claws paired, free, divaricate, simple with long stiff ventrobasal seta.

ABDOMEN. Ventrites 1–4 medially flat, ventrite 5 slightly convex; ventrite 1 medially about twice as long as laterally, as long as ventrites 2–3 combined, intercoxal process ogival, apically acuminate.

MALE TERMINALIA. Penis elongate. Tectum narrow but distinct; endophallus with copulatory sclerite divided into 2 symmetrical, elongate structures. Parameroid lobes of dorsal plate of tegmen fused and jointly evenly rounded at apex, devoid of setae. Spiculum gastrale asymmetrical; divergence of basal arms V-shaped.

Female Terminalia. Gonocoxites (Fig. 8N) elongate, narrowly triangular, narrowed apicad and rounded apically, with only a few setae; styli inserted apicolaterally, $2 \times$ as long as wide, bases distinctly separate, apices with 5–6 long setae, setal length subequal to that of styli. Sternite VIII (Fig. 8O) with basal arms symmetrical, $0.67 \times$ length of apodeme, merged at apex. Spermatheca (Fig. 8P) stocky, cornu wide and curved, nodulus rounded, collum and ramus not differentiated.

Sexual dimorphism

The sexes can be distinguished by the shape of ventrite 1 (convex in male, concave in female), and by the shape of the elytra (more elongate in male).

Remarks

The genus *Hadrocryptolarynx* gen. nov. is presently monotypic.

Key to the genera of Cryptolaryngini Van Schalkwyk, 1966

asymmetrical (Fig. 2). Southern Africa

25. *Hadrocryptolarynx major* Haran gen. et sp. nov. urn:lsid:zoobank.org:act:55B2B09A-2A4F-4D0D-996F-8E93E874C0E9 Figs 1X, 2X, 3X, 4X, 5X, 7M–P, 8F

Differential diagnosis

Hadrocryptolarynx major gen. et sp. nov. is at present the only species in its genus. See diagnostic characters in key to genera for differential diagnosis with species of *Cryptolarynx*.

Etymology

The species name *major* refers to the large body size of some specimens of the species, seemingly the largest among the Cryptolaryngini. The specific epithet is an adjective in the masculine form.

Material examined

Holotype

REPUBLIC OF SOUTH AFRICA • & "REPUBLIC OF SOUTH AFRICA. Western Cape Province, Klawer [13 km S]. 26.vii.2019. J. Haran leg." "31.902° S 18.630° E. at base of *Oxalis luteola*. JHAR02464_0101. Cirad-CBGP coll." "Holotype. *Hadrocryptolarynx major*. Haran 2023"; SAMC.

Paratypes

REPUBLIC OF SOUTH AFRICA – **Western Cape** • 1 \circlearrowleft , 1 \circlearrowleft ; same collection data as for holotype; CBGP • 1 \circlearrowleft , 1 \circlearrowleft ; same collection data as for holotype; NHMUK • 1 \circlearrowleft ; same collection data as for holotype; MNHN • 4 specs (preserved in ethanol); same collection data as for holotype; CBGP • 10 specs; Klawer 13 km S; 31.902° S, 18.630° E; 26 Jul. 2019; J. Haran leg.; at base of *Oxalis luteola*; JHAR02486; CBGP • 1 \circlearrowleft , 2 specs; Velddrif, 32.722° S, 18.194° E; 27 Jul. 2019; J. Haran leg.; near stands of *Oxalis pes-caprae*; JHAR02482; CBGP • 1 \circlearrowleft , 1 \hookrightarrow ; Worcester; 33.650° S, 19.417° E; 23 Sep. 1973; L. Schulze leg.; collected from flowers in Karoo garden; E-Y:148; TMSA • 1 \hookrightarrow ; 10 km WSW of Uitvlugt, Zandkraal Farm; 31.700° S, 18.767° E; 12 Sep. 1987; S. Endrödy-Younga leg.; dry coarse-sandy flat; E-Y:2490; TMSA • 2 \circlearrowleft \circlearrowleft 1 \hookrightarrow ; 5 km S of Vanrhynsdorp; 31.600° S, 18.733° E; 26 Sep. 1973; L. Schulze leg.; collected from Aizoaceae flowers; E-Y:162; TMSA • 1 \circlearrowleft ; Vanrhynsdorp S, Farm Wiedouw 309; 31.733° S, 18.783° E; 20–23 Sep. 1982; S. Louw leg.; NMBH 89711; SANC • 1 \hookrightarrow ; Namaqualand, Koekenaap dunes; 31.533° S, 18.233° E; 23 Sep. 1994; S. Endrödy-Younga and C.L. Bellamy leg.; pitfall traps 3 days; red sand dunes with patchy dense bushy vegetation; E-Y:3032; TMSA.

Description (♂)

Measurements. Body elongate, length 2.0–6.0 mm.

COLOUR AND VESTITURE. Body integument black, antennae, tibiae and tarsi reddish. Dorsal vestiture (pronotum + elytra) consisting of overlapping, recumbent, parallel-sided or bilaterally convex clothing scales, each 2–5 × as long as wide, truncate at apex, not aligned on interstriae, concealing integument. Colour of scales black, dark brown to pale brown, grey or white; darker scales usually concentrated medially over pronotum and on elytral interstriae 1–3; paler scales concentrated laterally and on pronotum and elytra, usually forming a transverse spot near middle of interstriae 1–3. Scales arising from strial punctures not different from those of rest of vestiture.

HEAD. Forehead slightly wider than epifrons near antennal insertions, scales recumbent. Eyes convex, in dorsal view distinctly exceeding outline of head, surrounded by a ring of short scales, on forehead directed towards occiput; distance between eye and scrobe less than width of an eye. Epifrons flat, as wide as forehead, epifrontal scales suberect and orientated laterad, towards scrobes, overlapping. Frons with 3 pairs of long erect lateral setae. Epistome without median seta. Antennae with funicle segment 1 longer than wide, as long as 2 and 3 combined, 2–4 subcylindrical, slightly angular on inside, 5–7 globular or moderately elongate.

THORAX. Pronotum moderately transverse (W:L ratio 1.15), widest near midlength, sides arcuate; apex and base subequal in width; integument densely punctate, spaces between punctures narrow, dull, surface regularly convex.

ELYTRA. Broadly ovate (W:L ratio 0.76), sides arcuate, widest near midlength.

Legs. Slender. Tibiae with apical mucro, inner margin bisinuate; protibiae curved in apical half; mesotibiae curved in apical third; metatibiae straight. Protarsi with segments 1 and 2 isodiametric; meso and metatarsi with segments 1 and 2 $2 \times$ as long as wide.

ABDOMEN. Ventrites 1–4 with pale, recumbent, plumose scales intermixed with white suberect setae; ventrite 5 with a few scales near base, elsewhere setose only; ventrites 1–2 slightly concave medially, 5 convex medially.

