

Two tribes hidden in one genus: the case of *Agaedioxenis* Villeneuve (Diptera: Tachinidae: Exoristinae)

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Received: 18 December 2014 / Accepted: 9 March 2015 / Published online: 3 April 2015
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Abstract The Afrotropical tachinid “genus” *Agaedioxenis* Villeneuve is taken here as an example of the challenges faced by dipterists in classifying one of the most diverse and species rich families of organisms on Earth. Our study has revealed “two tribes hidden in one genus”, with one lineage representing a genus belonging to the tribe Goniini (*Agaedioxenis*) and the other representing a genus belonging to Eryciini (*Eugaedioxenis* gen. nov.). The two genera have been revised through an integrative approach of morphology and genetics (COI barcode sequences). The genus name *Agaedioxenis* replaces that of *Gaedioxenis* Townsend as a valid genus name. *Agaedioxenis* is recognized from five species consisting of two previously described species (*Agaedioxenis setifrons* (Villeneuve) and *Agaedioxenis brevicornis* (Villeneuve) both comb. nov.) and three new species (*Agaedioxenis kirkspriggsi* sp. nov., *Agaedioxenis succulentus* sp. nov., and *Agaedioxenis timidus* sp. nov.). *Agaedioxenis propinqua* (Villeneuve) is recognized as a subjective synonym of *A. brevicornis* (Villeneuve), syn. nov., and by First Reviser action, the latter is chosen as the senior of the

two names. *Eugaedioxenis* gen. nov. is recognized based on two species, *Eugaedioxenis haematodes* (Villeneuve), type species and comb. nov., and *Eugaedioxenis horridus* sp. nov. All new species of both genera are described from South Africa. We further discuss how genetics, morphology, and natural history have contributed to revise the generic circumscription of *Agaedioxenis*, bringing about both the description of *Eugaedioxenis* and the revision of the suprageneric classification for these two taxa.

Keywords Diversity · DNA barcode · Genetic distance · New genus · New species · Parasitoids · Systematics · Taxonomic revision · Afrotropical Region

Introduction

An international effort is currently underway to prepare and publish the first *Manual of Afrotropical Diptera* (Kirk-Spriggs et al., <http://afrotropicalmanual.org/index.html>). A chapter will be devoted to each of the 108 families of flies known from the region, and an illustrated key to the genera of each family will be an integral part of each family's chapter. For parasitic flies of the family Tachinidae, there are several challenges associated with preparing a key to genera. First, there are significantly more genera of Tachinidae in the region than there are genera of any other family of Diptera (229 at last count, O'Hara 2014). Second, the classification of Afrotropical Tachinidae has received little attention since the catalogue and keys of Crosskey (1980, 1984). Third, even the classification of 30 years ago was, for practical reasons, seriously flawed phylogenetically for certain tribes of the Exoristinae (then known as the Goniinae).

Crosskey (1984: 202) was aware that the “externally visible adult morphology in Tachinidae frequently does not correlate very precisely with phyletic grouping”. This was

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particularly evident in the so-called Goniini-Carceliini-Sturmiini-Eryciini complex that Crosskey first discussed in his Australian conspectus (Crosskey 1973). Crosskey was familiar with the studies of the female reproductive system by Herting (1957, 1960) that revealed a lineage within this complex characterized by the production of a derived type of egg (termed “microtype”). He understood that a phylogenetic classification should take this into account, but noted that “it is impossible to adopt such a system as yet for the Australian fauna, in which the reproductive habit of most of the genera remains unstudied” (Crosskey 1973: 77). Crosskey (1973) thus followed a more traditional classificatory scheme that emphasized adult morphology and recognized four tribes in the complex: Carceliini, Eryciini, Goniini, and Sturmiini. Shortly thereafter, Mesnil (1975) formalized the results of Herting’s discoveries of the female reproductive system into a two-tribe system—the Goniini with microtype eggs and the Eryciini with macrotype eggs—but Crosskey (1976) maintained his four tribes for his Oriental conspectus and later for his Afrotropical catalogue and keys (Crosskey 1980, 1984).

An international team was formed in 2012 to investigate the phylogeny of the Tachinidae using morphological and molecular data (Stireman et al. 2013). It is anticipated that this study will result in a well-supported phylogeny that will aid in the development of a world classification of the family to replace the current regional classifications. This study, coinciding as it does with the *Manual of Afrotropical Diptera* project, has brought the Afrotropical Tachinidae under special scrutiny. We are endeavoring to modernize the supra-specific classification for the 1000-odd species, including reassigning the genera of Crosskey’s “Goniini-Carceliini-Sturmiini-Eryciini complex” along phylogenetic lines.

The “genus” *Agaedioxenis* Villeneuve is a prime example of the challenges faced by tachinidologists in classifying tachinids in general and resolving the Goniini-Carceliini-Sturmiini-Eryciini complex in particular. Villeneuve (1937) erected the genus, under the name *Gaedioxis*, for two new species and later (Villeneuve 1939) added two more new species and placed one of them in a new subgenus, *Agaedioxenis*. Crosskey (1980) followed this classification and assigned the genus to the Eryciini. Crosskey (1984) keyed out the species of *Gaedioxis* in two places in his key to Afrotropical eryciines, retaining the four species in one genus but noting that a revision was needed. Our study of *Gaedioxis sensu* Villeneuve and Crosskey has revealed two problems, one nomenclatural and the other phylogenetic. We review the nomenclatural history of the genus name and show that its valid name is *Agaedioxenis* Villeneuve, 1939, stat. nov. We further demonstrate that the “genus” is in reality “two tribes hidden in one genus”, with one lineage representing a genus with microtype eggs and belonging to Goniini (*Agaedioxenis*) and the other representing a genus with macrotype eggs and belonging to Eryciini

(*Eugaedioxenis* gen. nov.). The two genera are revised below, including the description of three new species of *Agaedioxenis*, the reassignment of *Gaedioxis haematodes* Villeneuve to *Eugaedioxenis* (comb. nov.), and the description of one new species of the latter genus.

Materials and methods

Specimens

Male terminalia were dissected and prepared for examination following the methods described by O’Hara (2002). After examination, the terminalia were rehydrated and preserved in glycerol in a plastic microvial pinned below the specimen. Composite focus-stacking images were produced from multiple images captured using a Nikon DS-L1 digital camera (Nikon, Tokyo, Japan) mounted on a Leica MZ12.5 (Leica, Wetzlar, Germany) stereomicroscope (habitus, head, wing, abdomen) or on a Leica DMLS (Leica, Wetzlar, Germany) compound microscope, and processed with CombineZM 1.0 (<http://combinezm.software.informer.com/>). Environmental scanning electron microscope (ESEM) digital images were taken with a Hitachi TM1000 (Hitachi, Tokyo, Japan).

Label data of primary types are given verbatim using the following symbols:

- / End of a line and beginning of the next
- // End of a label and beginning of the next (from top to bottom on the same pin)

Repositories of specimens are given in square brackets using the following acronyms:

BMNH	Natural History Museum [formerly British Museum (Natural History)], London, UK
CNC	Canadian National Collection of Insects, Ottawa, Canada
JOSC	J.O. Stireman collection at Wright State University, Dayton, Ohio, USA
MZUR	Zoological Museum, ‘Sapienza’ University of Rome, Rome, Italy
NMDA	Department of Arthropoda, Natal Museum, Pietermaritzburg, South Africa
NMB	National Museum, Bloemfontein, South Africa

Terminology

Morphological terminology essentially follows McAlpine (1981) with a few exceptions as described and discussed by Cerretti et al. (2014b [see in particular Supplementary File S2]). Sexual patches on the male abdominal tergites of Tachinidae were reviewed and discussed by Cerretti et al.

(2014a). The term “Code” is used for the *International Code of Zoological Nomenclature* published in 1999 by the International Commission on Zoological Nomenclature (hereafter as ICZN 1999).

Genetic analysis

DNA was extracted from ethanol-preserved legs of the holotype (MZUR) and one female paratype (JOSC) of *Agaedioxenis succulentus* and of the holotype of *Eugaedioxenis horridus* (MZUR) that were collected in the Western Cape province of South Africa in 2012 (Table 1). Similarly, DNA was extracted from 10 additional exoristine tachinid taxa previously collected by JOS in the USA (Table 1). Extractions were performed using the Puregene Tissue Kit (Qiagen Inc.), slightly modifying the manufacturer’s protocol. PCR amplifications (30 μ L) of COI mtDNA were composed of 13.35 μ L deionized H₂O, 3 μ L of 10x PCR buffer (TaKaRa), 3 μ L of 10 mM dNTPs, 4.5 μ L of 25 mM MgCl₂, 0.15 μ L of Taq polymerase (ExTaq, TaKaRa), 1.5 μ L of each primer (5 pmol/ μ L), and 1 μ L of DNA solution. The standard “barcode” sequencing primers LepF1 and LepR1 were used to amplify an approximately 700-bp fragment (e.g. Smith et al. 2006). After visualization on an agarose gel, samples were sent to the University of Arizona Genetics Core (uagc.arl.arizona.edu) for PCR product cleanup, quantification, sequencing reactions, and sequencing. In addition, 21 COI sequences of Exoristinae in the CNC were obtained from the *Barcode of Life Data System* (BOLD, www.boldsystems.org) (Ratnasingham and Hebert 2007), and 19 additional sequences were obtained from Genbank (primarily from Smith et al. 2007) (Table 1).

Sequencing output files were assembled and edited using CodonCode Aligner (CodonCode Corp.) and aligned using ClustalW and by eye in MEGA 6.0 (Tamura et al. 2013). A maximum parsimony analysis was conducted using MEGA 6.0 (Tamura et al. 2013), employing the SPR method with 10 initial random addition trees, retaining a maximum of 100 trees, and performing 500 bootstrap replicates. Maximum likelihood (ML) analysis was conducted using RAxML 8.0.24 (Stamatakis 2014) via the CIPRES Science Gateway (<https://www.phylo.org>). A GTRCAT substitutional model was used with threads = 6, Nruns = autoMRE, algorithm = “rapid bootstrap analysis and search for the best tree in one run”, and *Winthemia* sp. as the outgroup. A parallel Bayesian analysis was conducted using MrBayes 3.2.2 (Ronquist and Huelsenbeck 2003) with the following parameters: Nst=6, Rates=Invgamma, Ratepr=variable, all other priors=default, Nruns=2, ngen=100000, samplefreq=100, nchains=4, Burninfrac=0.25, contype=allcompat. Convergence was assessed using Tracer (Rambaut et al. 2014), and, despite wide variance in LnL, approximate stationarity was achieved within the first 25 % of generations. Trees were visualized in FigTree

v.1.4.1 (Rambaut 2014). In addition, we estimated distances (uncorrected and ML) using MEGA 6.0 with variances estimated with 500 bootstraps.

Results

Genetics

Phylogenetic relationships of the tribes Goniini and Eryciini were not well resolved in our parsimony, maximum likelihood or Bayesian analyses of COI sequences, and neither tribe was recovered as monophyletic in any analysis (Figs. 9 and 10). Bootstrap (bp.) and posterior probability (pp.) values were generally low for internal nodes above the level of genus, although erycines and goniines together form a somewhat well-supported clade (88 % pp., 36 % MP bp.), sister to the two blondeline taxa included (100 % pp., 49 % MP bp.).

Regardless of the analysis, representatives of the focal taxa of this study, *A. succulentus* and *E. horridus*, were reconstructed in highly divergent positions. The former taxon was recovered as sister to the goniine genus *Belvosia* Robineau-Desvoidy in all analyses, but support for this relationship was very weak (27 % pp., 13 % ML bp., 10 % MP bp.; the shortest MP tree supported a *Belvosia* (*Gonia* Meigen + *Agaedioxenis*) relationship, but bootstrap support was marginally higher for *Belvosia*+*Agaedioxenis*). *Eugaedioxenis* was recovered in a distant clade, grouping with the eryciine genera *Madremyia* Townsend and *Tsugaea* Hall in both Bayesian and MP analyses, but this relationship was only moderately supported (66 % pp., 41 % bp in the MP consensus tree) and was not recovered in the ML analysis. Still, *Eugaedioxenis* was recovered far from *Agaedioxenis* in the ML analysis (not shown) as sister to an eryciine, the long-branched *Ametadoria* Townsend. Overall genetic distance between *Agaedioxenis* and *Eugaedioxenis* was 11.5 % (raw “p” distance), with ML estimated distances ranging from 12.8 % (uniform rates) to 24.7 % (gamma distributed rates, $\gamma=0.2$). Mean (raw) distance between all (nominal) eryciine and goniine taxa was 10.5 % \pm 0.6 (S.E.), and mean composite ML distances ranged from 11.5 % \pm 0.8 (uniform rates) to 19.2 % \pm 2.2 % (gamma distributed rates).

Morphology

Key to identify *Agaedioxenis* Villeneuve and *Eugaedioxenis* gen. nov. among *Afrotropical* Tachinidae

1. Simultaneously: Parafacial covered with setulae; facial ridge with decumbent setae on lower 1/4–1/2; lower facial margin at least slightly visible in lateral view; ocellar setae well developed and proclinate; lower 1/2 of occiput and postgena covered with a majority of pale, hair-like setulae;

Table 1 Taxa sampled with BOLD and GenBank accession numbers

Taxon	tribe	Region	Collection	voucher ID	BOLD	GenBank
<i>Acantholespesia</i> sp. (Wood02)	Eryciini	Neotropical	CNC	DHJP0019146		GUI141836
<i>Agaeidioxenus succulentus</i> sp. nov.	Goniini	Afrotropical	MZUR	SA007		KP189255
<i>Agaeidioxenus succulentus</i> sp. nov.	Goniini	Afrotropical	JOSC	JASA02		KP189256
<i>Ametadoria</i> sp. (Wood01)	Eryciini	Neotropical	CNC	DHJP0018984		GUI141850
<i>Argyrochaetona</i> sp. nr. <i>cubana</i> Townsend	Eryciini	Neotropical	CNC	DHJP0019704		GUI141905
<i>Argyrophyllax</i> sp. (Wood03)	Goniini	Neotropical	CNC	DHJP0019087		GUI141945
<i>Argyrophyllax</i> sp. (Wood05)	Goniini	Neotropical	CNC	DHJP0018968		GUI142402
<i>Atacta</i> sp. nr. <i>brasiliensis</i> Schiner (DHJ02)	Goniini	Neotropical	CNC	DHJP0019009		GUI141963
<i>Atactosturmia</i> sp. (Wood03)	Goniini	Neotropical	CNC	DHJP0019616		GUI141964
<i>Avibrissosturmia</i> sp. (Wood04)	Winthermiini	Neotropical	CNC	DHJP0019808		GUI141966
<i>Belvosia</i> sp. (Woodley01)	Goniini	Neotropical	CNC	DHJP0015130		GUI140313
<i>Belvosia unifasciata</i> Robineau-Desvoidy	Goniini	Nearctic	JOSC	HMP070706.1		KP189258
<i>Blepharipa</i> sp. nr. <i>fimbriata</i> (DHJ12) Wulp	Goniini	Neotropical	CNC	DHJP00003111		EF180772
<i>Blepharipa tibialis</i> (Chao)	Goniini	Palaearctic	?	NA		EU433559
<i>Blondelia hyphantriae</i> Townsend	Blondeliini	Nearctic	JOSC	HMP807E12.6C		KP189246
<i>Carcelia</i> sp. nr. <i>formosa</i> (Aldrich & Webber)	Eryciini	Nearctic	JOSC	JOS706.3.1		KP189254
<i>Carcelia reclinata</i> (Aldrich & Webber)	Eryciini	Nearctic	CNC	CNC_DIPTERA_104459	CNCDC547-11	KP725265
<i>Chaetogaedia monticola</i> (Bigot)	Goniini	Nearctic	CNC	CNC_DIPTERA_104919	CNCDC1009-11	KP725270
<i>Chaetoglossa picticornis</i> Townsend	Goniini	Nearctic	JOSC	JOS807.1		KP189253
<i>Chrysoxorista dawsoni</i> (Sellers)	Goniini	Nearctic	CNC	CNC_DIPTERA_104088	CNCDC175-11	KP725274
<i>Drieto rhoeo</i> (Walker)	Eryciini	Nearctic	CNC	CNC_DIPTERA_104785	CNCDC875-11	KP725266
<i>Erynnia tortricis</i> (Coquillett)	Eryciini	Nearctic	CNC	CNC_DIPTERA_104008	CNCDC095-11	KP725263
<i>Engaeidioxenus horridus</i> sp. nov.	Eryciini	Afrotropical	MZUR	SA020		KP189257
<i>Eumea</i> sp. (Wood01)	Goniini	Nearctic	CNC	DHJP0019128		GUI142356.1
<i>Eunemorilla longicornis</i> (Reinhard)	Eryciini	Nearctic	CNC	CNC_DIPTERA_104305	CNCDC393-11	KP725272
<i>Frontiniella spectabilis</i> (Aldrich)	Goniini	Nearctic	CNC	CNC_DIPTERA_104748	CNCDC837-11	KP725260
<i>Gaediopsis rubentis</i> (Reinhard)	Goniini	Nearctic	CNC	CNC_DIPTERA_104018	CNCDC105-11	KP725261
<i>Gaediopsis setosa</i> Coquillett	Goniini	Nearctic	JOSC	JOS807.13.16		KP189252
<i>Gonia frontosa</i> Say	Goniini	Nearctic	JOSC	280406.5		KP189247
<i>Gonia pilosa</i> Brooks	Goniini	Nearctic	JOSC	JOS707.1.3		KP189248
<i>Hemisturmia</i> sp. nr. <i>tenuipalpis</i> (DHJ04) (Wulp)	Winthermiini	Neotropical	CNC	DHJP0008009		EF181326.1
<i>Hyphanthrophaga virilis</i> (Aldrich & Webber)	Goniini	Nearctic	CNC	CNC_DIPTERA_104654	CNCDC742-11	KP725255
<i>Leschenaultia bicolor</i> (Macquart)	Goniini	Nearctic	CNC	CNC_DIPTERA_103933	CNCDC020-11	KP725267
<i>Leschenaultia halisidiotae</i> Brooks	Goniini	Nearctic	CNC	CNC_DIPTERA_103939	CNCDC026-11	KP725254
<i>Lespesia aletiae</i> (Riley)	Eryciini	Nearctic	JOSC	GH71708.1		KP189249

Table 1 (continued)

Taxon	tribe	Region	Collection	voucher ID	BOLD	GenBank
<i>Lixophaga</i> sp. (Wood07)	Blondeliini	Neotropical	CNC	DHJP0037275		HQ548232.1
<i>Lydella griseascens</i> Robineau-Desvoidy	Eryciini	Palearctic	CNC	CNC_DIPTERA_104002	CNCDC089-11	KP725262
<i>Lydella radialis</i> (Townsend)	Eryciini	Nearctic	CNC	CNC_DIPTERA_104840	CNCDC930-11	KP725264
<i>Madremyia saundersii</i> (Williston)	Eryciini	Nearctic	JOSC	CA43		KP189250
<i>Myothyrriopsis</i> sp. (Wood02)	Eryciini	Neotropical	CNC	DHJP0019135		GU142661
<i>Nilea dimmocki</i> (Webber)	Eryciini	Nearctic	CNC	CNC_DIPTERA_105107	CNCDC1197-11	KP725258
<i>Patelloa pachyptiga</i> (Aldrich & Webber)	Goniini	Nearctic	CNC	CNC_DIPTERA_104619	CNCDC707-11	KP725256
<i>Patelloa pluriseriata</i> (Aldrich & Webber)	Goniini	Nearctic	CNC	CNC_DIPTERA_104624	CNCDC712-11	KP725273
<i>Patelloa</i> sp.	Goniini	Nearctic	JOSC	OHA29-04-06-039-040		KP189251
<i>Phebellia helvina</i> (Coquillett)	Eryciini	Nearctic	CNC	CNC_DIPTERA_104642	CNCDC730-11	KP725268
<i>Platymya confusiois</i> (Sellers)	Goniini	Nearctic	CNC	CNC_DIPTERA_104872	CNCDC962-11	KP725269
<i>Pseudosturmia</i> sp. (Wood12)	Goniini	Neotropical	CNC	DHJP0019045		GU142687
<i>Siphosturmia</i> sp. nr. <i>raftaei</i> (DHJ06) (Townsend)	Eryciini	Neotropical	CNC	DHJP0006118		EF182557
<i>Spallanzania hebes</i> (Fallén)	Goniini	Holarctic	CNC	CNC_DIPTERA_104878	CNCDC968-11	KP725257
<i>Sturniopsis parasitica</i> (Curran)	Eryciini	Afrotropical	?	453		DQ337202
<i>Tsugaea nox</i> Hall	Eryciini	Nearctic	CNC	CNC_DIPTERA_104643	CNCDC731-11	KP725259
<i>Winthemia</i> sp. nr. <i>tricolor</i> (DHJ02) (Wulp)	Winthemini	Neotropical	CNC	DHJP0008873		EF182567
<i>Zizyphomyia crescentis</i> (Reinhard)	Eryciini	Nearctic	CNC	CNC_DIPTERA_104835	CNCDC925-11	KP725271

prementum long and slender, 0.55–0.80 times as long as height of head; prosternum setose; proepisternal depression bare; the 3, strongest, basal postpronotal setae arranged in a line; 3 presutural acrostichal setae; 3 presutural and 3 or 4 postsutural (i.e., 3+3–4) dorsocentral setae; 1 presutural and 3 postsutural intra-alar setae; 3 postsutural supra-alar setae; first postsutural supra-alar seta longer than notopleural setae; 3–4 katepisternal setae; katepimeron and anepimeron bare; posterior lappet of metathoracic spiracle large, operculum-like; preapical anterodorsal setae of fore tibia at least as long and strong as preapical dorsal seta; mid tibia with 3–5, strong anterodorsal setae; costal spine well developed, at least as long as crossvein r-m; cs_4 about as long as cs_6 ; section of M between r-m and dm-cu longer than section between dm-cu and bend of M; hind tibia with 3–4 dorsal preapical setae2

- Other combination of characters [other Afrotropical Tachinidae]
- 2. Scutum with 3 postsutural dorsocentral setae. Compound eye covered with scattered, long ommatrichia (longest ommatrichia at least as long as three eye facets). Hind tibia with 4 strong dorsal preapical setae. Basicosta yellow. Mid-dorsal depression on abdominal syntergite 1+2 not extended back to hind margin of syntergite. Scutellum without erect preapical setae. Three katepisternal setae. Tibiae yellow. Male: 2 strong proclinate orbital setae (Figs. 1a, c; 2e, g). Female: tergite 5 long, conical, 1.1–1.3 times as long as tergite 4 (Fig. 4a–b); egg macrotype, membranous, fully embryonated *Eugaedioxenis* Cerretti, O'Hara and Stireman, **gen. nov.**
- Scutum with 4 postsutural dorsocentral setae. Compound eye bare. Hind tibia with 3 dorsal preapical setae. Basicosta black or blackish brown. Mid-dorsal depression on abdominal syntergite 1+2 extended back to hind margin of that segment. Scutellum with at least 1 pair of long, erect preapical scutellar setae. Usually 4 katepisternal setae. Tibiae dark. Male: proclinate orbital setae absent (Figs. 2a–d; 3a, c, e, g, i). Female: tergite 5 0.8–0.9 times as long as tergite 4 (Fig. 4c); egg microtype, planoconvex, fully embryonated and brownish black in dorsal view (Fig. 8a–d) *Agaedioxenis* Villeneuve

Tribe Eryciini

Eugaedioxenis Cerretti, O'Hara and Stireman, **gen. nov.**

(Figs. 1a–d; 2e–h; 4a–b, f; 5a–b; 6f; 7a–d)

<http://zoobank.org/urn:lsid:zoobank.org:act:FE7A5AB9-74D6-4627-8696-39D2398432E2>

Type species. *Gaedioxenis haematodes* Villeneuve, 1937, by present designation.

Diagnosis. Medium to large size, strongly bristly, flies characterized by the following combination of character states: Compound eye covered with scattered, long ommatrichia; parafacial covered with fine setulae; facial ridge with decumbent setae on lower 1/4–1/2; lower facial margin at least slightly visible in lateral view; prementum long and slender; 5 postpronotal setae, the 3, strongest, basal setae arranged in a line; scutum with 3 postsutural dorsocentral setae; katepimeron bare; first postsutural supra-alar seta longer than notopleural setae; preapical anterodorsal setae of fore tibia at least as long and strong as preapical dorsal seta; hind tibia with 4 strong preapical setae; basicosta yellow; mid-dorsal depression on abdominal syntergite 1+2 not extended back to hind margin of syntergite; male with 2 strong proclinate orbital setae; female with tergite 5 long, conical, 1.1–1.3 times as long as tergite 4; oviscapt slightly elongated and telescopically retracted within segment 5 (Fig. 7); egg macrotype, membranous, fully embryonated. No remarkable sexual dimorphism has been observed between male and female in head chaetotaxy, frons width, compound eye size or postpedicel length.

Etymology. The generic name is a composite word formed from *eu*, meaning true, and the tachinid genus-group name *Gaedioxenis* Townsend.

Hosts. Unknown.

Distribution. South Africa.

Eugaedioxenis haematodes (Villeneuve, 1937), **comb. nov.** (Figs. 1a–b, 2e–f, 4a, f, 5a–b, 6f)

Gaedioxenis haematodes Villeneuve, 1937: 207. Holotype male (CNC). Type locality: South Africa, Western Cape, between Somerset West and Strand [according to label data; published as “Colonie du Cap” (i.e., former Cape Province)].

Gaedioxenis haematodes: Crosskey (1980: 878), Afrotropical catalogue; Crosskey (1984: 288, 291), in key to genera of tropical and southern Africa.

Type material examined. Holotype ♂: ♂ // Somerset / W. Strand / Dr. Brauns. / Kapland [Cape of Good Hope] // *Gaedioxenis* / *haematodes* / Typ. Villen [label handwritten by Villeneuve] // *Gaedioxenis* / *haematodes* Vill. [handwritten by Mesnil] // L.P. Mesnil det., 1969 // TYPE [red label] // EX / L.-P. MESNIL / COLLECTION 1970 [CNC, in good condition except missing right fore leg]. **Other material examined.** 1♂, “Capland” [South Africa, Western Cape], Stellenbosch, 11.x.1925, Dr. H. Brauns (NMDA). 1♀, same data except xi.1924 (NMDA). 3♂♂, 1♀, [South Africa, Northern Cape], Calvinia District, Brandkop area, 14.x.1964, B. & P. Stuckenberg (NMDA).

Description.

Body length: 8–12 mm.

Male.

Colouration (Figs. 1a–b; 4a–b, f): Head ground colour black except genal groove, face, facial ridge and frontal vitta which are red. Head covered with whitish-grey reflecting microtomentum.