TERMINALIA. Body of penis elongate (W:L ratio 0.3), as long as temones, acuminate at apex, in profile downcurved in apical third. Tectum narrow but distinct; endophallus with copulatory sclerite divided

into two symmetrical, elongate structures. Parameroid lobes of dorsal plate of tegmen fused and jointly evenly rounded at apex, devoid of seta. Spiculum gastrale asymmetrical; divergence of basal arms V-shaped.

Sexual dimorphism

The sexes can be distinguished by the shape of the elytra (elongate and widest near midlength in male, shorter and widest at base in female) and by ventrites 1–2 (concave in male, convex in female), and half of females examined bear a series of long, suberect setae on interstriae 1–3–5–7.

Life history

Adults of *Hadrocryptolarynx major* gen. et sp. nov. were at several localities found in dense stands of *Oxalis luteola*, most specimens collected from the base of the plants. As in *Cryptolarynx*, some specimens were observed to form small holes in the soil, below the leaves of various surrounding plants (Fig. 70). The weevils are active during the day on open fields but may also climb onto vegetation. Adults were collected between July and September.

Distribution

Hadrocryptolarynx major gen. et sp. nov. was mostly collected in the northwestern regions of the Western Cape province, from Koekenaap to Velddrif and inland to Vanrhynsdorp and Worcester (Fig. 13).

Remarks

Specimens of *Hadrocryptolarynx major* gen. et sp. nov. were collected in sympatry with those of *C. spinicornis* sp. nov. Amplification of the standard mitochondrial barcode fragment failed repeatedly for this species, and the fragments of the only two specimens that successfully amplified (JHAR02464_0101 and JHAR02486_0101) yielded five regions with large nucleotide deletions. By contrast, all remaining nucleotides aligned well with those of the various species of *Cryptolarynx* sequenced and showed no traces of stop codons. This fragment is probably of pseudogene origin caused by a mismatch between the primers and the actual mitochondrial copy of the *COI* fragment.

Morphology of immature stages

Cryptolarynx variabilis Haran sp. nov.

Material examined

Eggs

REPUBLIC OF SOUTH AFRICA – **Western Cape •** 2 specs (preserved in ethanol); Stellenbosch; 33.949° S, 18.876° E; 20 Jul. 2018; J. Haran leg.; eggs deposited by reared adults collected on *Oxalis pes-caprae*; JHAR01185; CBGP. Determined by association with adults.

Larvae

REPUBLIC OF SOUTH AFRICA – **Western Cape •** 2 specs in second and third instar; Stellenbosch; 33.949° S, 18.876° E; 20 Jul. 2018; J. Haran leg.; in bulbs of *Oxalis pes-caprae*; JHAR01185; (larvae initially preserved in ethanol; then dissected and slide-mounted in Euparal (as in May 1993) for examination under compound microscope) MLPA (preserved in ethanol) • 1 spec. of undetermined instar; same collection data as for preceding; CBGP • 1 spec. in last instar (larva initially preserved in ethanol; then dissected and slide-mounted in Euparal (as in May 1993) for examination under compound microscope); Stellenbosch, Jan Marais Nature Reserve; 33.930° S, 18.875° E; 13 Sep. 2018; J. Haran leg.; in bulb of *Oxalis purpurea*; JHAR01497; MLP. Determined by association with adults.

Pupa

REPUBLIC OF SOUTH AFRICA – **Western Cape •** 1 spec. (preserved in ethanol); Stellenbosch; 33.942° S, 18.873° E; 9 Aug. 2018; J. Haran leg.; in bulb of *Oxalis lanata*; JHAR01247; CBGP. Determined by association with adults.

Descriptions

Egg

Length 0.8–1.0 mm; width 0.2–0.3 mm, widest near midlength. Slightly curved. Yellow.

Larva (Figs 9A-B, 10A-I)

Measurements. Maximum body length 4.62 mm; head width 0.55 mm.

HABITUS. Body very robust, curved, widest at thorax and anterior abdominal segments; setae pallid and inconspicuous, the longer setae slender, fine; cuticle with minute asperities; posterior third of head capsule in repose partially retracted into pronotum.

HEAD. Subcircular in outline, about as long as wide; posterior margin rounded, not emarginate. Epicranial line short, about $0.3 \times length$ of head capsule. Frontal lines and endocarina absent. Hypopharyngeal bracon hyaline, without maculae. Postoccipital margin simple, without condyles. Cranial setae well developed, in modal numbers: fs3, 4, 5 long, fs1, 2 shorter, fs3 placed outward of fs4 and behind fs5, des1, 2, 3, 4, 5, well developed, des4 shorter, pes1-4 minute; epicranial sensillum present, close to des2 and pes4; les1, 2 long; vcs1, 2 long.

Stemmata. Present as two pigmented dark spots, anterior stemma larger than posterior one.

Antennae. Situated on dorso-anterior margin of head; membranous basal segment bearing sensorium and eight smaller sensilla externally; sensorium broadly conical, about isodiametric or slightly longer than wide, circular in apical view.

CLYPEUS. Pigmented at base; *cls1*, 2 well developed; sensillum closer to *cls1*.

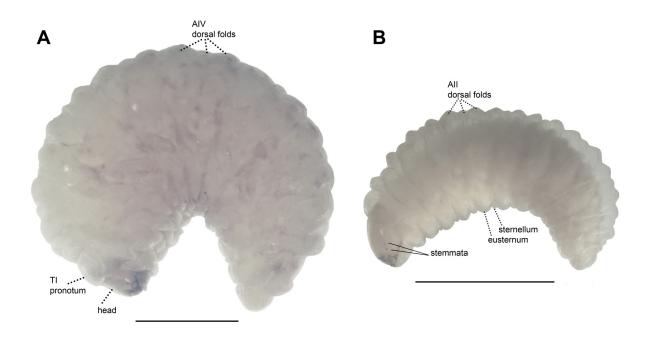


Fig. 9. Habitus of larvae of *Cryptolarynx variabilis* sp. nov., lateral view. **A.** Last-instar larva (TI, pronotum; AIV, fourth abdominal segment). **B.** Early second-instar larva (AII, second abdominal segment). Scale bars = 1.0 mm.