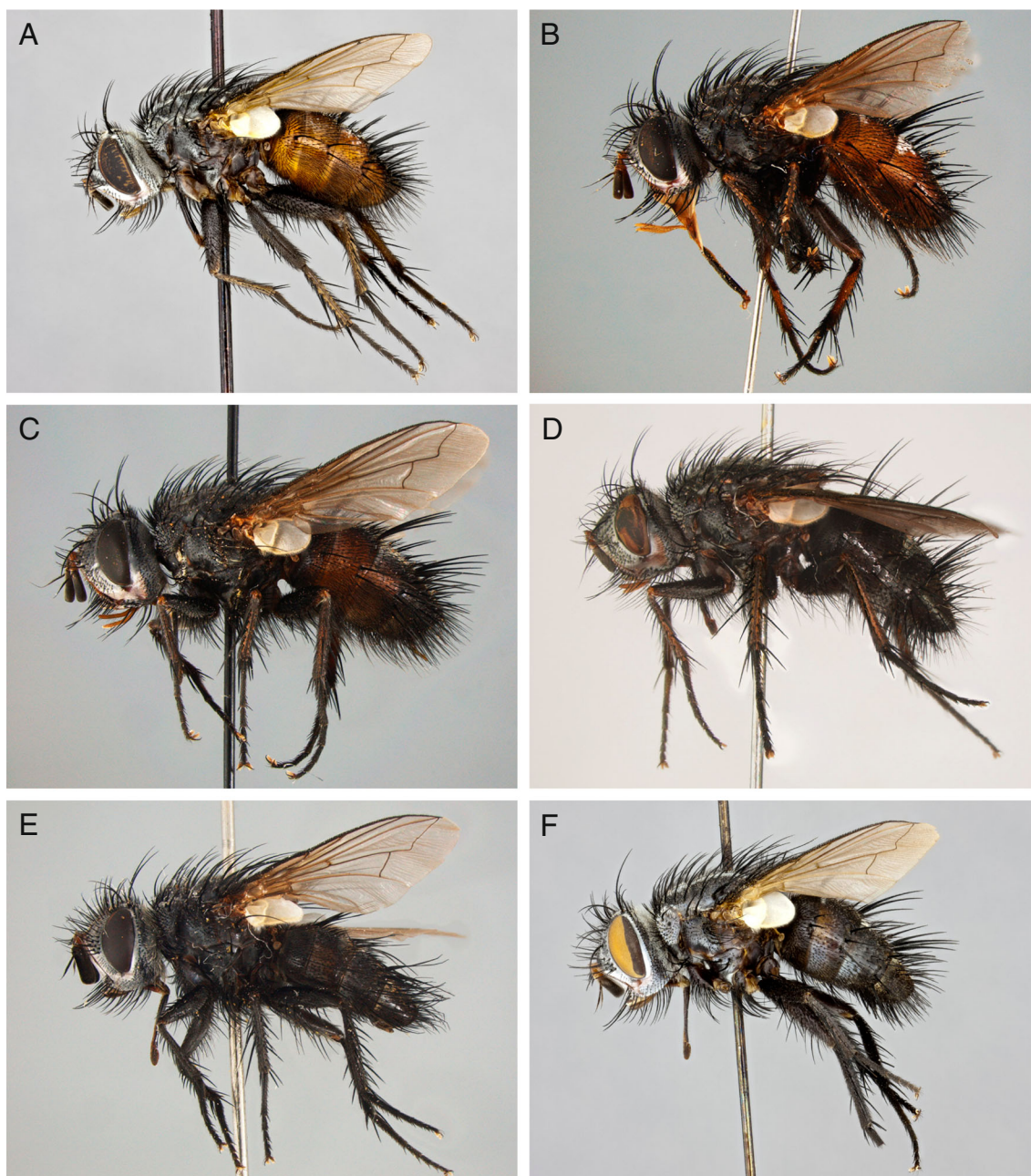


Fig. 1 a–b *Eugaedioxenis* gen. nov. *haematodes* (Villeneuve) habitus in lateral view: a male (holotype); b female. c–d *Eugaedioxenis horridus* gen. et sp. nov. habitus in lateral view: c male (holotype); d female

(paratype). e–f *Agaedioxenis setifrons* (Villeneuve), habitus in lateral view: e male; f female (holotype)

Scape and pedicel reddish yellow; postpedicel and arista black. Palpus yellow. Thorax (except scutellum) black with light grey reflecting microtomentum; scutellum varying from red on apical 2/3 to almost entirely red. Presutural area of scutum with 4, well outlined, dark vittae (lateral pair subtriangular, median pair straight and narrow); postsutural area of scutum, when viewed from behind, with 5 dark vittae, 3 extending length of postsutural area and 2 on anterior portion only and continuous with median pair on presutural area. Femora and tarsi black, tibiae yellow. Tegula black; basicosta yellow. Wing membrane mostly hyaline,

shading into yellowish antero-proximally. Abdomen mostly red with a median longitudinal dark vitta usually extending to tip of tergite 5 (median vitta tapers posteriorly, ending before posterior margin of tergite 5 in two examined specimens). Weak, grey reflecting micromentum present dorsally from syntergite 1+2 to tergite 5, without forming a distinct basal band.

Head (Figs. 1a; 2e): Compound eye covered with scattered ommatrichia, irregular in length (longest ommatrichia are at most as long as 4 eye facets). Frons 1.3–1.4 times as wide as compound eye in dorsal view. Inner and outer vertical setae

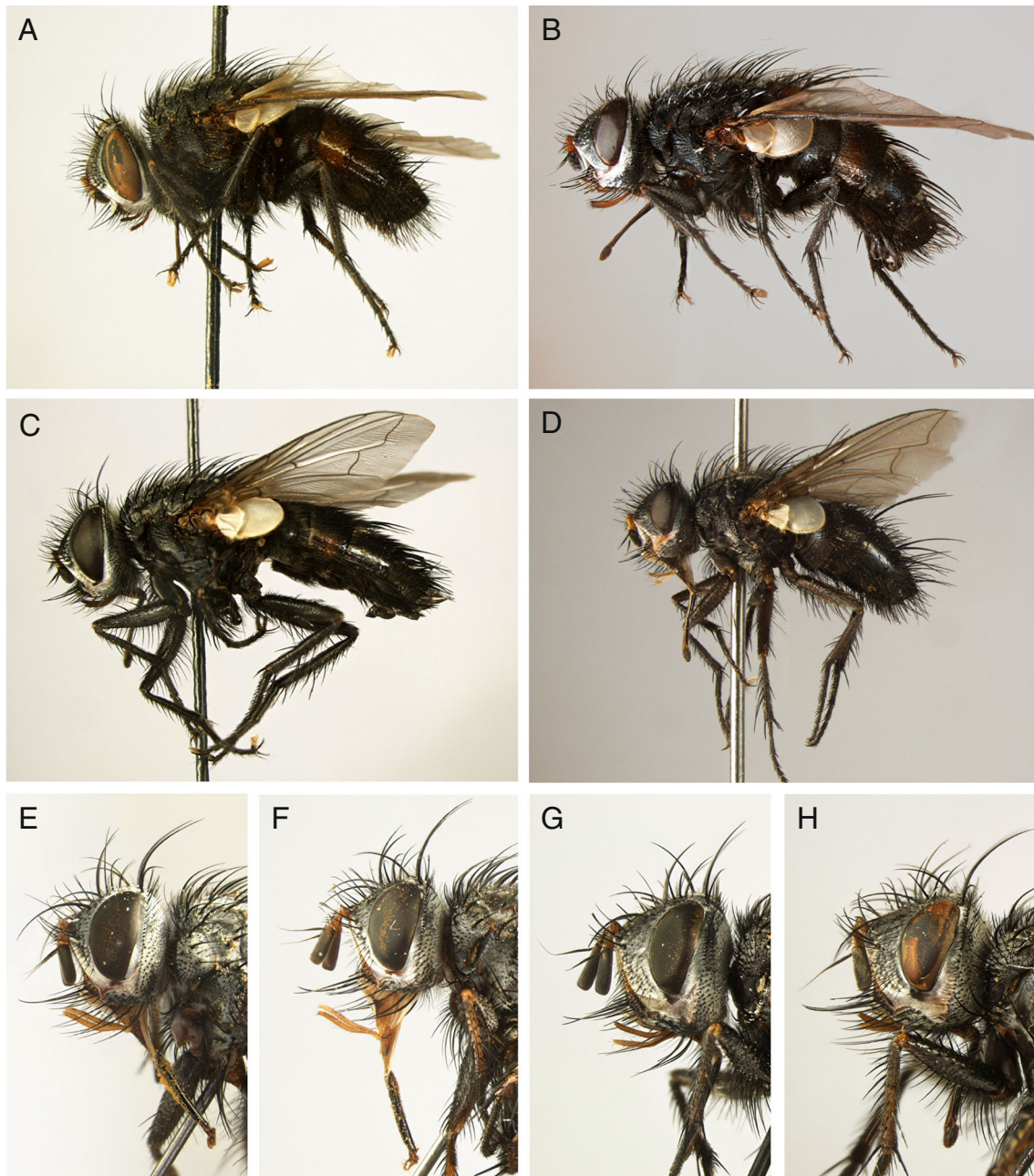


Fig. 2 **a** *Agaedioxis brevicornis* (Villeneuve), male, habitus. **b** *Agaedioxis kirkspriggi* **sp. nov.**, male (holotype) habitus. **c** *Agaedioxis succulentus* **sp. nov.**, male (holotype) habitus. **d** *Agaedioxis timidus* **sp. nov.**, male (holotype) habitus.

e–f *Eugaedioxis* **gen. nov.** *haematodes* (Villeneuve) head in lateral view: **e** male; **f** female. **g–h** *Eugaedioxis horridus* **gen. et sp. nov.** head in lateral view: **g** male (holotype), **h** female (paratype)

long and robust in both sexes (outer vertical seta latero-clinate). Ocellar seta strong, proclinate. Fronto-orbital plate with only fine setulae lateral to frontal setae. Two upper reclinate orbital setae (only 1 in one specimen). Two strong proclinate and 2 strong latero-clinate orbital setae. Parafacial flat, at its narrowest point 1.1–1.3 times as wide as postpedicel; parafacial covered with fine, long, black setulae. Facial ridge usually slightly concave, with robust decumbent setae on lower 1/4–1/3. Vibrissa strong, arising slightly above level of

lower facial margin. Face flat. Lower facial margin slightly visible in lateral view. Postpedicel 1.7–2.0 times as long as pedicel. Arista apparently bare, thickened on basal 2/5. First aristomere shorter than wide; second aristomere about 1.0–1.5 times as long as wide. Genal dilation well developed. Gena in profile 0.27–0.33 times as high as compound eye. Occiput convex; posterodorsal portion of occiput with 1–2 irregular rows of black setulae behind postocular row. Rest of occiput and postgena almost entirely covered with fine, pale setae.



Fig. 3 a–b *Agaedioxenis setifrons* (Villeneuve) head in lateral view: a male; b female. c–d *Agaedioxenis brevicornis* (Villeneuve) head in lateral view: c male; d female. e–f *Agaedioxenis kirkspriggsi* sp. nov. head in lateral view: e male (holotype); f female. g–h *Agaedioxenis*

succulentus sp. nov. head in lateral view: g male (holotype); h female. i *Agaedioxenis timidus* sp. nov., male (holotype) head in lateral view. j–k Male left hind tibia in posterodorsal view: j *Agaedioxenis kirkspriggsi* sp. nov. male (holotype); k *Agaedioxenis brevicornis* (Villeneuve)

Palpus long and narrow, sub-cylindrical. Prementum slender, 0.7–0.8 times as long as height of head.

Thorax: Four or 5 postpronotal setae, 3 strong, basal setae arranged in a straight line; 1 strong anterior seta arising in front of mid basal one; 1 additional postpronotal seta usually present between and slightly posteriorly to the line of outer basal and mid basal postpronotal setae. Scutum with 3+3

acrostichal setae; 3+3 dorsocentral setae; 1+3 intra-alar setae; 1 or 2 posthumeral setae; 1+3 supra-alar setae (first postsutural supra-alar seta longer than notopleural setae); notopleuron with 2 strong setae, equal in length and thickness; postalar callus with 2 or 3 setae [when 3, then 1 is weaker than notopleural setae]. Anatergite bare. Prosternum with several long setulae on lateral margin. Proepisternal depression bare.

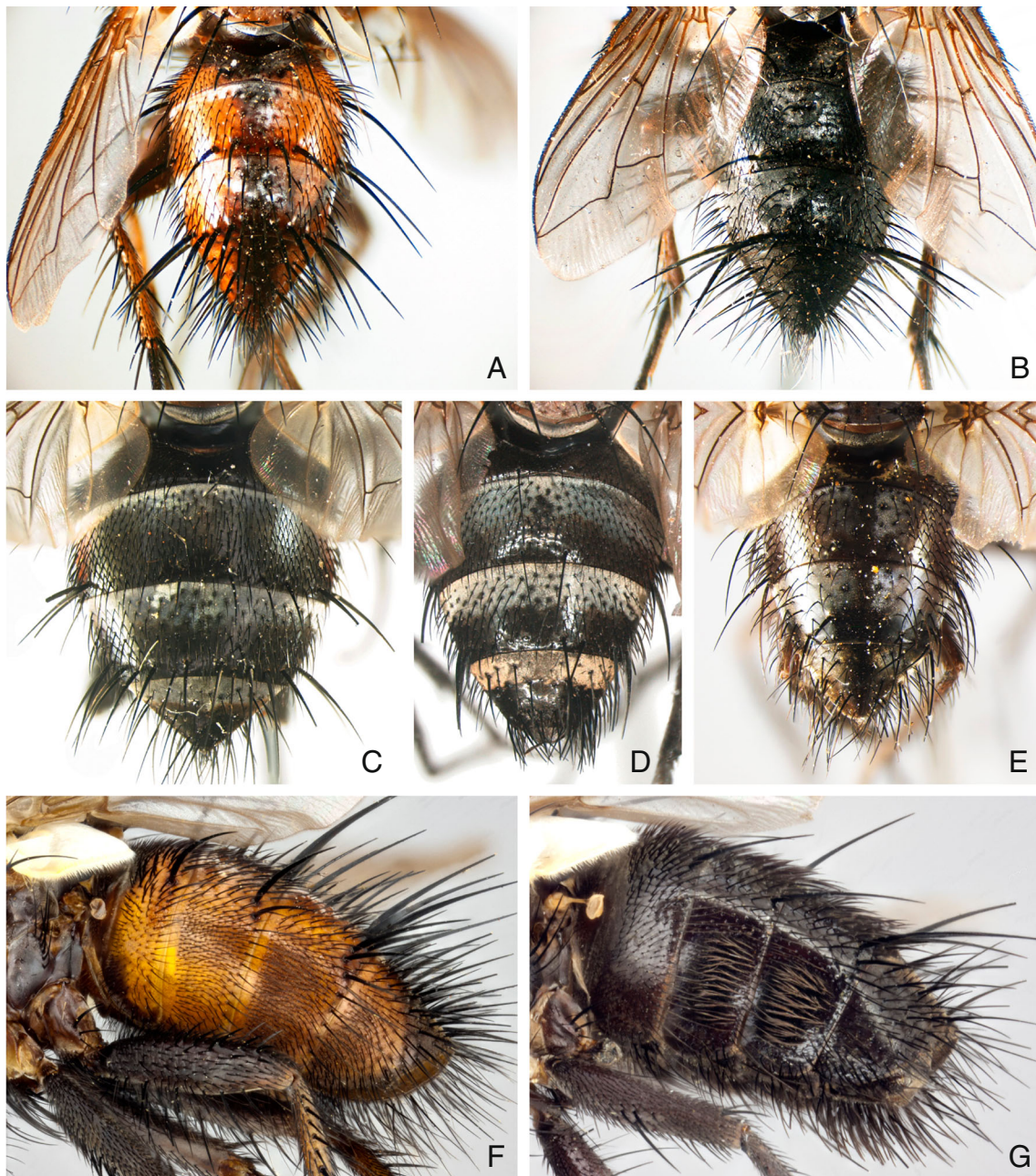


Fig. 4 a–c Female abdomen: **a** *Eugaedioxenis* **gen. nov.** *haematodes* (Villeneuve); **b** *Eugaedioxenis* *horridus* **gen. et sp. nov.** **c** *Agaedioxenis succulentus* **sp. nov.** **d–e** Male abdomen: **d** *Agaedioxenis kirkspriggsi* **sp. nov.** (holotype); **e** *Agaedioxenis timidus* **sp. nov.** (holotype). **f–g** Male

abdomen in lateral view showing the sexual patches: **f** *Eugaedioxenis* **gen. nov.** *haematodes* (Villeneuve); **g** *Agaedioxenis brevicornis* (Villeneuve)

Katepimeron bare or nearly so. Usually 3 katepisternal setae (nearly in line) [holotype with 4 setae on right side, fourth seta below middle seta]. Anterior and posterior lappets of metathoracic spiracle unequal in size (posterior lappet larger, operculum-like). Scutellum with 1 pair of crossed apical setae (standing slightly erect), varying from 1/2 (holotype) to 2/3 as long as subapical setae; 1 pair of subapical setae, 1 pair of lateral setae, and 1 pair of basal setae; lateral and subapical setae strong and subequal in size; 1 pair of widely separated discal

setae; preapical setae absent. Postmetacoxal area membranous.