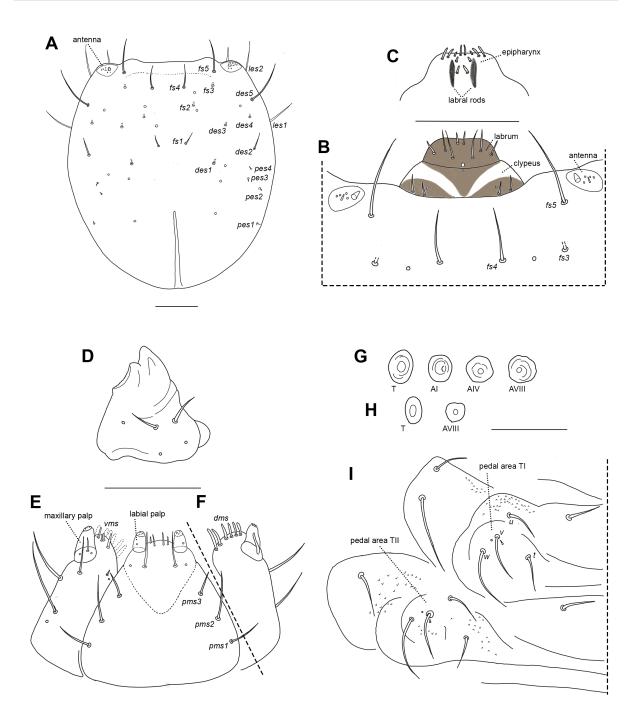


Fig. 10. Larva of *Cryptolarynx variabilis* sp. nov., morphological structures (drawn from second-instar larva, except A and G from last-instar larva). **A.** Head capsule, dorsal view (*fs*, frontal setae; *des*, dorsal epicranial setae; *pes*, posterior epicranial setae; *les*, lateral epicranial setae). **B.** Clypeus and labrum, including a portion of head with antennae. **C.** Epipharynx. **D.** Mandible. **E.** Maxilla and labium, ventral view. **F.** Maxilla, dorsal view. **G.** Spiracles of thorax and abdominal segments I, IV and VIII, last-instar larva. **H.** Spiracles of thorax and abdominal segment VIII, second-instar larva. **I.** Pro- and mesothorax, ventral view (one half), showing pedal areas with setae named in the former. Scale bars = 0.1 mm.

LABRUM. Transverse, completely pigmented, anterior margin evenly rounded; labral setae *lms1* well developed; single basal sensillum present, median (lateral) sensilla absent; labral rods (seen on epipharyngeal side) subparallel, rather short, acute at apices.

EPIPHARYNX. With three *als*; *ams1* conspicuous; *mes1*, 2 between labral rods, *mes1* pair slightly less apart than *mes2* pair.

Mandibles. Bidentate at apex, with obtuse tooth on cutting edge; transversely rugose on exterior lateral surface; *mds1*, *2* aligned transversely.

MAXILLAE. Each stipe with 1 seta at base, 2 palpiferal setae and 1 minute seta plus sensillum near base of mala; maxillary malae with 4 *vms*, median 2 smaller, and with 6 elongated *dms* in a row; maxillary palps 2-segmented, 1 seta on basal segment, none on distal segment.

LABIUM. Postmentum with *pms1* pair more widely apart than *pms2*, 3 pairs; premental sclerite hardly distinct, its posterior extension subtriangular, posterior margin V-shaped, anterior extension indistinct; labial palps 1-segmented; ligula wide.

THORAX. Spiracles placed on pronothorax, oval, annular, without airtubes. Pronotum pigmented, not divided by median line, with 9 setae. Meso- and metathorax with 1 prs and 4 pds. Pedal area with 4 clearly distinct setae (t, u, v and w); the longest (v and w) placed on a lobe slightly distinct in the pedal area; some minute additional setae present (e.g., v').

ABDOMEN. Spiracles of AI–VIII placed laterally, of similar size as thoracic spiracle, subcircular, without airtubes. Segments AI–VII with 3 dorsal folds, prodorsum and postdorsum both similarly prominent. AVIII with prodorsum and postdorsum distinct. AIX with dorsum somewhat expanded over AX (in mature larva). AX with anus subterminal; lateral anal lobes and dorsal anal lobe larger than ventral anal lobe.

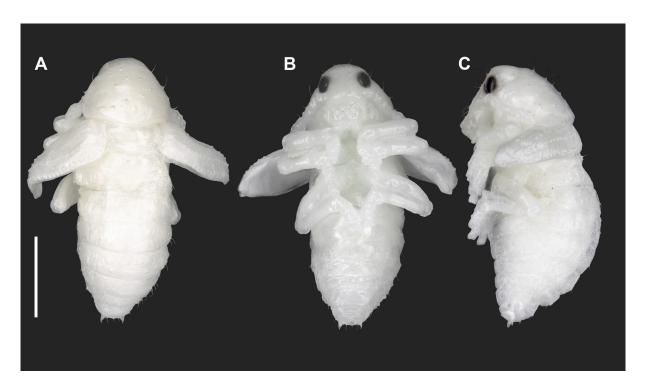


Fig. 11. Habitus of pupa of *Cryptolarynx variabilis* sp. nov., dorsal (\mathbf{A}), ventral (\mathbf{B}) and lateral (\mathbf{C}) views. Scale bar = 1 mm.

Table 1. List of species and host plant associations of the species of *Cryptolarynx* Van Schalkwyk, 1966 and *Hadrocryptolarynx* Haran gen. nov. * = reared from bulbs of host plant; + = sequences available for at least one population of the species.

Genus	species	Host associations	COI	EF1
Cryptolarynx	armatus sp. nov.	O. obtusa, O. cf. suteroides		+
	carinatus sp. nov.	O. purpurea	+	+
	cederbergensis sp. nov.	O. obtusa	+	+
	endroedyi sp. nov.	_		
	estriatus (Marshall, 1957)	_		
	falciformis sp. nov.	_		
	hirtulus sp. nov.	O. obtusa*	+	+
	homaroides sp. nov.	_		
	luteipennis sp. nov.	Oxalis spp.	+	+
	marshalli sp. nov.	O. imbricata	+	+
	muellerae sp. nov.	_		
	namaquanus sp. nov.	O. obtusa	+	+
	oberlanderi sp. nov.	O. depressa	+	+
	oberprieleri sp. nov.	O. glabra	+	+
	pilipes sp. nov.	_		
	pyrophilus sp. nov.	O. pes-capreae	+	+
	robustus sp. nov.	Oxalis spp.	+	+
	san sp. nov.	O. luteola, O. obtusa, O. cf. hirta	+	+
	spinicerus sp. nov.	O. cf. luteola, O. obtusa, O. cf. odorata		+
	squamulatus sp. nov.	O. obtusa	+	+
	subglaber sp. nov.	O. lanata, O. purpurea, O. tenuifolia	+	+
	variabilis sp. nov.	O. pes-capreae *, O. purpurea*	+	+
	vitis (Marshall, 1957)	O. glabra	+	+
	sp. 1	O. obtusa	+	+
	sp. 2	O. cf. purpurea	+	+
	sp. 3	O. obtusa	+	+
	sp. 4			
	sp. 5	O. obtusa		+
	sp. 6			
Hadrocryptolarynx gen. nov.	major gen. et sp. nov.	O. luteola, O. obtusa, Oxalis spp.		