Legs: Fore tibia with 2–3 strong posterior setae. Preapical anterodorsal seta of fore tibia well developed, about 2/3 as long as preapical dorsal seta. Fore claws about as long as fifth tarsomere (sometimes slightly longer). Mid tibia with 3–5 anterodorsal setae. Submedian ventral seta of mid tibia present. Hind tibia with several anterodorsal setae, irregular in size (i.e., not forming a comb-like row). Preapical posteroventral

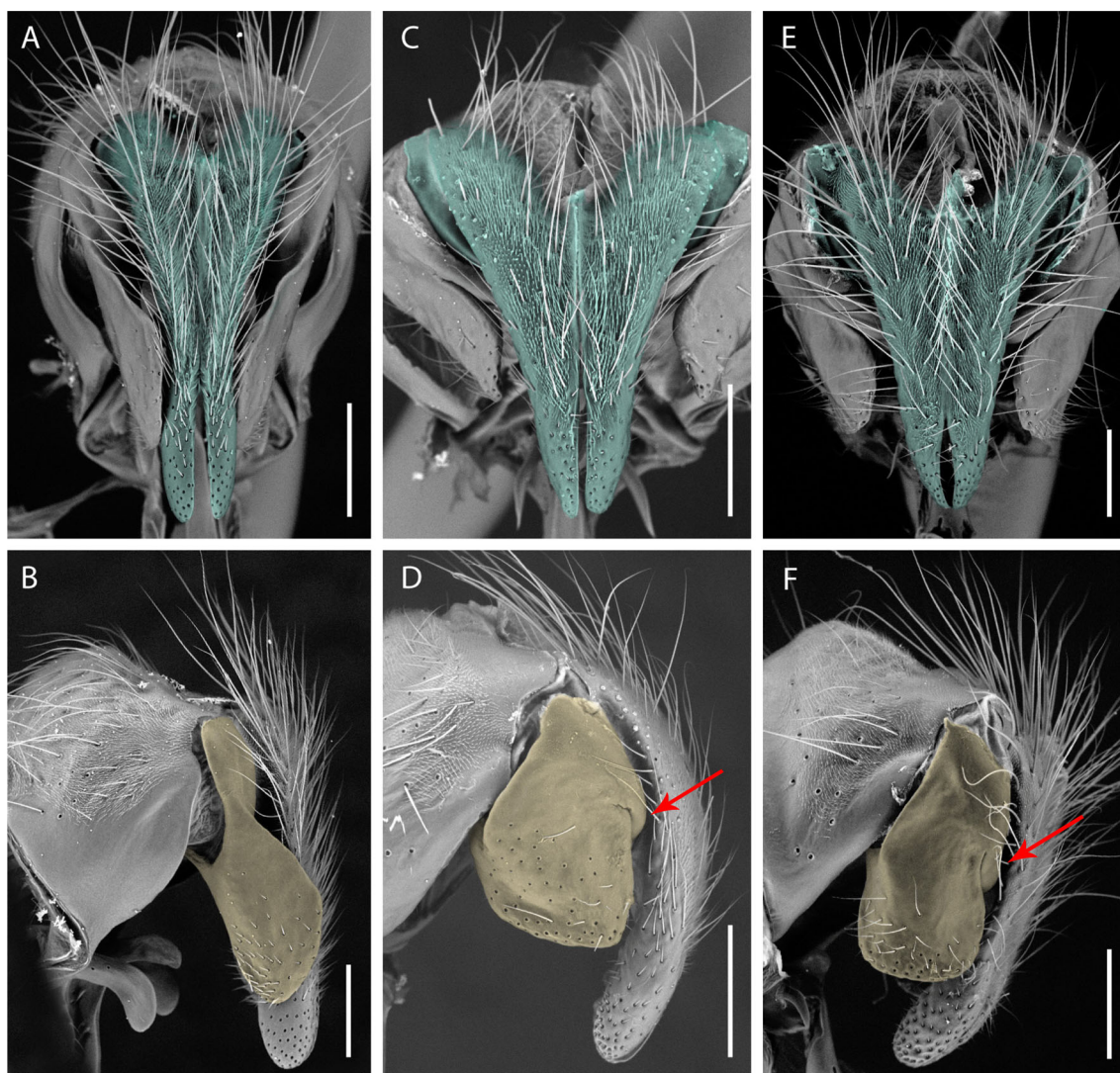


Fig. 5 a–b *Eugaedioxenis* gen. nov. *haematodes* (Villeneuve), epandrial complex in posterior (a) and lateral (b) view. c–d *Agaedioxenis setifrons* Villeneuve, epandrial complex in posterior (c) and lateral (d) view. e–f *Agaedioxenis brevicornis* (Villeneuve), epandrial complex in

posterior (e) and lateral (f) view. Scale bar 0.2 mm. [red arrow indicates postero-proximal lobe of surstylus. Colour coding: green = cerci; yellow = surstylus]

seta of hind tibia moderately well developed, varying from 1/2 to 2/3 as long as preapical anteroventral seta. Hind tibia with 4 dorsal preapical setae.

Wing: Costal spine well developed, about 1.5 times as long as crossvein r-m. Vein R_{4+5} with 2–3 setulae at base. Bend of vein M nearly right-angled. Costal sector cs_2 ventrally bare. Costal sector cs_4 about as long as cs_6 . Section of M between crossveins r-m and dm-cu clearly longer than section between dm-cu and bend of M. Section of M between dm-cu and bend of M shorter than postangular section of M. Cell r_{4+5} closed at wing margin or short petiolate. Wing membrane uniformly covered with microscopic setulae.

Abdomen (Fig. 4f): Ventral edges of syntergite 1+2 and tergites 3 and 4 entirely overlapping the corresponding sternites. Mid-dorsal depression of syntergite 1+2 not extending posteriorly to hind margin of syntergite (i.e.,

confined to approximately anterior 4/5). Syntergite 1+2 with 2 pairs of median marginal setae (inner median pair less than half as long as outer median pair, and only barely noticeable in holotype), and 1 pair of lateral marginal setae; tergite 3 with 3 pairs of median marginal setae (inner median pair 1/3–2/3 as long as outer median pairs), and 2 pairs of lateral marginal setae; tergite 4 with a complete row of regular marginal setae; tergite 5 covered with erect setae, not arranged in rows. Tergites 3 and 4 with several median discal setae about as long and robust as inner median marginal setae. Tergites 4 and 5 ventrally with sexual patches (i.e., patches of appressed fine setulae with underlying glandular organs) (Fig. 4f; cf. Cerretti et al. 2014a) (barely visible patches sometimes also on tergite 3 [incl. holotype]). Tergite 5 about 0.9–1.0 times as long as tergite 4.

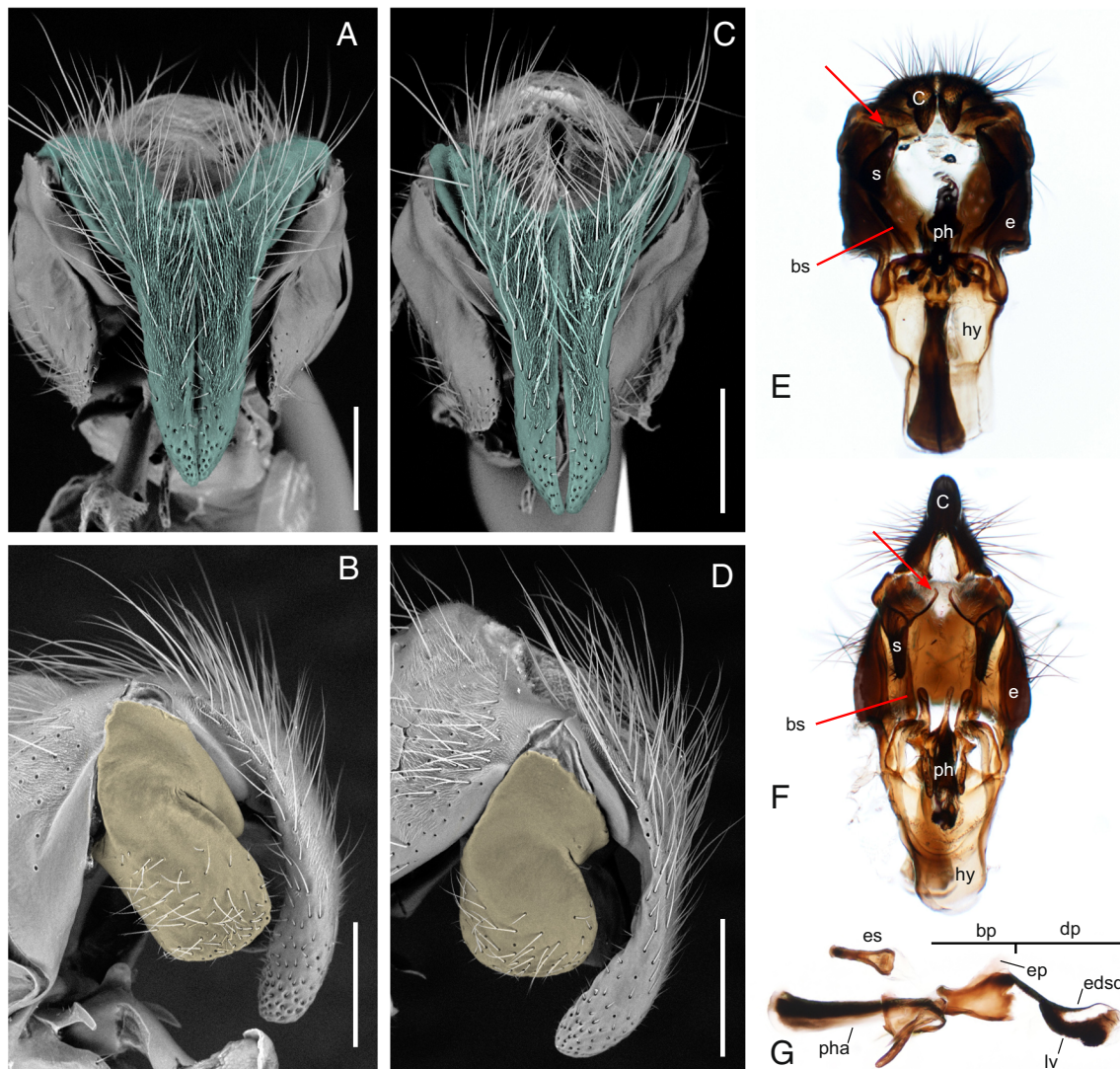


Fig. 6 a–b *Agaediioxenis succulentus* sp. nov. (holotype), epandrial complex in posterior (a) and lateral (b) view. c–d *Agaediioxenis kirkspriggsi* sp. nov. (holotype), epandrial complex in posterior (c) and lateral (d) view. Scale bar 0.2 mm. e *Agaediioxenis brevicornis* (Villeneuve), male terminalia in ventral view. f *Eugaediioxenis* gen. nov. *haematodes* (Villeneuve), male terminalia in ventral view. g *Agaediioxenis kirkspriggsi* sp. nov. (holotype), phallus, phallapodeme and ejaculatory

apodeme in lateral view. [Arrow indicates median, proximal apophysis of surstylus. Colour coding (a–d): green = cerci; yellow = surstylus. Abbreviations (e–g): bp basiphallus, bs bacilliform sclerite, c cerci, dp distiphallus, e epandrium, edsd extension of dorsal sclerite of distiphallus, ep epiphallus, es ejaculatory apodeme, hy hypandrium, lv lateroventral region of distiphallus, ph phallus, pha phallapodeme, s surstylus.]

Male terminalia: Tergite 6 more or less plate-like but indented anteriorly at mid point, not fused with segment 7. Synergosternite 7+8 relatively narrow. Sternite 6 asymmetrical and right side connection to segment 7 narrowly membranous. Sternite 5 with anterior margin almost straight; posterior margin with a deep median U-shaped cleft. Membranous transverse band on sternite 5 well developed. Epandrium short and convex. Lateral epandrial lobe not developed. Cerci in posterior view long and narrow, distally only slightly separated (Fig. 5a). Surstylus well developed, only slightly shorter than cerci, more or less lobe-like in lateral view (Fig. 5b), not fused with epandrium; with several short setulae on lateral and medial surfaces. Bacilliform sclerite rod-shaped and narrowly

fused to surstylus anterobasally; surstylus with a long and narrow median, proximal apophysis (Fig. 6f). Hypandrial arms not fused posteromedially. Pregonite well developed, sub-triangular, moderately hook-shaped distally and provided with fine setulae along posterior margin. Postgonite narrow, distally rounded and gently bent anteriorly. Intermedium well developed. Ejaculatory apodeme present, small. Basal processes of basiphallus present. Epiphallus well developed and arising dorsally on basiphallus, in sub-basal position. Ventral wall of distiphallus concave. Lateroventral region of distiphallus sclerotized. Medioventral ridge of distiphallus not developed. Extension of dorsal sclerite of distiphallus well developed (Fig. 6g).

Fig. 7 a–c *Eugaedioxenis* gen. nov. *haematodes* (Villeneuve), first instar: **a** habitus in lateral view (scale bar 0.1 mm); **b** Cephaloskeleton in dorsal view; **c** Cephaloskeleton in lateral view. **d** Oviscapt (segments 6 to 9) in lateral view



Female (Figs. 1b, 2f).

Oviscapt slightly elongated and telescopically retracted within segment 5 (Fig. 7d); egg membranous, macrotype. Eggs are stored fully embryonated within a long and spiralling common oviduct.

For other characters, female differs from male as follows:

Thorax: Fore claws 0.5–0.7 times as long as fifth tarsomere. Abdomen: Tergite 5 sub-conical, 1.1–1.3 times as long as tergite 4 (Fig. 4a).

Distribution. Afrotropical: South Africa (Northern Cape, Western Cape).

***Eugaedioxenis horridus* Cerretti, O'Hara and Stireman, sp. nov.**

(Figs. 1c–d, 2g–h, 4b)

<http://zoobank.org/urn:lsid:zoobank.org:act:221425B1-CA8A-4BC7-875F-5FD23373FBF1>

Type material. Holotype ♂: South Africa: Western Cape / Anysberg Nature Reserve at: / 33°26'37.76"S 20°47'29.25"E / 14.X.2012, 840 m (hilltop) / P. Cerretti, J. Stireman, J. O'Hara, / I. Winkler & A.H. Kirk-Spriggs leg // SA020 [MZUR]. Paratype ♀: Sth Africa Cape Prov / 10 km E Garies [Northern Cape] / 3017DB 3.ix.1981 / J. Londt, L. Schoeman / and B. Stuckenberg. / Succulent Karoo [NMDA].

Etymology. The species epithet derives from the Latin adjective *horridus* meaning bristly.

Recognition. *Eugaedioxenis horridus* shares many characters with congener *E. haematodes* in regard to habitus, wing venation and chaetotaxy, but is distinguishable from it in its darker colouration of abdomen (Fig. 1a–d) and remarkably different morphometric ratios of the head (Fig. 2e–h) (see key below).

Description.

Body length: 11–12 mm.

Male.

Colouration: Head ground colour black except genal groove and facial ridge which are red, and frontal vitta which is brown. Head covered with grey reflecting microtomentum. Scape and pedicel reddish yellow; postpedicel and arista black. Palpus yellow. Thorax (except scutellum) black; scutellum mostly black with red tip. Presutural area of scutum with 4 well outlined dark vittae (lateral pair subtriangular, median pair straight and narrow); postsutural area of scutum, when viewed from behind, with 5 dark vittae, 3 extending length of postsutural area and 2 on anterior portion only and continuous with median pair on presutural area. Femora and tarsi black, tibiae yellow. Tegula black; basicosta yellow. Wing membrane mostly hyaline, shading into yellowish antero-proximally. Syntergite 1+2 black dorsally, red lateroventrally, dorsally covered with weak, grey microtomentum. Tergites 3 and 4 mostly black dorsally, largely red lateroventrally; grey reflecting microtomentum present on both tergites but dense only on tergite 4. Tergite 5 entirely black and covered with weak brownish microtomentum.

Head (Figs. 1c, 2g): Compound eye covered with scattered ommatrichia, irregular in length (longest ommatrichia are at most as long as 4 eye facets). Frons 1.7–1.9 times as wide as compound eye in dorsal view. Inner and outer vertical setae long and robust in both sexes (outer vertical seta latero-clinate). Ocellar seta strong, proclinate. Fronto-orbital plate with only short setulae lateral to frontal row. Two upper reclinate orbital setae. Two strong proclinate and 2 strong latero-clinate orbital setae. Parafacial convex, at its narrowest point 2.0–2.3 times as wide as postpedicel; parafacial covered with fine, long, black setae. Facial ridge straight to slightly concave just above vibrissa, with robust decumbent setae on lower 1/2. Vibrissa strong, arising slightly above lower facial margin. Face flat. Lower facial margin slightly visible in lateral view. Postpedicel 1.7–2.0 times as long as pedicel. Arista bare, thickened on basal 1/2. First

aristomere shorter than wide; second aristomere about 1.5 times as long as wide. Genal dilation well developed, narrow. Gena in profile about 0.4–0.5 times as high as compound eye. Occiput convex; posterodorsal portion of occiput with 1–2 irregular rows of black setulae behind postocular row. Rest of occiput and postgena almost entirely covered with fine, pale setae. Palpus long and narrow, sub-cylindrical. Prementum slender, 0.60–0.65 times as long as height of head.

Thorax: Five postpronotal setae, 3 strong, basal setae arranged in a straight line; 1 strong anterior seta arising in front of mid basal one; 1 additional postpronotal seta present between and slightly posteriorly to the line of outer basal and mid basal postpronotal setae. Scutum with 3+3 acrostichal setae; 3+3 dorsocentral setae; 1+3 intra-alar setae; 3 posthumeral setae; 1+3 supra-alar setae (first postsutural supra-alar seta longer than notopleural setae); notopleuron with 2 strong setae, equal in length and thickness; postalar callus with 3 setae. Anatergite bare. Prosternum with several long setulae on lateral margin. Proepisternal depression bare. Katepimeron bare. Three katepisternal setae (nearly in line). Anterior and posterior lappets of metathoracic spiracle unequal in size (posterior lappet larger, operculum-like). Scutellum with 1 pair of crossed apical setae (standing slightly erect) about 2/3 as long as subapical setae; 1 pair of subapical, 1 pair of lateral setae, and 1 pair of basal setae; lateral and subapical setae subequal in size; 1 pair of widely separated discal setae; preapical setae absent. Postmetacoxal area membranous.

Legs: Fore tibia with 2 strong posterior setae. Preapical anterodorsal seta of fore tibia about as long and robust as preapical dorsal seta. Fore claws about as long as fifth tarsomere. Mid tibia with 5 anterodorsal setae. Submedian ventral seta on mid tibia present. Hind tibia with several anterodorsal setae, irregular in size. Preapical posteroventral seta of hind tibia well developed, about 2/3 as long as preapical anteroventral seta. Hind tibia with 4 dorsal preapical setae.

Wing: Costal spine well developed, about 1.5 times as long as crossvein r-m. Vein R₄₊₅ with 2–3 setulae at base. Bend of vein M nearly right-angled. Costal sector cs₂ ventrally bare. Costal sector cs₄ about as long as cs₆. Section of M between crossveins r-m and dm-cu clearly longer than section between dm-cu and bend of M. Section of M between dm-cu and bend of M shorter than postangular section of M. Cell r₄₊₅ closed at wing margin. Wing membrane uniformly covered with microscopic setulae.

Abdomen (Fig. 1c): Ventral edges of syntergite 1+2 and tergites 3 and 4 entirely overlapping the corresponding sternites. Mid-dorsal depression of syntergite 1+2 not extending posteriorly to hind margin of syntergite. Syntergite 1+2 with 2 pairs of median marginal setae (inner median pair less than 1/2 as long as outer median pair), and 1 pair of lateral marginal setae; tergites 3 with 3 pairs of median marginal setae (inner median pair about 1/3 as long as outer median pairs) and 2 pairs of lateral marginal setae; tergite 4 with a complete row of marginal setae; tergite 5 covered with erect setae not arranged in rows. Tergites 3 and 4

with several median discal setae about as long and robust as inner median marginal setae. Tergites 3 to 5 ventrally with sexual patches. Tergite 5 about 0.9–1.0 times as long as tergite 4.

Male terminalia: not examined.

Female (Figs. 1d, 2h, 4b) differs from male as follows:

Colouration: Scutellum almost entirely red. Abdomen entirely black in ground colour (Figs. 1d, 4b). **Legs:** Fore claws about 0.7 times as long as fifth tarsomere. **Abdomen:** Tergite 5 sub-conical, 1.2 times as long as tergite 4 (Fig. 4b).

Distribution. Afrotropical: South Africa (Northern Cape, Western Cape).

Key to species of *Eugaedioxenis* gen. nov.

1. Frons at its narrowest point 1.3–1.4 times as wide as compound eye in dorsal view. Parafacial at its narrowest point 1.1–1.3 times as wide as width of postpedicel (Figs. 1a–b, 2e–f). Abdomen mainly reddish with a narrow median black vitta on syntergite 1+2 to tergite 5 (Fig. 4a) *E. haematodes* (Villeneuve)
- Frons at its narrowest point 1.7–1.9 times as wide as compound eye in dorsal view. Parafacial at its narrowest point 2.0–2.3 times as wide as width of postpedicel (Figs. 1c–d; 2g–h). Abdomen mainly black with dark red sides (Fig. 4b) in male, entirely black in female *E. horridus* Cerretti, O'Hara and Stireman, sp. nov.

Tribe Goniini

Agaedioxenis Villeneuve, 1939, stat. nov.

(Figs. 1e–f, 2a–d, 3a–k, 4c–e, g, 5c–f, 6a–e, g, 8a–d)

Gaedioxenis Villeneuve, 1937: 206. *Nomen nudum* (proposed after 1930 without designation of type species from two included species).

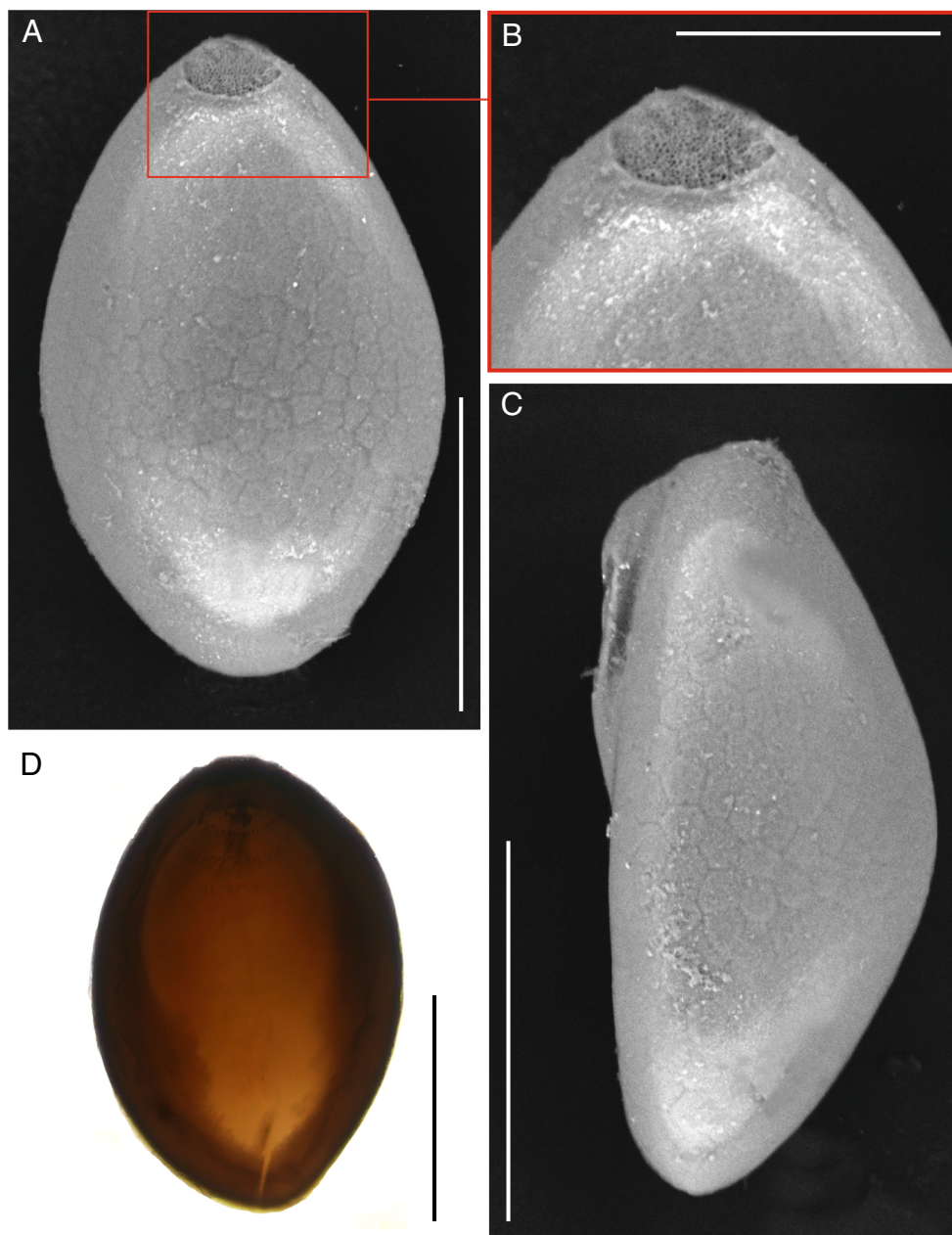
Gaedioxenis Villeneuve, 1939: 1. *Nomen nudum* (proposed after 1930 without designation of type species from two included species).

Agaedioxenis Villeneuve, 1939: 2 (as subgenus of *Gaedioxenis* Villeneuve, 1937 [*nomen nudum*]). Type species: *Gaedioxenis (Agaedioxenis) brevicornis* Villeneuve, 1939, by monotypy.

Gaedioxenis Townsend, 1943: 335. Type species: *Gaedioxenis setifrons* Villeneuve, 1937, by original designation.

Review of genus-group names. Villeneuve (1937) proposed the new genus *Gaedioxenis* for two new species, *G. setifrons* and *G. haematodes*. Later, Villeneuve (1939) added two new species to this genus, *Gaedioxenis propinqua* and *G. brevicornis*, placing the latter in a new subgenus, *Agaedioxenis*. The type species of the genus-group name *Agaedioxenis* was thus fixed by monotypy as *G. (A.) brevicornis*. In neither of Villeneuve's papers was a type species

Fig. 8 a–d *Agaedioxenis brevicornis* (Villeneuve): **a–c** ESEM images of egg: **a–b** dorsal view; **c** lateral view (scale bar 0.05 mm). **d** Light microscope images of egg with ready to hatch first instar visible within



fixed for *Gaedioxenis* from among the two species described in 1937 or the two species available for type species fixation in 1939 (*G. setifrons* and *G. propinqua*; *G. haematodes* was not mentioned in this work and *G. brevicornis* was fixed as type species of *Agaedioxenis*). Townsend (1943: 335) attempted to remedy this situation by designating *G. setifrons* as the type species of *Gaedioxenis* (by “designation herein”). Crosskey (1980: 878) followed this interpretation, attributing authorship of *Gaedioxenis* to Villeneuve, 1937 and the type species designation to Townsend (1943) [as 1941, treating the “Addenda and corrigenda” to Part XI of Townsend’s (1941) *Manual of Myiology* as published at the same time as the rest of the volume].

Evenhuis et al. (2008) discovered that earlier interpretations of *Gaedioxenis* were contrary to the *Code* that required the description of a new genus after 1930 to “be accompanied by the fixation of a type species in the original publication” (Article 13.3 of ICZN 1999). Thus, *Gaedioxenis* was unavailable from Villeneuve (1937, 1939) and took authorship and date from Townsend (1943). This interpretation was discussed in more detail by Evenhuis et al. (2015).

We agree with Evenhuis et al. (2008) and Evenhuis et al. (2015) that *Gaedioxenis* is correctly attributed to Townsend (1943), but we do not treat this name as valid. The genus-group name *Agaedioxenis* Villeneuve, 1939 has priority over *Gaedioxenis* Townsend, 1943 and is the valid name of the

genus when these names are treated as subjective synonyms, as they are herein.