Remarks

The smaller larva examined (Fig. 9B) may correspond to the second instar (body length 2.40 mm; head width 0.39 mm). It agrees with the last-instar larva in the characters described above (Fig. 10A–I), including the spiracles. Differences between early- and later-instar larvae involve relative dimension of structures, with the head (in relation to body), the antennae and stemmata being relatively larger

in earlier instars, and the pigmentation and level of sclerotisation of body areas tend to increase in successive instars.

Pupa (Fig. 11A–C)

Colour white, cuticle smooth. Setae (given for one side of body) inconspicuous, pallid, placed on small tubercles on head (with 1 vs, 1 sos; rostrum with 2 brs; without setae on mandibular theca) and pronotum (with 2 aps, 3 lps, 2 bps, and 3 dps). Rostrum reaching procoxae. Pronotum 1.3× as wide as long, rounded laterally, tapering anteriorly. Mesonotum 1.5× as long as metanotum. Primary pterothecae (elytral sheaths) well developed, covering hindlegs (when folded onto body, as in Fig. 6L); secondary pterothecae absent (adult without hindwings). Femora without apical setae. Abdominal segments I–IV of subequal width; segments V–VIII tapered gradually towards terminal IX, the latter with posterior processes ("pupal urogomphi") small, pointed at sclerotised apex.

Molecular analyses

DNA-grade specimens were obtained for 18 of the 24 known species of South African Cryptolaryngini. Fragments of the *COI* and *EFI* genes were successfully amplified for, respectively, 16 and 17 species (Table 1). Preliminary PhyML analyses conducted on separate genes showed a consistent arrangement,

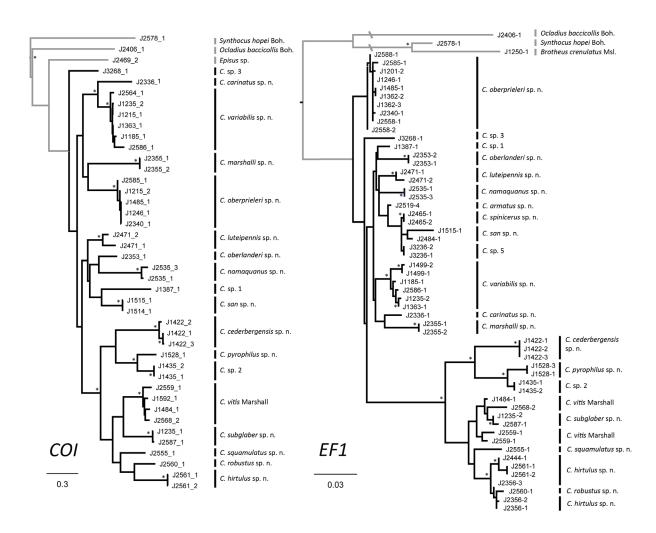


Fig. 12. PhyML gene trees of *COI* and *EF1* gene fragments of species of *Cryptolarynx* Van Schalkwyk, 1966 (1000 bootstrap replicates). *: node support > 80.

with the *C. vitis* group forming a cluster nested with *C. cederbergensis* sp. nov., *C. pyrophilus* sp. nov. and *C.* sp. 2 (bt values: 91% and 84% for *COI* and *EF1*, respectively; Fig. 12). Relationships between other species or species groups were less stable between gene trees. Uncorrected p-distances between closely related species ranged from 10% to 20% for *COI* (Supp. file 1). At intraspecific level, distances ranged up to 10% for this DNA fragment between populations of *C. vitis*. In the *C. vitis* group, several closely related species showed incomplete phylogenetic sorting in their current concept in regard to the *COI* gene (*C. vitis* / *C. subglaber*; *C. hirtulus* / *C. robustus*). Although less densely sampled, relationships between these species were better resolved with *EF1*.

Life history

General life cycle

Weevils of Cryptolarynx and Hadrocryptolarynx gen. nov. are active in the austral winter, with adults encountered between the end of June and the middle of October and a peak of abundance of many species occurring in July and August. However, sporadic records of some species of Cryptolarynx also exist for February (C. vitis). In contrast, adults of Perieges in the Palaearctic Region are active during spring and autumn (April and September). Detailed observations of the life cycle are only available for C. variabilis sp. nov. (a population in Stellenbosch; JHAR01185). The first adults there emerge in late June to early July and start their maturation feeding on aerial parts of surrounding vegetation. They remain mainly on the soil surface at the base of their host plants, becoming active and moving on the ground in open areas only during the hottest hours of the day. Mating was observed in early July, and gravid females with mature eggs were found at the end of July. Oviposition was observed in late September and occurs directly onto the immature and non-sclerified bulbs of Oxalis pes-caprae and O. purpurea when the vegetative parts of the plants may begin to decline. Females reach the bulbs by digging vertical holes in the ground with their mandibles. In clayish soils, holes are distinct on the surface in the vicinity of stems of species of Oxalis. Larvae were observed in Oxalis bulbs from early December to March. Oviposition and early development of the larvae occur in such a way that the tunics of the bulbs are allowed to sclerify before weevil damage starts. As a result, attacked bulbs are intact from the outside and the larvae are sealed inside. Larvae entirely consume the fleshy parts of the bulb, leaving no trace thereof. They do not produce any frass (Fig. 6K). The size of the last larval instar (and then of the resulting adult) depends on the size of the bulb, as also observed for other weevils that develop in limited substrates (de Medeiros et al. 2014). Variation in the size of Oxalis bulbs therefore explains the variability in the sizes of adult males and females of C. variabilis. After reaching the last instar, larvae undertake a period of inactivity during the summer. Pupation takes place inside the bulb around March (Fig. 6L). Mature larvae and freshly emerged adults of C. variabilis (Fig. 6K, M) are often found in the bulbs at this time, but pupae are rare, indicating a very brief pupal stage. Teneral adults of C. variabilis remain in the bulbs until emergence. Emergence takes place via a circular hole made in the basal or lateral parts of the bulbs (Fig. 6I). Adults of C. luteipennis sp. nov. newly emerged from bulbs were collected in late July and those of C. hirtulus sp. nov., C. squamulatus sp. nov. and C. armatus in August, suggesting that different species of Cryptolarynx may have chronologically specific and partly different life cycles.