Diagnosis. Medium to large size, moderately bristly, exoristine characterized by the following combination of character states: Compound eye bare; parafacial covered with fine setulae; facial ridge with decumbent setae approximately on lower 1/4; lower facial margin protruded and clearly visible in lateral view; prementum long and slender; 4 or 5 postpronotal setae, the 3, strongest, basal setae arranged in a line; scutum with 4 postsutural dorsocentral setae; katepimeron bare or at most with 1–2 hair-like setulae on anterior 1/4; first postsutural supra-alar seta longer than notopleural setae; preapical anterodorsal setae of fore tibia at least as long and strong as preapical dorsal seta; hind tibia with 3 strong dorsal preapical setae; basicosta brownish black; mid-dorsal depression on abdominal syntergite 1+2 extended back to hind margin of that segment; male without proclinate orbital setae; female with tergite 5 normally developed, sub-conical, 0.8–0.9 times as long as tergite 4; egg microtype, planoconvex, fully embryonated; convex side hard-shelled, blackish brown, with 1 subcircular aeropilar area attached to anterior margin. Sexual dimorphism involves head chaetotaxy and morphometric ratios of head; specifically females have proclinate and latero-clinate orbital setae, a wider frons and in some cases also a shorter postpedicel.

Hosts. Unknown.

Distribution. South Africa, Zimbabwe.

***Gaedio Xenis setifrons* (Villeneuve, 1937), comb. nov.**

(Figs. 1e–f, 3a–b, 5c–d)

Gaedio Xenis setifrons Villeneuve, 1937: 207. Holotype female (CNC). Type locality: South Africa, Western Cape, Stellenbosch.

Gaedio Xenis setifrons: Villeneuve (1939: 1); Townsend (1943: 335), type species designation; Crosskey (1980: 878), Afrotropical catalogue; Crosskey (1984: 291), note in key to genera of tropical and southern Africa; Evenhuis et al. (2008: 14), newly recognized as type species of *Gaedio Xenis* Townsend; Evenhuis et al. (2015), type species of *Gaedio Xenis* in list of Townsend genus-group names.

Type material. Holotype ♀: [blank small red square label] // Capland / Stellenbosch / Nov-10 1925 / Dr. H. Brauns. // *Gaedio Xenis* / *setifrons* / Villen. / Typ. [label handwritten by Villeneuve] // *Gaedio Xenis* / *setifrons* Vill. [handwritten by Mesnil] / L.P. Mesnil det., 1969 // TYPE [red label] // EX / L.-P. MESNIL / COLLECTION 1970 [CNC, in good condition except missing both front legs]. **Other material examined.** 1♂, South Africa, Western Cape, West Coast National Park, 33° 07' 31" S 18° 03' 38" E 30 m, J.G.L. & A. Londt, 13.ix.2001, Seeberg area, lagoon bush; 1♀, South Africa, Cape Prov., 10 km E Garies, 3017DB, 3.ix.1981, J. Londt, L. Schoeman and B. Stuckenberg, Succulent Karoo (both in NMDA).

Description.

Body length: 10.5–11.0 mm.

Male.

Colouration: Head ground colour black except genal groove and facial ridge which are dark red, and frontal vitta which is dark brown. Head covered with whitish-grey reflecting microtomentum. Scape and pedicel reddish yellow; postpedicel and arista black. Palpus blackish or brownish (reddish brown in holotype). Thorax (except scutellum) black; scutellum anteriorly and anterolaterally black turning to red on posteromedian 1/2. Presutural area of scutum with 4 dark vittae (lateral pair subtriangular, median pair straight and narrow); postsutural area of scutum, when viewed from behind, with 5 dark vittae, 3 extending length of postsutural area and 2 on anterior portion only and continuous with median pair on presutural area. Legs black. Tegula and basicosta black. Wing membrane hyaline. Abdomen almost entirely black in ground colour, only faintly reddish laterally on tergite 4 or on both tergites 3 and 4. Tergites 3 and 4 with a band of whitish reflecting microtomentum on anterior 1/2; tergite 5 with a narrow band of whitish and brownish reflecting microtomentum on anterior 1/4–1/3.

Head (Figs. 1e, 3a): Compound eye bare. Frons 1.33 times as wide as compound eye in dorsal view. Inner and outer vertical setae long and robust (outer vertical seta latero-clinate). Ocellar seta strong, proclinate. Fronto-orbital plate with 2 irregular rows of several strong medio-clinate setae lateral to lower frontal setae. Four to 6 upper reclinate orbital seta (2 of them latero-clinate). Proclinate orbital setae absent. Parafacial flat, at its narrowest point about 0.8 times as wide as postpedicel; parafacial covered with fine, long, black setae. Facial ridge concave, with decumbent setae on lower 1/4–1/5. Vibrissa strong, arising slightly above or at level of lower facial margin. Face slightly raised and usually visible in lateral view. Lower facial margin protruded and clearly visible in lateral view. Postpedicel about 4 times as long as pedicel. Arista bare, thickened on basal 4/5 or more. First aristomere at most as long as wide; second aristomere about 3–5 times as long as wide. Genal dilation well developed. Gena in profile ca. 0.4 times as high as compound eye. Occiput slightly convex; posterodorsal portion of occiput with 2 irregular rows of black setulae behind postocular row. Rest of occiput and postgena almost entirely covered with fine, pale setae. Palpus long and narrow, sub-cylindrical. Prementum slender, 0.60–0.75 times as long as height of head.

Thorax: Four postpronotal setae, the 3 strongest basal setae arranged in a straight line; 1 strong anterior seta arising in front between mid basal and inner basal setae. Scutum with 3+3 acrostichal setae; 3+4 dorsocentral setae; 1+3 intra-alar setae; 3 posthumeral setae; 1+3 supra-alar setae (first postsutural supra-alar seta longer than notopleural setae); notopleuron with 2 strong setae, equal in length and thickness; postalar callus with 2 strong setae, 1 additional, smaller seta may be

present. Anatergite bare. Prosternum with several long setulae on lateral margin. Proepisternal depression bare. Katepimeron bare or with 1 fine setula anteriorly. Four katepisternal setae. Anterior and posterior lappets of metathoracic spiracle unequal in size (posterior lappet larger, operculum-like). Apical scutellar setae strong, crossed and varying from almost horizontal to slightly erect. One pair of subapical scutellar setae, 1 pair of lateral setae, and 1 pair of basal setae; lateral scutellar setae about 4/5 as long as subapical setae; 1 pair of widely separated discal setae and 1–2 pairs of strong, erect preapical setae, irregular in length. Postmetacoxal area membranous.

Legs: Fore tibia with 2 posterior setae. Preapical anterodorsal seta of fore tibia distinctly longer than preapical dorsal seta. Fore claws shorter than fifth tarsomere. Mid tibia with 3–5 anterodorsal setae. Submedian ventral seta on mid tibia present. Row of anterodorsal setae of hind tibia very irregular in size (i.e., not forming a comb-like row). Preapical posteroventral seta of hind tibia distinctly shorter than preapical anteroventral seta. Hind tibia with 3 dorsal preapical setae (mid-dorsal one shorter than preapical anterodorsal and preapical posterodorsal).

Wing: Costal spine well developed, about twice as long as crossvein r-m. Vein R_{4+5} with 2–3 setulae at base. Bend of vein M nearly right-angled. Costa sector cs_2 ventrally bare. Costal sector cs_4 longer than cs_6 . Section of M between crossveins r-m and dm-cu clearly longer than section between dm-cu and bend of M. Section of M between dm-cu and bend of M shorter than postangular section of M. Cell r_{4+5} closed at wing margin. Wing membrane uniformly covered with microscopic setulae.

Abdomen: Ventral edges of syntergite 1+2 and tergites 3 and 4 entirely overlapping corresponding sternites. Mid-dorsal depression of syntergite 1+2 extending posteriorly to hind margin of that segment. Syntergite 1+2 with 2 pairs of equally strong median marginal setae, and 2–3 pairs of lateral marginal setae; tergite 3 with 2 pairs of median marginal setae and 4 pairs of lateral marginal setae; tergite 4 with a complete row of regular marginal setae; tergite 5 with erect marginal and discal setae not arranged in rows. Tergites 3 and 4 with irregular median discal setae barely distinguishable from strong erect general setulae (median discal setae more developed on tergite 4). Tergites 3 to 5 without sexual patches. Tergite 5 about 0.9–1.0 times as long as tergite 4.

Male terminalia (Fig. 5c–d): Tergite 6 divided into 2 large hemitergites, not fused with segment 7. Syntergosternite 7+8 relatively broad. Sternite 6 asymmetrical and right side connection to segment 7 narrowly membranous. Sternite 5 with anterior margin almost straight; posterior margin with a deep median U-shaped cleft. Membranous transverse band on sternite 5 well developed. Epandrium short and convex. Lateral epandrial lobe not developed. Cerci in posterior view long and sub-triangular, distally only slightly separated. Surstylus laterally compressed, shorter than cerci; distal 2/3 rounded in lateral view and proximally not fused with epandrium; with several short setulae on both lateral and medial surfaces.

Bacilliform sclerite rod-shaped and fused to surstylus antero-basally; surstylus with a stout median, proximal apophysis, visible in lateral view in form of a postero-proximal lobe (Fig. 5d, red arrow). Hypandrial arms strongly approximated, not fused posteromedially. Pregonite well developed, sub-triangular, hook-shaped distally. Postgonite narrow, distally pointed and gently bent anteriorly. Intermedium well developed. Ejaculatory apodeme present, small. Basal processes of basiphallus present. Epiphallus very short and membranous (barely distinguishable), arising dorsally in distal position (i.e., close to junction between basiphallus and distiphallus) (as in Fig. 6g). Ventral wall of distiphallus concave. Lateroventral region of distiphallus sclerotized. Medioventral ridge of distiphallus not developed. Extension of dorsal sclerite of distiphallus well developed (as in Fig. 6g).

Female differs from male as follows:

Head (Figs. 1f, 3b): Frons 1.40–1.51 times as wide as compound eye in dorsal view. Fronto-orbital plate with 1 irregular row of several strong medioclinate setae lateral to lower frontal setae. Two or 3 upper reclinate orbital setae, 2 strong proclinate orbital setae, and 2 laterocline orbital setae. Postpedicel about 2.5 times as long as pedicel. **Thorax:** Postalar callus with 2 setae. **Legs:** Hind tibia with 3 dorsal preapical setae subequal in size. **Abdomen:** Syntergite 1+2 with 2 pairs of median marginal setae, inner pair weak. Tergite 3 with 1 strong and 1 weak pair of median marginal setae and 2 or 3 pairs of lateral marginal setae; tergite 5 sub-conical, 0.9 times as long as tergite 4.

Distribution. Afrotropical: South Africa (Western Cape).

Remarks. *Agaedioxenis setifrons* is morphologically divergent and is separable from congeners by having a different shape of the antennae and head and by having apical scutellar setae well developed and crossed. Moreover, males of *A. setifrons* do not have sexual patches on abdominal tergites, which otherwise characterize the remaining species; i.e., *A. brevicornis*, *A. kirkspriggsi*, *A. succulentus* and *A. timidus*. Sexual patches on tergites 3 and 4, although present also in several other Goniini and Eryciini (see Cerretti et al. 2014a), may represent a homoplasious autapomorphy supporting monophyly of this group of species.

***Agaedioxenis brevicornis* (Villeneuve, 1939), comb. nov.**

(Figs. 2a, 3c–d, k; 4g, 5e–f; 6e, 8a–d)

Gaedioxenis (*Agaedioxenis*) *brevicornis* Villeneuve, 1939: 1. Holotype male (BMNH). Type locality: Zimbabwe, Mutare [as “Umtali”] District.

Gaedioxenis brevicornis: Crosskey (1980: 878), Afrotropical catalogue.

Gaedioxenis propinqua Villeneuve, 1939: 2. Holotype female (not located). Type locality: South Africa, KwaZulu-Natal [as “Natal”]. **Syn. nov.**

Gaedioxenis propinqua: Crosskey (1980: 878), Afrotropical catalogue.

Note about synonymy. *Gaedioxenis brevicornis* and *Gaedioxenis propinqua* were described in the same paper by Villeneuve (1939). We consider these names to be subjective synonyms, with the former based on a male and the latter on a female of the same species. Acting as the First Reviser, we select *G. brevicornis* as the senior synonym (Article 24.2.2 of the *Code*, ICZN 1999).

Note about the holotype of *Gaedioxenis brevicornis* Villeneuve. The holotype is pinned sideways on a micropin (minuten) and double-mounted on a rectangular card. The head is detached and glued, face up, to the same card. The left fore leg and right hind leg are missing. The specimen is otherwise in good condition but generally rather dirty (D. Whitmore, pers. comm. April 2014).

Material examined. 1♂, “Capland” [South Africa, Western Cape], Stellenbosch, 10.ix.1926, Dr. H. Brauns (NMDA). 1♂, same data except 13.ix.1926 (NMDA). 1♀, same data except 15.x.1926 (NMDA). 1♀, same data except 21.x.1926 (NMDA). 1♂, same data except 25.x.1926 (NMDA). 1♂, Kapstadt [South Africa, Western Cape, Cape Town], 13.x–7.xi.1958, Lindner (CNC). 1♀, “Natal” [South Africa, KwaZulu-Natal], Mooi River, Willow Grande, Well Brook, 18.x.1913, R.C. Wroughton (CNC, abdomen missing). 2♂♂, “S. Rhodesia” [Zimbabwe], “Umtali Dist.” [Mutare District], Vumba Mountains, iii.1938, A. Cuthbertson (CNC, labelled by Villeneuve as a paratype of *Gaedioxenis brevicornis* but the species was described from a single male).

Description.

Body length: 9–12 mm.

Male.

Colouration: Head ground colour black except genal groove and facial ridge which are dark red. Head covered with grey reflecting microtomentum. Scape and pedicel yellow to reddish brown; postpedicel and arista black. Palpus mainly yellow and usually with blackish tip. Thorax (except scutellum) black; scutellum anteriorly black turning into red on posterior 2/3 or more. Presutural area of scutum with 4 well-outlined dark vittae (lateral pair subtriangular, median pair straight and narrow); postsutural area of scutum, when viewed from behind, with 5 dark vittae, all extending length of postsutural area though ending shortly anterior to transverse suture. Legs black. Tegula and basicosta black. Wing membrane hyaline. Abdomen almost entirely black in ground colour, sometimes faintly reddish laterally on tergite 4. Tergites 3 and 4 with a band of whitish reflecting microtomentum on anterior 1/3 or less, tergite 5 with at most a narrow band of whitish or brownish reflecting microtomentum.

Head (Figs. 2a, 3c): Compound eye bare. Frons 0.70–0.85 times as wide as compound eye in dorsal view. Inner vertical seta long and robust. Outer vertical seta not or only slightly [often varying within single specimens] differentiated from postocular row. Ocellar seta strong, proclinate. Fronto-orbital plate with an irregular row of strong medioclinate setae lateral to frontal setae running most of length of frontal setae but

decreasing in size on upper portion, sometimes with several additional strong setae on lower portion. Two to 4 upper reclinate orbital setae. Proclinate and laterocline orbital setae absent. Parafacial flat, at its narrowest point 1.30–1.45 times as wide as postpedicel; parafacial covered with fine, long, black setae (sometimes confined to lower 1/2 of parafacial). Facial ridge concave, with decumbent setae on lower 1/4–1/5. Vibrissa strong, arising at or slightly above level of lower facial margin. Face slightly raised and usually barely visible in lateral view. Lower facial margin protruded and clearly visible in lateral view. Postpedicel 1.1–1.2 times as long as pedicel. Arista apparently bare, thickened on basal 1/2–3/4. First aristomere at most as long as wide; second aristomere about 1.0–1.5 times as long as wide. Genal dilation well developed. Gena in profile 0.28–0.43 times as high as compound eye. Occiput flat or slightly convex; posterodorsal portion of occiput with 1–2 irregular rows of black setulae behind postocular row. Rest of occiput and postgena almost entirely covered with fine, pale setae. Palpus long and narrow, sub-cylindrical. Prementum slender, 0.55–0.65 times as long as height of head.

Thorax: Four postpronotal setae, the 3 strongest basal setae arranged in a straight line; 1 strong anterior seta arising between mid basal and inner basal setae. Scutum with 3+3 acrostichal setae; 3+4 dorsocentral setae; 1+3 intra-alar setae; 1 to 3 posthumeral setae; 1+3 supra-alar setae (first postsutural supra-alar seta longer than notopleural setae); notopleuron with 2 strong setae, equal in length and thickness; postalar callus with 2–3 setae. Anatergite bare. Prosternum with several long setulae on lateral margin. Proepisternal depression bare. Katepimeron bare. Four katepisternal setae. Anterior and posterior lappets of metathoracic spiracle unequal in size (posterior lappet larger, operculum-like). Apical scutellar setae varied from absent to long and thin, if present then divergent. One pair of subapical scutellar setae, 1 pair of lateral, and 1 pair of basal setae; lateral and subapical setae subequal in size or lateral pair slightly shorter; 1 pair of widely separated discal setae and 1–2 pairs of strong, erect preapical setae. Postmetacoxal area membranous.

Legs: Fore tibia with 2 posterior setae. Preapical anterodorsal seta of fore tibia about as long and robust as preapical dorsal seta. Fore claws longer than fifth tarsomere. Mid tibia with 3–5 anterodorsal setae. Submedian ventral seta on mid tibia present. Row of anterodorsal setae of hind tibia very irregular in size (i.e., not forming a comb-like row) (Fig. 3k). Preapical posteroventral seta of hind tibia distinctly shorter than preapical anteroventral seta. Hind tibia with 3 dorsal preapical setae (mid-dorsal one usually shorter than preapical anterodorsal and preapical posterodorsal setae).

Wing: Costal spine well developed, about 1.2 times as long as crossvein r-m. Vein R₄₊₅ with 2–3 setulae only at base. Bend of M vein obtuse. Costa sector cs₂ ventrally bare. Costal sector cs₄ about as long as cs₆. Section of M between crossveins r-m and dm-cu clearly longer than section between dm-cu and bend of M. Section of M between dm-cu and bend

of M shorter than postangular section of M. Cell r_{4+5} closed at wing margin or short petiolate. Wing membrane uniformly covered with microscopic setulae.

Abdomen (Fig. 4g): Ventral edges of syntergite 1+2 and tergites 3 and 4 entirely overlapping corresponding sternites. Mid-dorsal depression of syntergite 1+2 extending posteriorly to hind margin of syntergite. Syntergite 1+2 with 1 pair of median marginal setae, and 1–3 pairs of lateral marginal setae; tergite 3 with 1 pair of median marginal setae, and 1–2 pairs of lateral marginal setae (the longest median marginal setae 0.9–1.3 times as long as corresponding tergite measured at its maximum median length); tergite 4 with a complete row of marginal setae; tergite 5 with erect marginal and discal setae not arranged in rows. Tergites 3 and 4 usually without median discal setae; short median discal setae occasionally present only on tergite 4. Tergites 3 and 4 ventrally with a pair of sexual patches (Fig. 4g). Tergite 5 about 0.9–1.0 times as long as tergite 4.

Male terminalia (Figs. 5e–f, 6e): Tergite 6 divided into 2 hemitergites, not fused with segment 7. Syntergosternite 7+8 relatively narrow. Sternite 6 asymmetrical and right side connection to segment 7 narrowly membranous. Sternite 5 with anterior margin almost straight; posterior margin with a deep median U-shaped cleft. Membranous transverse band on sternite 5 well developed. Epandrium short and convex. Lateral epandrial lobe not developed. Cerci in posterior view long and sub-triangular, distally only slightly separated. Surstylus laterally compressed, shorter than cerci; distal 2/3 rounded in lateral view and proximally not fused with epandrium; with several short setulae on both outer and inner surfaces. Bacilliform sclerite rod-shaped and fused to surstylus antero-basally; surstylus with a stout median, proximal apophysis (Fig. 6e, red arrow), visible in lateral view in form of a postero-proximal lobe (Fig. 5f, red arrow). Hypandrial arms strongly approximated, fused or not fused posteromedially. Pregonite well developed, sub-triangular, hook-shaped distally. Postgonite narrow, distally pointed and gently bent anteriorly. Intermedium well developed. Ejaculatory apodeme present, small. Basal processes of basiphallus present. Epiphallus very short and membranous, arising dorsally in distal position (i.e., close to junction between basiphallus and distiphallus) (as in Fig. 6g). Ventral wall of distiphallus concave. Lateroventral region of distiphallus sclerotized. Medioventral ridge of distiphallus not developed. Extension of dorsal sclerite of distiphallus well developed (as in Fig. 6g).

Female differs from male as follows:

Head: Frons 1.20–1.33 times as wide as compound eye in dorsal view. Two or 3 upper reclinate orbital setae, 2–3 strong proclinate orbital setae and 2 latero-clinate orbital setae. Outer vertical seta well developed, latero-clinate. **Thorax**: Fore claws 0.7–0.9 times as long as fifth tarsomere.

Egg (Fig. 8a–d): Length: 217–232 μm ; width: 117–132 μm . Shape: plano-convex. Microsculpture of thick, dorsal chorion: smooth with a barely visible polygonal microsculpture; one subcircular aeropilar area is present on

anterior edge of egg. Colour: dorsal side and lateral margins blackish brown, mid-ventral, flat side whitish to pale yellow.

Distribution. Afrotropical: South Africa (KwaZulu-Natal, Western Cape), Zimbabwe.

***Agaedioxenis kirkspriggsi* Cerretti, O'Hara and Stireman, sp. nov.**

(Figs. 2b, 3e–f, j, 4d, 6c–d, g)

<http://zoobank.org/urn:lsid:zoobank.org:act:4A4A9BA3-FD22-4ACD-9132-893DAB95AE17>

Type material. Holotype ♂: Malaise trap, *Leucosidea* [error for *Leucosidea*]-dominated scrub // RSA, Free State, Harrismith / Mooihokop / 28° 10' 50.0" S 29° 10' 51.1" E / 14-16.ix.2009, ca. 1800 m / A.H. Kirk-Spriggs // Entomology Dept. / National Museum / P.O. Box 266 / Bloemfontein 9300 / South Africa // BMSA (D) 10351 [NMB]. Paratypes: 3♂♂, 1♀: same data as holotype [1♂ 1♀ in NMB, 1♂ in MZUR, 1♂ in CNC].

Etymology. Dedicated to our colleague Dr Ashley Kirk-Spriggs (NMB), who collected the type specimens.

Description.

Body length: 7–11 mm.

Male differs from *A. brevicornis* as follows:

Colouration: Abdominal tergite 3 with a band of whitish reflecting microtomentum on anterior half (Fig. 4d). **Head** (Figs. 2b, 3e): Frons 0.75–0.85 times as wide as compound eye in dorsal view. Parafacial flat, at its narrowest point 1.25–1.62 times as wide as postpedicel. Postpedicel 1.13–1.50 times as long as pedicel. Gena in profile 0.24–0.29 times as high as compound eye. Prementum 0.66–0.75 times as long as height of head. **Legs**. Hind tibia with a comb-like row of 15–20 anterodorsal setae with only one larger seta in submedian position (Fig. 3j). **Male terminalia**: As in *A. brevicornis* except for shape of cerci in posterior view (Fig. 6c) and shape of surstylus in lateral view (Fig. 6d); phallus as in Fig. 6g.

Female. Differs from male as follows:

Head (Fig. 3f): Frons 1.06 times as wide as compound eye in dorsal view. Two or 3 upper reclinate orbital setae, 3 strong proclinate orbital setae and 2 latero-clinate orbital setae. Outer vertical seta well developed, latero-clinate. **Thorax**: Fore claws about as long as fifth tarsomere.

Distribution. Afrotropical: South Africa (Free State).

***Agaedioxenis succulentus* Cerretti, O'Hara and Stireman, sp. nov.**

(Figs. 2c, 3g–h, 4c, 6a–b)

<http://zoobank.org/urn:lsid:zoobank.org:act:A63F53B9-30CB-4544-B437-042827FD983D>

Gaedioxenis brevicornis: Cerretti et al. (2013: 23), misidentification.

Type material. Holotype ♂: SA007 // South Africa, Western Cape / Ceres Bergfynbos Reserve at: / 33° 23' 1.91" S 19° 17' 20.16" E / 12.X.2012, 459 m, P. Cerretti, J. Stireman, J. O'Hara / I. Winkler & A.H. Kirk-Spriggs leg. [MZUR].

Paratypes: 1 ♀: SA006 // [same data as holotype] [MZUR]; 1 ♀ [same data as holotype] [JOSC].

Etymology. The specific epithet derives from the habitat in which the type specimens were collected, the Succulent Karoo, and should be treated as a Latin adjective.

Description.

Body length: 10.0–11.4 mm.

Male differs from *A. brevicornis* as follows:

Head (Figs. 2c, 3g): Frons 0.65 times as wide as compound eye in dorsal view. Parafacial flat, at its narrowest point 1.18–1.54 times as wide as postpedicel. Postpedicel 1.12–1.35 times as long as pedicel. Gena in profile 0.21–0.38 times as high as compound eye. Prementum 0.60–0.65 times as long as height of head. *Abdomen:* Abdominal tergite 3 with 2 pairs of median marginal setae (outer pair slightly shorter). *Male terminalia:* As in *A. brevicornis* except for shape of cerci in posterior view (Fig. 6a) and shape of surstylus in lateral view (Fig. 6b).

Female differs from male as follows:

Head (Fig. 3h): Frons 1.15–1.25 times as wide as compound eye in dorsal view. Two or 3 upper reclinate orbital setae, 2–4 strong proclinate orbital setae and 2 laterocline orbital setae. Outer vertical seta well developed, laterocline. *Thorax:* Fore claws about 0.9 times as long as fifth tarsomere. *Abdomen:* Abdominal tergite 3 with a complete row of median marginal setae (Fig. 4c).

Distribution. Afrotropical: South Africa (Western Cape).

***Agaedioxenis timidus* Cerretti, O’Hara and Stireman, sp. nov.**

(Figs. 2d, 3i, 4e)

<http://zoobank.org/urn:lsid:zoobank.org:act:42D3708E-CF9D-40B2-ABB9-158CB696F15A>

Type material. Holotype ♂: Kapstadt [Cape Town] / 13.X–7.XI.1958 / Lindner leg. // *Agaedioxenis / brevicornis* / L.P. Mesnil det, 1969 // EX / L.-P. MESNIL / COLLECTION 1970 [CNC].

Etymology. The species epithet is derived from the Latin adjective *timidus*, meaning shy, alluding to the fact that this species has been rarely collected.

Description.

Body length: 7.0 mm.

Male differs from *A. brevicornis* as follows:

Colouration: Scutellum black, shading into dark brown apically. Abdomen entirely black with wide bands of weak and barely visible greyish microtomentum on anterior 4/5 or more (tergite 3) or anterior 1/2 (tergite 4) (Fig. 4e). *Head* (Figs. 2d, 3i): Frons 0.83 times as wide as compound eye in dorsal view. Parafacial at its narrowest point 1.66 times as wide as postpedicel. Postpedicel 1.08 times as long as pedicel. Second aristomere about 2.6 times as long as wide. Gena in profile 0.43 times as high as compound eye. Prementum slender, about 0.75 times as long as height of head. *Abdomen:*

The longest median marginal setae of tergite 3, at least twice as long as corresponding tergite measured at its maximum median length. *Male terminalia:* not examined.