Host plants

Cryptolarynx and Hadrocryptolarynx gen. nov. are closely associated with species of Oxalis. The weevils track the appearance and growth of their host plants by emerging at the base of the aerial parts early in the growing season in autumn and then being active during and after the flowering season in winter and spring, and they spend the heat and drought of summer as immature stages in the protective environment of the subterranean bulbs of their host plants (Fig. 6I, K–L). Host plant species were established for C. variabilis sp. nov. and C. oberprieleri sp. nov., of which larvae, pupae and teneral adults were found in the bulbs of O. pes-caprae, O. purpurea and O. glabra. For the other species, species of Oxalis

growing in close vicinity were only recorded and specific host associations could not be confirmed. The fact that different species of *Oxalis* often occur in local sympatry makes it difficult to link particular species of *Cryptolarynx* with a specific host plant, especially given that the weevils may still be active when the aerial parts of their *Oxalis* host have already withered away. Adults of *Cryptolarynx* and *Hadrocryptolarynx* appear to be polyphagous, as they have been found feeding on leaves of several plant species in the surrounding vegetation, such as *Vitis vinifera* (*C. vitis*; Marshall 1957), *Moraea* sp. (*C. estriatus*; Oberprieler *et al.* 2007), Poaceae (*C. variabilis*, *C. vitis*; pers. obs. JMH) and *Arctotheca calendula* (*C. pilipes* sp. nov.). They seem, however, to avoid consumption of the foliage of their own *Oxalis* larval host and would eat its leaves only in non-choice lab conditions or when all surrounding vegetation is senescent. The level of damage to *Oxalis* bulbs is variable. In *C. variabilis*, for example, between 5% and 25% of bulbs were attacked in the few sites investigated. The rearing of specimens from bulbs collected in the field did not reveal any natural enemies such as parasitoids, but remains of adults were found in spider webs under stones. Bulbs, including those containing weevil larvae, are also intensively eaten by rodents during summer.

Distribution and habitat

Cryptolarynx and *Hadrocryptolarynx* gen. nov. are so far only known to occur in the Mediterranean-climate and semi-arid regions of the Greater Cape Floristic Region in the Western and Northern Cape provinces of South Africa, with *Cryptolarynx* recorded from Namaqualand in the north to the Swellendam area in the south and inland to the Great Escarpment (Sutherland area) and *Hadrocryptolarynx* from Namaqualand to Vanrhynsdorp and Worcester (Fig. 13).

The habitats of *Cryptolarynx* and *Hadrocryptolarynx* gen. nov. correspond with those of their *Oxalis* hosts. *Cryptolarynx* species occur in Fynbos, Nama Karoo, Renosterveld and Succulent Karoo vegetation types and on various soil types, from clayish to sandy and from very fine to coarse sandstones and on flat habitats from sea level to 1500 m on the Great Escarpment, but they seem to be absent from steep slopes and mountain tops. *Hadrocryptolarynx major* gen. et sp. nov. was recorded mainly in the Succulent Karoo biome, more rarely in the Fynbos biome, and on more or less coarse sandy soils from the seashore to about 60 km inland, always on plains. The species of both genera occur mainly in open habitats but sometimes also under dense forest canopy.

Behaviour

The adults of Cryptolarynx and Hadrocryptolarynx gen. nov. are diurnal, spending the day on the soil surface in the vicinity of their larval host plants (Fig. 7A, E). On open fields they start moving during the warmer hours of the day, occasionally climbing onto vegetation in large numbers for a few hours on hot afternoons. The adults of some species can run very fast on hot sands, possibly to avoid predation or heat (C. san sp. nov.; Fig. 7L). Around sunset they disappear from the soil surface to hide in little holes they form under debris, stones or leaves that effectively conceal the ground, such as those of *Haemanthus* L. (Amaryllidaceae) or *Lachenalia J. Jacq.* (Hyacinthaceae) (*Hadrocryptolarynx major* gen. et sp. nov., Fig. 70). The broad, short and flexible head with its flat eyes and stout mandibles seems to be adapted for digging holes and tunnels into the soil. The weevils are well camouflaged on the ground, their colour and vestiture largely matching the colour and texture of the soil substrate (Fig. 6A-B). When disturbed or threatened, they feign death and retract their head and appendages (Figs 6B, 7A, 7E), as many weevils do. When the danger recedes, they start moving again but with the antennae remaining hidden in the space between head and prosternum (Fig. 8C) and only the clubs protruding below the mouthparts. Seven months after a natural fire near Montagu, a large migration of adults of *C. pyrophilus* sp. nov. (JHAR01528) took place from unburnt vegetation to the burnt areas, where plants of some species of Oxalis (mainly O. pes-caprae) were emerging. Oxalis plants often emerge and flower prolifically in the first or second year after a fire, leading to vigorous growth of the plants, which the weevils appear to be

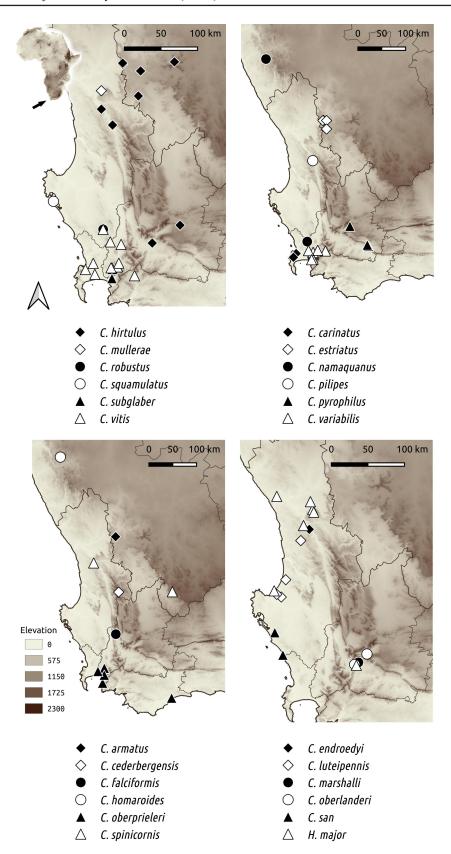


Fig. 13. Distribution maps of species of *Cryptolarynx* Van Schalkwyk, 1966 and *Hadrocryptolarynx* Haran gen. nov.

able to detect from a distance. Species of *Cryptolarynx* show a moderate to high tolerance to heat in the adult stage, when compared to other weevils (Javal *et al.* 2023). As larvae and teneral adults are enclosed in bulbs and cannot move, this tolerance has been proposed to be an adaptation to survive during the summer, when bulbs can be very close to the surface of the ground.

Discussion

Species diversity

This study highlights the large diversity of Cryptolaryngini that exists in the southwestern parts of South Africa. Only two species were known since Marshall's (1957) original description of *Cryptolarynx*. Oberprieler *et al.* (2007), from an assessment of particularly the material collected by S. Endrödy-Younga and colleagues of the former Transvaal Museum in Pretoria during the 1970s and 1980s, estimated the number of species in the genus as 18, including an aberrant species recognised as representing a different genus (Oberprieler 2014) and here described as *Hadrocryptolarynx major* gen. et sp. nov. The discovery of the larval hosts of the South African Cryptolaryngini and focussed surveys of stands of *Oxalis* by the first author of this paper (JMH) during 2018 and 2019 resulted in the recognition of 22 species as here newly described, which brings the number of described species of Cryptolaryngini in South Africa to 24, and another six are left undescribed for the moment. However, the level of endemism in this group and the rate of discoveries of new species over the two years of sampling by JMH suggest that the diversity of this tribe in southern Africa is far from being fully known. *Oxalis* comprises about 200 species in southern Africa, and even if Cryptolaryngini are restricted to the Greater Cape Floristic Region, as appears to be the case, their diversity may be considerably larger and their distribution extend northwards into southern Namibia and eastwards along the southern coast of the Western Cape province.

Cryptolarynx is remarkably homogeneous in habitus, but several stable morphological features of the males (mainly the genitalia and ventrite 1) provide reliable diagnostic characters to distinguish the species. Interspecific genetic distances based on mitochondrial (COI) and nuclear (EF-I) gene fragments were found to be consistent and corroborate the species distinctions derived from morphological characters. For two pairs of species, incongruences were found between morphological and nucleargene species delimitation, suggesting that these species as currently recognised may comprise multiple cryptic genetic lineages. Interspecific distances found between closely related species for COI (10–20%) are high for insects (Hebert et al. 2003) including beetles (Woodcock et al. 2013). At intraspecific level, distances ranged up to 10% for this DNA fragment in the current concepts of the species, suggesting that the commonly applied "barcode-gap" to define species genetically is inapplicable in this group. It is likely that the flightless condition of Cryptolaryngini enhances the intraspecific and probably also the interspecific genetic divergences by geographical isolation and drift of populations and species. It should be noted that Cryptolarynx species in the Cape Town area occur mainly in flat Renosterveld patches that are isolated from each other by unsuitable Fynbos patches. In addition, the frequent cycles of natural fires in this area may strengthen the barrier effect of Fynbos patches for such small and flightless insects.

At most localities, several species of *Cryptolarynx* were found together in stands of multiple *Oxalis* species. This suggests that some species divergence may have occurred in alignment with larval host species. However, at least one species (*C. variabilis* sp. nov.) was found to be able to complete its larval development on two co-occurring species of *Oxalis*, *O. purpurea* and *O. pes-caprae*, and host records suggest that an *Oxalis* species can serve as larval host for several species of *Cryptolarynx*, depending on geographical location. Thus, it is unclear to what extent host plant divergence may have driven speciation in these weevils, but the system represents an interesting model to explore the processes of diversification of phytophagous insects in the Greater Cape Floristic Region. Due to their local diversity, abundance and limited dispersal, the South African Cryptolaryngini also represent potential candidates to estimate the conservation value of Renosterveld patches from an arthropod perspective.

Systematic position of Cryptolaryngini

Due to their pedotectal male genitalia, the Cryptolaryngini phylogenetically fall outside the "higher" Curculionidae (Oberprieler 2014; Shin et al. 2018), i.e., the CEGH and CCCMS clades (Gunter et al. 2016). The "lower" Curculionidae comprise a clade formed by the subfamilies Dryophthorinae Schönherr, 1825 and Platypodinae Shuckard, 1840 and a range of taxa of uncertain relationships to each other (Shin et al. 2018), which retain the plesiomorphic condition of the pedotectal aedeagus and lack the synapomorphies that defines the clade of "higher" Curculionidae. Because of the widely varying and conflicting classifications of these taxa, Oberprieler (2004) combined the tribes with pedotectal aedeagus into a single subfamily Brachycerinae (sensu lato), though acknowledging that this likely constitutes a paraphyletic grade (Oberprieler et al. 2007). Oberprieler (2014) discussed the chequered classification history of these taxa, in particular of the Erirhinini, in greater detail and recognised seven tribes in Brachycerinae: Brachycerini Billberg, 1820, Cryptolaryngini, Erirhinini Schoenherr, 1825, Himasthlophallini Zherikhin, 1991, Tanysphyrini Gistel, 1856, Myrtonymini Kuschel, 1990 and Raymondionymini Reitter, 1913, with Bagoini Thomson, 1859 possibly constituting an eighth. Molecular phylogenetic analyses of weevils undertaken since (Gillett et al. 2014, 2018; Gunter et al. 2016; Mugu et al. 2018; Shin et al. 2018; Baird et al. 2021) affirmed the non-monophyly of Brachycerinae sensu lato, but have not resolved this conundrum mainly because of insufficient taxon sampling, even though several key genera, such as Brachycerus Olivier, 1789, Ocladius Schoenherr, 1825, Echinocnemus Schoenherr, 1843 and Bagous Germar, 1817 have been included in most of them. As a result, and because Cryptolaryngini have never been included in any large-scale molecular phylogenetic analysis, the phylogenetic position and classificatory status of this tribe remain indeterminate. Preliminary results of a study in progress, analyzing the phylogeny of this group using nuclear ribosomal markers and mitochondrial COI, corroborate the placement of Cryptolarynx among the earliest-divergent curculionids and suggest a close relationship with Stenopelmus Schoenherr, 1835 (Marvaldi et al. 2022) itself of uncertain position (Erirhininae, Stenopelmini sensu Alonso-Zarazaga & Lyal (1999); Tanysphyrini sensu Oberprieler 2014).

Resolution of this issue is beyond the scope of the present study, but its assessment of a much larger number of species and especially of the larval and pupal characters of *Cryptolarynx* enables it to make an additional contribution to the debate.

Cryptolarynx was initially considered as unique and unrelated to other weevil groups due to its globular body shape and the head and short rostrum being retractable into a large ventral recession in the prothorax (Marshall 1957) marked by prominent lateral flanges abutting onto the procoxae. Such a short, broad ventral recession also exists in Perieges as well as in some other genera of Brachycerinae s. lat. with a relatively short rostrum, such as Brotheus Stephens, 1829, Byrsops Germar, 1829 and Synthocus Schoenherr, 1842 of Brachycerini, and comparable recessions of the prosternum also occur in numerous brachycerine genera with a longer rostrum, varying from broad and shallow with distinct lateral carinae, as in Raymondionymini, to narrower and deeper and forming a rostral canal that may reach posteriad to between the mesocoxae, as in the Ocladius group of Erirhinini (Oberprieler 2014). The prosternal recession of Cryptolarynx is unusual in that the row of dense setae that brush over the eyes when the head in retracted is not located on the rim of the lateral flanges but much deeper inside, so that the flanges do not represent the anterior prothoracic margin, whereas in other brachycerines with a ventral prothoracic recession (including Perieges) these setae are located on the rim or just inside and usually on a pronounced ocular lobe of the prothoracic margin. A similar condition to that of Cryptolarynx occurs in Bagoinae, however, although the lateral flanges in this taxon do not directly abut onto the procoxae.