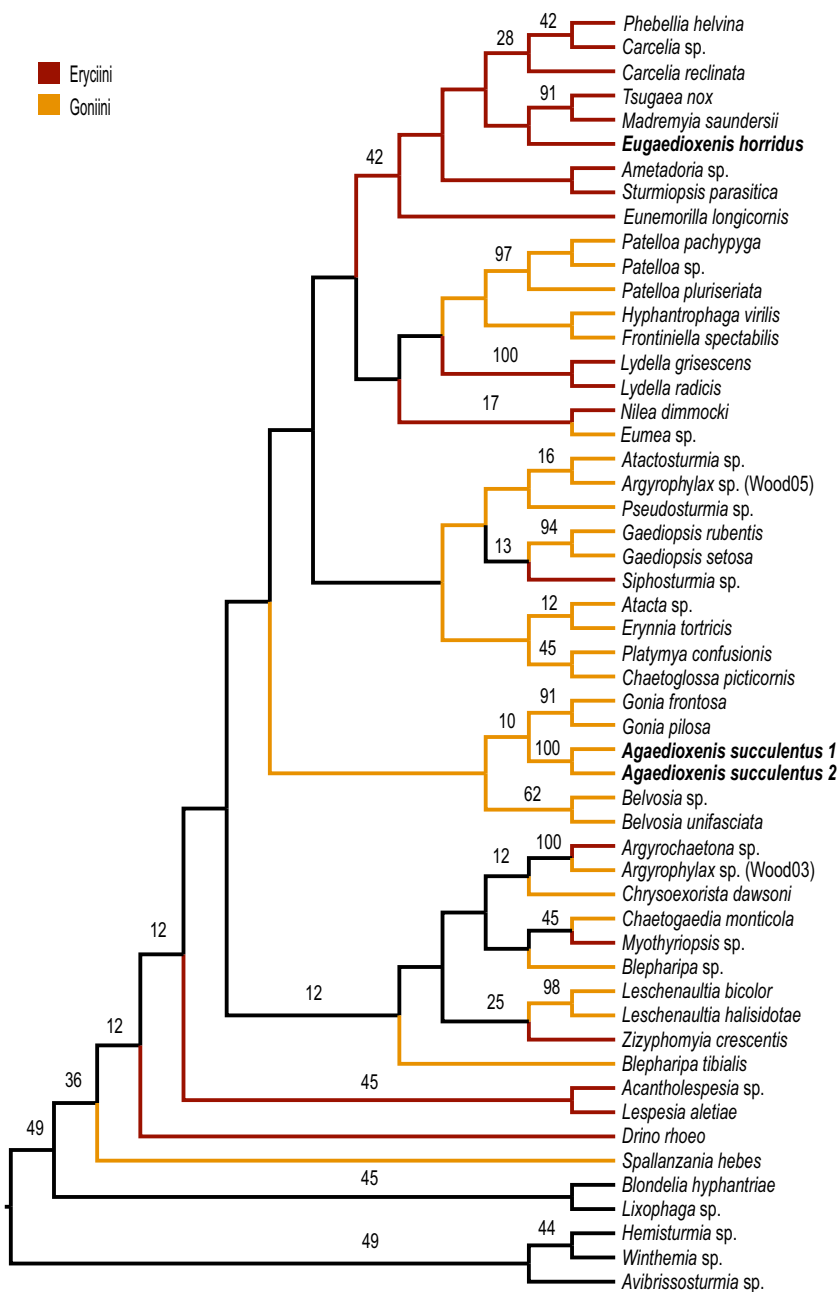
Female unknown.

Distribution. Afrotropical: South Africa, Western Cape (known only from the type locality of Cape Town).

Key to species of *Agaedioxenis* Villeneuve

1. Postpedicel 4 (♂), 1.9–2.4 (♀) times as long as pedicel (Figs. 1e–f; 3a–b). Second aristomere 3–5 times as long as its diameter at midlength. Arista thickened on about its basal 4/5. Scutellum with crossed apical setae. Female: frons about 1.4–1.5 times as wide as compound eye in dorsal view; 2 upper reclinate orbital setae, 2 strong proclinate orbitals, 2 strong laterocline orbital setae. Male: frons 1.33 times as wide as compound eye in dorsal view; abdomen without sexual patches *A. setifrons* (Villeneuve)
- Postpedicel 0.9–1.5 times as long as pedicel (Figs. 2a–d; 3c–h). Second aristomere at most 2.6 times as long as its diameter at midlength. Arista thickened on its basal 1/2–2/3. Apical scutellar setae varying from diverging to sub-parallel, sometimes reduced or absent. Female: frons about 1.00–1.35 times as wide as compound eye in dorsal view; 2–4 strong proclinate orbital setae and 1–2 laterocline orbital setae. Male: frons 0.65–0.90 times as wide as compound eye in dorsal view; tergite 3 and 4 with sexual patches ventrally (Fig. 4g) 2
2. Abdominal syntergite 1 + 2 (♂) and tergite 3 (♂♀) with 4 or more median marginal setae. Male: Frons about 0.65 times as wide as compound eye in dorsal view; cerci in posterior view as in Fig. 6a; surstylus in lateral view as in Fig. 6b *A. succulentus* Cerretti, O’Hara and Stireman, sp. nov.
- Abdominal syntergite 1 + 2 and tergite 3 with 2 median marginal setae. Male: Frons 0.75–0.85 times as wide as compound eye in dorsal view; cerci and surstylus not as above [male terminalia of *A. timidus* not examined] 3
3. Longest median marginal setae of tergite 3 at least twice as long as tergite 3 measured at its maximum median length (Fig. 2d). Second aristomere about 2.5 times as long as wide. Scutellum almost entirely black, only dark brown apically. Abdominal microtomentum weak and not forming distinct basal bands (Fig. 4e). [female unknown] *A. timidus* Cerretti, O’Hara and Stireman, sp. nov.
- Longest median marginal setae of tergite 3 0.9–1.3 times as long as same tergite measured at its maximum median length. Second aristomere at most 2 times as long as wide. Scutellum reddish yellow at least on apical 1/3. Abdominal microtomentum in form of distinct basal bands 4

Fig. 9 The most parsimonious tree recovered from maximum parsimony analysis of representative eryciine (*red*) and goniine (*yellow*) taxa based on COI sequence data (treelength 1721). Numbers above bars indicate bootstrap probabilities of branches (500 replicates). Only probabilities >10 % are reported. The focal taxa in the current study, *Agaedioxenis* and *Eugaedioxenis*, are indicated in *bold*



4. Hind tibia with a comb-like row of 15–25 anterodorsal setae with only one larger seta in submedian position (Fig. 3j). Basal band of microtomentum on abdominal tergite 3 confined on anterior half (Fig. 4d). Male: terminalia as in Fig. 6c–d
 *A. kirkspriggsi* Cerretti, O’Hara and Stireman, sp. nov.
- Anterodorsal setae on hind tibia not arranged in a regular comb-like row (i.e., with at least three setae longer and stronger than others, Fig. 3k). Basal band of microtomentum on abdominal tergite 3 confined on anterior 1/3. Male: terminalia as in Fig. 5e–f
 *A. brevicornis* (Villeneuve)

Discussion

If it is through a rigorous implementation of cladistic principles that systematics plays a fundamental role in evolutionary biology, then it is the task of taxonomists to improve the classification of living organisms by identifying monophyletic assemblages, removing inconsistencies, and instituting taxonomic changes to better reflect evolutionary history.

It is apparent from our integrative study of morphology and genetics that *Agaedioxenis sensu* Crosskey (1980, 1984, as *Gaediopsis*) represented a polyphyletic assemblage of species that were combined under one genus due to a

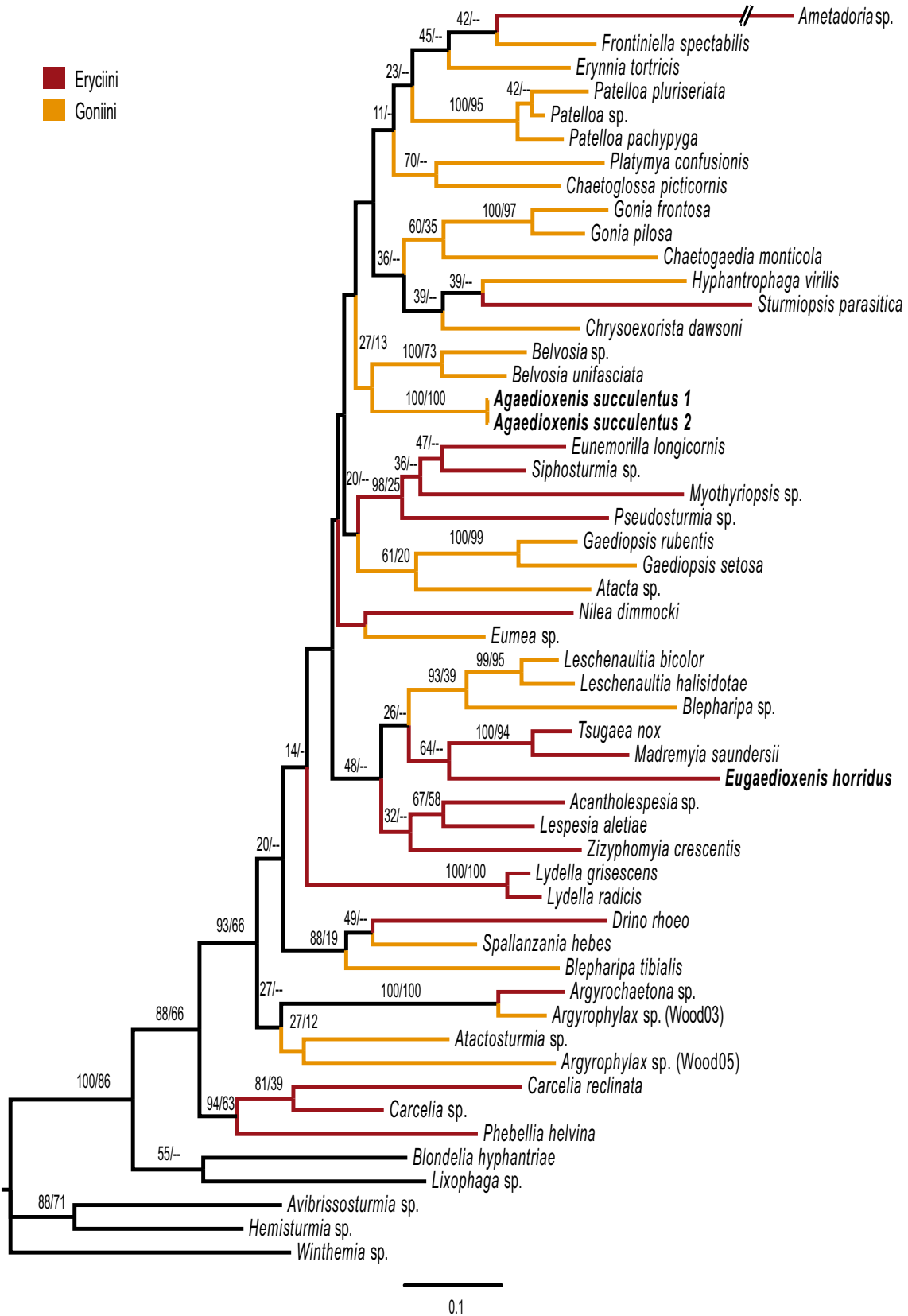


Fig. 10 A summary tree from Bayesian analysis of representative exoristine taxa based on COI sequence data with posterior probabilities and ML bootstrap probabilities above branches (pp./bp.). Only probabilities >10 % are reported. Eryciini are red, Goniini are yellow, and focal taxa are in bold

misleading combination of external traits. Although all examined females share a long and coiled common oviduct (uterus) capable of retaining large quantities of eggs, dissection of the female genitalia has revealed two different reproductive strategies.

We did not observe females in the act of laying their eggs, but there are several morphological traits from which we can infer a lot about their oviposition behaviour. *Eugaedioxenis haematodes* and *E. horridus* produce macrotype, membranous eggs, which are laid ready to hatch. Also, females of these species have a relatively long, conical tergite 5 and an oviscapt that is slightly elongated and telescopically retracted within segment 5. These traits are characteristic of several eryciine genera that deposit their eggs directly on hosts (e.g. some species of *Phryxe* Robineau-Desvoidy and *Erycia* Robineau-Desvoidy). Females of *Agaedioxenis* have an unmodified tergite 5, short oviscapt and produce microtype, plano-convex, hard-shelled eggs. These eggs are of the type that are laid ready to hatch on the food plants of their hosts, and must be swallowed by feeding hosts before they can hatch and the first instars can penetrate into the host's haemocoel through the gut wall (see Herting 1960; Wood 1987; Mellini 1991). As mentioned in the "Introduction" section, tachinids sharing this reproductive strategy are grouped within the tribe Goniini (cf. O'Hara 2013). Other than egg morphology there are no known characters that unambiguously separate the Eryciini from the Goniini (see Tschorsnig 1985; Cerretti and Barraclough 2007), and it is therefore necessary to examine the female genitalia and eggs of a species in this group to determine to which tribe it belongs.

Monophyly of the Eryciini has been questioned by several authors due to the lack of synapomorphies defining this tribe, in contrast to the Goniini, which are widely accepted as a monophyletic group (Herting 1960; Wood 1987), well supported by at least three morphological autapomorphies (Cerretti et al. 2014b). Using molecular data, the hypothesis of Goniini monophyly was rejected by Stireman (2002), while more recently, it was upheld by Tachi and Shima (2010). In particular, Stireman (2002), using two genes (EF1 α and 28S rDNA), found taxa of Eryciini and Goniini interspersed within a single clade, i.e., not forming two distinct clades. On the other hand, Tachi and Shima (2010), using four genes (16S, 18S, 28S rDNA, and white), reconstructed the Eryciini as a paraphyletic grade from which a monophyletic Goniini arose. These results are consistent with the assumption that increasing the number of loci should lead to an increase in phylogenetic resolution (e.g. Rokas and Carroll 2005).

Our analyses of "barcode" sequences yielded contrasting topologies with very low branch support, but consistently recovered both the Eryciini and Goniini as nonmonophyletic and *Agaedioxenis* and *Eugaedioxenis* in highly divergent positions (see the "Results" section and Figs. 9 and 10). Also interesting is that all analyses yielded Eryciini + Goniini as a

well-supported monophyletic assemblage (Figs. 9 and 10). To comment further on the monophyly of the Eryciini and Goniini is beyond our present scope, because COI sequences are clearly not informative enough to robustly resolve relationships at this level. However, the overall genetic distance between *Agaedioxenis* and *Eugaedioxenis* is higher than the mean genetic distance between all the eryciines and goniines we tested. Furthermore, *Agaedioxenis* was always reconstructed as sister to a member of the Goniini and *Eugaedioxenis* was always reconstructed as sister to an eryciine, although the identity of that sister taxon varied across analyses. Therefore, despite instability in the trees, genetic data clearly indicate that these two taxa are not closely related, corroborating the morphological evidence of their phylogenetic disparity.

Acknowledgments We would like to thank Ashley Kirk-Spriggs (NMB), Burgert Muller (NMDA), and Nigel Wyatt (BMNH) who enabled our studies of the valuable material preserved in their institutions. Thanks to Daniel Whitmore (BMNH) for information about the holotype of *A. brevicornis* and to Mara Tisato (Centro Nazionale Biodiversità Forestale, Verona, Italy) for help composing plates. Thomas Pape (Natural History Museum of Denmark, Copenhagen) provided the nomenclatural advice on the interpretation of Villeneuve's genus-group names. Finally, we thank Knut Rognes (University of Stavanger, Stavanger, Norway) and an anonymous reviewer for their constructive comments on earlier drafts of this manuscript.

Funding This work was supported by U.S. National Science Foundation DEB-1146269 to principal investigators J.O.S. and J.E.O. and to major collaborator P.C.

Conflict of interest The authors declare that they have no conflict of interest.

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