With the larger number of South African Cryptolaryngini now known, some differences between *Cryptolarynx* and *Perieges* as reported by Oberprieler (2014) no longer hold: the number of setae on the mandibles ranges from 4 to 8 in *Cryptolarynx* and is ca 20 in *Hadrocryptolarynx* gen. nov. (4

in *Perieges*); ventrite 1 of the male has a concavity and cuticular sculpture only in some species of Cryptolarynx and not in Hadrocryptolarynx (also not in Perieges), the penis body is more variable in Cryptolarynx and can be elongate as in Perieges, the copulatory sclerite is single and complex in some *Cryptolarynx* as it is in *Perieges* (divided into two symmetrical elongate structures in *Hadrocryptolarynx* and several Cryptolarynx species), the longitudinal rows of denticles in the endophallus are lacking in Hadrocryptolarynx and several species of Cryptolarynx, the parameroid lobes are asetose in Hadrocryptolarynx as they are in Perieges, and the number and arrangement of setae on the parameroid lobes in Cryptolarynx are very variable. The following characters remain valid to distinguish the South African Cryptolaryngini from Perieges: tarsi flattened (cylindrical in Perieges), claws with a ventrobasal seta (absent in Perieges), maxillae paucisetose (plurisetose, with dense long setae, in Perieges), spiculum gastrale asymmetrical (symmetrical in Perieges), gonocoxites with normal styli (with extrose apical teeth in *Perieges*). Also the median position of the epistomal setae in *Cryptolarynx* and *Hadrocryptolarynx* (often reduced to a single seta and sometimes absent) appears to be unique to these two genera, as in *Perieges* the epistome bears 1–2 pairs of setae in the normal position (further apart and closer to the anterior margin), as is also the case in all other genera of Brachycerinae that have epistomal setae. The condition of a separate galea and lacinia of the maxillae as present in Cryptolarynx and Perieges also occurs in Hadrocryptolarynx and Stenopelmus (AEM pers. obs.), but whether this indicates a phylogenetic relationship needs further investigations as the condition also occurs in some genera of Entiminae (Thompson 1992; Oberprieler 2014).

The larva of *Cryptolarynx* has morphological features that place the genus firmly in the family Curculionidae sensu lato, the sister group of Brentidae (synapomorphies in Marvaldi *et al.* 2002; Marvaldi unpubl.). These features are: thoracic legs absent, thoracic spiracles placed on prothorax, abdominal segments with 3 folds on dorsum and with sternellum developed (Fig. 9A–B). Three other larval features of *Cryptolarynx* are plesiomorphic in Curculionidae and suggest a relatively basal position of the genus: postoccipital condyles absent (not developed), sensillum present near setae *des2* and *pes4* and labrum with single basal sensillum and without median (lateral) sensilla.

Although the larva of Cryptolarynx seems to have the des3 setae located on the frontal area, instead of on the epicranium, this condition cannot be established with certainty because the frontal lines are obsolete. The des3 setae are positioned in the frontal lines or on the frons in Brachycerinae sensu lato (Oberprieler 2014) as well as in members of the CEGH clade. Also, a vestigial to absent endocarinal line characterises the larvae of *Brachycerus*, *Ocladius*, *Desmidophorus* Dejean and several "erirhinines" (May 1993; Marvaldi 1997, 2000; Morimoto & Kojima 2006). The larva of Cryptolarynx has the frontal setae 5 (fs5) well developed and more so than fs4. A similar condition occurs in the larvae of Stenopelmus and some Erirhinini sensu stricto (e.g., Notaris Germar, 1817), in which fs5 are distinctly stronger than fs4 (which can even be minute). In contrast, in the known larvae of Brachycerus and most other taxa classified in Brachycerinae sensu lato (van Emden 1952; Louw 1990; May 1993; Marvaldi 1997) the strongest setae on the frons are fs4 (with fs5 well developed to minute), as is the case in many Curculionidae. Some other characters, such as mandibles with transverse rugae on the exterior lateral surface, the shape of the labral rods (subparallel, short and acute at apex), the general body form (robust and curved, with prominent prodorsal and postdorsal abdominal folds) and spiracles without airtubes (in mature larvae) occur in the larvae of Cryptolarvnx, Brachycerus and Desmidophorus (van Emden 1952; May 1993; Marvaldi 1997; Morimoto & Kojima 2006; AEM pers. obs.), but these features are also present in several other weevil clades and do not necessarily indicate common ancestry. Besides, the larva of Cryptolarynx does not have the character states deemed to be autapomorphic for Brachycerus (e.g., flat antennal sensorium) and *Desmidophorus* (e.g., mandibles unidentate at apex and with two sulcate cutting edges). The larvae of Cryptolarynx and Stenopelmus are quite different in body shape, in accordance with their particular habits (associated with geophytic and aquatic plants, respectively), but they have similar characters, especially on the head and mouth-parts that may be of phylogenetic significance (Marvaldi et al. in prep). Among these are mandibular setae (mds1 and mds2) transversely placed, maxillary mala with 6 elongated and slightly curved *dms* labial palps 1-segmented (also in some species of *Bagous* and some Tanysphyrini); the proximal pair of postmental setae of labium (*pms1*) more widely apart than *pms2*,3 (also in *Ocladius*). Their pupae also show similarities in general appearance and structure, i.e., the posterior processes being very small and pointed with a sclerotised apex and the abdominal segments lacking setae on the ventrolateral areas.

Regarding life history traits, this study found that *Cryptolarynx* larvae develop endophytically in the bulbs of species of *Oxalis*. This lifestyle resembles that of Brachycerini, whose larvae develop in the bulbs or tubers of geophytes or stems of aloes (e.g., Louw 1990; May 1993; Howden 1995; Germann 2003; Oberprieler 2014). The life history of *Brachycerus* differs from that of *Cryptolarynx* in that the mature larvae leave the bulb and pupate in an earthen cell in the soil (Louw 1990; Germann 2003), but those of *Synthocus* (and perhaps other genera of Byrsopina) seem to pupate inside the bulbs as adults of *S. ornithoglossi* Marshall, 1956 have been found in the bulbs of *Ornithoglossum* (Marshall 1956). The larval hosts of Brachycerini also differ from those of *Cryptolarynx* in being exclusively monocotyledonous plants (Liliopsida) (Oberprieler 2014), phylogenetically unrelated to the eudicotyledonous Oxalidaceae, and the subterranean bulbs of *Oxalis* are only superficially similar storage organs and not homologous with monocot bulbs.

Potential biological control of invasive Oxalis

Several South African species of *Oxalis* have been introduced overseas and become invasive weeds. *Oxalis pes-caprae* is listed among the ten worst invasive species in Europe (Vilà *et al.* 2010) and has an ecological and economic impact on invaded ecosystems (reviewed in McLaughlan *et al.* 2014). Control of weedy species of *Oxalis* is difficult and largely ineffective (Marshall 1987), and only one potential biological control agent has so far been identified, a moth whose larvae feed on the aerial parts of the plants (Kluge & Claassens 1990). We here record the first phytophagous insects feeding on the bulbs of species of *Oxalis* including *O. pes-caprae*, weevils of the genera *Cryptolarynx* and *Hadrocryptolarynx* gen. nov. As the feeding of their larvae results in the destruction of the bulbs of the plants, they have the potential to control the vegetative proliferation, which is the main reproductive means of species of *Oxalis* in invaded areas. Further, available biological data indicate that the larvae of *Cryptolarynx* and *Hadrocryptolarynx* are specialised feeders of *Oxalis* and have no other natural host plants, which makes these weevils potentially suitable candidates for biological control of weedy *Oxalis* species outside of their native ranges. The adult weevils, however, have the potential to feed on various other plants, including grapevine (*Vitis vinifera*) and are consequently regarded as quarantine pests in some countries, e.g., Israel.

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Appendices

Appendix 1. PCR primers and conditions (M13 tails from Ivanova *et al.* (2007) highlighted).

Gene	Primer		Reference
COI	HCO2198	CAGGAAACAGCTATGACTAAACYT CDGGATGBCCAAARAATCA	Folmer <i>et al.</i> (1994), modified by Germain <i>et al.</i> (2013)
		CAGGAAACAGCTATGACTAAACYT	
		CAGGATGACCAAAAAAYCA	
		CAGGAAACAGCTATGACTAAACTT	
		CWGGRTGWCCAAARAATCA	
	LCO1490	TGTAAAACGACGGCCAGTTTTCAA	
		CTAAYCATAARGATATYGG	
		TGTAAAACGACGGCCAGTTTTCAA	
		CWAATCATAAAGATATTGG	
EF1	F2_557F	GAACGTGAACGTGGTATYACSAT	Brady et al. (2006)
	F2_1118R	TTACCTGAAGGGGAAGACGRAG	

Appendix 2 (continued on next page). GenBank accession numbers for the COI and EF1 genes.

Specimen ID	Species	EF1a GB Accession	COI GB Accession
JHAR01250_0101	Brotheus crenulatus	OP882554	OP918978
JHAR01387_0101	Cryptolarynx sp. 1	OP882530	OP919008
JHAR01435_0101	Cryptolarynx sp. 2	OP882520	OP918997
JHAR01435_0102	Cryptolarynx sp. 2	OP882521	OP919007
JHAR03236_0101	Cryptolarynx sp. 5	OP882558	_
JHAR03236_0102	Cryptolarynx sp. 5	OP882559	_
JHAR03268_0101	Cryptolarynx sp. 3	OP882504	OP918986
JHAR02519_0101	Cryptolarynx armatus	OP882553	_
JHAR02519_0104	Cryptolarynx armatus	OP882505	_
JHAR02336_0101	Cryptolarynx carinatus	OP882537	OP919004
JHAR01422_0101	Cryptolarynx cederbergensis	OP882524	OP919009
JHAR01422_0102	Cryptolarynx cederbergensis	OP882522	OP918995
JHAR01422_0103	Cryptolarynx cederbergensis	OP882523	OP918996
JHAR02356_0101	Cryptolarynx hirtulus	OP882511	_
JHAR02356_0102	Cryptolarynx hirtulus	OP882512	_
JHAR02356_0103	Cryptolarynx hirtulus	OP882513	_
JHAR02444_0101	Cryptolarynx hirtulus	OP882517	_
JHAR02561_0101	Cryptolarynx hirtulus	OP882515	OP918984
JHAR02561_0102	Cryptolarynx hirtulus	OP882516	OP918985
JHAR02471_0101	Cryptolarynx luteipennis	OP882525	OP918987
JHAR02471_0102	Cryptolarynx luteipennis	OP882526	OP918988
JHAR02355_0101	Cryptolarynx marshalli	OP882546	OP919017
JHAR02355_0102	Cryptolarynx marshalli	OP882547	OP918989
JHAR02535_0101	Cryptolarynx namaquanus	OP882548	OP918982
JHAR02535_0103	Cryptolarynx namaquanus	OP882549	OP918983
JHAR02353_0101	Cryptolarynx oberlanderi	OP882550	OP919016
JHAR02353_0102	Cryptolarynx oberlanderi	OP882551	_
JHAR03227_0101	Cryptolarynx oberlanderi	OP882557	_
JHAR02558_0101	Cryptolarynx oberprieleri	OP882541	_
JHAR02558_0102	Cryptolarynx oberprieleri	OP882538	_
JHAR01201_0102	Cryptolarynx oberprieleri	OP882542	_
JHAR01246_0101	Cryptolarynx oberprieleri	OP882540	OP919006
JHAR01485_0101	Cryptolarynx oberprieleri	OP882544	OP919011
JHAR02340_0101	Cryptolarynx oberprieleri	OP882543	OP919001
JHAR02585_0101	Cryptolarynx oberprieleri	OP882545	OP918980
JHAR01528_0101	Cryptolarynx pyrophilus	OP882503	OP919015
JHAR01528_0103	Cryptolarynx pyrophilus	OP882519	_
JHAR02560_0101	Cryptolarynx robustus	OP882514	OP918992
JHAR01515_0101	Cryptolarynx san	OP882552	OP919013

Appendix 2 (continued). GenBank accession numbers for the COI and EF1 genes.

Specimen ID	Species	EF1a GB Accession	COI GB Accession
JHAR02484_0101	Cryptolarynx san	OP882529	<u> </u>
JHAR01514_0101	Cryptolarynx san	_	OP919012
JHAR02465_0101	Cryptolarynx spinicornis	OP882527	_
JHAR02465_0102	Cryptolarynx spinicornis	OP882528	_
JHAR02555_0101	Cryptolarynx squamulatus	OP882518	OP918994
JHAR01235_0101	Cryptolarynx subglaber	OP882507	OP918998
JHAR02587_0101	Cryptolarynx subglaber	OP882508	OP918990
JHAR01185_0101	Cryptolarynx variabilis	OP882536	OP919003
JHAR01235_0102	Cryptolarynx variabilis	OP882533	OP918999
JHAR01363_0101	Cryptolarynx variabilis	OP882534	OP919002
JHAR01499_0101	Cryptolarynx variabilis	OP882531	_
JHAR01499_0102	Cryptolarynx variabilis	OP882532	_
JHAR02586_0101	Cryptolarynx variabilis	OP882535	OP918979
JHAR02588_0101	Cryptolarynx variabilis	OP882539	_
JHAR01215_0101	Cryptolarynx variabilis	_	OP919005
JHAR01215_0102	Cryptolarynx variabilis	_	OP919000
JHAR02564_0101	Cryptolarynx variabilis	_	OP918981
JHAR01484_0101	Cryptolarynx vitis	OP882509	OP919010
JHAR02559_0101	Cryptolarynx vitis	OP882506	OP918993
JHAR02568_0102	Cryptolarynx vitis	OP882510	OP918991
JHAR01592_0101	Cryptolarynx vitis	_	OP919014
JHAR02469_0102	Episus sp.	_	OP918976
JHAR02406_0101	Ocladius baccicollis	OP882556	OP918975
JHAR02578_0101	Synthocus hopei	OP882555	OP918977

Supplementary material

Supp. file 1. Uncorrected p-distances between specimens based on COI and EF1. https://doi.org/10.5852/ejt.2023.877.2151.9151